Microbiome-assisted restoration of degraded marine habitats: a new nature-based solution?

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Microorganisms interact with all biological components in a variety of ways. They contribute to increase the efficiency of marine food webs and facilitate the adaptation of multicellular organisms to climate change and other human-induced impacts. Increasing evidence suggests that microbiomes are essential for the health of marine species, for maintaining productive marine ecosystems, and thus for the sustainable functioning of the global biosphere. Marine microbiomes are typically species- or habitat-specific and are susceptible to environmental and human-driven changes. The microbiota of seagrasses, macroalgae, mangroves or tropical corals benefits their hosts by increasing their fitness, contributing to the removal of toxic compounds, conferring protection against pathogens, and/or supporting nutrient requirements. Alterations of the microbiomes might have negative consequences on species' health, survival, and overall ecosystem functioning. Despite the key ecological role of microbiomes in all ecosystems, their potential for the restoration of degraded habitats is still largely unexplored. Here we present a literature survey of the existing information on the microbiota associated with habitat-forming species and suggest that the resilience/recovery of damaged marine habitats can depend largely on the changes in the microbiota. Nature-based solutions relying on microbiome analyses (also through omics approaches) enable health monitoring of transplanted organisms/metacommunities and potential identification/production of probiotics/bio-promoters to stabilize unhealthy conditions of transplants. In the context of international strategies concerning ecological restoration, the use of the scientific knowledge acquired on the marine microbiome deserves to be exploited to assist both traditional and innovative restoration approaches. The success of habitat restoration may depend on our ability to maintain, along with the restored species and habitats, a functional microbiota.

KEYWORDS

marine ecosystem restoration, microbiome, corals, seagrasses, macroalgae, habitat-forming species

1 Introduction

Microorganisms support the existence and resilience of all life forms (Gilbert and Neufeld, 2014). They are crucial for the maintenance of healthy and productive marine ecosystems and for the sustainable functioning of the global biosphere (Trevelline et al., 2019). Microorganisms are intimately associated with animals, plants, and algae, and contribute to their nutrition, defence, immunity, and development (Pita et al., 2018; Stévenne et al., 2021). The prevalence of these associations implies that multicellular organisms can no longer be considered as individual entities, but rather as "holobionts" (consisting of the host, the microbiota, and the interactions among them). Consequently, the impact of climate changes and human pressures on multicellular organisms as well as their resilience will also depend on the responses of their associated microbiota, which will be essential to achieve an environmentally sustainable future (Doney et al., 2012; McFall-Ngai et al., 2013; Petersen and Osvatic, 2018).

It is recognized that microorganisms have the potential to adapt to climate change scenarios (e.g., global warming, ocean acidification, oxygen depletion) and human-induced impacts (e.g., pollution due to chemical contaminants, eutrophication) (Danovaro et al., 2011; Torda et al., 2017; Cavicchioli et al., 2019). Micro-organisms, indeed, thrive in the most extreme environments on Earth, from the coldest to warmest habitats, from the acid and hypersaline environments to anoxic systems, even at the highest pressures of the deep sea (Boetius et al., 2015; Dick, 2019; Manea et al., 2019; Hiraoka et al., 2020). It has been also extensively documented that marine microbiota can allow multicellular organisms to thrive in extreme marine habitats by conferring them the ability to cope with conditions incompatible with life (Danovaro et al., 2017; Sogin et al., 2020) by regulating the maintenance of their fitness, conferring them resistance and resilience (Bang et al., 2018). Microorganisms can also be sentinels of the impact of climate change and/or pollution on the holobionts (Conte et al., 2021; Corinaldesi et al., 2022) revealing early their health conditions (Peixoto et al., 2022).

Despite the key ecological role of microbiota in all ecosystems, their potential for restoration actions of degraded habitats and pollution control is still largely unexplored. Due to the rapid decline of marine ecosystems and their associated biodiversity (Danovaro et al., 2020; Orfanidis et al., 2021), both in coastal and deep-sea habitats, ecological restoration actions appear to be the most promising strategy to rebuild them (Cebrian et al., 2021; Fraschetti et al., 2021). This practice refers to the process able to assist the recovery of degraded, damaged, and destroyed ecosystems (Gann et al., 2019), thus retrieving lost biodiversity and ecosystem services (i.e., nutrient cycling, primary and secondary production, maintenance of genetic diversity, habitat provisioning, pollution control, carbon storage, erosion prevention). To revert the trajectory of degradation of most ecosystems on Earth and to accelerate the recovery of damaged ecosystems, the United Nations has declared the Decade on "Ecosystem Restoration" 2021-2030.

The strategies and techniques for ecological restoration of different marine habitats/ecosystems (e.g., seagrass beds, macroalgae forests, reef-forming corals) are mostly already available, but these do not consider the role of the microbial component. The International Coral Reef Society (ICRS) has recently published a scientific policy document that underlines the importance of "driving innovation by developing new approaches, where current solutions are not sufficient to address the coral reef emergency" (Knowlton, 2021). Accordingly, the declaration of the Decade on Ecosystem Restoration by the United Nations has sparked interest in the methods needed to implement best practices for maximum gain.

In the present literature survey, we provide an overview of the diversity and role of the microbiome (Berg et al., 2020) in marine habitats/ecosystems to shed light on the importance of integrating this component into future restoration plans. To the extent possible, we will draw parallels with microbiome-based restoration in the terrestrial environment, which is a much more advanced scientific field than in the marine environment, to identify key aspects and pathways in the recovery of degraded marine ecosystems. In this regard, the use of microbial inoculants and microbiome engineering will be addressed, emphasizing the challenges and pitfalls of these practices in the marine environment.

2 Microbiome-based restoration of marine ecosystems: lessons learnt from terrestrial ecosystems

Ecological restoration in the marine environment is certainly a much younger field of scientific application than the terrestrial one (Saunders et al., 2020). In terrestrial ecosystems, it has been reported that the success of ecological restoration largely depends on soil microbial assemblages that degrade plant-associated organic substances, thus improving the physicochemical characteristics of the soil (Trivedi et al., 2013; Calderón et al., 2017). In addition, plant-associated microbes (e.g., the rhizosphere and endophytic microbiomes) provide nutrients, minerals, and vitamins and protect plants against biotic and abiotic stress (Vandenkoornhuyse et al., 2015; Dubey et al., 2019).

Especially, with the advent of the -omics approaches it has been possible to identify key microbiomes and their metabolites in different environments at unprecedented resolution. In terrestrial ecosystems, there is evidence that the core microbiota is essential for the maintenance of the functional stability of soil microbiomes, nutrient cycling, and plant establishment in reforested ecosystems and that it should be integrated into the policy and management strategies of ecological restoration plans (Jiao et al., 2022). In this regard, soil inoculation techniques and the use of carriers for inoculants have been assessed to promote plant growth. In particular, *Rhizobium* inoculants have been commercially produced worldwide (Catroux et al., 2001; Deaker et al., 2004) as well as *Azospirillum brasilense* and *Bacillus pumilus* (Cassán et al., 2020). Manipulative experiments highlighted that the soil community is an important driver of plant-community development and that manipulation of the soil community is a key step for successful restoration (Wubs et al., 2016).

A large-scale, six-year-old field experiment on terrestrial habitats has shown that the application of soil inoculants is a powerful tool to promote ecosystem restoration and steer plant community development depending on the origin of the soil inoculum (Wubs et al., 2016). Other studies have reported that inoculation of soils with mycorrhizal fungi can also increase the growth performance of plants and that local mycorrhizal fungi strains outperform commercial strains. Co-inoculation of different native mycorrhizal fungi species can improve plant growth with positive implications for restoration ecology (Crossay et al., 2019). A key role is indeed represented by the species richness of the inoculum (Hu et al., 2021). Previous investigations indicated that the use of consortia that contained more *Pseudomonas* strains produced beneficial effects on plant growth. Consistently, it has been also documented that the transfer of whole soil communities, enriched in plant grow-promoting consortia, is more effective than the addition of individual species or strains in restoration actions (Emam, 2016; Bulot et al., 2017). Another interesting finding obtained in terrestrial ecology is that soil transplantation experiments at large-spatial scales are more successful than at smaller-spatial scales (Kardol et al., 2009; Pywell et al., 2011; Jaunatre et al., 2014). Several investigations have also indicated that environmental and biological factors such as nutrient loads and interactions among soil biological communities can influence the success of transplantation (De Deyn et al., 2004; Van Elsas et al., 2012). However, several studies concluded that it is currently unclear if the inoculant or soil transplantation effects will be transient or whether they will last through plant generations, and it is necessary to better deepen scientific research on plant-microbe interactions for sustainable agriculture (Hu et al., 2021).

