The Integral Role of the Coastal Microbiome in Mangrove Conservation

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Abstract

Mangroves are intertidal forests that bridge the gap between terrestrial and marine environments. They live at the edge of their tolerance in habitats rife with abiotic stressors such as fluctuations in salinity and temperature, yet mangroves are among the most productive ecosystems in the world. They are also among the most vulnerable to climate change and anthropogenic degradation, and are in steep decline globally. Providing important services economically, ecologically and environmentally, mangroves support a plethora of human activities, stabilizing coastlines, supporting marine food webs, sequestering vast amounts of carbon, cycling nutrients, trapping sediment and filtering water. This research examines the existing literature on the microbiome, biochemistry, ecological role, and conservation initiatives surrounding mangroves. My aim is the synthesis of a holistic approach to improving transplantation practices, supporting the success of mangrove reforestation. Mangrove reforestation initiatives are adapting priorities to include conservation and biodiversity, but success rates and longevity of transplants remain low. Inoculation of mangrove seedlings raised in nurseries, away from their natural habitats, shows promise in bolstering the success rates of seedling transplantation. Studies have correlated bacterial and fungal inoculants with increased biomass, increased resistance to stressors, increased root stability, increased plant productivity and reduced uptake of phytotoxic metals. These increases in performance are not attributed to a single microbial species, but rather a combination of bacterial and fungal inoculants. The interactions of these species is not yet well-understood but may hold pertinent insight for the successful reforestation of mangroves, and the rehabilitation of coastal ecosystems across the globe.

Keywords: Mangrove, microbiome, nutrient cycling, reforestation, mangrove management, sustainable development goals

Introductory Information

Mangroves are highly productive intertidal forests that bridge the gap between fresh and salt water and host countless species from every kingdom of life. Survival in these demanding ecosystems is made possible through specialized structures and processes to counteract changes in salinity, temperatures and sea level, among other abiotic stressors. Mangroves provide integral resources and services to both terrestrial and marine ecosystems while hosting a great deal of biodiversity (Allard at el., 2020). The resources and services provided by mangroves are important ecologically and economically to many stakeholders; mangroves are known to directly support over seventy human activities, from commercial forests to coastal fisheries (Kathiresan, 2012). Additionally, mangroves serve as buffers from extreme weather events, act as nurseries during the early life-stages of various ecologically and economically important animals, filter and purify water, facilitate nutrient cycling and carbon sequestration, provide organic matter that serves as an ecological base for complex marine food webs, and stabilize coastlines (Katherisan, 2012; Holguin et al., 2001).

Mangroves form close relationships with various microbes and these relationships generally support mangrove processes and development, playing an essential role in the productivity of coastal ecosystems (Holguin et al., 2001; Allard et al., 2020). Associated microbial communities play a significant role in the transformation of detritus into nutrients, such as phosphorus and nitrogen, preparing them for uptake by surrounding vegetation that further supports other organisms in the ecosystem (Holguin et al., 2001). In return for these services, mangrove-root exudates serve as nutrition for the microorganisms involved (Holguin et al., 2001). While it is well-known that the coastal microbiome is integral to nutrient cycling and other ecosystem processes in mangroves, the importance of microbial diversity and interaction in seedling development and transplantation is not well understood, as environmental conditions and species' associations make this information highly specific and difficult to ascertain. Seedlings grown in nurseries can be inoculated with growth-promoting microorganisms to support development, and this will likely improve transplantation success rates (Holguin et al., 2001).

Purpose & Relevance

The purpose of this research is to amalgamate the existing literature concerning microbial interactions in mangrove ecosystems, outline the significance of the microbial role in mangrove reforestation, and identify strategies to bolster nursery and transplantation efforts going forward. Mangroves are economically, ecologically, and environmentally important ecosystems. As such, they relate to several of the United Nations' Sustainable Development Goals, including SDG 13: Climate Action, SDG 14: Life Below Water, and SDG 15: Life on Land.

SDG 13: Climate Action

The thirteenth SDG, Climate Action, focuses on mitigating the impacts of climate change globally, and particularly in vulnerable regions. Part of the ongoing strategy includes collecting and distributing funds to developing countries so that they may both adapt to climate change and invest in sustainable development. This is in large part due to the cost and casualties resulting from the deleterious consequences of climate change, which continue to intensify (UNDP, 2022a). By nature, SDG 13 is interdisciplinary and will contribute to the achievement of other SDGs as they are integrated in purpose and strategy. Providing support to developing countries will entail disaster-prevention measures and investment in sustainable resource management, which includes the conservation and restoration of coastal ecosystems. The primary goal if SDG 13 is to contain the increasing global mean temperature to below 2°C, and ideally below 1.5°C. This goal is both urgent and important, as greenhouse emissions are presently 50% greater than they were in 1990 (UNDP, 2022a).

