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Environmental Microbiome

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Microbiome matters: how transplantation methods and donor origins shape the successful restoration of the seagrass *Posidonia oceanica*

Arnaud Boulenger[1,2*], Tânia Aires[3], Aschwin H. Engelen[3], Gerard Muyzer[4], Michel Marengo[2] and Sylvie Gobert[1,2]

Abstract

Background *Posidonia oceanica* forms extensive seagrass meadows in the Mediterranean Sea, providing key ecosystem services. However, these meadows decline due to anthropogenic pressures like anchoring and coastal development. Transplantation-based restoration has been explored for decades, yet the role of the plant-associated microbiome in restoration success remains largely unknown.

Results 16 S rRNA gene amplicon sequencing was used to investigate how different transplantation methods and donor origins influence the bacterial communities of *P. oceanica* cuttings two years post-transplantation. We tested three transplantation methods, iron staples, coconut fiber mats, and BESE elements, and compared them with control meadows and donor populations from two different origins: naturally uprooted storm-fragments and intermatte cuttings manually harvested from established meadows. Our results show that transplantation methods strongly shape bacterial communities in seagrass roots. Iron staples promoted microbial assemblages most similar to natural meadows, likely due to direct sediment contact enhancing recruitment of key functional bacterial orders such as *Chromatiales* and *Desulfobacterales*. In contrast, BESE elements and coconut fiber mats displayed dissimilar bacterial communities compared to control meadows, likely due to material composition and physical separation between the cuttings and the sediment. Donor origin had only subtle effects on bacterial communities' structure, although intermatte cuttings showed higher abundances of *Candidatus* Thiodiazotropha, a genus thought to be involved sulfur oxidation and nitrogen fixation.

Conclusion Our results demonstrate that transplantation methods strongly influence root-associated bacterial communities. Limited sediment contact in elevated substrates delayed the establishment of key functional bacteria, highlighting the importance of direct interaction with the sediment microbial pool. These results imply that restoration strategies should prioritize methods enhancing sediment–root interactions to support microbial recovery. Incorporating microbiome considerations, such as optimized substrates or microbial inoculation, could improve the resilience and long-term success of *P. oceanica* restoration.

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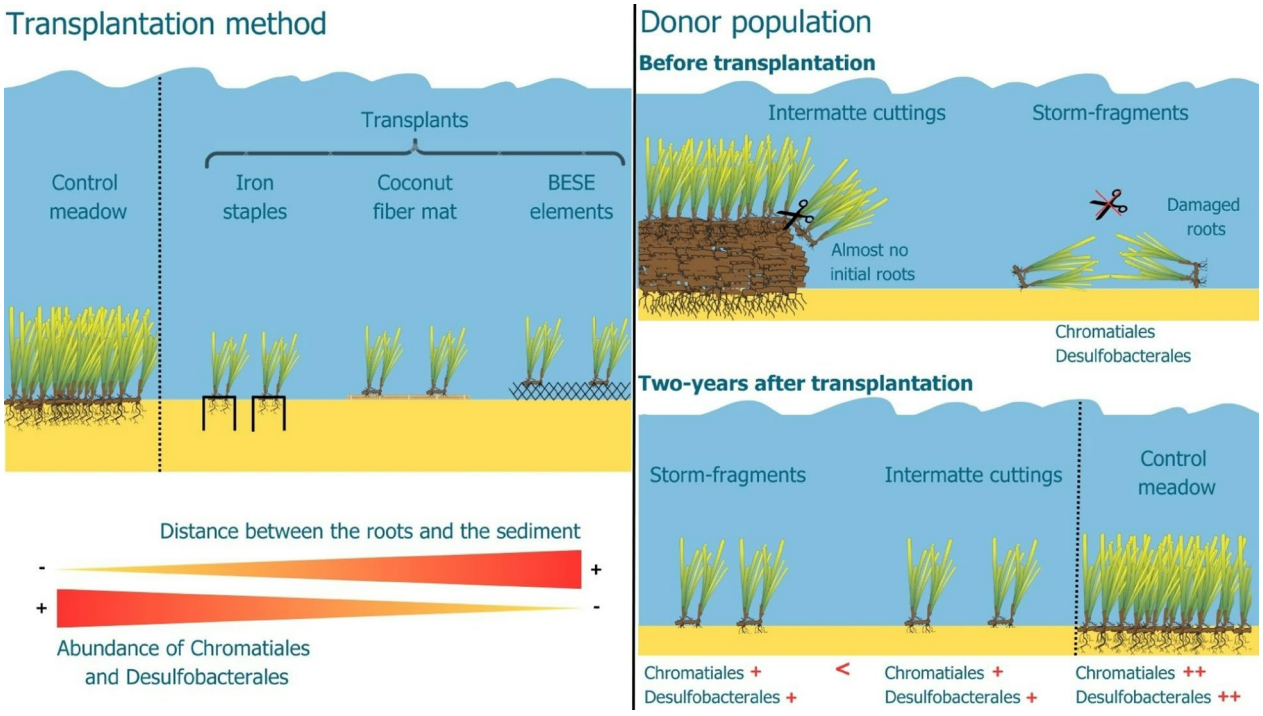
Graphical Abstract



Keywords Holobiont, Microbiome, Rhizosphere, Restoration, Seagrass, Symbiosis, Transplantation

Background

Seagrasses are marine flowering plants that colonised the aquatic environment about 100 million years ago and are widely distributed in coastal waters worldwide, except in Antarctica [1, 2]. They are key benthic ecosystem engineers (sensu [3]) that form three-dimensional meadows providing essential habitats and nursery grounds for marine life [4–6]. Those meadows stabilize soft sediments and diminish wave intensity and turbulence, offering coastal protection against erosion [7, 8]. Furthermore, they sequester large amounts of CO_2, thus mitigating anthropogenic emissions [2, 9, 10]. Despite the ecological and economic significance of seagrass meadows, climate change, and human activities, such as agricultural activities, coastal urbanization, dredging, trawling, and anchoring, have severely impacted those ecosystems [11, 12]. These ongoing reductions in seagrass coverage are especially detrimental to large slow-growing seagrass species such as *Posidonia oceanica* (L.) Delile, which forms extensive meadows in the Mediterranean Sea.

The alarming global decline of seagrass meadows has prompted a surge in restoration efforts [13, 14]. For *P. oceanica* meadows active restoration, it can be achieved through sod transplantation, which has shown promising results [15]. One of the major advantages of this technique lies in preserving the sediment and the underlying matte of the meadow, along with its associated microbiome [15]. The second active restoration technique involves transplanting seeds or cuttings into degraded areas. The challenge of transplanting cuttings lies in their long-term anchoring and adaptation to new environmental conditions, such as a modified substrate [16–18]. Despite several decades of seagrass restoration research, the role of microbial communities in these processes remains largely overlooked [19].

Microbial communities that reside within (endophytic) and on the surface of (epiphytic) plants' tissues can act as functional drivers for their host by forming complex co-associations, impacting terrestrial plant health and productivity [20–22]. These microorganisms enhance nutrient availability through nitrogen fixation and the mineralization of organic compounds, produce phytohormones that stimulate root and shoot development, and help alleviate plant stress [23–25]. Yet, our understanding of plant-microbial interactions in marine environments is still limited [26]. However, recent studies in salt marshes highlight the potential significance of these interactions. Daleo et al. [27] found that mycorrhizal fungi enhance nutrient uptake in dense-flowered cordgrass (*Spartina densiflora*). Likewise, seagrasses form symbiotic relationships with various microorganisms both above and below ground [26, 28–30] [31–33]. For

example, seagrasses are associated with sulfide-oxidizing bacteria to reduce toxic sulfide accumulation [34, 35]. Additionally, some bacteria on seagrass leaves and roots produce antimicrobial molecules that may protect the plants by selectively targeting pathogens and biofouling organisms [36, 37]. However, marine restoration is a more recent scientific discipline than terrestrial restoration [38]. In terrestrial ecosystems, there is evidence that the core microbiota plays a crucial role in maintaining the functional stability of soil microbiomes, nutrient cycling, and plant establishment in reforested areas. This microbiota should also be considered in marine restoration plans' policy and management strategies [39]. Considering the potentially beneficial microbial interactions in seagrasses, further research is required to understand better their implications for restoration efforts' success or failure [19, 26]. A recent guide on *P. oceanica* restoration has emphasized the need for further research on plant-sediment interactions, particularly regarding associated bacterial communities [40]. Notably, recent reviews fail to mention the role of microbial communities in *P. oceanica* restoration [41, 42], highlighting a critical knowledge gap. While microbial studies have been conducted on some temperate [43] and tropical [44, 45] seagrass species, *P. oceanica* remains largely unstudied in this context.

In our study, *P. oceanica* cuttings collected from donor populations from two different origins were transplanted onto various biodegradable materials. Two years after transplantation, leaf and root samples were collected from the transplants and nearby control meadows for bacterial community characterization. We hypothesized that transplantation methods would shape distinct bacterial communities due to the material composition and physical structure of the transplantation supports, as well as their proximity to the sediment, with methods allowing closer sediment contact favouring communities more similar to natural meadows. We further hypothesized that donor origin would influence initial bacterial community composition, but that these differences would diminish over time as communities adapt to the transplantation site. Finally, we hypothesized that bacterial communities in transplants would gradually converge towards those of natural meadows over time, reflecting a progressive recovery of the microbiome after transplantation.