In terrestrial ecology, it has been also reported that plants and their roots have evolved "a cry for help" response to resist environmental and anthropogenic stress, by developing adaptive strategies including the production of metabolites with direct defensive effects and molecules that attract beneficial (micro) organisms for protection (Rizaludin et al., 2021). In a recent study, the "cry for help" concept was also supported by the results of a field experiment, in which durum wheat (*Triticum turgidum L.* var. *durum*) naturally infected with the crown rot pathogen *Fusarium graminearum* enriched for *Stenotrophomonas rhizophila* (SR80) in the rhizosphere and root endosphere (Liu et al., 2021). After reintroduction, the SR80 strain induced resistance against canopy rot and improved grain growth. The rhizosphere microbiome is thus a reservoir of efficient helpers that plants can specifically exploit to cope with one or more stressors. Deciphering their communication can provide fundamental knowledge for the future development of plants resistant to multiple stressors also in marine ecosystems.
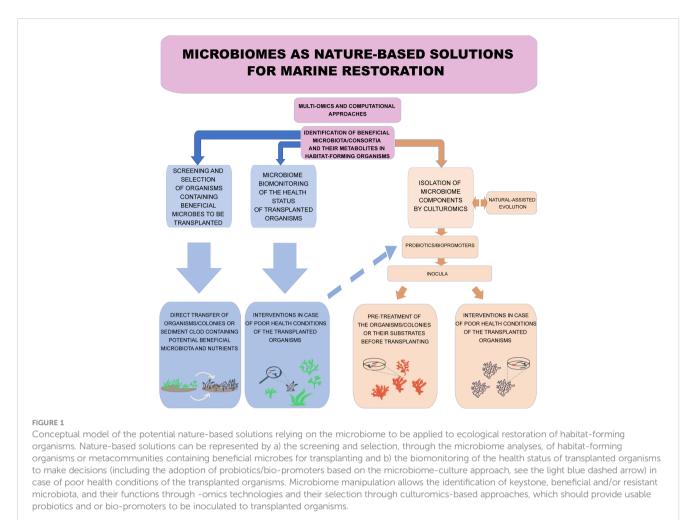
If the integration of the microbiome in the design and management of terrestrial restoration actions is under experimentation, in the marine environment this is still far from being taken into consideration. This wide gap is due to the greater complexity of the marine submersed environment compared to the terrestrial one, its high variability due to hydrodynamic forcings, and the difficulty of applying and managing bacterial inoculants. Furthermore, while on land, vegetation is the main (practically the

only) biological component that structures the landscape, in the marine environment even animal components such as corals can form habitats. Therefore, scientific research on the role and application of the microbiome in restoration ecology has a more complex job to do. However, knowledge accumulated in terrestrial microbiome-based restoration may inspire marine ecosystem restoration.

3 Microbiome selection to boost the restoration success of marine ecosystems

As it becomes more evident that microbiomes power ecosystem-level processes and resilience to anthropogenic and climate-driven impacts, scientific interest in microbiome engineering is increasing. Microbiome selection (which is part of the wider field of microbiome engineering but excludes any form of genetic manipulation) aims at improving host fitness with designed microbial communities (Mueller and Sachs, 2015). Microbiome selection thus foresees the desired modulation of the tailored microbiome to enhance a selected microbiome-dependent host phenotype. To this aim chemical-based (prebiotics and antibiotics), cellular-based (probiotics and microbiota transplants), phage-based (bacteriophages), or host-mediated microbiome-modulation approaches can be implemented (Li et al., 2022).

Traditionally, the modulation of the host-associated microbiome to tailor a desired phenotype was mainly performed empirically, thus completely blind concerning the compositional and functional features of the target microbiome, just relying on the use of allochthonous probiotics and prebiotics (i.e., compounds that foster growth or activity of beneficial microorganisms such as bacteria and fungi) as possible providers of the desired functions (Peixoto et al., 2022; Figure 1). The current multi-omics era is changing our capacity to study and understand the microbiome in their native ecosystems. From an operational point of view, the identification of the microbiome features being responsible for a desired function foresees 4 phases: (i) microbiome sampling, biobanking and multi-omics assessment; (ii) microbiome modelling and networks construction; (iii) assembly of *de novo* Microbiome-Assembled Genomes (MAGs) and (iv) construction of genome-scale metabolic models. The identification of the microbiome modules and their metabolic interactions allows the knowledge-based implementation of microbiome-based approaches - in terms of selected bio-promoters and bio-inocula – piloting these modules, their components, and their web of interactions.

The recovery and selection of beneficial and resistant microorganisms can be obtained through specific culture media (Peixoto et al., 2017), whose selection and implementation can be also carried out based on the genome-scale metabolic models of the tailored beneficial microorganisms, allowing the in-depth understanding of their nutritional requirements (Liu et al., 2010). However, only a minor fraction of marine microbes are actually cultivable even using the best available colturomics-based approaches (Rodrigues and de Carvalho, 2022). In addition, if we

FIGURE 1

Conceptual model of the potential nature-based solutions relying on the microbiome to be applied to ecological restoration of habitat-forming organisms. Nature-based solutions can be represented by a) the screening and selection, through the microbiome analyses, of habitat-forming organisms or metacommunities containing beneficial microbes for transplanting and b) the biomonitoring of the health status of transplanted organisms to make decisions (including the adoption of probiotics/bio-promoters based on the microbiome-culture approach, see the light blue dashed arrow) in case of poor health conditions of the transplanted organisms. Microbiome manipulation allows the identification of keystone, beneficial and/or resistant microbiota, and their functions through -omics technologies and their selection through culturomics-based approaches, which should provide usable probiotics and or bio-promoters to be inoculated to transplanted organisms.

consider that only a few marine isolates are endowed with the technological properties necessary for their implementation in concrete biotechnological applications, such as marine probiotics (e.g., the ability to grow as axenic culture in pilot bioreactors) it is clear that at present only a tiny fraction of the diversity of marine microbiomes can be exploited to produce probiotics (Wang et al., 2021a). These selected microorganisms can be inoculated at different life stages of the host using similar approaches to those already used in agriculture for probiotics (Backer et al., 2018). The inoculation of beneficial microorganisms can be performed using microencapsulation and nanoparticles as well as saline suspension and substrates for the microbial immobilization adopted in terrestrial ecosystems (Vassilev et al., 2020; Balla et al., 2022) and aquaculture systems (Prado et al., 2020). However, the delivery of microorganisms (microbial inoculum) in marine environments is a major challenge due to dilution in the water column and dispersion by currents and the difficulty of controlling interactions with a wide range of micro- and macro-organisms naturally present in these systems. Therefore, the immobilization of the microbial cells could be one of the approaches that might be adopted to overcome this problem (Peixoto et al., 2021).

Microbiome manipulation to improve host health could be based on other approaches such as microbiome-assisted evolution, used to accelerate adaptation on natural taxa to select those that show the highest resilience against stress and thus increase the fitness of the transplanted species (Van Oppen et al., 2015). In this case, experimental evolution studies involve the maintenance of organisms under controlled conditions and the monitoring of their response over several generations (Figure 1). Organisms are expected to adapt to these conditions through selection due to random natural genetic mutations, trans-generationally stable epigenetic modifications and/or through the acquirement of adaptive changes in the associated microbiome (Henry et al., 2021; Maire and van Oppen, 2022; Mueller and Linksvayer, 2022). Even though the selected pressures cannot dictate what adaptive traits will appear, these factors may select beneficial changes at the microbiome level (Maire and van Oppen, 2022). These microbiome-dependent adaptive changes can be characterized by multi-omic approaches, allowing the complete understanding of the correspondent functional traits, and opening the opportunity for their engineering.

