

TAILORED RESTORATION RESPONSE: PREDICTIONS
AND GUIDELINES FOR WETLAND RENEWAL

REVIEW ARTICLE

Aiding coastal wetland restoration via the belowground soil microbiome: an overview

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The United Nations Decade of Ecosystem Restoration was announced in 2021 to highlight the need for collective efforts to revive degraded ecosystems. Plant above- and belowground microbiomes are fundamental to plant health and ecosystem functioning. Plant aboveground microbiomes have received considerably more attention than the belowground microbiome, especially in the context of coastal plant restoration. Thus, there is fundamental gap in our understanding of the role belowground microbiomes play in restoration success in saltmarsh and mangrove ecosystems. Here, we outline potential pathways and challenges associated with including the belowground microbiome in mangrove and saltmarsh restoration via a conceptual framework and an overview of current literature. We highlight the large gap of knowledge that exists in plant–microbe literature as it pertains to coastal restoration warranting future research. More research is needed to significantly advance both fundamental and applied knowledge through better understanding of the importance of coastal microbiomes to restoration success by stakeholders and funding bodies.

Key words: germination, mangrove, revegetation, rhizosphere, root, saltmarsh

Implications for Practice

- Coastal wetland restoration success may be enhanced by incorporating assessment of belowground soil microbial communities that affect plant survival and health.
- Microbial ecologists and land managers need to collaborate to trial solutions for facilitating coastal wetland restoration that would be cost effective and viable long term.

Introduction

Preventing, halting, and reversing the degradation of ecosystems worldwide are the central goals of the United Nations Decade of Ecosystem Restoration announced in 2021. The rapid deterioration of terrestrial and coastal ecosystems calls for coordinated efforts to prevent further degradation and assist in more informed restoration management plans. Coastal ecosystems, such as mangroves and saltmarshes, are highly productive and valuable marine coastal habitats (Barbier et al. 2011; Costanza et al. 2014). They are of a significant value to humans providing key ecosystem services, including water filtration, storm surge protection, carbon storage and sequestration, recreation and serving as biodiversity reservoirs (Macreadie et al. 2021; Farrer et al. 2022). Analyses of global mangrove distribution have found that 75 % of mangroves are concentrated in 15 countries (Giri et al. 2011). Indonesia (3,112,989 ha), Australia (977,975 ha), Brazil (962,683 ha) and Mexico (741,917 ha) have the highest area of mangroves (Giri et al. 2011). Saltmarsh global

distribution has been estimated to be between 2.2 to 40 Mha (Pendleton et al. 2012); however, a recent, that is, 2017 global study, reported and mapped saltmarshes across 43 countries and territories with a combined area of approximately 5.5 Mha (Mcowen et al. 2017). The United States (1,723,410 ha), Australia (1,325,854 ha), Russian Federation (700,719 ha), China (549,506 ha), and Europe (356,947 ha) have the highest area of saltmarshes (Mcowen et al. 2017).

However, these coastal ecosystems are experiencing extensive degradation due to sea level rise, pollution, erosion, and pressure from introduced invasive species (Jankowski et al. 2017; Birnbaum et al. 2021; Zengel et al. 2022). For example, surveys of mangrove global coverage in the early 2000s revealed a decline of more than 35%, with a predicted future decline at 1–2% per year (Valiela et al. 2001; Duke et al. 2007). Mangrove decline has been predominantly attributed to their clearing for forestry, agriculture, and urban expansion, as well as their conversion to

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aquaculture ponds across the tropics as well as die-backs from climate change-driven impacts (Valiela et al. 2001; Bayraktarov et al. 2016; Sippo et al. 2018; Abhik et al. 2021). It has been estimated that saltmarshes have declined by 25 to 50% compared to their global historic coverage (Duarte et al. 2008; Crooks et al. 2011). Saltmarshes have been significantly modified by drainage for agriculture, coastal eutrophication, and replacement by mangroves due to climate change (Gedan et al. 2009; Deegan et al. 2012; Saintilan et al. 2014). Some of these threatening external physical processes may cease after change in land use and restoration activities (e.g. releasing of grazing pressure or tidal reinstatement), with time allowing for ecosystem recovery through natural expansion of nearby vegetation and follow-on climate change mitigation benefits (e.g. blue carbon; Lovelock et al. 2022). Alternatively, active restoration may be required in instances where lack of recruitment and altered, detrimental habitat conditions prevent successful establishment and growth (Silliman et al. 2015; Billah et al. 2022). Direct planting of seeds, seedlings, saplings, or small trees, can enhance the survival of