Methods

Study area

Samples were collected by SCUBA-diving in May 2024 in a sub-bay of Calvi Bay, Alga Bay (8°43′52′′ E; 42°34′20′′ N), located in front of the oceanographic research station STARESO (Calvi, Western Corsica, France) (Fig. 1). This bay harbours extensive seagrass meadows of *P. oceanica*, spanning around 0.78 km² at depths ranging from 3 m to 37 m [17]. Significant anchoring activity in the area has caused a substantial reduction in these seagrass meadows [46], and restoration efforts by cuttings' transplantation on dead matte took place in the spring of 2022 [47]. As the availability of donor material for transplanting is one of the main constraints in *P. oceanica* meadows restoration, donor populations of two different origins were used as planting material: naturally uprooted seagrass fragments drifting on the seafloor (referred to as storm-fragments) and fragments of *P. oceanica* rhizomes manually extracted from donor meadows. The storm-fragments were collected from various locations near STARESO during scuba dives ranging from 6 to 28 m depth. The manual extraction of *P. oceanica* fragments from donor meadows was performed on a healthy *P. oceanica* meadow located on the erosion side of a natural sandy intermatte at 15 m depth (Fig. S1) [48]. The later cuttings are hereafter referred to as 'intermatte cuttings'. The cuttings were attached to the seafloor using three different types of biodegradable artificial structures: (i) iron staples, (ii) biodegradable mat in natural coconut fibre woven mesh (referred to as coconut fiber mat), and (iii) BESE-elements® (BESE Ecosystem Restoration Products, Culemborg, The Netherlands) (Fig. 2). The storm-fragments and intermatte cuttings were spatially interspersed within each structure, and the structures were spaced approximately 3 m apart. This experimental design was replicated in seven sites, and two control meadows were selected in close vicinity to the experimental sites.

Sampling strategy

Transplanted *P. oceanica* fragments were collected two years after transplantation along with environmental samples (i.e., sediment and seawater). Seven replicates of *P. oceanica* transplants were collected for each combination of transplantation method and donor origin. Five individual seagrass fragments were collected at the two control sites, also with environmental samples. This resulted in a total of 52 fragments and a total of 104 plant samples as leaves and roots were separated. Each seagrass fragment (cutting or control plant) was uprooted and washed with seawater from the sampling location to remove sediment, epiphytes and any loosely attached material. The seawater in excess was shaken off. A portion of approximately 1 cm² in the middle section of the second most external leaf was collected from one sampled shoot per individual fragment. If present, pen roots and hair roots were sampled. Sediment cores (20 cm depth x 5 cm diameter) were collected from the dead matte in close vicinity to the experimental restoration sites ($n = 20$) and control meadows ($n = 10$). From those cores, sediment samples of a volume of approximately 1 mL were collected at a depth of 1–10 cm, representing the seagrass's root depth. Seawater samples with a

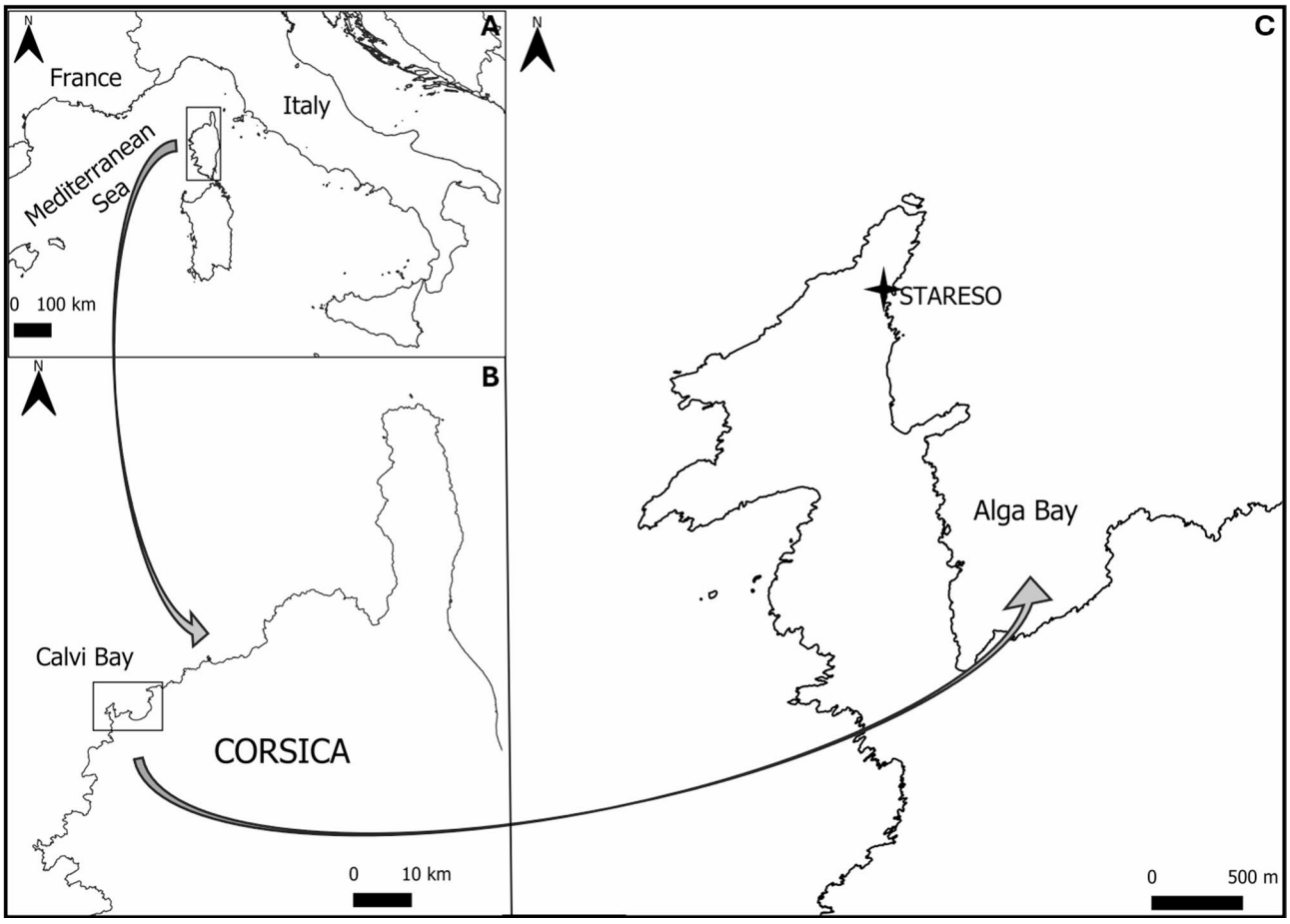


Fig. 1 The location of the study area: (**A**) Corsica Island in the North-Western part of the Mediterranean Sea; (**B**) Northern part of Corsica and Calvi Bay; (**C**) Location of the STARESO marine station and Alga Bay (Calvi, Corsica) where the samples were collected

volume of 120 mL were collected above the dead matte at each of the seven experimental restoration sites, with two replicates per site (total $n = 12$), and inside the seagrass meadows' canopy for the two control meadows, with three replicates per meadow (total $n = 6$). The seawater was filtered using 0.22 µm Sterivex™ unit with a sterile 120 mL syringe (MF-Millipore Membrane, Merck KGaA, Darmstadt, Germany). The leaves, roots, sediment samples, and filters were directly preserved in DNA/RNA Shield (ZymoResearch, California, USA) and stored at − 20 °C until DNA extraction. Environmental contaminants were removed from the dataset using the above-mentioned sediment and seawater controls to ensure only seagrass-associated bacterial communities were retained for diversity analyses.

DNA extraction and amplicon sequencing

DNA was extracted from all samples using the Quick-DNA™ Miniprep Kit (ZymoResearch, California, USA) following the manufacturer's instructions for 'Solid Tissue Samples' (page 6 of the manual). Filters from the Sterivex™ casing were removed according to Cruaud et al. [49] that demonstrated significantly increased DNA yields. For all the samples, including sediment and seawater filters, in the lysis step, tungsten beads, and an automatic homogenizer (Vortex-Genie® 2, Scientific Industries) (for 10 min at a maximum speed) were used for a more efficient mechanical lysis. After DNA extraction, the samples were sent to Novogene GmbH (Munich, Germany) for DNA amplification and sequencing. PCR was performed on extracted DNA to amplify the V5–V7 region of 16S rRNA gene using the primer pairs 799F and 1193R (forward primer, 5′-AACMGGATTAGATACCCKG-3′; reverse primer, 5′-ACGTCATCCCCACCTTCC-3') [50]. The samples were pooled in equal proportions based on their molecular weight and DNA concentrations (using Qubit Invitrogen®) and purified using magnetic beads. The sequencing libraries were generated, and paired-end (2 × 250 bp) sequencing was performed on an Illumina MiSeq PE250 system following the manufacturer's guidelines.