The experimental evolution of coral-associated bacteria is at the stage of hypothesis, and it has been not implemented yet (Rosado et al., 2019; Maire and van Oppen, 2022). Although scientific literature is available on the possibilities of exploiting microbiome selection and probiotic supply to improve the resistance and resilience of natural ecosystems (especially concerning coral reefs), the implementation of these technologies in restoration plans is still far from being reached. Several gaps in knowledge
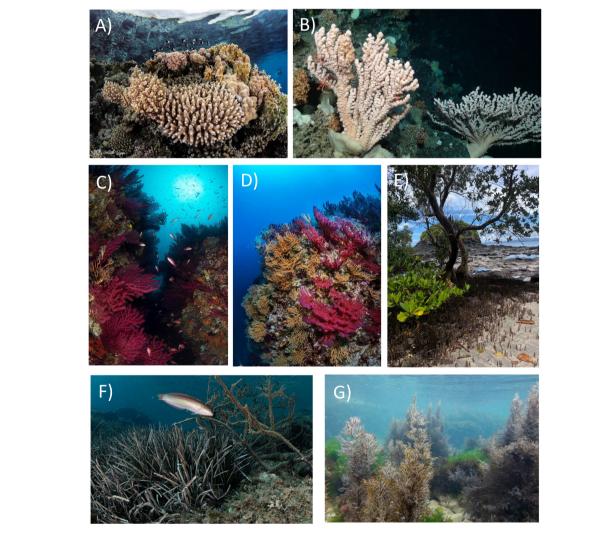
and practical issues (e.g., in the approaches of target microorganisms and the industrial production of pro-biotics and bio-promoters) need to be filled (Peixoto et al., 2022) to make the most of the potential of the microbiome in the restoration ecology.

4 Microbiomes of marine habitat-forming species: integration into ecological restoration approaches

Many of the marine restoration efforts have been focused on coral reefs of shallow-coastal ecosystems contrary to what has been carried out for cold-water corals, and mesophotic bioconstructions (Fraschetti et al., 2021). Tropical coral transplantation is also one of the pioneering approaches to marine ecological restoration (Boström-Einarsson et al., 2020). This is due to several reasons, including the high ecological and economic importance of these habitats, their easy accessibility, and the rapid decline they are facing

due to climate change and other anthropogenic impacts (Rivera et al., 2020; Ferse et al., 2021). At the same time, wide information is available on microbial assemblages associated with coral reefs, also justified by the desire to identify microbial diseases that contribute to their decline in the world's oceans (Li et al., 2022). Despite this, the microbiome has not yet been factored into effective plans to restore coral reef ecosystems. However, it could contribute to the success of their restoration, and to that of other bioconstructions and even deep habitat-forming species (Figure 2). The general habitat characteristics of the microbiomes and their potential in the restoration of different bioconstructions is described here below.

4.1 Coral reefs, coral gardens, and cold-water corals

Reef-building corals (Figure 2) - Awareness of the rapid decline of coral reefs worldwide due to anthropogenic impacts and climate

FIGURE 2
Habitat-forming species, which can be involved in the microbiome-based-restoration. **(A)** Coral reef (image credits by Gabriella Luongo); **(B)** cold-water corals; **(C, D)** coral gardens (credits by Gabriella Luongo); **(E)** mangroves; **(F)** seagrass meadows (credits by Gabriella Luongo), and **(G)** macroalgal forests (credits by AFRIMED project).

change has spurred restoration efforts, which are now widely applied using several approaches (Pandolfi et al., 2003; Bellwood et al., 2004; Vaughan, 2021) including coral gardening, transplantation of coral fragments, micro-fragmentation, and the use of artificial substrates (Boström-Einarsson et al., 2020). In the last decade studies of the coral microbiome have allowed expanding knowledge of the diversity and functions of microorganisms associated with reef-building corals (Van Oppen and Blackall, 2019). There is evidence that coral-associated microorganisms play a key role in the cycling and/or supply of nutrients (e.g. carbon, nitrogen, and sulfur) to corals or their symbiotic algae (e.g., Symbiodiniaceae), in the protection of corals (possibly through the production of antimicrobial compounds), in improving larval settlement (Van Oppen and Blackall, 2019) and resilience to environmental stressors, which can lead to coral diseases (Bourne et al., 2016; Vanwonterghem and Webster, 2020). Available studies indicate that the diversity of coral-associated bacteria far outnumbers that of archaea (two archaeal phyla versus at least 39 bacterial phyla described and candidate; Gardner et al., 2023). However, few studies have specifically focused on archaea, mainly because of technical limitations e.g., primer specificity (Gantner et al., 2011; Apprill et al., 2015; Parada et al., 2016), thus it is possible that their diversity is greater than what is known to date.

The most common coral-associated bacterial taxa belong to Gammaproteobacteria, Alphaproteobacteria, Bacteroidetes, Cyanobacteria, Firmicutes, and Tenericutes, while the coral-associated archaea mostly affiliate with Euryarchaeota and Nitrososphaerota (syn. Thaumarchaeota) (Table 1; Huggett and Apprill, 2019). Available data for coral-associated fungi are currently limited and only in recent research, some taxa such as *Aspergillus*, *Clonostachys*, *Mortierella*, *Cladosporium*, *Wicherhamomyces*, *Simplicillium*, *Cutaneotrichosporon*, and *Penicillium* have been identified (Cheng et al., 2023). The microbiome of different coral species can change over time and across different geographic regions, and microbiome shifts can depend also upon environmental stressors as well as coral health (Hernandez-Agreda et al., 2018; Morrow et al., 2022). It has been also reported that coral adults have a less diverse and more stable microbiome than larvae and early recruits, suggesting a selection process during coral maturation (Epstein et al., 2019) and that microbiome is fine-tuned to meet the needs of a particular host in a certain environment (Van Oppen and Blackall, 2019). Given the complexity of studying the whole coral microbiome, scientific research is increasingly focusing on core microbial taxa that persist within the host across different spatial and temporal scales (Hernandez-Agreda et al., 2017; Dunphy et al., 2019). The core microbiome is indeed composed of common taxa, host and habitat-specific (Sweet and Bulling, 2017), which form stable and persistent symbiotic interactions with corals to provide key functions (Shade and Handelsman, 2012; Shafquat et al., 2014; Ainsworth et al., 2015; Chu and Vollmer, 2016). A less stable core microbiome could indicate a higher susceptibility of the holobiont to environmental stress (Ziegler et al., 2016). Therefore, the analysis of the core microbiome is essential to inform holobiont health status, which in turn is also fundamental for outlining strategies for coral restoration (Hernandez-Agreda et al., 2016; Sweet and Bulling, 2017).

The top five reef-building coral species used in restoration projects are *Acropora cervicornis*, *Pocillopora damicornis*, *Stylophora pistillata*, *A. palmata*, and *Porites cylindrica* (Boström-Einarsson et al., 2020). In general, the dominant taxa of bacterial assemblages associated with corals are assumed to be their healthy symbiotic state (Hernandez-Agreda et al., 2017 and references within). Bacterial members belonging to the genus *Endozoicomonas* are dominant in corals although their contribution to the entire microbial assemblage is highly variable within individuals of the same species and among different species (Hernandez-Agreda et al., 2017; Robbins et al., 2019; Rosales et al., 2019; Vanwonterghem and Webster, 2020). There is evidence that *Endozoicomonas* members are beneficial symbionts of the coral hosts with a role in biofilm production (that promotes surface colonization of other bacteria), sulphur metabolism, the cycling of carbohydrates and the provision of proteins to the host (Jessen et al., 2013; Ainsworth et al., 2015; Pootakham et al., 2019; Krishnaswamy et al., 2023). *Endozoicomonas* can have a mutualistic relationship with the endosymbiotic dinoflagellate partner *Symbiodinium*. This relationship has been suggested to be critical to the success of coral restoration (Bernasconi et al., 2019). However, a broad spectrum of other microorganisms (e.g., bacteria, archaea, viruses and eukaryotic microbes) may play a key role in maintaining coral health (Van Oppen et al., 2009; Ainsworth et al., 2017) and beneficial microorganisms should be identified specifically for each coral species, regional location, and stage of development (Peixoto et al., 2017).