mangrove and saltmarsh wetlands in the short term, but can be challenged by species growth strategies that impact recovery, physical disturbances, and poor site selection or lack of community support, which can lead to longer-term restoration failures (Bayraktarov et al. 2016; Lee et al. 2019; Lewis et al. 2019; Lovelock & Brown 2019). Restoration projects in mangroves and saltmarshes have been predominantly focused on measuring aboveground plant responses (Bayraktarov et al. 2016), neglecting the assessment of the belowground soil health and compatibility with plants. However, plants are highly reliant on soil microbial communities to withstand stressful environments because of high salinity, flooding, drought, or low nutrient concentrations (Farrer et al. 2022). The potential of plant–microbial interactions in improving the success of restoration in mangroves and saltmarshes has been rarely explored (see Farrer et al. 2022 and Srivastava et al. 2017 for reviews of plant–microbe interactions in coastal and aquatic systems).

Saltmarsh and mangrove ecosystems are dominated by plants that form belowground associations with soil microbial

The role of soil microbes in ecological restoration

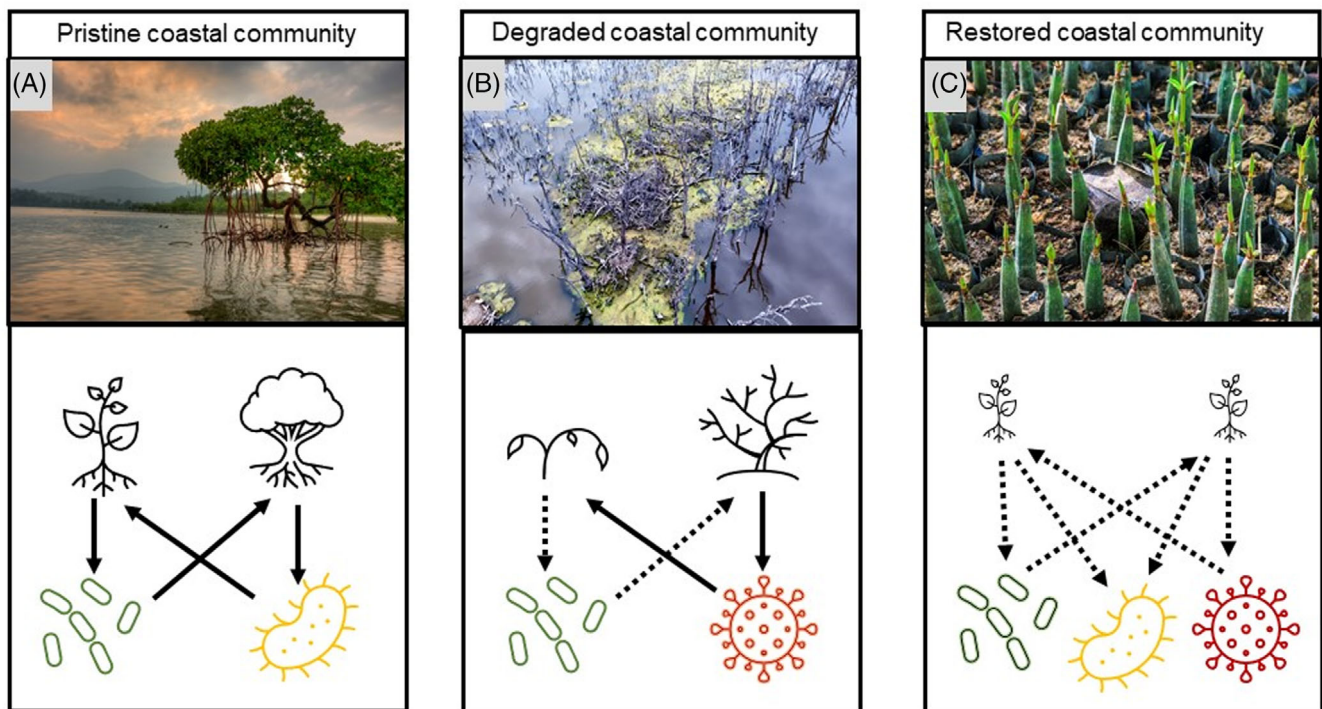


Figure 1. Conceptual diagram showing the role of soil microbes in coastal saltmarsh and mangrove communities. Soil microbes include whole communities (microbiome), as well as individual microbes, that may have significant interactions with the host plant. (A) Pristine coastal community, where plants may form diverse established associations with microbial communities (e.g. mutualistic [green] and symbiotic [yellow]; solid lines) that have evolved over longer time periods. (B) Degraded coastal community where some beneficial plant–microbe associations have weakened (dashed lines) due to the degradation. Degradation may also facilitate shifts whereby soil microbial communities associated with a pristine ecosystem are replaced by opportunistic communities that are thriving in altered abiotic conditions (e.g. following an oil spill). These new communities may not confer benefits to the host (or ecosystem functions) or represent/replace the beneficial communities. Thus, there is potential for dysbiosis to develop. Some forms of pressures may also cause complete ecosystem loss. Mutualistic [green] and commensalistic associations [orange] shown. (C) Restored coastal community with replanted seedlings or saplings may form associations with both, that is, (1) with propagules of the soil microbial communities from the pristine source community, and (2) with the soil microbial remnants from the degraded coastal community. The initial plant–microbe associations may be weak (dashed lines) following the restoration. In the absence of further degradation, these associations are expected to strengthen and diversify. In some instances, however, there is natural regeneration occurring when the negative pressures that caused the degradation are removed. Mutualistic [green], symbiotic [yellow] and antagonistic [red] associations shown.