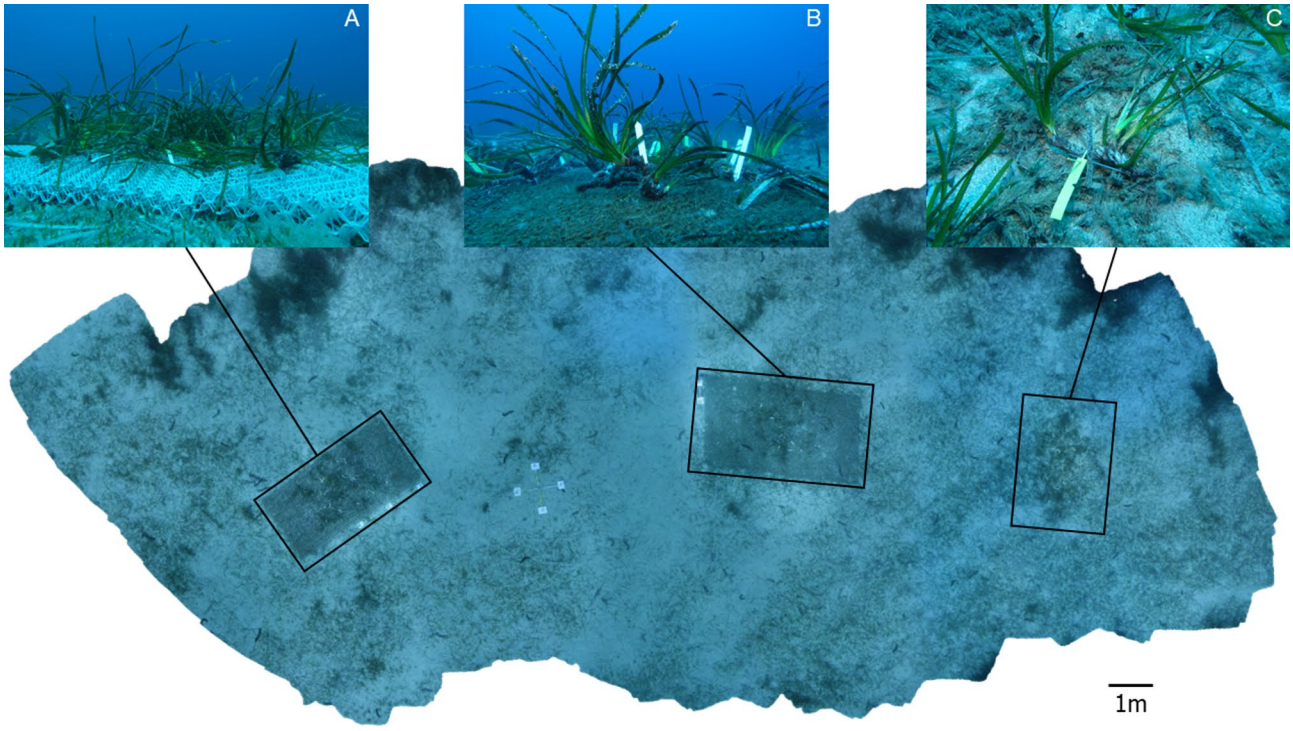


Fig. 2 Orthomosaic of one of the seven experimental sites. It represents a dead matte area with the three different P. oceanica transplantation methods tested in this study (black rectangles): (**A**) BESE elements, (**B**) coconut fiber mat, and (**C**) iron staples

Bioinformatic analysis

The raw dataset consisted of a total of 6,360,321 sequences. The sequences were depleted from barcodes and primer sequences and were trimmed for quality with the fastp (version 0.23.1) software. Sequences with ambiguous base calls, as well as chimeras, were removed. The de-duplicated or unique sequences were denoised using DADA2 [51] to obtain initial ASVs. Taxonomy was assigned to ASVs using the SILVA reference database (version 138). From the resulting ASV table, eukaryotic organelle sequences (i.e., chloroplasts and mitochondria) and unassigned sequences were removed. The resulting absolute ASV table was used for all downstream analyses. Rarefaction curves were used to assess sampling depth (Fig. S2). Due to the important differences in the number of sequences among samples (7312–70,118 sequences), the samples were normalized by rarefaction to the minimum number of sequences (7312) per sample to adjust for those differences (Fig. S2). Library size normalization is required for meaningful alpha and beta diversity analysis. Therefore, the rarefied ASVs table resulted in 1,118,736 high-quality sequences, clustered in 40,028 ASVs.

Bacterial community richness and diversity: alpha diversity analysis

Before calculating alpha diversity indices, all the ASVs with a relative abundance above 0.01% in seawater and sediment samples were classified as 'environmental bacteria' and removed from the rarefied ASVs table. Bacterial community richness was assessed using the number of ASVs (S), while diversity was evaluated using the Shannon (H') and Simpson (1-λ') indices. The exponential function was applied to the Shannon's diversity index to determine the true Shannon diversity (i.e., the effective number of species), following the methodology outlined by Lundberg et al. [52]. The seagrass samples within the 'donor population of intermatte cuttings' did not have roots, which is why this level within the group factor 'sample tissue' is absent in the following analyses. The normality and linearity of the residuals were tested by visual inspection of the residuals versus fitted values plot and with a Shapiro-Wilks test. The homogeneity of variances was checked using Levene's test. Data visualisation and assumptions were checked using RStudio software version 4.3.2 (RStudio Inc., Boston, MA, USA). As the data were not normally distributed, and to maximize comparability with the beta diversity analysis (as in [53]), PERMANOVAs were used to determine significant differences between samples origins and the transplantation methods, according to sample tissue. Two two-factor PERMANOVAs were performed. The first PERMANOVA was computed with the following factors: 'Sample tissue' (fixed factor with two levels) and 'Transplantation method' (fixed factor with five levels). The second PERMANOVA was computed with the following

factors: 'Sample tissue' (fixed factor with two levels) and 'Sample origin' (fixed factor with five levels). All the factors and respective interactions were tested. After square root transformation of the data, the resemblance matrix was constructed based on Euclidean distances, and the number of permutations was set to 999. Monte Carlo tests were performed when permutations were fewer than 100 [54]. Community richness, diversity indices and one-way PERMANOVAs were done using the PRIMER-E + PERMANOVA software version 7.0.24 (PRIMER-E, Auckland, New Zealand).

Bacterial community structure: beta diversity analysis

Differences in community structure were visualized with Canonical Analysis of Principal coordinates (CAP), based on a Bray-Curtis dissimilarity matrix after square root transformation of the rarefied ASVs table. CAP analysis was chosen as it allows to constrain the ordination based on explanatory variables, which is a better match for a priori hypothesis testing plots, enabling to assess specific relationships between sample groupings and environmental or experimental factors. PERMANOVAs were used to test for statistical significance of the differences among samples nature, samples origins, and transplantation methods. The same PERMANOVA designs as described in Sect. 2.4.1 were used. Moreover, a one-way PERMANOVA test for the factor "Sample nature" (fixed factor with four levels) was performed to assess the differentiation among the seagrass samples and the environmental samples. Differential abundance analysis using Linear Discriminant Analysis (LDA) Effect Size (LEfSe) [55] was performed to identify the top 20 significant orders and ASVs contributing to the differences observed among groups. This analysis employed the Kruskal-Wallis rank test with an adjusted *p*-value threshold of 0.05. The Log LDA Score was set to 1.0, and significant orders and ASVs were ranked in descending order based on their LDA scores. The CAPs were done using RStudio software version 4.3.2, the PERMANOVAs were done using the PRIMER-E + PERMANOVA software version 7.0.24 and the LEfSe analysis was performed in MicrobiomeAnalyst [56].

Results

Taxonomic composition at the order level

The three most abundant bacterial orders for the leaf samples of the control meadows were *Rhizobiales*, *Burkholderiales*, and *Bacillales*, while *Chromatiales*, *Corynebacteriales*, and *Desulfobacteriales* were the three most abundant in the root samples of the control meadows. (Figures 3 and 4; Table S1, S2).

Rhizobiales was also the first most abundant order of the leaves from transplants attached to iron staples, while it was the second most abundant order of the leaves of the transplants on the coconut fiber mats (Fig. 3; Table S1). *Burkholderiales* was the most abundant order for those latter samples, while it was *Bacillales* for the leaves on the transplants on the BESE element and from cuttings of the donor populations (Fig. 3; Table S1). For the roots, *Chromatiales* was the second most abundant bacterial order on iron staple samples, with *Microtrochales* being more abundant (Fig. 3, Table S1). *Rhizobiales* was the most abundant for the coconut fiber mat samples, *Pseudomonadales* for the BESE element samples, and *Enterobacterales* for the donor populations samples (Fig. 3; Table S1). Although *Desulfobacterales* was the third most abundant order in the roots of the control meadows (9.44%), it was only present in the roots of iron staples (0.84%) and coconut fiber mats (0.15%) samples (Fig. 3; Table S1).