Previous studies suggested that coral transplantation can affect coral microbial assemblages thus increasing the susceptibility of the corals to diseases (Casey et al., 2015). This finding reinforces the need to investigate the microbiome of coral reefs to increase the success of the restoration actions (Garren and Azam, 2012; Moriarty et al., 2020). In this regard, probiotics can also be adopted for disease mitigation (Peixoto et al., 2019). For example, marine bacteria isolated from *Acropora palmata* and other corals were found to produce anti-bacterial molecules against a broad spectrum of pathogens, including *Serratia marcescens* which is a pathogen known to lead to the disease 'white pox' (Ritchie, 2006; Alagely et al., 2011). This method was also tested on cnidarians affected by whitepox disease revealing beneficial effects.

Transplant-induced coral diseases could combine with the adverse effects of climate change, thus hampering successful restoration. Despite it has been reported that the coral microbiome can acclimatize to climate-driven changing conditions (including pH acidification, and heatwaves) enriching its functions related to nitrogen metabolism, host nutrition, and increased resistance (Biagi et al., 2020; Palladino et al., 2022; Prada et al., 2023), monitoring microbiome changes in restoration projects could be useful for predicting the effects of multiple stressors.

Recent studies have also suggested that microbiome manipulation could enhance heat tolerance and help corals survive the effects of ocean warming (Doering et al., 2021). From this perspective, microbiome engineering could represent a powerful tool to mitigate disease-associated threats, increase corals' stress tolerance to perturbations, and improve coral resilience in the face of ongoing climate change (Li et al., 2022).

TABLE 1 Examples of microbial taxa of habitat-forming species which could have a key role in restoration activities.

Habitat	Habitat forming taxa	Microbial taxa	Isolation	Potential functions	Reference
Cold-water corals	*Lophelia pertusa, Desmophyllum pertusum* (former *Madrepora oculata*)	*Endozoicomonas*, Entomoplasmatales, Spirochaetales, Rickettsiales	no	Core members of the microbiome with a role in pathogens protection; protein and carbohydrate transport and cycling	(Chapron et al., 2020)
Coral gardens	*Paramuricea clavata, Eunicella cavolinii*	*Endozoicomonas*	no	Core members of the microbiome with a role in pathogens protection; protein and carbohydrate transport and cycling	(van de Water et al., 2017)
	Corallium rubrum	Spirochaetaceae	no	Core members of the microbiome with a role in pathogens protection	(van de Water et al., 2016)
Reef-building corals	*Acropora cervicornis, Pocillopora damicornis, Stylophora pistillata, A. palmata*, and *Porites cylindrica*	γ-proteobacteria, α-proteobacteria, Bacteroidetes, Cyanobacteria, Firmicutes, Tenericutes, Euryarchaeota, Nitrososphaerota (syn. Thaumarchaeota)	Some strains	Biofilm production and nutrient provisioning	(Huggett and Apprill, 2019)
	Pocillopora damicornis	Consortium including five *Pseudoalteromonas* sp., *Halomonas taeanensis, Cobetia marina* related species strains	yes	Coral bleaching mitigation	(Rosado et al., 2019)
	Pocillopora sp., *Porites* sp.	Fresh tissue homogenates	no	Coral bleaching reduction	(Doering et al., 2021)
Seagrass meadows	*Zostera japonica, Z. marina, Halophila stipulacea*	Bacteroidetes, γ-proteobacteria, α-proteobacteria, δ-proteobacteria, β-proteobacteria, Epsilonbacteria, Actinobacteria, Verrucomicrobia, Planctomicetes, Cyanobacteria	yes	Nitrogen fixation, phosphorous solubilization and organic matter mineralisation	(Tarquinio et al., 2019)
	Posidonia oceanica, Cymodocea serrulate, H. uninervis, Thalassia hemprichii, H. ovalis	α-proteobacteria, γ-proteobacteria, δ-proteobacteria, Actinobacteria, Firmicutes, Bacteroidetes	no	Plant metabolism contribution	(Crump and Koch, 2008; Tarquinio et al., 2019)
	Zostera marina	*Labyrinthula zosterae*	yes	Parasitic bacteria, which causes Wasting Disease	(Muehlstein et al., 1991)
Mangroves	*Avicennia marina*	*Oceanobacillus picturae*	yes	Enhancing plant growth	(El-Tarabily and Youssef, 2010)
Macroalgal forests-	*Saccharina latissima*	α-proteobacteria, γ-proteobacteria, Bacteroidota, and Planctomycetes	no	n.a.	(Burgunter-Delamare et al., 2022)
	Fucus vesiculosus	Planctomycetes	yes	Biofilm formation; degradation of organic matter of plant and algal cell walls	(Lage and Bondoso, 2014; Parrot et al., 2019)
	Nereocystis luetkeana	Microbiome including 6 phyla and 19 families	no	Assimilation of dissolved organic matter, involved in alginate metabolism, vitamin B12 biosynthesis, and nitrogen reduction	(Weigel et al., 2022)
Cystoseira sensu lato	*Cystoseira compressa*	Verrucomicrobia, Actinobacteria	no	Utilization of organic carbon sources	(Mancuso et al., 2016)
		Ruegeria, Nautella, Aquimarina, Loktanella, Saprospira, and *Phaeobacter*	no	Pathogens	(Mancuso et al., 2016)
	Caulerpa cylindracea, Agarophyton vermiculophyllum	58 bacterial species	yes	Protective role/pathogens	(Saha and Weinberger, 2019)

For each habitat microbial taxa and their functions are reported.

Knowledge of corals' ability to acquire new microbiome components to mitigate the negative effects of environmental stress led to the development of the "Coral Probiotic Hypothesis" based on the identification of strains of dinoflagellates and microbes able to promote the growth and persistence of the host under shifting environmental conditions (Epstein et al., 2019). Theoretically, a coral treated with an inoculum of these microorganisms taken from a stress-adapted conspecific should adapt or acclimatize to that stress more rapidly (Epstein et al., 2019). The "Coral Beneficial Microorganisms" (CBM) concept provides procedures to further apply the "Coral Probiotic Hypothesis" by identifying potential selected advantageous mechanisms provided by the microbiome, isolating these beneficial microbes, and experimentally testing them for their role in coral resilience to environmental perturbations, both *in situ* and in controlled conditions (e.g., aquaria, Peixoto et al., 2017). This concept and its applications might be also translated to other habitat-forming species, including vegetated habitats.

Pioneering studies have shown that the microbiome can be shaped through inoculation with cultured bacterial isolates (Welsh et al., 2017; Damjanovic et al., 2019), while other investigations have tested the probiotic potential of these inoculations to assess improvements in coral health and resistance under different types of stress (Fragoso Ados Santos et al., 2015; Jacquemot et al., 2018; Rosado et al., 2019). For example, a consortium of native (isolated from *Pocillopora damicornis* and surrounding seawater) putatively beneficial microorganisms for corals, including *Pseudoalteromonas* sp., *Halomonas taeanensis* and *Cobetia marina* strains was added to coral colonies to increase resistance to bleaching (Table 1; Rosado et al., 2019). In a recent transplantation study of two cosmopolitan reef-building corals, *Pocillopora* sp. *and Porites* sp., from the Andaman Sea in Thailand, heat-sensitive corals were transplanted with donor microbiomes using fresh tissue homogenates produced from heat-tolerant conspecific donor corals, thus bypassing time-consuming culturing and screening for beneficial bacteria from healthy donors and allowing the transmission of the "unculturable" microbiome fraction (Table 1; Doering et al., 2021). The inoculation reduced coral bleaching under heat stress suggesting its beneficial effect and the potential of a probiotic intervention to support success in coral restoration.

Overall, based on the available information, although the microbiome offers important opportunities for coral restoration and re-establishing self-sustaining and functional habitats, its use has been made on a limited spatial scale and is still at an experimental level.