communities (Fig. 1A). Biogeochemical nutrient cycling of carbon and nitrogen relies on both plants and belowground microbial communities that together play a central role in making them available to living organisms. Soil microbial communities increase plant stress tolerance, enhance seedling establishment, and provide protection from soil borne pathogens (Kumar & Verma 2018; Igwe & Vannette 2019; Liu et al. 2021)—key functions that are likely important during the colonization of new soils in extreme (e.g. anoxic, hypersaline, potentially polluted from previous land use) coastal conditions. A recent review by Farrer et al. (2022) provided a comprehensive overview of several plant–microbe symbioses (i.e. mycorrhizae, nitrogen fixers, endophytes, rhizosphere microbes, and pathogens) in coastal ecosystems and their importance in coastal restoration.

Despite how essential microbiomes are to coastal wetland ecology and health, there is yet to be a broad uptake of incorporating microbial responses or microbiome interventions in mangrove and saltmarsh restoration (Allard et al. 2020; Bayraktarov et al. 2020). Here, the focus is to propose a conceptual framework for the roles that the belowground microbiome may play during restoration of mangrove and saltmarsh ecosystems (Fig. 1), with a particular emphasis on how the microbiome communities and functions can enhance plant establishment and revegetation success. We draw on known and potential relationships between the plant and soil/rhizosphere microbiomes, as well as current restoration techniques. By developing this framework, we outline research opportunities, as well as challenges when considering these belowground processes during ecological coastal restoration (Fig. 1B & 1C). Lastly, we provide an overview of published literature that assessed or included belowground microbial community analyses in coastal mangrove or saltmarsh restoration.

Potential Pathways for Soil Microbiomes to Accelerate Coastal Wetland Restoration

Improving and utilizing our knowledge of soil and rhizosphere microbiomes has become an important component to ecological restoration and soil management frameworks across many terrestrial biomes and degradation scenarios (de Deyn & Kooistra 2021; Coban et al. 2022), including a strategy to support the Decade of Restoration (Aronson et al. 2020). The roles and benefits that microbiome provide to degraded ecosystems include bioremediation of polluted or contaminated soils and improving biogeochemical conditions (Allard et al. 2020; Coban et al. 2022), as well as improving plant nutrient acquisition, productivity, and defense (Allard et al. 2020; Trivedi et al. 2020; Farrer et al. 2022). In coastal ecosystems, including saltmarshes and mangroves, developing our understanding and characterization of the holobiont is a critical step to identifying the roles and utility of belowground microbiomes in restoration scenarios (Trevathan-Tackett et al. 2019; Allard et al. 2020). Holobiont is defined as the complex relationship between communities of microorganisms (the “microbiome”) and the environment or their hosts (Vandenkoornhuysen et al. 2015; Trevathan-Tackett et al. 2019). For example, coastal rhizospheres include functional groups that are critical