For the samples grouped according to their origin, *Rhizobiales* was the most abundant order in storm-fragment leaf samples as in the control meadows leaf samples (Fig. 4; Table S2). *Burkholderiales* was the most abundant in the leaves of intermatte cuttings, as well as in the leaves of storm-fragment donor population, while *Bacillales* was the most abundant in the leaves of intermatte cutting donor population (Fig. 4; Table S2). *Microtrichales* were dominating the roots of storm-fragments while *Rhizobiales* were the most abundant in the roots of intermatte cuttings (Fig. 4; Table S2). In those two groups, *Pseudomanadales* was the second most abundantorder, followed by *Chromatiales* in the third position while it was the first most abundant order in roots of control meadows (Fig. 4; Table S2). *Enterobacterales* was the most abundant order in the roots of the storm-fragment donor population (Fig. 4; Table S2). Although *Desulfobacterales* was the third most abundant order in the roots of the control meadows (9.44%), it was only present in the roots of storm-fragments at a very low relative abundance (0.89%) (Fig. 4; Table S2).

Bacterial community richness and diversity: alpha diversity analysis

The effects of transplantation method, sample origin, and their interaction with sample tissue (leaf vs. root) on bacterial alpha diversity (number of observed ASVs, exponentiated Shannon index, and Simpson index) were evaluated. Among the three diversity metrics, only the number of observed ASVs showed significant differences for the factors transplantation method (Table S3), sample origin (Table S8), and their respective interaction with sample tissue (Fig. 5; Table S3, S8). In contrast, no significant effects were detected for Shannon or Simpson indices (Fig. 5B, C, E, F; Table S6, S7, S11, S12). Pairwise PERMANOVA tests indicated that the significant differences in the number of observed ASVs were driven exclusively by root samples. Roots from donor populations

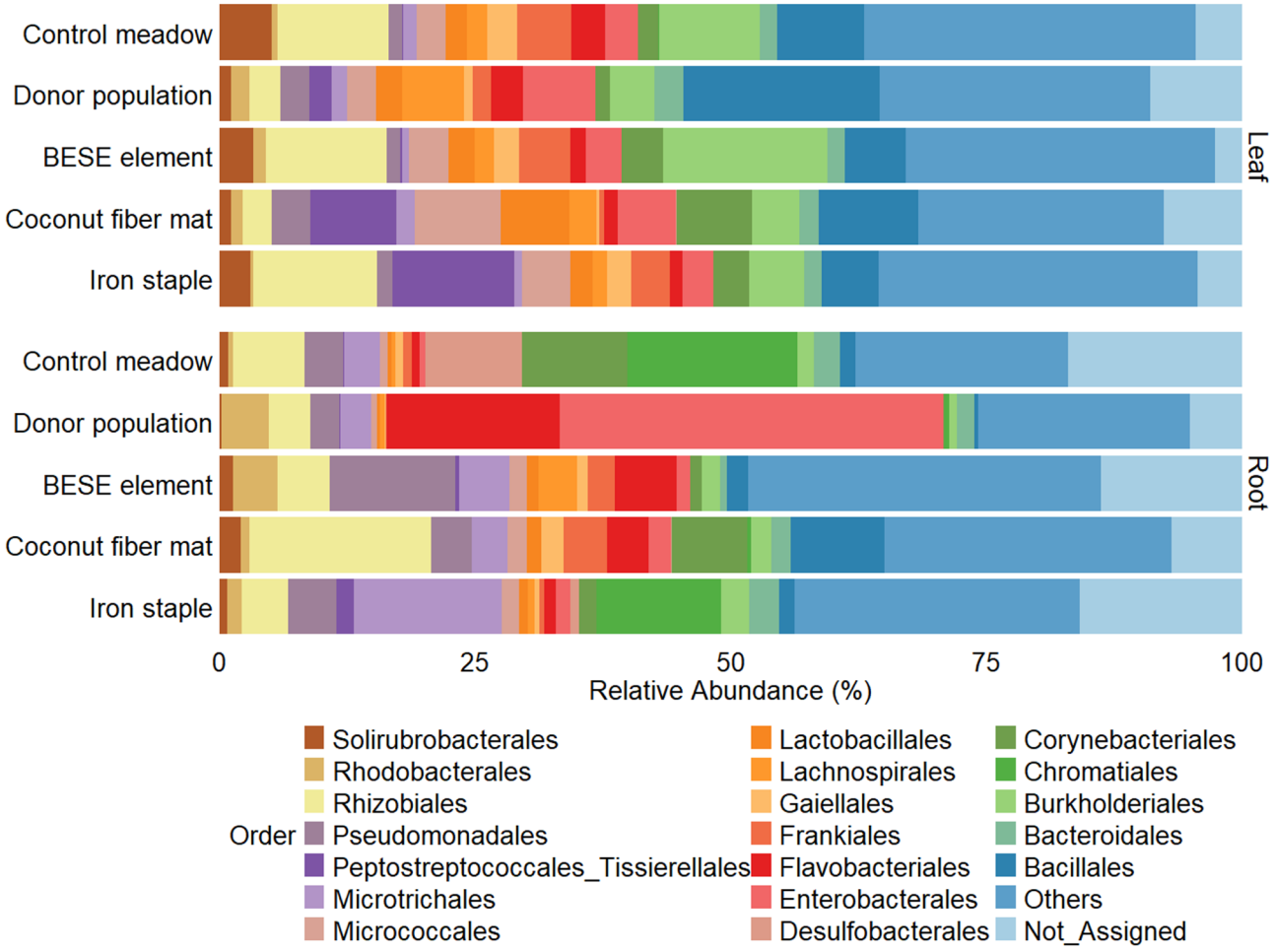


Fig. 3 Distribution of bacterial communities, at the order level, associated with the different tissues (leaf and root) of transplanted P. oceanica cuttings and control meadows as a function of transplantation method

prior to transplantation exhibited significantly higher number of ASVs compared to roots from transplanted plants (all transplantation methods and origins) and control meadows (Fig. 5, A, D; Table S4, S5, S9, S10). No significant differences were observed for leaves (Fig. 5, A, D; Table S4, S5, S9, S10). All the *p*–*v*alues for the alpha diversity statistical analysis are reported in Supplementary Tables S3–S12.

Bacterial community structure: beta diversity analysis

The variation in bacterial community structure (beta diversity) among sample types (leaf, root, sediment, water), transplantation methods, and sample origins was evaluated using CAP ordination, PERMANOVA, and Linear Discriminant Analysis (LDA) Effect Size (LEfSe). Bacterial community structure displayed a clear differentiation between unvegetated areas (i.e., dead matte) and vegetated areas (i.e., control meadow) for both water and sediment samples (Fig. 6; Table S16, S20). No differentiation was observed between sample tissues. Instead, clustering was primarily driven by transplantation method (Fig. 6A) and sample origin (Fig. 6B).

For the transplantation method, CAP ordination revealed that the control meadow samples were more similar to the transplants on iron staples (Fig. 6A). Donor populations, transplants on BESE elements and coconut fiber mats formed a separate cluster (Fig. 6A). Pairwise PERMANOVA tests indicated that leaf communities did not differ significantly among transplantation methods or between transplants and control meadows (Table S16). In contrast, root communities of control meadows differed significantly from those transplanted on coconut fiber mats, BESE elements, and from donor populations (Table S16). No significant difference was detected between control meadow roots and those transplanted using iron staples (Table S16). Differential abundance analysis supported these results, highlighting several ASVs and bacterial orders enriched in control meadow roots compared to transplants on coconut fiber mats, BESE elements, and donor populations. The most notable were ASV23 (*Gammaproteobacteria*), ASV27 (*Candidatus*