Gorgonian forests (Figure 2) - Gorgonian forests include corals belonging to the Anthozoan subclass of Octocorallia, which comprise soft corals (e.g., sea fans and sea whips - order Alcyonacea-, sea pens -order Pennatulacea-), and blue corals (order Helioporacea). They represent corals of conservationist interest as they act as ecosystem engineers, supporting high biodiversity levels (Ballesteros, 2006; Poulos et al., 2013; Sánchez, 2017; Angiolillo and Canese, 2018; van De Water et al., 2018a). Over the last 30 years, gorgonian gardens have been reported to be highly vulnerable to episodic climate-driven events as well as to anthropogenic activities and diseases (Smith and Weil, 2004;

Sánchez et al., 2014; Girard and Fisher, 2018; Garrabou et al., 2019). Some coral species in the Mediterranean Sea including *Corallium rubrum, Paramuricea clavata*, and *Eunicella cavolini*, are regressing in different coastal areas (Barnes, 2010; Angiolillo and Canese, 2018; Verdura et al., 2019; Gómez-Gras et al., 2021; Topçu et al., 2023). Similarly, the soft coral *Dendronephthya australis* has been listed as endangered in Australia (Larkin et al., 2023). For this reason, these species have been a target of restoration experiments in the field and in aquaria (i.e., to assist *in situ* recovery) (Ballesteros, 2006; Ponti et al., 2014; Ingrosso et al., 2018; Montero-Serra et al., 2018; Verdura et al., 2019; Steinberg et al., 2020; Casoli et al., 2022; Topçu et al., 2023). Also, gorgonians collected as by-catch can be a valuable resource for the restoration of impacted ecosystems (Montseny et al., 2019; Casoli et al., 2020; Montseny et al., 2020).

Only a few studies have been carried out to test the efficiency of transplanting to rehabilitate gorgonian populations in impacted areas reporting contrasting results in terms of survival rate (30%-90% in 2.5 years; Linares et al., 2008; Fava et al., 2010; Montseny et al., 2019; Casoli et al., 2022). The design of any restoration procedure must take into account the likelihood of mortality of coral colonies before transplanting since this can affect the initial attachment effort necessary to increase the success of the restoration process. To this aim, microbiome analyses including the detection of pathogens can help to anticipate these actions by identifying stressed colonies that visually do not show any signs of alteration (Corinaldesi et al., 2022).

Octocoral-microbe interactions compared to those of Scleractinia have attracted a lower interest, with only a limited number of studies focused on their associated microbiota (van De Water et al., 2018a), thus limiting understanding of the role of the microbiome in gorgonian health. Available information indicates that in natural conditions, the core microbiome of gorgonians is stable (van de Water et al., 2016; van de Water et al., 2018b) over space and seasons as in the case of *E. cavolini, P. clavata* and different Caribbean Octocorals, which are generally dominated by Endozoicomonadaceae (Table 1; Bayer et al., 2013; Vezzulli et al., 2013; van de Water et al., 2017; McCauley et al., 2020; van de Water et al., 2020) or Spirochaetaceae mostly associated with *C. rubrum* (van de Water et al., 2016; van de Water et al., 2018b; Corinaldesi et al., 2022). Thus, a shift in the composition of the core microbiome of these species after transplantation actions can represent an early warning indicator of stressful conditions that can decrease the success rate of the restoration actions. Considering that newly established coral populations need 30-40 years to show an adequate colony size distribution (Montero-Serra et al., 2018), it is quite difficult to assess the restoration success after only a few years (Linares et al., 2008; Duarte et al., 2020). This constraint is mainly due to the short time scale (3-4 years) of funded projects aimed at promoting some restoration actions and experiments. Consequently, long-term monitoring programs, including analyses of the microbiome associated with transplanted organisms, should be planned over a longer time scale to provide more comprehensive information about the factors influencing microbiome dysbiosis, thus allowing the implementation of possible intervention actions to keep microbiome eubiosis in future restoration activities.

Cold-water corals (Figure 2) - Cold-water corals are key habitat-forming species, producing complex three-dimensional structures over wide areas, which foster biodiversity hotspots including species of high commercial interest (Roberts et al., 2009; Angiolillo and Canese, 2018). These corals are generally found in the deep sea (Roberts et al., 2009), particularly on continental margins, seamounts and canyons (Montseny et al., 2021). These ecosystems are threatened by multiple human activities such as commercial bottom fisheries, hydrocarbon exploration and extraction (Ramirez-Llodra et al., 2011; Ragnarsson et al., 2017; Montseny et al., 2021) and ongoing climate changes (Danovaro et al., 2017; Portilho-Ramos et al., 2022). Most restoration actions in marine ecosystems have been conducted in shallow waters (Bakker et al., 2002; Hughes and Paramor, 2004; Fraschetti et al., 2021), including tropical coral reefs (Rinkevich, 2005; Precht and Robbart, 2006; Young et al., 2012; Deignan and McDougald, 2022) and gorgonian forests (Linares et al., 2008; Fava et al., 2010; Weinberg, 2019; Basconi et al., 2020; Duarte et al., 2020; Montseny et al., 2021). The restoration of deep-sea habitats, including cold-water corals has been delayed due to the technological challenges associated with their remoteness, water depth (below 200 m), and high costs of intervention (Van Dover et al., 2014; Da Ros et al., 2019). It has been estimated that the cost of deep-sea ecosystem restoration might be up to 3–4 orders of magnitude higher than that of shallow-water ecosystems (Barbier et al., 2014). The most used techniques for active cold-water coral restoration are transplantation techniques from a healthy donor reef to a degraded reef, and the use of artificial structures (Brooke et al., 2006; Dahl et al., 2012; Jonsson et al., 2015; Montseny et al., 2021). Additionally, it may be necessary to harvest and maintain cold-water corals *ex situ* (i.e., in aquaria before returning them to their natural habitat. However, the slow growth rates of cold-water corals, the stress experienced by corals during harvesting, such as thermal changes, and the complexity of replicating their natural environment in the laboratory are some of the most important barriers to successful active restoration (Orejas et al., 2019). To overcome all these problems, improving underwater technologies and long-term monitoring strategies, as well as expanding knowledge about species interactions, are key steps in deep-sea restoration. To increase the success rate of transplantations, we would also benefit from a better understanding of the role and composition of coral-associated microbiomes and particularly of the beneficial taxa, which can be markers useful to select healthy coral colonies suitable for transplantation actions and to monitor over time the holobiont health status.

Information on the microbiomes of the cold-water corals in the frame of deep-sea restoration is still very limited. Spirochaetes or Endozoicomonas have been suggested to be bacterial taxa supporting the physiology of *Desmophyllum pertusum* (former *Lophelia pertusa*) and *Madrepora oculata* (Kellogg et al., 2009; Meistertzheim et al., 2016; Neave et al., 2016). However, the *Desmophyllum pertusum* microbiome appears to be more variable in terms of composition than the microbiome of *M. oculata* (Meistertzheim et al., 2016; Galand et al., 2018). An investigation of the microbiome during an *in situ* transplanting of *Desmophyllum pertusum* and *M. oculata* revealed shifts of some bacterial taxa (such

as Entomoplasmatales, Spirochaetales, Rickettsiales and Endozoicomonas; Table 1; Chapron et al., 2020). In addition, the microbiome-based analyses were useful in investigating the habitat preference for the two cold-water species (i.e., *D. pertusum* did not show a strict preference for habitat due to its higher capacity to acquire bacteria from the surrounding waters, whereas *M. oculata* did) (Chapron et al., 2020). This could be crucial information in deep-water coral restoration as well as the potential presence of pathogens in gorgonians, which could hinder their recovery. Deep-sea ecosystem restoration appears to be the biggest challenge among marine habitat restoration actions; the microbiome could help address this challenge.

4.2 Restoration of vegetated habitats: seagrass meadows, mangroves, and macroalgal forests

Seagrass meadows, mangroves and macroalgal forests support high biodiversity levels by providing food, habitat, and shelter to a variety of marine organisms. They also underpin many important ecosystem functions and services such as primary and secondary productivity, C sequestration (acting as a "blue carbon" storage system; Duarte, 2017), the provision of nursery areas for endangered and commercially important species, protection from coastal erosion (Duffy et al., 2019). However, these meadows/forests are facing dramatic decline worldwide, so effective restoration efforts are urgently needed to recover their associated key ecosystem functions and services (Paling et al., 2009; Tan et al., 2020; Cebrian et al., 2021; Dahdouh-Guebas and Cannicci, 2021; Dunic et al., 2021). We detail below the general characteristics of the microbiomes of these vegetated ecosystems and perspectives for their potential application to the restoration of such habitats.