to sulfide detoxification (Rolando et al. 2022) and nutrient acquisition (Davis et al. 2011; Rolando et al. 2022), in addition to helping the plants cope with salinity, drought and oxidative stress (Hueso et al. 2011; Mohapatra et al. 2021). Observing how the root and rhizosphere microbiome develops when pioneering species expand habitat into new areas may provide key insight into the taxa or functions within the microbiome that assist in revegetation. Further, characterization of the soil and microbiomes during restoration failures may be informative, particularly where antagonistic microbiota or stressful belowground conditions may be linked to plant mortality and reduced establishment or expansion. Based on current restoration practices for coastal wetlands, we outline opportunities where belowground microbiomes could aid in saltmarsh and mangrove restoration success, either indirectly or directly, providing examples where possible (summarized in Table 1).

Microbial inoculations or transfers are direct pathways to manipulate the belowground microbiome to enhance plant germination, establishment, and expansion. The microbial inoculum can be sourced from pristine adjacent to restoration sites and sub-selection of plant-growth-promoting bacteria or fungi would need to be cultured and amplified in the laboratory conditions to ensure high transferable density in the field. The few examples that exist for emergent coastal plants include rhizosphere bacteria showing suppression activity to fungal pathogens (Mavrodi et al. 2018), and bacteria enhancing seed germination (Figueira et al. 2019; Mesa-Marín et al. 2019) and seedling root length (Soldan et al. 2019). Such studies hold promise for coastal wetland rhizospheres as hotspots for beneficial microbiome members (Trevathan-Tackett et al. 2019; Allard et al. 2020). However, a well-known drawback for applying inocula is that microbiota often cannot be grown in culture, thereby limiting our scope for isolating individual microbial taxum or a consortium of taxa that may be essential for plant root health. Transferring an intact rhizosphere as part of a cluster of multiple plants and surrounding the soil has been shown to improve transplant success by maintaining root oxygenation and soil stability (Silliman et al. 2015). Likewise, the rhizosphere microbiome within the transplant plug could initially provide benefits to the plants in the new environment. Over time the surrounding soil microbiomes will become more important as the roots expand and the rhizosphere microbiomes change due to plant selection and recruitment of microbiota from the new soils (Fig. 1) (Duarte et al. 2012; Wang et al. 2016; Mavrodi et al. 2018).

Soil manipulations represent pathways for indirectly altering the soil microbiome in a way that benefits or enhances revegetation. For coastal ecosystems, tidal reinstatement may have the power to alter the edaphic conditions and soil microbiome prior to, and potentially in facilitation of, revegetation by saltmarshes (Lynum et al. 2020). Soil amendments have been used to facilitate coastal plant restoration activities by creating new space for revegetation (Billah et al. 2022), or adding specific resources to help plant growth (e.g. biochar; Cai et al. 2021). We know little about the rhizosphere response to soil amendments in relation to restoration success, but some studies suggest microbial taxa or functional traits may respond

Table 1. List of potential pathways to improve belowground microbiome function, potential impact of chosen pathway during restoration, as well as potential challenges.

Pathway to Improve Belowground Microbiome Function	Description of the Pathway and Potential Impact During Restoration	Potential Challenges	References
(1) Microbial inoculum	Plant-growth-promoting bacteria or fungi to accelerate plant and seedling growth or nutrient uptake Treatment of plant rhizosphere or soil with an inoculum before outplanting, including but not limited to bioremediation	Need detailed understanding of plant–microbe interactions to identify beneficial microbial inoculum and avoid pathogen introduction Expensive at-scale	Holguin et al. (2001); Bledsoe and Boopathy (2016); Figueira et al. (2019); Mesa-Marín et al. (2019); Farrer et al. (2022)
(2) Transference via clustered transplants (outplants) or seeds	Transference of rhizosphere from multiple plants in a plug (and surrounding soil) maintains rhizosphere microbiome and conditions, thereby reducing stress and promoting establishment Transference of parent microbiota to the seed to assist in germination and establishment, e.g. seed coating with beneficial microbes that assist with establishment	Requires nursery or sourcing plants from a natural ecosystem Little known about seed associated microbial communities of coastal plants	Silliman et al. (2015); Wang et al. (2016); Muñoz-Rojas et al. (2018); Nelson (2018)
(3) Artificial structures	Stabilization of the soil near or surrounding the plant may reduce erosion and allow for enhanced root and seed establishment, and thereby rhizosphere development and germination success	Prior knowledge of elevation and hydrology is required in order to plant in areas where establishment will be successful	Temmink et al. (2020); Fivash et al. (2021)
(4) Soil or environmental manipulation	Indirectly altering soil microbiota conducive to revegetation by altering the environment to predisturbance conditions Inorganic nutrient, organic matter, and/or biochar addition to facilitate root growth or seed germination Manual aeration of soil to mimic oxygenation by bioturbation Planting of fast-growing nontarget species (e.g. legumes) to improve soil conditions and stability that would promote natural establishment of the target species	Predisturbance environmental condition records are not always available Time consuming and costly Prior ecological knowledge of nontarget species required to avoid soil modification that favors the nontarget species, e.g. legumes changing the nutrient balance in soil and modifying soil conditions that promote bacteria beneficial to legumes	Lorenzo et al. (2010); Begam et al. (2017); Matzke and Elsey-Quirk (2018); Lynum et al. (2020); Cai et al. (2021); Qiu et al. (2021)