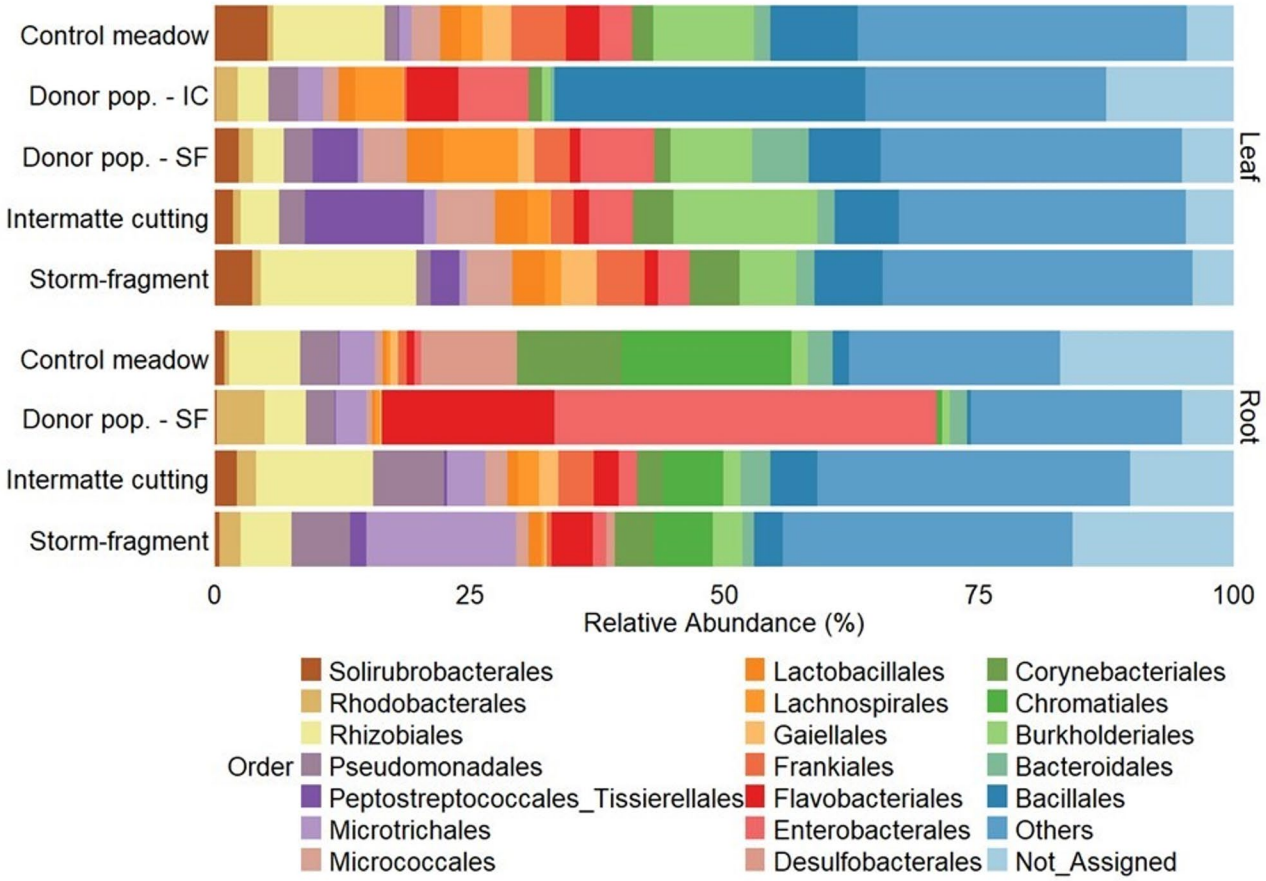


Fig. 4 Distribution of bacterial communities, at the order level, associated with the different tissues (leaf and root) of transplanted P. oceanica cuttings and control meadows as a function of sample origin. "Donor pop.-IC" - donor population of intermatte cuttings before transplantation, "Donor pop.- SF" donor population of storm-fragments before transplantation

Thiodiazotropha), ASV79 (Desulfosarcinaceae), and the bacterial orders *Chromatiales*, *Desulfobacterales*, *Desulfobulbales*, and *Spirochaetales* (Fig. 7; Table S21). Additional pairwise comparisons showed that the roots of donor populations before transplantation differed significantly from those transplanted on coconut fiber mats and iron staples, but not from those on BESE elements (Table S16).

For sample origins, CAP ordination showed three distinct clusters: one for control meadow samples, another grouping intermatte cuttings, storm-fragments, and donor populations of intermatte cuttings, and a third composed of donor populations of storm-fragments, which were the most dissimilar from control meadows (Fig. 6B). Pairwise PERMANOVA tests showed no significant differences among leaf communities from different the different sample origins (Table S20). In contrast, root communities of control meadows differed significantly from those of storm-fragments and intermatte cuttings (Table S20). Differential abundance analysis revealed ASVs and bacterial orders driving these differences, including ASV79 (*Desulfosarcinaceae*) and ASV23 (*Gammaproteobacteria*), which were more abundant in control meadow roots compared to transplanted roots (Fig. 8A; Table S22). ASV27 (*Candidatus* Thiodiazotropha) was also enriched in control roots relative to storm-fragments but showed slightly higher abundance in intermatte cuttings (Fig. 8A; Table S22). Conversely, ASV19 (*Gammaproteobacteria*) was higher in storm-fragments compared to control meadows (Fig. 8A; Table S22). At the order level, *Desulfobacterales*, *Chromatiales*, and *Desulfobulbales* dominated in control meadow roots compared to both intermatte cuttings and storm-fragments (Fig. 8B; Table S22). Further pairwise tests showed that donor populations of storm-fragments before transplantation differed significantly from their transplanted counterparts two years later, as well as from intermatte cuttings and control meadows (Fig. 6B; Table S20). No significant difference was detected between the two transplanted types (i.e., intermatte cuttings and storm-fragments) after two years (Fig. 6B; Table S20).

All the *p*–*v*alues for the beta diversity statistical analysis are reported in Supplementary Tables S13–S20. The lowest taxonomical levels of the ASVs represented in

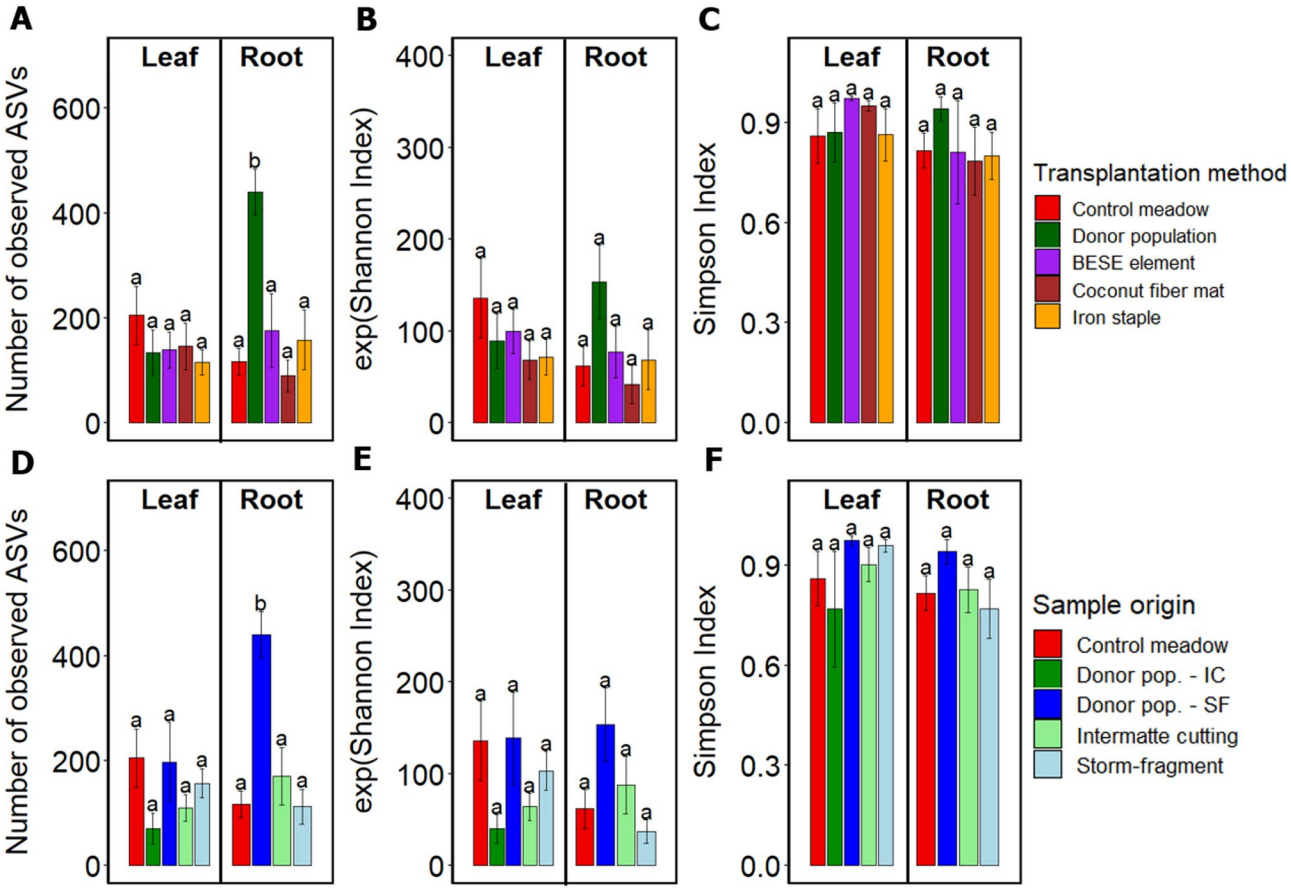


Fig. 5 Mean number of observed ASVs (**A**, **D**), exponentiated Shannon Index (**B**, **E**), and Simpson Index (**C**, **F**) of bacterial communities associated with the different tissues (leaf and root) of the transplanted P. oceanica seagrass cuttings and control meadows as a function of transplantation method (**A**, **B**, and **C**) and sample origin (**D**, **E**, and **F**). "Donor pop.-IC" - donor population of intermatte cuttings before transplantation, "Donor pop.- SF" donor population of storm-fragments before transplantation. Statistically significant differences ($p < 0.05$) within tissues are represented by different lowercase letters (a, b)

Figs. 7A and 8A are reported in Supplementary Tables S21 and S22, respectively.