Seagrass meadows (Figure 2) - Classical seagrass restoration practices have obtained contrasting results in different coastal habitats, either testing bare-root transplanting, alternative methods such as deploying multiple plants in larger cores, planting seagrass seeds or using biodegradable containers (Zhou et al., 2014; van Katwijk et al., 2016; Da Ros et al., 2021; Mokumo et al., 2023). There is broad consensus that harnessing positive biological interactions, including those between seagrass and microbiota, can increase restoration success (Halpern et al., 2007; Silliman et al., 2015; Tan et al., 2020; Valdez et al., 2020). Different members of the seagrass microbiota can indeed benefit their hosts (recently reviewed by (Ugarelli et al., 2017; Tarquinio et al., 2019; Conte et al., 2021). Epiphytic diazotrophic bacteria can increase nutrient bioavailability through nitrogen fixation and phosphorous solubilization while sulphate-reducing bacteria play a similar role in the rhizosphere and roots through anaerobic nitrogen fixation and organic matter mineralisation (Table 1; Welsh, 2000; Hamisi et al., 2009; Sharma et al., 2013; Tarquinio et al., 2019; Mohr et al., 2021). Several microbes involved in growth-promotion activities in plants or macroalgae (like *Kocuria* sp.*, Vibrio* sp.*, Methylophilus* sp.*, Alteromonas macleodii, and Marinomonas* sp.) have been described also as epi- or endophytic microbes of seagrasses, hence hypothesized to play a similar role (Tarquinio et al., 2019). As in

terrestrial plants, seagrass roots and rhizosphere are also enriched with beneficial sulphide-oxidising bacteria able to remove the otherwise toxic H_2S produced by the sulphate-reducing bacteria during organic matter degradation (Conte et al., 2021) while sulphate-reducing bacteria have been suggested to detoxify from ethanol (another phytotoxin produced by the seagrass fermentative metabolism in the dark) (Ugarelli et al., 2017). Similarly, methanol (a waste by-product of seagrass metabolism known to inhibit plant growth and seed germination; Abanda-Nkpwatt et al., 2006) has been suggested to be consumed by methylotrophic bacteria (Methylophilaceae and Methylophagaceae), which are typically associated with seagrasses (Adamczyk et al., 2022). An additional protective mechanism of seagrasses can be attributed to microbes capable of producing antioxidant enzymes (e.g., *Marinomonas mediterranea* MMB-1), which can alleviate their oxidative stress by scavenging extracellular toxic radicals (Sanchez-Amat et al., 2010; Tarquinio et al., 2019). Additional plant-protection features, including the production of antiviral, antiparasitic, antibacterial and anti-biofouling compounds have been described or inferred for several bacteria (e.g., Actinobacteria) directly isolated from seagrasses or identified by metabarcoding (Marhaeni et al., 2010; Tarquinio et al., 2019; Boontanom and Chantarasiri, 2020). Such microbial products are supposed to benefit the seagrass by promoting healthy microbe-host interactions and contrasting potentially harmful outbreaks.

Bacteria have been by far the main target of seagrass microbiome studies, even though it can be expected that future research will provide evidence also on the relevance of archaea, as anticipated from terrestrial plants (Jung et al., 2020; Ayangbenro and Babalola, 2021). Similarly, the importance of fungi in fostering plant fitness is well-known in terrestrial ecosystems (Averill et al., 2022; Busby et al., 2022). As far as seagrasses are concerned, studies on fungi and other eukaryotic microbiota associated with them have mainly focused on pathogens and parasites like labyrinthulids, oomycetes and Phytomyxea (Sullivan et al., 2018; Ettinger and Eisen, 2019; Ettinger and Eisen, 2020), therefore the potentially beneficial functions and implications of microbial eukaryotes for the seagrass holobiont are still largely unknown (Wainwright et al., 2019; Ettinger et al., 2021; Liu et al., 2022).

Despite the growing awareness of the key role of the microbiome in seagrass health, little is still known about the possibility of using and/or modulating specific components of the seagrass microbiota to enhance transplantation success at large spatial scale (Trevathan-Tackett et al., 2019; Unsworth et al., 2019; Tan et al., 2020; Unsworth et al., 2022). Recent investigations on seagrass transplantation have demonstrated the importance of implementing a more holistic approach based on the "holobiont" concept, which argues that 'macrobial' hosts and their associated microbiota form a coherent biological entity and we need to consider them together to understand the ecology of hosts and their interactions (McFall-Ngai et al., 2013; Wang et al., 2021b). Milbrandt et al. (2008) showed that seagrass transplanting performed using portions of the original bulk sediments can increase transplant success, compared to the use of sterile sediment. Similarly, preliminary studies reported that seagrass seeds germinate and grow more quickly after the addition of their original sediments than in fully sterile sand (Boyer

and Wyllie-Echeverria, 2010). These results suggested that seagrass transplanting may be more successful if using the plant's autochthonous sediments, possibly also thanks to the beneficial microbes living in it (Tarquinio et al., 2019). Indeed, as for other terrestrial organisms (Jiang et al., 2022; Sorbara and Pamer, 2022; Morales Moreira et al., 2023), also the seagrass microbiome (including bacteria, archaea, fungi and other microbial eukaryotes associated with the leaves, roots and surrounding sediments) has been proposed to potentially increase the seagrass host fitness, resistance to environmental stressors and hazards and resilience (Fahimipour et al., 2017; Crump et al., 2018; Tarquinio et al., 2019; Trevathan-Tackett et al., 2019; Unsworth et al., 2019; Wainwright et al., 2019; Chen et al., 2022; Unsworth et al., 2022). For example, Fuggle et al. (2023), investigated the influence of root and sediment microbiomes on *Zostera muelleri* growth under stressful conditions (i.e., excess nutrient load). They found that the disruption of the root microbiome caused reduced seagrass growth under stressful conditions, thus inducing an uncoupling between bacteria involved in sulphate reduction and sulphide oxidation. These findings suggest a "cry for help" mechanism also for seagrass as observed in terrestrial plants, which under stress conditions attract beneficial (micro) organisms for protection (Meena et al., 2017; Khan et al., 2021). This mechanism indicates that the seagrass-microbiota interactions can influence host resilience. A recent study on *in-situ* seagrass (*Zostera marina*) transplanting investigated the changes in microbial assemblages after transplanting (Adamczyk et al., 2022), showing that the microbiota rapidly changed after transplanting and was strongly influenced by environmental conditions. In addition, this investigation revealed a stable microbiome core of the seagrass leaves represented by methanol-utilizing bacteria suggesting their relevant role for seagrass health, in view of transplanting and ecosystem restoration purposes.

Further investigations pointed out the need to re-think the holobiont concept in a "meta-holobiont" perspective (i.e., a network of holobionts that can exchange biomolecules and microbiota across generations, thus impacting the fitness of both biological scales: holobionts and meta-holobionts; Vannier et al., 2019). This new concept could have direct implications for seagrass restoration, as also exemplified by the *in-situ* evidence that mutualism between seagrasses and lucinid bivalves, which host sulphide-oxidizing gill symbionts, can reduce the sulphide-induced stress (Valdez et al., 2020; van der Geest et al., 2020). Other examples include the investigation conducted by Schenck et al. (2023), which performed a transplanting experiment of *Zostera marina ex-situ*, with its pathogenic parasite *Labyrinthula zosterae* (Table 1). The authors reported that changes in the host microbiome may influence the outcome of the host–parasite interactions, which would have direct implications for seagrass restoration and conservation management. Similarly, another study carried out by O'Connor et al. (2022) conducted an *in situ* reciprocal transplanting experiment with *Zostera marina* with and without its epiphytic macroalgal symbiont *Smithora naiadum*, showing that the presence of *Smithora* changes the *Zostera* leaf microbiota, thus suggesting a possible role of the microbiota in the plant-macroalgae symbiosis.

Overall, recent studies support the expectation that since the seagrass microbiome has a crucial role in the seagrass meta-

holobiont (Vannier et al., 2019; Valdez et al., 2020) by enhancing nutrient uptake, immunity, and tolerance to environmental and anthropogenic stressors, its examination can represent a useful tool to increase restoration success. In this regard, the first milestone would be to define best practices in meta-holobiont transplanting, by emulating terrestrial microbiome studies (Emam, 2016; Bulot et al., 2017).