The goals of SDG 13 are particularly relevant to mangroves, as their multi-faceted role includes functions that mitigate the effects of natural disasters and sequester vast amounts of carbon in biomass and sediment—mangroves are among the most carbon-rich forests in tropical regions (Donato et al., 2011). In addition, natural disasters often leave developing countries particularly vulnerable in terms of food security and clean water, both of which are supported by mangroves (Allard et al., 2020). The conservation and continued reforestation of mangroves is essential to achieving SDG 13 and supporting sustainable coastal development, as they cover up to 24 million hectares in 112 countries, with over 41% in south or southeast Asia and over 23% in Indonesia (Katherisan and Bingham, 2001). Mangroves live at the edge of their threshold in high-stress environments, and are particularly vulnerable to shifts in temperature, salinity, and sea-level rise (Wee et al., 2019).

SDG 14: Life Below Water

The fourteenth SDG, Life Below Water, is concerned with understanding and regulating several abiotic factors of the worlds' oceans, such as water chemistry, temperature, and currents. These factors impact biotic components of these ecological regions and, through their role in climate regulation, these factors not only determine the viability of life under water, but also significantly impact life in every ecosystem across the globe (UNDP, 2022b; UN Decade for Ocean Science and Sustainable Development, 2022). Additionally, over 3 billion people rely on coastal or marine biodiversity for their livelihoods, from fisheries to forestry products. Oceans play a significant role in the cycle of atmospheric carbon, absorbing about 30% of anthropogenic CO^2, consequently leading to a steep increase in ocean acidification. Since the industrial revolution, there has been a 26% rise in ocean acidification which produces dire consequences for marine life by making habitats unlivable, altering behavior and interrupting physiological regulatory processes (UNDP, 2022b; Di Santo, 2019). Beyond acidification and abiotic factors, marine life is also threatened by anthropogenic pollution, from microplastics to oil spills. The degradation of oceanic ecosystems threatens the structure, function and benefits of marine systems at large (UN Decade for Ocean Science and Sustainable Development, 2022).

This goal is particularly relevant, given the United Nations Decade of Ocean Science for Sustainable Development, declared from 2021 to 2030. This initiative has been delegated to UNESCO's Intergovernmental Oceanographic Commission (IOC). IOC works collaboratively through its 150 Member States to expand scientific and institutional capacity in order to meet myriad goals laid out by the UN General Assembly, including the Sustainable Development Goals (UNESCO, 2022). It is designed to reverse the decline in ocean health through a global community of expert collaboration.

SDG 14 is relevant to mangroves because they are among the most biodiverse ecosystems on the planet and particularly along the coast. They play an essential role in the life cycles of multiple ecologically and economically important species, acting as feeding grounds, breeding grounds, and nurseries during the juvenile stages of many fish, mollusks and crustaceans (Katherisan, 2012). In addition to supporting early life stages of marine animals, mangroves provide foundational organic matter for complex marine food webs, and cycle nutrients that further support these webs (Allard et al., 2020). In addition to their roles in ecosystem functioning, mangroves and their associated microbes have been shown to filter water and remediate pollution (dos Santos et al., 2011; Kohlmeier et al., 2005; Valiela et al., 2018).

SDG 15: Life on Land

The final SDG related here is the fifteenth, Life on Land. This SDG addresses plant life from agriculture to forests, relating their benefits for humans as well as their ecological importance. Deforestation and desertification have transformed over 16 million hectares globally, disproportionately impacting marginalized communities struggling with poverty. Over 80% of terrestrial species rely on forests, and reduction in natural habitats further endangers those species beyond reducing food security (UNDP, 2022c). In addition to reversing ecosystem degradation and declines in biodiversity, this goal aims to support global food and water security, protect endangered species, mitigate the impacts of climate change, and help developing countries to adapt to new climatic conditions.

Supporting these goals and others, the United Nations Decade on Ecosystem Restoration aspires to halt ecosystem degradation and engage in restoration and conservation in order to prevent catastrophic climate change. This initiative is led by the UN Environment Programme and the Food and Agricultural Organization of the United States. It incorporates global political approaches in tandem with grassroots conservation to build momentum behind terrestrial and marine ecosystem restoration (UN Decade for Ecosystem Restoration, 2022). Their strategy entails allocating the proper funding for research and action, involving the global community, incentivizing restoration, and inciting cultural and rhetorical changes in the relationship between consumption and conservation.