Discussion

To our knowledge, this is the first study to investigate the influence of transplantation methods and donor origins on the bacterial communities associated with *P. oceanica* cuttings transplanted into dead matte areas. Overall, our findings show that while bacterial diversity remained broadly stable across treatments, the composition of root-associated microbiomes was strongly mainly by the transplantation method and to a lesser extent by the donor origin. Among the transplantation methods, iron staples promoted microbial assemblages most similar to control meadows, whereas coconut fiber mats and BESE elements led to more distinct communities. Moreover, donor origin influenced the abundance of specific bacterial taxa, such as *Candidatus* Thiodiazotropha, which was more abundant in intermatte cuttings compared to storm-fragments. These patterns suggest that both the physical characteristics of the transplantation method and the initial microbial pool associated with donor material play a critical role in shaping the microbial trajectory of seagrass roots after restoration.

Bacterial community dynamics in transplanted P. oceanica cuttings

The analysis of alpha diversity showed that the Shannon and Simpson indices remained similar across all treatments for both leaves and roots, indicating a consistent balance between species richness and evenness regardless of the transplantation method or donor origin. However, a notable pattern emerged for the roots of donor populations originating from storm-fragments, which exhibited significantly higher ASV richness compared to the roots of control meadows and transplanted cuttings. This elevated richness may reflect the presence of low-abundance taxa, which do not strongly affect diversity indices sensitive to dominant species. Such a pattern suggests that the roots of the donor populations experience

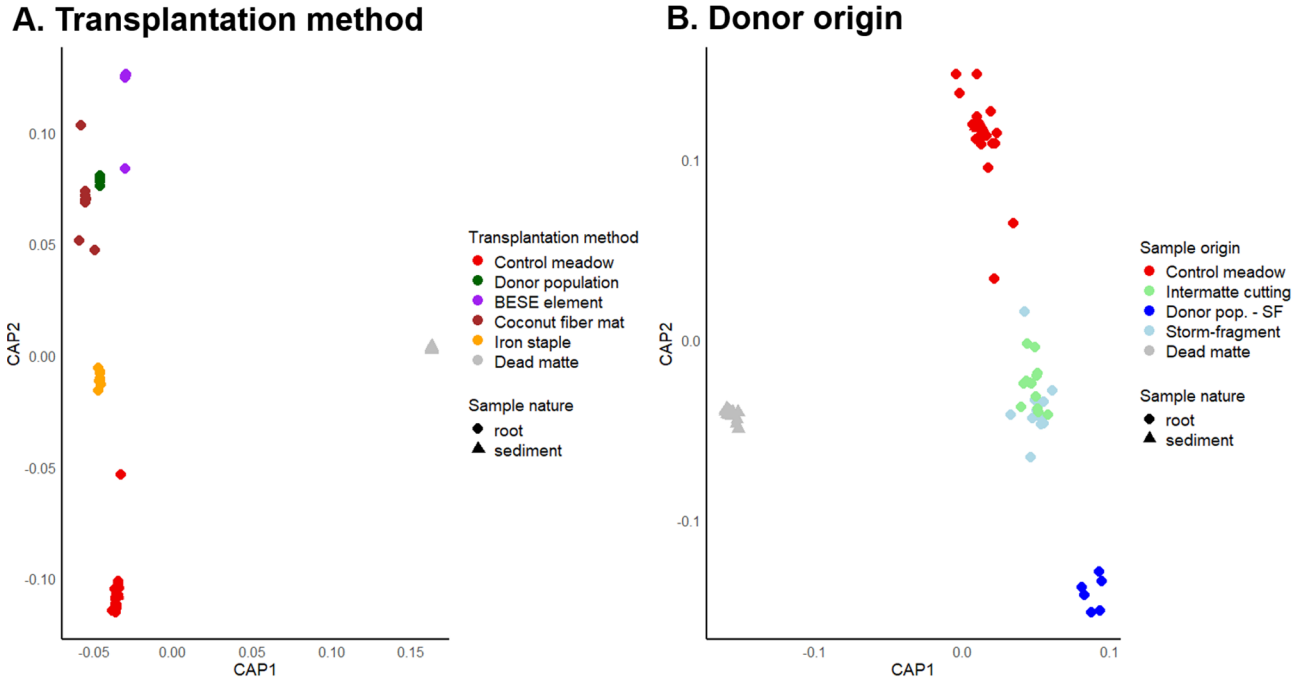


Fig. 6 Canonical analysis of principal coordinates (CAP) ordination plot based on Bray–Curtis dissimilarity matrix of square root transformed bacterial abundances showing canonical axes that best discriminate the bacterial communities associated with the different tissues (leaf and root) of the transplanted P. oceanica seagrass plants and control meadows, as well as sediment and seawater, as a function of transplantation method (**A**) and sample origin (**B**). "Donor pop.-IC" - donor population of intermatte cuttings before transplantation, "Donor pop.- SF" donor population of storm-fragments before transplantation

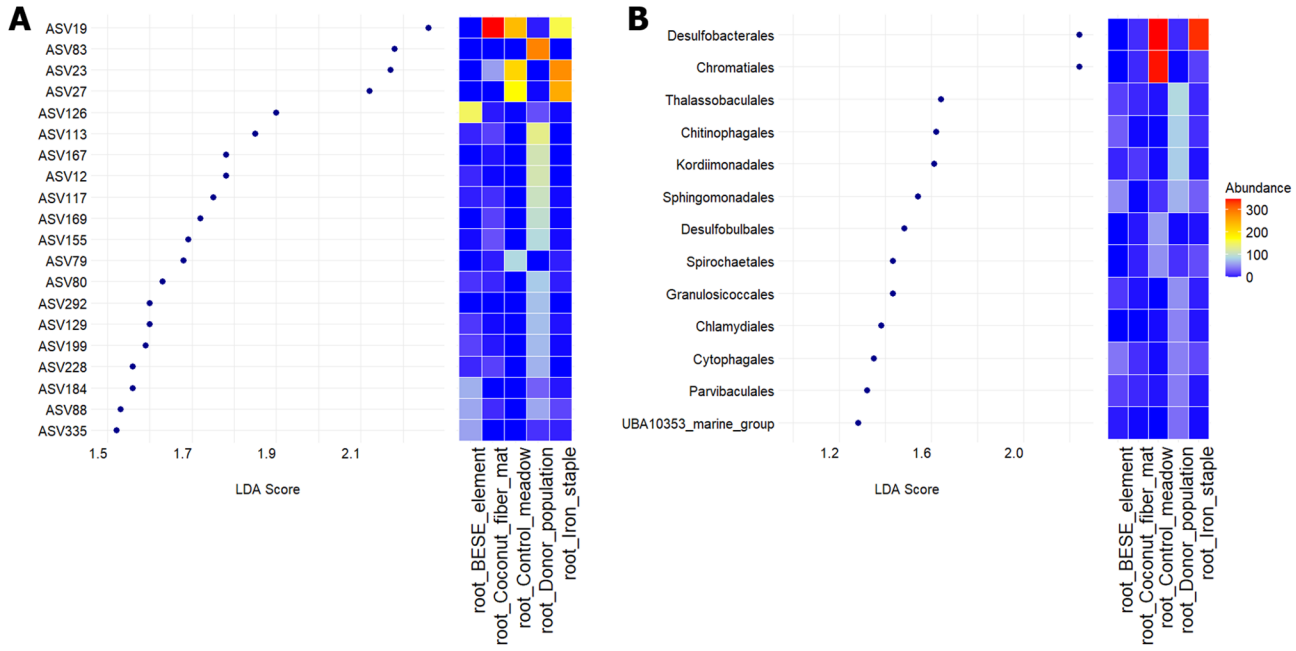


Fig. 7 Linear Discriminant Analysis (LDA) Effect Size (LEfSe) plots displaying the most differentially abundant (**A**) ASVs and (**B**) bacterial orders from P. oceanica seagrass roots according to the experimental factor 'transplantation method'. Differentially abundant features were determined using the Kruskal-Wallis rank test (adjusted *p*-value cut off = 0.05), with the Log LDA Score value adjusted to 1.0 and significant ASVs/taxa given in descending order from the highest to lowest LDA score