in a way that benefits the vegetation (Santini et al. 2019; Cai et al. 2021). Physical interventions that improve the soil before revegetation, such as artificial structures, aeration, and pre-planting of nontarget species (Begam et al. 2017; Fivash et al. 2021; Qiu et al. 2021), may indirectly improve rhizosphere microbiome development and function and promote restoration success by improving soil oxygenation and stability. For both the direct and indirect interventions, there is still the possibility that harmful microbiota or pollution could persist from previous land use or degradation activities and could impact revegetation success (Fig. 1C). Bioremediation of the soil itself may be needed to improve the soil microbiome and biogeochemical condition, with potential for enhancing in situ microbial populations that can degrade pollutants, e.g. hydrocarbons and heavy metals (Ramsay et al. 2000; Cabral et al. 2019).

Challenges Associated With Taking Soil Microbes Into Consideration in Ecological Restoration

We have discussed above some of the pathways that can be undertaken to enhance saltmarsh and mangrove restoration success by incorporating soil microbial communities into ecological restoration practices. However, there are many considerations and challenges remaining before the full potential of soil microbial communities can be harnessed for more successful and cost-effective restoration outcomes.

- (1) **Knowledge gaps:** Our understanding of soil microbial communities in saltmarsh and mangrove ecosystems is fundamentally still very limited and geographically biased (Trevathan-Tackett et al. 2019), requiring fundamental descriptive studies of natural belowground microbiomes, as well as their responses to restoration (e.g. monitoring

during active restoration like hydrological restoration, as well as natural colonization and expansion). For example, ecological restoration studies are heavily skewed toward North American ecosystems and high-income economies (Wortley et al. 2013; Bayraktarov et al. 2020; Cadier et al. 2020). Further, we need to understand who are the site-specific core members of the soil microbiomes, the function they serve to the plants and subsequently to the entire ecosystem. For example, changes in microbial communities have been consistently linked with changes in soil pH, soil moisture, phosphorus availability, and labile organic carbon pools (Hermans et al. 2017; Delgado-Baquerizo et al. 2018; Isobe et al. 2020; Ramírez et al. 2020). Quantifying the relative composition of soil pathogens in soil prior to restoration is important to predict the seedling establishment potential. If the soil microbial diversity is low or pathogen dominated, the seedling survival and establishment may be greatly compromised. However, surveying pathogen loads in soil during restoration is not a common practice, to our knowledge. Another important consideration is better understanding plant reliance on beneficial microbes in their roots. For example, legumes (Fabaceae) often require the presence of compatible nitrogen fixing bacteria (*Rhizobia*) for seedling establishment and growth (Birnbaum et al. 2017; Gorzelak et al. 2020).