The conservation and reforestation of mangroves is imperative for the success of SDG 15 as they are among the most biodiverse coastal ecosystems and are foundational to complex marine food webs through the provisioning of food, habitats and growth zones (Katherisan and Bingham, 2001). Mangroves support a diverse array of fauna, from pollinators to zooplankton to burrowing epifauna that underpin coastal fisheries, water filtration and nutrient cycling. The structure of pneumatophores creates an enclosed habitat, attracting vulnerable species to seek refuge in the roots of the mangal, furthering the protection of threatened and endangered species (Katherisan and Bingham, 2001). Beyond fauna, the mangal supports various flora, funga and surrounding ecosystems such as seagrasses, which rely on shade and filtration from mangroves to thrive (Katherisan and Bingham, 2001). The management of mangroves is complex and requires knowledge about both ecological and social interactions, as they are dynamic environments with a range of specific challenges (Dahdouh-Guebas et al., 2020).

Methodology

The synthesis of this information is the result of an extensive literature review, incorporating scholarly research and web pages from official organizations such as the United Nations. Using databases such as EBSCO, Google Scholar, Science Direct Journals, BioOne and JSTOR, I applied filters for peer-review on articles and books. The sources that I focused on included primary and secondary research where biotic and abiotic factors were measured and assessed relative to individual mangroves or mangrove ecosystems. The outcomes ranged from discovering the function of secondary metabolites in fungi to measuring water quality downstream versus upstream of ecosystem disturbance events. Analyses were conducted and results contrived via laboratory work, bioinformatic analysis, field measurements, and other approaches. Upon collection of well-cited, key sources covering mangroves broadly, as notated on ResearchGate, I scoured each article’s references for further information on the given area. While sourcing web pages, I only selected sites directly affiliated with the organizations discussed and ensured that the page ended in “.org” or “.edu”. Articles and book chapters were obtained in November of 2021 and January, February and March of 2022, while websites were accessed in March and April of 2022. I then analyzed these sources and categorized the material into sections to facilitate clear communication of my findings. Priority was given to sources that were well-cited and had already undergone peer-review. This may impose several limitations due to bias, recentness of publication and positionality of researchers, as the opportunity to publish and timelines for publication are not universal.

Why do Mangroves Matter?

Human Importance

With such a broad and foundational role in coastal ecology, mangroves have a notable influence on human communities, marine ecosystems and organisms, and the environment at-large. Mangroves provide numerous resources that support human activities—while many of these resources are primarily utilized by coastal communities, they have traction in communities across the globe. These resources have a significant impact on the economy; they may include timber, charcoal, fish, molluscs, crustaceans, medicinal extracts, livestock feed and more The estimated value of one hectare of mangrove forest ranges from $2,000 – $9,000 annually, although this fluctuates based on location and management (Katherisan, 2012).

Mangrove trees are often used as timber or charcoal, as the wood is known for its durability and caloric density—charcoal from mangroves is roughly five times more efficient than Indian coal, among other alternatives. Leaves and other debris are used by local communities for roofing, baskets, bottle stoppers, and other products (Katherisan, 2012). There are many cultural and medicinal uses of mangroves and mangrove-dependent species in Indigenous cultures, with extracts shown to treat myriad pathogens in humans, animals, and plants (Katherisan and Bingham, 2001). A few of these products are targeted toward ailments such as epilepsy, high blood pressure, leprosy, rheumatoid arthritis, and may even have applications for incurable viral infections like AIDS (Katherisan, 2012).

In addition to supplying resources to build and support coastal communities, mangroves play an important role in food production. These forests serve as grazing grounds for local livestock, including goats, sheep, camels and buffalo. They also provide seeds that act as feed for fisheries in areas such as West Bengal. Outside of industrial fisheries and agriculture operations, one hectare of mangroves yields as much as 767 kg of wild fish and crustaceans: systems categorized as “high-producing” generally yield around 500 kg or more (Katherisan, 2012). Managed mangroves can produce up to $11,300 per hectare annually, which is on par with yields from intensive shrimp farming (Primavera and Esteban, 1991). In many areas, mangroves are significant for apiculture, supporting the production of honey and wax. For example, Siddiqi et al. 1997 estimated that approximately 185 tons of honey and 44.4 tons of wax are harvested annually from the western mangrove forests in Bangladesh, as cited by Katherisan 2012.

Ecological Importance

The ecological importance of mangroves is paramount, as these trees form the foundation for the mangal. Mangrove trees, in concert with the fungi, bacteria, plants, and animals that they host, constitute the “mangal”—the mangrove swamp. “Mangrove” is generally used to refer to an individual tree, whereas “mangal” refers to the entire mangrove forest community. Mangals are responsible for nutrient cycling, coastal protection, provision of breeding and feeding grounds for marine life, water filtration, ecosystem productivity and carbon sequestration (Allard et al., 2020; Katherisan, 2012; Miryeganeh and Saze, 2021).