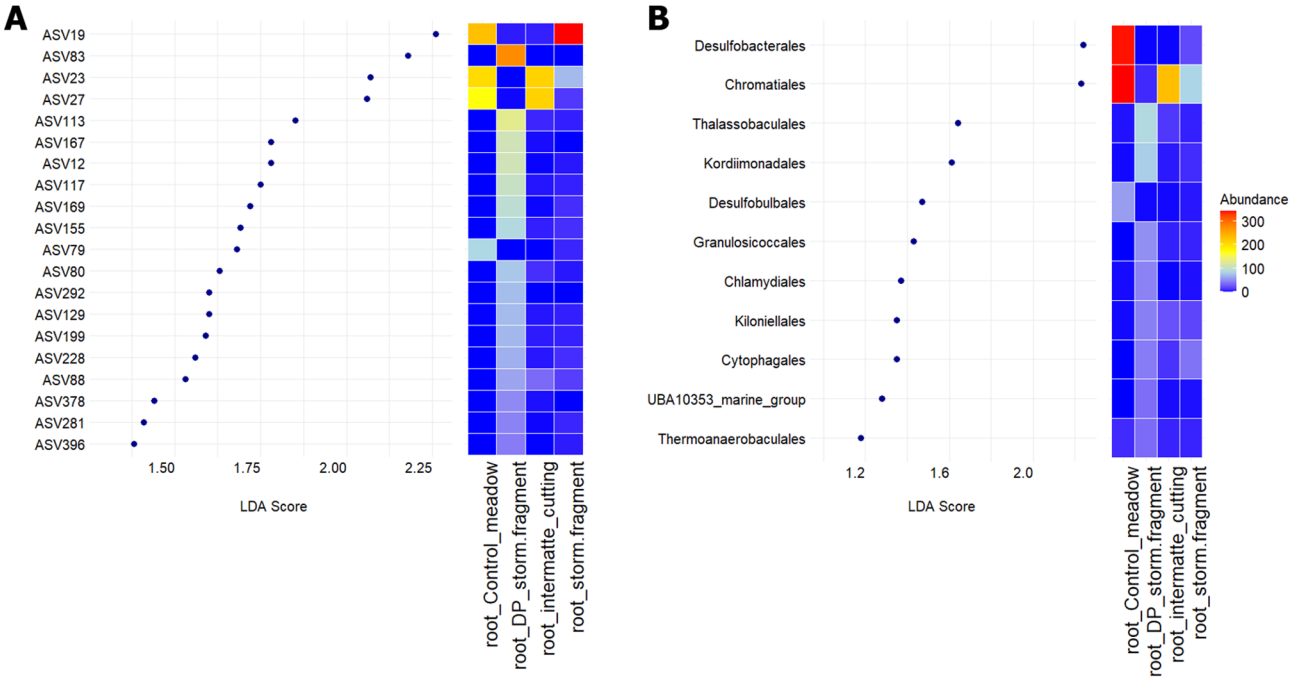


Fig. 8 Linear Discriminant Analysis (LDA) Effect Size (LEfSe) plots displaying the most differentially abundant (**A**) ASVs and (**B**) bacterial orders from P. oceanica seagrass roots according to the experimental factor 'sample origin'. Differentially abundant features were determined using the Kruskal-Wallis rank test (adjusted *p*-value cut off = 0.05), with the Log LDA Score value adjusted to 1.0 and significant ASVs/taxa given in descending order from the highest to lowest LDA score

opportunistic colonization by microbial taxa. The roots of the donor populations, originating from storm-fragments drifting on the seafloor without anchoring in sediment, likely encounter diverse microbial sources, enhancing their richness through exposure to a larger pool of water and sediment-associated bacteria. Indeed, surrounding sediment and seawater generally harbor a higher bacterial richness than seagrass tissues [35, 45].

Following transplantation, environmental conditions gradually stabilize, and this stabilization is mirrored in the bacterial communities, which progressively resemble those found in established control meadows [57, 58]. In these mature meadows, long-term interactions between roots and their environment promote the development of a more specialized and functionally optimized bacterial community. This results in a potentially reduced ASV richness and change in bacterial community structure, as the host plant selectively supports beneficial microbial taxa over time [34, 59]. Such specialized communities are shaped by plant-derived exudates and rhizosphere-specific gradients in oxygen and redox potential [58, 60, 61]. Medium and long-term studies are needed to determine whether the roots of the transplants will eventually develop a bacterial structure similar to that of the control meadow, as root age plays a key role in microbial colonization in long-lived seagrasses such as *P. oceanica* [62, 63].

Furthermore, the roots of the control meadows were significantly enriched in the bacterial orders *Chromatiales*, *Desulfobacterales*, and *Desulfobulbales* compared to the roots of storm-fragments and intermatte cuttings two years after transplantation. *Chromatiales* have been identified as key bacterial groups dominating the rhizosphere of seagrasses [28, 34] and salt marsh vegetation [63, 64]. *Chromatiales* are involved in sulfur oxidation processes, and it is thought that they are critical in mitigating sulfide toxicity within the root zones [34, 62, 64]. In addition, the most abundant genus among the *Chromatiales* was *Candidatus* Thiodiazotropha, which has been demonstrated as a key endosymbiont in the coastal cordgrass *S. alterniflora* [63]. Originally discovered in symbiosis with bivalves from the family *Lucinidae*, these endosymbionts fix carbon and provide both carbon and nitrogen to their host by harnessing energy from the oxidation of reduced sulfur compounds [65–68]. Coastal vegetated plants benefit from their symbiosis with members of the *Candidatus* Thiodiazotropha genus, as it helps mitigate sulfide toxicity [35] and links sulfide oxidation to carbon and nitrogen fixation. Although nitrogen is likely transferred to the plant host, the precise mechanism behind this transfer remains to be fully understood and warrants further investigation [63, 69]. Secondly, *Desulfobacterales* and *Desulfobulbales* are sulfate-reducing bacteria (SRB) capable of nitrogen fixation, commonly found in high abundance within the root microbiome of

seagrasses [34, 45, 60, 63, 70]. Moreover, SRB can oxidize ethanol [71] in the rhizosphere, potentially representing a mutually beneficial interaction between plants and bacteria. Indeed, despite producing hydrogen sulfide, these bacteria help detoxify the rhizosphere by metabolizing ethanol released by the plant roots [34]. Furthermore, it could be hypothesized that a mutualistic relationship exists between *Desulfobacterales and Desulfobulables*, which produce sulfide, and *Chromatiales*, which uses the oxygen released by the seagrass roots as the terminal electron acceptor for sulfide oxidation [72]. Finally, *Desulfobulbales* are not exclusively composed of SRB but also include genera known as cable bacteria (e.g., *Candidatus* Electrothrix), which can couple oxygen reduction with sulfide oxidation over centimeter-scale distances within the sediment [60, 73, 74]. These bacteria may also enhance nitrogen availability for seagrasses by indirectly promoting dissimilatory nitrate reduction to ammonium (DNRA) through the dissolution of iron sulfides [75] and/or by facilitating nitrogen fixation [76].

The essential functions provided by these bacterial orders strongly influence the health and productivity of seagrass meadows [60, 70], particularly under stressful environmental conditions such as those induced by transplantation [33, 43, 58]. Numerous studies have reported reduced morphological traits in transplanted *P. oceanica* compared to control meadows [47, 77, 78], yet no conclusive explanation has been established for this phenomenon. Further research is needed to determine whether the limited development of *P. oceanica* cuttings is directly linked to their associated bacterial communities.

Contribution of donor origins to bacterial communities associated with transplanted P. oceanica cuttings

Although the donor population of intermatte cuttings lacked initial roots at the time of transplantation, the intermatte cuttings successfully established microbial communities similar to those of the storm-fragments. This illustrates the ability of roots to recruit and stabilize functional microbial communities over time, even under disturbed conditions, by progressively shaping the microbial community as plants grow and modify the surrounding sediment [33, 58, 60, 79].

Moreover, the diversity and overall structure of bacterial communities associated with storm-fragments and intermatte cuttings showed no significant differences two years after transplantation. From a microbiological perspective, this finding suggests that both donor origins are equally suitable for transplantation onto dead matte in a restoration context. However, the notably higher abundance of *Chromatiales*, particularly the genus *Candidatus* Thiodiazotropha, in the roots of intermatte cuttings raises intriguing questions about their potential functional advantages compared to storm-fragments. Given the critical role of this genus in sulfur oxidation and nitrogen fixation processes [35, 63], further research are needed to determine if the higher abundance of *Candidatus* Thiodiazotropha could contribute to increased plant performance, such as higher nitrogen content in transplanted seagrass tissues.

Furthermore, mesocosm experiments involving the inoculation of specific strains from this bacterial genus, although these have yet to be isolated, could help clarify their direct contribution to nutrient cycling and plant health [25, 80]. In addition, ^{15}N-DNA stable isotope probing would provide valuable evidence of active nitrogen fixation by this genus within the roots of intermatte cuttings [81–83]. Such approaches could shed light on whether microbial differences, even when subtle, can influence the long-term success and resilience of transplanted *P. oceanica* cuttings.

Influence of transplantation methods in shaping bacterial communities associated with P. oceanica cuttings

As expected, our results showed that bacterial communities associated with *P. oceanica* roots are more affected by transplantation methods than those associated with leaves. Among the tree tested transplantation methods, cuttings secured with the iron staples exhibited a bacterial community structure most similar to that of the control meadow. In contrast, marked dissimilarities were observed between bacterial community associated with the control meadow, and those associated with cuttings transplanted using coconut fiber mats, BESE elements, and even the donor populations.

The three transplantation methods differed in the material composition of anchoring structures used to attach the cuttings to the seafloor (i.e., iron, coconut fibers, or starch-derived polymers) and the level of structural complexity they provided. Coconut fiber mats and BESE elements offered greater structural complexity compared to the iron staples. Additionally, these methods varied in the distance maintained between the cuttings and the sediment surface.