- (2) **High costs of microbial profiling and associated data analysis:** Although the novel molecular tools to analyze microbial communities are becoming increasingly affordable, the associated total costs of collecting soil samples, appropriate storage in the cold or freezing conditions in the field, preparing samples for high-throughput DNA sequencing for microbial analysis and having the suitable facilities is very costly and the process time-consuming, especially for practitioners and land managers leading the restoration efforts on the ground. For example, the average cost of amplicon-based microbial profiling for soil bacteria or fungi (extracted DNA) at a commercial lab is AU\$/US \$50–120/sample. The total costs of a one-off analysis can quickly escalate depending on the number of samples. For instance, analysis of 100 soil samples for bacterial and fungal profiling using sequencing technologies at a commercial laboratory in Australia may cost, on average, ca. AU \$10,000. Typically, ecological restoration may require repeat soil sampling for monitoring the outcomes of restoration practices, and thus the associated costs for repeat soil microbial sampling may quickly grow into tens of thousands of dollars. Obtaining soil microbial profiling data requires involvement of either a microbial ecologist or an expert in microbiology, who can aid scientifically accurate data collection, analysis, and interpretation of bioinformatics data, although the bioinformatics pipelines are increasingly becoming more use-friendly and accessible (Fierer et al. 2021). If an expert is not included in the project, internal upskill may be required that is financially costly and not always possible. These challenges are also relevant to other sequencing approaches, such as (shotgun) metagenomics

and eDNA monitoring, which provide information on microbiome community and functional potential and the monitoring of target organisms of interest (microbes, animals, and plants), respectively, (e.g. Foster et al. 2020; Saenz-Agudelo et al. 2022).

- (3) **Long-term monitoring, funding, and scalability:** Depending on the recovery parameters of interest and project scale, it may take years or decades before restored wetlands reach conditions of natural reference wetlands (e.g. typical long-term monitoring over 5–15 years; Wortley et al. 2013; Cadier et al. 2020). The timeframes needed to achieve target biodiversity and ecosystem functions conflict with government and industry funding (i.e. 1–3 years). Further, ecological restoration is very context-dependent and a “one-size-fits-all” approach to restoration is challenging and thus limiting the scalability of the restoration projects across large areas. One solution to assess the response of key restoration conditions within spatiotemporal and funding constraints are space-for-time and chronosequence approaches. For instance, sampling sites that represent a range of restoration or community succession responses, e.g. from natural reference and longer-term restored sites to newly restored and business-as-usual sites, would help identify the core microbial community members and functions that may be important to enhancing restoration success (Wang et al. 2016; Jiao et al. 2022). Such studies from the terrestrial and coastal realms have shown that restoration enhances the annual and seasonal stability of the belowground microbiome (revegetation of saltponds with mangroves; Tran et al. 2019), and that soil source, such as dredge spoil used in the restoration activity, influences rhizosphere community formation (revegetation of saltmarsh; Mavrodi et al. 2018). Long-term restoration has also been shown to enhance beneficial fungal and prokaryotic functional groups associated with sulfide oxidation, plant-growth-promoting, and pathogen suppression functions (Mavrodi et al. 2018; Yan et al. 2018). With this approach, however, controlling for or measuring environmental variables in cross-site comparisons will be key to constraining the influence of nonrestoration influences in order to detect restoration-driven responses on the belowground microbiomes.

Systematic Review of Saltmarsh and Mangrove Restoration Studies Where Belowground Microbiome Has Been Considered

To understand how much belowground microbiomes have been considered in ecological restoration in saltmarshes and mangroves globally, we performed a systematic quantitative literature review by searching the Scopus database (Elsevier, Atlanta, GA, U.S.A.) on 20 October 2022. Scopus database was searched through title, abstract and keywords using the search string:(mangrove OR saltmarsh) AND (fung* OR bact* OR microb* OR path*) AND (restoration OR “ecological restoration”). Available literature until October 2022 was included.

Table 2. The full list of studies that assessed soil belowground communities and ecological restoration in saltmarsh and mangrove ecosystems. NA, not available or not applicable. Asterisk indicates studies that compared soil microbial communities in reference or control site with restored saltmarsh or mangrove ecosystem.