Mangroves (Figure 2) - Mangroves are highly productive and valuable habitat-forming species in tropical marine ecosystems, that are facing a rapid human-induced decline worldwide and need large-scale restoration interventions (Romañach et al., 2018; Birnbaum and Trevathan-Tackett, 2022). Mangrove restoration is technically feasible in appropriate locations (Lewis, 2005), but projects often have failed because of the unsuitability of the transplanting sites (Lee et al., 2019), largely associated with the presence of plant growth-promoting microbiota living in the sediment (Holguin et al., 2001).

The failures obtained so far in mangrove restoration, suggest the need to explore in more detail the mangrove-microbe interactions and develop microbial-based interventions (Lee et al., 2019; Allard et al., 2020; Birnbaum and Trevathan-Tackett, 2022).

Classical microbiological research (mainly, non-omics approaches) has provided plentiful examples of mangrove-associated microbes (i.e., bacteria and fungi) with a role in plant health such as the production of growth-promoting phytohormones (Xu et al., 2018), metabolites that protect the plant against stress (Lata et al., 2018), the provision of nutrients through nitrogen fixation and the phosphate solubilization (Jha et al., 2011; Fukami et al., 2018), as well as the degradation of contaminants (Sipahutar and Vangnai, 2017), which can alleviate the toxic effects of soil pollutants on the plant (Siraj et al., 2023 and references within). However, mangrove-microbiota interactions have been scarcely explored for their potential to enhance mangrove restoration success (Holguin et al., 2001; Birnbaum and Trevathan-Tackett, 2022). Pioneering laboratory work inspired by terrestrial research on plant-growth-promoting bacteria (PGPB) found that the inoculation of mangroves with diazotrophic cyanobacteria isolated by the mangroves themselves resulted in rapid colonization of the roots and the transfer of N from the N_2-fixing bacteria to the plant (Holguin et al., 2001 and references therein). Successively, El-Tarabily and Youssef (2010), reported a phosphate-solubilizing bacterium (*Oceanobacillus picturae*) isolated from the mangrove *Avicennia marina* rhizosphere, able to strongly enhance plant growth, and suggested its possible use in reforestation programs (Table 1). The same authors also studied endophytic mangrove actinobacteria, describing one of the most promising strains (*Streptomyces mutabilis*) able to promote mangrove growth under laboratory conditions (El-Tarabily et al., 2021). Janarthine and Eganathan (2012), isolated one endophytic bacterial strain (*Sporosarcina aquimarina*) from pneumatophores *of Avicennia marina*, which enhanced the growth of different species of mangroves. Similarly, Soldan et al. (2019) isolated bacterial endophytes from mangrove propagules, describing one *Gordonia terrae* strain able to strongly promote the mangrove propagule germination and root colonization ability.

Overall, the available evidence supports the expectation that the mangrove microbiota can have great potential to help increase mangrove restoration success. However, additional research is needed to advance both theoretical and applied knowledge, by integrating classical microbiological studies with meta-omics, also performing microbiome-assisted mangrove transplant experiments in the field (Allard et al., 2020; Birnbaum and Trevathan-Tackett, 2022).

Macroalgal forests (Figure 2) - Among macroalgal forests, kelps (brown algae in the order Laminariales) play essential roles as ecosystem engineers in temperate coastal marine environments. Besides the ecosystem services provided, they are also important in many industries to produce alginates, human food supplements or food for abalone aquaculture (Burgunter-Delamare et al., 2022 and citations therein). Climate change and anthropogenic impacts are contributing to the global decline of the macroalgal forests making it increasingly urgent to restore these habitats (Mills et al., 2017). The history of kelp forest restoration, based on transplanting, seeding, grazer control, and artificial reefs (Eger et al., 2022), revealed that interactions between kelps and its associated microbiome can be crucial for obtaining successful restoration (Eger et al., 2022). The microbial partners, indeed, regulate and support their metabolism, health, fitness, resistance to pathogens, and adaptation to environmental changes (Wiese et al., 2009; Goecke et al., 2010; Dittami et al., 2016; Burgunter-Delamare et al., 2020).

Most available studies on the kelp microbiome are descriptive (i.e., focused on microbiome composition and distribution, and the interactions with environmental conditions; Lachnit et al., 2011; King et al., 2023). Knowing the environment and host characteristics shaping the kelp microbiota is important, as this may have implications on how we design restoration and/or future-proofing programs (Wood et al., 2019). Previous investigations documented that kelp and brown algae-associated microbiota is typically dominated by Alphaproteobacteria, Gammaproteobacteria, and Bacteroidota (Burgunter-Delamare et al., 2022 and citations therein; Table 1). In perennial species, such as *Saccharina latissima*, differences in the assemblage composition have been observed between different parts of the individuals, for example between apex and meristem. This is due to the algal growth mainly occurring in the meristem region, and younger meristem tissues are typically less colonised by bacteria (Burgunter-Delamare et al., 2022). Planctomycetes, which were observed predominantly in the *S. latissima* apex, have been observed also in other species, such as the brown algae *Fucus vesiculosus*, and are typical components of algal biofilms (Table 1; Lage and Bondoso, 2014; Parrot et al., 2019). The *N. luetkeana* blades' bacterial genomes spanned 6 phyla and 19 families and included common alga-associated microbial symbionts such as those belonging to the genus *Granulosicoccus*. Key functions encoded in kelp-associated bacterial genomes included dissolved organic matter assimilation, alginate metabolism, vitamin B12 biosynthesis, and nitrogen reduction from nitrate and urea to ammonium, potentially providing the host kelp with vitamins and reduced nitrogen compounds (Weigel et al., 2022). Field studies conducted on the bull kelp (*Nereocystis luetkeana*) microbiota, compared with other different substrates and the surrounding water column, revealed that new kelp blade tissues were colonized by markedly distinct microbial taxa (Table 1; Weigel and Pfister,

2021; Ramírez-Puebla et al., 2022). This suggests that microbial establishment on algae surfaces is more than just an attraction to a polysaccharide-rich surface and that host-specific factors may deter some surface-associated marine microbial taxa (Ramírez-Puebla et al., 2022; Weigel et al., 2022). Microbes can also be useful to sustain food webs in kelp forests as indicated by an experimental study based on the manipulation of bacterial abundances in kelp biofilm (Singh et al., 2021).

Despite the increasing interest in the diversity and functions of the algal microbiome, only a few studies have gone beyond the structural and functional description of the microbiomes and evaluated the responses to experimental inoculation of target microorganisms (Vairappan et al., 2001; Peng and Li, 2013) or assessed the role of microbiome in restoration actions (Eger et al., 2020). These approaches may be useful to identify beneficial or pathogenic microbes and to help in enhancing kelp performance and/or confer resistance or resilience to future environmental conditions. Although some studies tested the responses of the microbiomes of different kelp species (*Macrocystis pyrifera* and *Ecklonia radiata*; Minich et al., 2018; Qiu et al., 2019) to climate changes (e.g., increased temperature and partial pressure of carbon dioxide (pCO_2), how these changes will module the holobiont responses in restoration interventions is still practically unknown. This will be another challenge for restoration practices.