Influence of transplantation material composition on root-associated bacterial communities

The three transplantation methods differ in the type of material used to anchor the cuttings to the seafloor. The composition of the coconut fiber mats and BESE elements could explain the differences in bacterial community structure compared to the control seagrass meadows. The coconut fiber mats consist of a natural coconut fiber woven mesh with a high lignin content and, therefore, an increased hydrophobicity and resistance to microbial degradation [84–87]. However, high abundance of bacterial taxa specialized in lignin degradation was not observed in the root samples from the transplants

growing on the coconut fiber mats. BESE elements are composed of biodegradable potato-waste-derived Solanyl C1104M (Rodenburg Biopolymers, Oosterhout, the Netherlands), which could likely serve as a carbon source for microbial colonization [88]. The most differentiating bacterial taxon between the roots of the transplants on the BESE elements and the plants from the other groups was ASV126, which belongs to the order *Pseudomonadales*. *Pseudomonadales* abundance is influenced by nutrient availability, particularly ammonium and phosphate, and they thrive in environments rich in labile organic carbon [89]. Laboratory experiments on BESE elements biodegradation have shown that this compound releases a significant amount of dissolved organic carbon, soluble reactive phosphorus, and nitrate [88], which might have favoured *Pseudomonadales*. Moreover, members of this order are key contributors to the degradation of different biodegradable polymers [90, 91]. Furthermore, *Pseudomonadales* have also been found to be highly abundant in *P. oceanica* 'banquettes' [92], which consist of banks of dead leaf material on the beaches [93]. These bacteria are common in copiotrophic communities as they possess polymer-degrading enzymes [94–96], as well as ligninolytic and chitinolytic activity [96, 97] which makes them effective in seagrass leave decomposition [98]. Given the significant accumulation of dead *P. oceanica* leaves within the BESE elements (Fig. S3), this deposition could also explain the higher presence of *Pseudomonadales* in the roots of transplants on BESE elements compared to the other transplantation methods tested in this study. Further studies are needed to compare the core microbiome of the bacterial biofilm developing on the surface of restoration substrates with the root microbiome of the transplants. This would help assess the extent to which the transplantation material leaves its bacterial signature on the root microbiome of the seagrass transplants.

Effects of transplantation material structure and sediment contact on root-associated bacterial communities

Besides material composition, the three transplantation methods also differed in the height of the cuttings relative to the sediment and the underlying dead matte. The rhizomes and roots of the cuttings attached with iron staples have direct contact with the dead matte. In contrast, the cuttings on the coconut fiber mats are separated from the dead mat by the 5 mm thickness of the coconut fiber mats. As for the cuttings on the BESE elements, these layers measure 6 cm in height, creating a gap between the roots of the cuttings and the dead matte. This variation in positioning could influence the degree of interaction between the roots and the sediment microbial pool, affecting the recruitment and establishment of bacterial communities. Indeed, it is well established that plants recruit their root-associated microbiome from a larger pool of soil microbes, and the initial structure of this microbial pool plays a critical role in shaping the structure of root microbial communities [34, 99–101]. Cuttings anchored closer to the sediment may have increased exposure to beneficial sediment-associated bacteria. In contrast, elevated cuttings could encounter different oxygen and nutrient gradients, potentially promoting the proliferation of distinct bacterial groups. This could explain the observed differences in community structure and the varying degrees of similarity to the control meadows' bacterial communities. The reduced abundance of *Chromatiales* and *Desulfobacterales* in transplants on coconut fiber mats and BESE elements may be linked to limited initial recruitment due to reduced exposure to the sediment microbial pool, delaying the establishment of beneficial plant-microbe interactions. The use of iron staples appears to promote a more rapid microbial recovery, likely due to the direct contact between the roots and the sediment microbial pool, which closely resembles the microbial community of control meadows, despite differences in the dead matte bacterial community structure.

Moreover, empirical observations of the sampled cuttings revealed significant differences in root length and complexity two years after transplantation, whereas there were no initial differences at the time of planting (Fig. S4). The roots of transplants on coconut fiber mats and BESE elements were notably smaller than those of control meadows and transplants on iron staples (Fig. S4). Plant exudates released by the roots into the sediment promote microbial colonization through chemotaxis and attract key microbial partners that enhance plant fitness within the seagrass rhizosphere [70, 102, 103]. This interaction might be weaker or delayed in transplants on coconut fiber mats and BESE elements due to their limited initial contact with the sediment microbial pool. Further research is needed to determine the influence of bacterial communities on the root system development of *P. oceanica transplants*.

Perspectives for microbiome-driven seagrass restoration

The results discussed in this study highlight the effects of transplantation methods and donor origins on the bacterial communities associated to *P. oceanica* transplants and point to several promising research and application pathways. A key next step involves extended monitoring to evaluate the medium-term (5 years) and long-term (10 years) dynamics of microbial communities in transplants compared to control meadows. Such monitoring would clarify whether the observed differences in bacterial community composition between transplants and control meadows attenuate over time and whether distinct transplantation methods and donor origins ultimately converge toward similar bacterial assemblages. Moreover, the bacterial orders *Desulfobacterales* and *Chromatiales*

emerged as key contributors to the dissimilarity between control meadows and transplants. Further research is now warranted to elucidate how these taxa influence the overall fitness of transplanted seagrasses.

Furthermore, managing or manipulating microbial functions and communities are widely recognized as established methods in the bioremediation of terrestrial and aquatic ecosystems [104], and could be applied to marine ecosystem restoration. These methods leverage beneficial microbial interactions to optimize nutrient cycling, enhance plant stress tolerance, and accelerate ecosystem recovery [104, 105]. For example, plant growth-promoting rhizobacteria have demonstrated their effectiveness in enhancing seagrass growth, improving biomass production, rhizome elongation, and nitrogen uptake while also mitigating sulfide toxicity through microbial shifts in sulfur and iron cycling [25, 105]. Further research is needed to assess the effects of inoculating *Desulfobacterales* and *Chromatiales* strains into *P. oceanica* cuttings and to evaluate their potential influence on transplant morphology, growth, and overall development. Tailored pre- and probiotic treatments could help optimize microbial consortia, as demonstrated by their success in terrestrial and aquaculture systems [33, 104]. Collectively, these approaches could not only enhance initial transplant success but also ensure the long-term stability and ecological functionality of restored meadows.

Conclusion

To our knowledge, the present study is the first to investigate the succession of bacterial communities associated with the leaves and roots of *P. oceanica* transplants in a restoration project using different transplantation methods and donor origins. Our results reveal that while the overall alpha diversity of bacterial communities remains relatively stable across treatments, the root-associated microbiome exhibits pronounced shifts in composition compared to control meadows, particularly in the abundance of key bacterial orders such as *Chromatiales* and *Desulfobacterales*. Among the tested approaches, cuttings anchored with iron staples developed bacterial communities most similar to those of natural meadows, highlighting the critical role of direct sediment contact in facilitating the recruitment of functionally beneficial microbial partners. Conversely, cuttings transplanted on coconut fiber mats and BESE elements displayed more distinct microbial assemblages, likely influenced by differences in material composition, structural complexity, and sediment interaction.

Furthermore, the study shows that donor origin (storm-fragments or intermatte cuttings) does not significantly affect the long-term structure of root microbiomes two years after transplantation. This suggests that both sources are microbiologically suitable for restoration, although subtle differences in specific taxa, such as the higher abundance of *Candidatus* Thiodiazotropha in intermatte cuttings, raise intriguing questions about potential functional advantages related to nutrient cycling and sulfide detoxification.

Despite initial differences in bacterial community structure, the transplants displayed progressive stabilization towards conditions like those of control meadows, indicating the potential for long-term success with appropriate management strategies. These results emphasize the need for long-term monitoring to assess the full recovery and resilience of bacterial communities over time. By combining optimized transplantation methods with microbiome-targeted interventions, future restoration efforts could accelerate ecosystem recovery and enhance the stability and functionality of restored seagrass meadows. Overall, this study provides a foundational understanding of how transplantation methods and donor origins influence microbiome dynamics, laying the groundwork for improved methodologies that leverage beneficial plant-bacteria interactions for the sustainable recovery of degraded seagrass ecosystems.

Supplementary Information

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Supplementary Material 1

Supplementary Material 2

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Author contributions

AB: Conceptualization, Field Sampling, Methodology, Formal Analysis, Investigation, Writing, Visualization; TA: Conceptualization, Methodology, Formal Analysis, Investigation, Writing; AHE: Conceptualization, Methodology, Formal Analysis, Investigation, Writing, Visualization, Supervision; GM: Conceptualization, Methodology, Formal Analysis, Investigation, Writing, Visualization, Supervision; MM: Conceptualization, Writing, Supervision, Funding; SG: Conceptualization, Writing, Supervision, Funding. All authors read and approved the final manuscript.

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Data availability

The sequence reads from all samples collected during this study were deposited in the NCBI data bank (BioProject accession number PRJNA1221124).

Declarations

Competing interests
The authors declare no competing interests.

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