No.	Author (Year)	Country	Ecosystem	Substrate	Microbial Analysis		Type of Restoration
					Microbial Community	(Inferred/Direct, Details)	
1	Luke et al. (2017)	Australia	Mangrove	Soil	NA	Inferred (microbial processes)	Case study, approximately 10 years since restoration
2	Santini et al. (2019)*	Australia	Saltmarsh	Soil	Bacteria, eukaryotes, archaea	Direct (sequencing)	Case study, approximately 20 years since restoration
3	Huang et al. (2022)	China	Mangrove	Soil	Bacteria (diazotrophs)	Direct, not specified	Chronosequence, 3, 10 years since restoration
4	Wei et al. (2021)*	China	Mangrove	Soil	NA	Direct (PLFA)	Comparison of restored (17 years since restoration) with reference site
5	Xiao et al. (2020)*	China	Saltmarsh	Soil	Fungi	Direct (sequencing)	Analysis of 16-year-old restoration site
6	Lin et al. (2021)*	China	Mangrove	Soil	Bacteria	Direct (sequencing)	Comparison of unvegetated mudflat, invasive <i>Spartina alterniflora</i> stands, 1, 8, 10-year <i>K. obovata</i> restoration areas, and reference site
7	Cheng et al. (2022)	China	Mangrove	Soil	Bacteria	Direct (sequencing)	Mangrove reforestation
8	Mai et al. (2022)*	China	Mangrove	Soil	Bacteria	Direct (sequencing)	Comparison of two artificial mangrove forests with unvegetated mudflat control site
9	Xu et al. (2020)	China	Saltmarsh	Soil	Eukaryotes (ciliates)	Direct (culture)	Comparison of restored <i>Scirpus mariqueter</i> meadow, <i>S. alterniflora</i> -invaded meadow, and bare mudflats and tested how ciliates were influenced by a recent restoration
10	Chen et al. (2020)	China	Mangrove	Soil	NA	Inferred (microbial composition)	Long-term restoration
11	Ma et al. (2021)	China	Mangrove	Soil	Bacteria	Direct (sequencing)	Mangrove reconstruction
12	Begam et al. (2017)	India	Mangrove	Soil	Bacteria	Direct (culture)	Mudflat stabilization
13	Ojeda-Morales et al. (2022)	Mexico	Mangrove	Soil	Bacteria	NA	Restoration post oil spill
14	Duarte et al. (2012)	Portugal	Saltmarsh	Soil	NA	Inferred (microbial enzymatic and respiratory activity)	Ecosystem monitoring during a 1-year revegetation trial
15	Burden et al. (2013)	United Kingdom	Saltmarsh	Soil	Bacteria	Inferred (microbial respiration)	Managed realignment
16	Piehlner et al. (1998)*	United States	Saltmarsh	Soil	Bacteria	Inferred (nitrogenase activity)	Comparison between restored 1-year-old and 6-year-old marsh and a reference site
17	Pietroski et al. (2015)	United States	Saltmarsh	Soil	NA	Inferred (microbial biomass)	Oil spill remediation
18	Barry et al. (2022)	United States	Saltmarsh	Soil	Bacteria	Inferred (microbial respiration) and direct sequencing	Tidal restoration
19	Janousek et al. (2007)*	United States	Saltmarsh	Soil	Bacteria	Direct (microscopy)	Comparison between natural and restored saltmarsh
20	Tatariw et al. (2021)*	United States	Saltmarsh	Soil	NA	Inferred (compared denitrification and dissimilatory nitrate reduction to ammonium rates)	Comparison between natural site and 32-year restored site

Table 2. Continued

No.	Author (Year)	Country	Ecosystem	Substrate	Microbial Community	Microbial Analysis (Inferred/Direct, Details)	Type of Restoration
21	Craft et al. (2003)*	United States	Saltmarsh	Soil	NA	Inferred (via microbial processes, i.e. soil organic carbon mineralization)	Chronosequence of 1- to 28-year-old, and reference site
22	Cooke & Lefor (1990)	United States	Saltmarsh	Host associated	Fungi (Arbuscular Mycorrhizal Fungi)	Direct (root staining for colonization)	10-year restoration project
23	Lynum et al. (2020)*	United States	Saltmarsh	Soil	Bacteria	Direct (sequencing)	Passive restoration/induced by restoration of tidal flooding. Before-After, Control-Impact approach
24	Cagle et al. (2020)	United States	Saltmarsh	Soil	Bacteria	Direct (sequencing)	Habitat restoration after oil spill
25	Bernhard et al. (2012)*	United States	Saltmarsh	Soil	Bacteria	Direct analysis (Terminal Restriction Fragment Polymorphism)	Tidal flow restoration
26	Wood et al. (2017)*	United States	Saltmarsh	Soil	NA	Inferred (enzyme activity, microbial biomass carbon and nitrogen, potentially mineralizable nitrogen)	Comparison between restored (dredged river sediment) and natural marshes

This search returned 177 papers in Scopus. All articles were imported into Covidence (Covidence systematic review software, Veritas Health Innovation, Melbourne, Australia) for title, abstract and full text screening. 151 studies were excluded, because they did not meet the criteria as follows: microbial communities not assessed (64 studies), ecological restoration not conducted (55 studies), review (14 studies), not in English language (6 studies), and other (12 studies; e.g. not mangrove or saltmarsh).