The canopy-forming macroalgae Cystoseira *sensu lato* (s.l.) (Figure 2G; including the *Cystoseira, Gongolaria* and *Ericaria* genera; Smith et al., 2023), are among the most important brown macroalgal forests, which are object of restoration projects for their key ecological role in coastal habitats (Cebrian et al., 2021) and provision of ecosystem services (including potential pharmaceuticals; Zbakh et al., 2020). Although available studies on the microbiome of *Cystoseira s.l.* forests are very limited, an investigation on *Ericaria amantacea* showed a core of associated bacterial families (including Rhodobacteraceae, Flavobacteriaceae, Alteromonadaceae, Vibrionaceae, and Halomonadaceae) also present in other brown algae suggesting a great plasticity of the microbiome of these macroalgae (Malfatti et al., 2023). Other studies carried out on *C. compressa* showed a distinct microbiota from the surrounding water column, with only a few taxa in common (Table 1; Mancuso et al., 2016). At the same time, a clear successional pattern in the epiphytic bacteria of *C. compressa* was observed, with the gradual appearance of specific bacterial taxa (e.g., Verrucomicrobia, Actinobacteria) over the growing season (Mancuso et al., 2016). An increase of bacteria affiliated with Rhodobacteraceae, which comprise six potential pathogenic genera, *Ruegeria, Nautella, Aquimarina, Loktanella, Saprospira,* and *Phaeobacter*, was also observed in aged thalli of *C. compressa*. These bacteria could influence the health and ecology of the algae, suggesting a possible role of the microbiome in contributing to the extensive ongoing declines of populations of *Cystoseira s.l.* in the Mediterranean Sea. In this regard, information on red macroalgae revealed that their decline is caused by bacterial diseases, such as the case of *Delisea pulchra* affected by bleaching also in combination with temperature rise events (Case et al., 2011; Campbell et al., 2014). However, the microbiome can also prevent the establishment of pathogenic microbes (Abdul Malik et al., 2020). An example is the study conducted on the seaweed *Phyllospora comosa* (Fucales,

Seirococcaceae), where a "core" of microbial taxa (i.e., present on all individuals sampled) was considered responsible for multiple functions, including biological defence (Wood et al., 2022). The capacity of aquatic macrophytes to "garden" protective microorganisms to the benefit of strengthened disease resistance has been demonstrated in the model invasive seaweed holobiont *Agarophyton vermiculophyllum* (Saha and Weinberger, 2019). This species is characterized by beneficial microbiota on its surface that protects from bacterial pathogens. Metabolites from the holobiont surface reduce the settlement of opportunistic pathogens and promote the settlement of other beneficial bacteria (Saha and Weinberger, 2019). Other functions can be attributed to the interactions between seaweeds and microbiomes; for example, investigations conducted on non-indigenous and invasive algae, such as *Caulerpa cylindracea* and *Agarophyton vermiculophyllum* (Table 1; Saha and Weinberger, 2019; Morrissey et al., 2021), reported a key role of microbiomes in their success in quickly colonizing new areas.

The tight relationship between macroalgae and microbiota suggests that they interact as a unified functional entity (i.e., holobiont), therefore, future restoration interventions cannot ignore the microbiome component (Morrissey et al., 2021). This holds true especially in the light of future climate change scenarios, which can determine shifts in macroalgal microbiomes and may lead to host disease, with potential cascading impacts on associated ecosystems (Qiu et al., 2019). In this regard, it remains largely unexplored how the interactions between macroalgae and microbes are affected by environmental stressors (van der Loos et al., 2019). Macroalgae–microbe interactions have been recognized as drivers of acclimatization to environmental changes as in the case of the brown alga *Ectocarpus*, whose ability to acclimate to salinity gradients has been attributed to their microbial associations (Dittami et al., 2016). In addition, it has been reported that the responses of macroalgae to various environmental perturbations, such as heat stress and nutrient enrichment, may depend on the niche-specific microbiota of macroalgae (i.e., endo-microbiota, epi-microbiota and rhizo-microbiota) (Morrissey et al., 2021). For example, in *C. cylindracea*, endomicrobiota has been reported to have the highest resistance, but the lowest resilience to environmental stress.

Given the rate at which macroalgal forests and other marine habitats are changing and given the predicted increases in the frequency and magnitude of multiple stressors, the need for subtidal marine macrophyte restoration efforts is evident (Wood et al., 2022). Future macroalgal forest restoration may rely on resistance and resilience of the associated microbiomes, therefore exploiting the provided probiotic functions to facilitate the holobiont adaptation to environmental stress, will be a step forward in the macroalgae forest restoration (Ghaderiardakani et al., 2020). Investigations into the selection and use of inoculants and probiotics in macroalgae restoration are very limited. A recent study based on metabarcoding analysis suggested that some bacterial taxa (*Postechiella, Winogradskyella, Roseovarius* and *Arenibacter*) are the main responsible for algal growth and potential candidates for probiotic consortia promoting the growth of *Ericaria amentacea* (Phaeophyceae) seedlings

(Malfatti et al., 2023). Molecular analysis of the microbiome of macroalgal forests based on metagenomic approaches can be a valuable tool for biomonitoring and predicting their health status, thus guiding restoration actions. However, we urgently need to increase the number of *in situ* investigations of the macroalgal forest microbiome in different habitats and environmental conditions and at different spatial scales to understand more about how to use the microbiome in restoration actions.

5 Microbiomes as nature-based solutions for marine ecosystem restoration

Nature-based solutions (i.e., actions that are inspired by, supported by, or copied from nature), also those relying on microbes, are gaining momentum globally as a concept to address ecological and societal challenges. Here, we advocate for combining these two concepts to incorporate microbiome analysis into nature-based solutions for the restoration actions of different habitat-forming marine species (Figure 1).

Microbiome characterization and identification of beneficial microbial taxa or their potential metabolites can be used for screening and selection of the "meta-community and meta-ecosystem" (e.g., plants and their sediment containing microbiota and nutrients) to be transplanted. Traditionally, this screening and selection was done empirically (e.g., visually) but, nowadays we can leverage multi-omics and computational approaches (e.g., metabarcoding, metagenomics and meta-transcriptomics) to identify organisms, colonies or sediment clods to be translocated to the restoration site or to identify the most suitable substrate for larval/propagule settlements (Jorissen et al., 2021). Changes in the composition of microbiome are, indeed, considered an early warning of holobiont health (Glasl et al., 2019; Corinaldesi et al., 2022), therefore microbiome analysis might be particularly useful in deep-sea ecosystems (e.g., cold-water corals) for the selection of healthy organisms and their monitoring once translocated/transplanted. The biomonitoring of the microbiome of habitat-forming species is now possible thanks to well-consolidated methodologies and ready-to-use technologies. However, it does not represent a way to remediate failed restoration interventions, but rather a strategy for the early detection of potential pathogens and for making quick decisions, for example, to stop the spread of disease (Pollock et al., 2011; Traylor-Knowles et al., 2022). Probiotic and bio-promoter supplements could, once their efficacy has been demonstrated, not only increase the resistance of the holobiont (e.g., to coral bleaching and other stress factors) before transplanting, but also stabilize it or improve its health conditions after transplanting. Other microbiome-based strategies for addressing restoration intervention include isolating microbiome components through culturomics-based approaches, which allow the selection of microbes producing usable probiotics and or bio-promoters to be inoculated to transplanted organisms. Other methods based on culturomics include the natural microbiome-assisted evolution, used to select microbial taxa that show the greatest resilience to

stress and thereby increase the fitness of transplanted species. However, these approaches are characterized by drawbacks (e.g., difficulties in culturing marine bacteria and in producing probiotics), which make their application difficult, especially for large-scale interventions. Given the urgency of implementing marine ecosystem restoration, culturomics-based approaches need to be optimized.

6 Conclusions

Microbiota can respond and adapt more rapidly than their associated pluricellular organisms to climate change and anthropogenic stressors, potentially increasing holobiont resilience to novel environmental conditions (Duarte, 2017; Martin et al., 2019). Due to their great potential, microbiome-based approaches can be very useful for the recovery of degraded ecosystems, contributing to their resilience and the achievement of the UN objectives of sustainability and habitat restoration. In the context of international strategies concerning ecological restoration, the use of the scientific knowledge acquired on the marine microbiome deserves to be exploited to assist both traditional and innovative restoration approaches. Taking a cue from the positive results obtained in terrestrial ecosystems, especially from reforestation experiments, there is ample space to exploit the potential of the microbiome in the restoration of different habitat-forming species. Although the use of microbiomes is still in its infancy in marine ecosystem restoration, it is being successfully applied in the restoration of coral reefs and experimentally in seagrass beds and macroalgal forests. The delay in the use of microbiomes in marine restoration is more relevant for deep-sea ecosystems due to technological and logistical difficulties. Therefore, upgrading the portfolio of technology tools for supporting such approaches, especially in deep-sea ecosystems (e.g., collecting samples in the long-term monitoring of deep-sea communities) is, as well, needed to effectively make microbiome-based restoration feasible in the future. Marine microbial nature-based restoration is an emerging and promising sector to accelerate and expand the spatial scale of blue restoration plans and to increase success of restoration initiatives.

Author contributions

CC conceived the review and its structure. RD, MC, AD'A and CG contributed to the manuscript design. CC, SB, MC, ER, SV contributed to the first draft and the different sections of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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

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