From the final 26 studies, the following data were extracted including the country where the research was conducted, ecosystem type (i.e. saltmarsh or mangrove), microbial community and how it was assessed (direct or inferred), and type of restoration. The results from the 26 studies are summarized in Table 2.

We found that approximately 50% of studies were from the United States (11), followed by China (9), Australia (2), India (1), Mexico (1), Portugal (1), and United Kingdom (1) (Table 2). Saltmarshes and mangroves were studied in 16 and 10 studies, respectively, although there were regional differences. For example, all studies from the United States were from saltmarshes. Studies from China were all but two from mangroves (Table 2). Microbial communities were predominantly assessed from soil or sediment in all but one study that analyzed arbuscular mycorrhizal fungi in plant roots (Cooke & Lefor 1990). Bacteria were the most common microbial group reported in 14 studies, fungi were reported in 2 studies, archaea from 1 study, and 7 studies did not report which microbial community was assessed or the microbial community was inferred by analyzing microbial activity or processes (Table 2). In mangroves, the type of restoration ranged from mudflat stabilization to mangrove reforestation and reconstruction to comparing chronosequences ranging from 1 year to 17 years since restoration, using predominantly next generation sequencing to assess microbial communities (Table 2). In saltmarshes, the type of restoration ranged from oil spill remediation to comparisons between restored and reference sites (Table 2). In total, 12 out of 26 studies compared soil microbial communities between restored and reference natural sites (Table 2).

In terms of how soil microbial assemblages responded to restoration and compared to reference sites, there were limited, or contrasting findings reported. For example, Wei et al. (2021) found no significant differences in phospholipid fatty acid (PLFA) profiles and microbial metabolism between mangrove sites. Bernhard et al. (2012) found that the bacterial community composition in restored saltmarsh sites was not significantly different from the undisturbed sites, although there were significant differences in bacterial community stability. Santini et al. (2019) reported that the microbial (i.e. bacterial, archaeal) community assessment in saltmarshes indicated that restored and natural saltmarsh habitats were similar at a phylum level, except for a higher proportion of Proteobacteria in the rhizosphere of saltmarshes from the regenerated habitat. These authors also reported that the abundance of *Desulfuromonas* and *Geobacter* was associated with high carbon and nitrogen densities in soils indicating that these genera may be key for the recovery of ecosystem characteristics in saltmarshes. Other authors found a stronger fungal network in saltmarshes within Ascomycota

(e.g. Sordariales, Aspergillus, Hypocreales, and *Cladosporium herbarum*) in restored marshes, but with a lower diversity of halophilic taxa (e.g. *Chytridiomycota*) in comparison with natural saltmarshes (Xiao et al. 2020). Lynam et al. (2020) found that the microbial communities in three compared habitats within the restored marsh were different from reference marshes, and both the prokaryotic and fungal communities within saltmarsh *Phragmites australis* and *Typha* sp. habitats became more similar to reference marshes during the first 2 years after restoration. Taken together, the review of current literature suggests there is conflicting and inconclusive evidence on soil microbial responses to restoration and geographic biases in plant–soil research as it pertains to coastal restoration.

These results show that there is still limited application of soil microbiome and a paucity of information about the rhizosphere microbiome responses to coastal restoration. This exercise also highlights the opportunity for fundamental research on the belowground microbial community diversity in coastal ecosystems and how these soil microbial communities could be harnessed to improve the outcomes of coastal restoration projects in both above- and belowground compartment.

Conclusions

The belowground microbiome holds a huge potential to enhance coastal restoration efforts. Before this knowledge can be harnessed, better understanding of plant–microbe belowground associations in coastal ecosystems is needed via on-ground studies that would provide a baseline on soil microbial diversity. We have highlighted potential pathways and acknowledged the associated challenges and suggested opportunities for direct and indirect interventions based on current restoration techniques within and outside of coastal restoration. While the list is not exhaustive and will likely be developed over time, we hope that this review will create further discussions toward improving the outcomes of coastal restoration. There are challenges to assessing belowground microbiome responses; however, we are hopeful that the field will see significant advancements in both fundamental and applied knowledge through technological advances, collaborative efforts, and increased understanding of the importance of coastal microbiomes to restoration success by stakeholders and funding bodies.

LITERATURE CITED

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