Mangroves and their associated microbes play an integral role in moving nutrients with low mobility, such as phosphorus, which is accomplished with the assistance of Arbuscular Mycorrhizal fungi (AMF) (D’Souza, 2016). These fungi play a significant role in carbon and nitrogen cycles, and also reduce the uptake of phytotoxic heavy metals (D’Souza, 2016; Willis et al., 2013). Mangrove soils have notable metal-binding capacities due to the presence of microbial communities, and can act as heavy metal sinks until disturbance causes them to shift to heavy metal sources (Katherisan and Bingham, 2001). Beyond cycling nitrogen and phosphorus, bacterial and fungal communities associated with mangroves break down detritus, transforming it into organic matter that serves as the basis for complex marine food webs (Katherisan and Bingham, 2001).

Lateral roots from mangroves stabilize the soft, silty sediments and reduce coastal erosion, while simultaneously acting as a buffer against natural disasters such as cyclones, wave action and tides, tsunamis, flooding, and sea level rise (Katherisan and Bingham, 2001). One study even found that the buffer provided by mangals was significant enough to reduce the effects of a Category 5 storm to a Category 3 storm (Liu et al., 2013).

The mangal swamp traps sediments, effectively filtering the water to produce a clear environment for fish; they host myriad organisms capable of filtering pollutants, such as bacteria or bivalves (Yam et al., 2013). In addition to filtration of sediments and pollutants, mangroves provide protection from UV-B radiation to mangal inhabitants. Mangroves have a high tolerance to UV-B radiation and are adapted to hot, arid climates: their foliage produces flavonoids that screen out UV radiation, protecting the ecosystem from the deleterious effects of exposure (Katherisan and Bingham, 2001).

Environmental Importance: Carbon Sequestration

Finally, mangals impact the environment significantly, as they are key players in the carbon sequestration and are integral to complete calculations of oceanic and global carbon budgets (Cameron et al., 2019). Beyond contributing to the cycling and provision of organic carbon, mangroves and their associated microbes sequester 50 times the amount of carbon as other tropical forest ecosystems and lead in coastal ecosystem sequestration, storing 2.4 times the amount of carbon as salt marshes and 5.2 times the amount stored from seagrasses (Katherisan and Bingham, 2001). This carbon storage takes place both above- and below-ground, with high ratios occurring in the first few meters of below-ground sediment, which is rich in organic matter, dominates tropical coastlines and is often referred to as “mangrove peat” (Katherisan and Bingham, 2001). The anoxic conditions of these sediments trap carbon for longer time periods than terrestrial forest storage, with carbon stores 3 to 5 times greater than their terrestrial counterparts (Cameron et al., 2019).

Beyond providing basal nutrients for their relative ecosystems, mangroves also play a disproportionate role in carbon sequestration and atmospheric exchange, as opposed to terrestrial ecosystems (Donato et al., 2011; Cameron et al., 2019). Carbon sequestration occurs through accumulated biomass as well as long-term soil storage, with anoxic soil conditions allowing for storage timescales exponentially greater than terrestrial counterparts, when undisturbed (Cameron et al., 2019). Mangrove forests store more carbon in their soils per hectare than most any other ecosystems, particularly in terms of long-term carbon storage (Donato et al., 2011). This carbon sequestered in marine ecosystems, commonly referred to as “coastal blue carbon,” is a significant factor in discussions of climate change, and conservation of these ecosystems should be considered seriously when attempting to reduce greenhouse emissions (Allard et al., 2020; Cameron et al., 2019; Donato et al., 2011).

Mangroves remove carbon dioxide from the atmosphere through photosynthesis and utilize microbial communities to fix more carbon than tropical oceanic phytoplankton (Cheung et al., 2018; Katherisan and Bingham, 2001). Bacteria consume most of the carbon in interstitial waters, metabolizing it as biomass, storing it in the sediment, or mineralizing and releasing it as dissolved organic matter (Holguin et al., 2001). Environments with high carbon-concentration result in increased biomass—mangroves have a significantly higher ratio of aerial biomass to below-ground biomass than upland forests (2.5:1 from 4:1), improving soft sediment stabilization (Katherisan and Bingham, 2001). The above-ground biomass of mangroves is estimated around 3,700 trillion grams (Tg) of carbon, sequestering 14 – 17 Tg of carbon annually. Organic matter-rich soils at depths ranging from 0.5 m – 3 m account for between 49% and 98% of mangrove carbon storage (Katherisan and Bingham, 2001). Global primary production by mangroves is estimated at 218 Tg annually, and is a significant contributor to oceanic carbon by export, sediment burial and mineralization of fixed carbon (Katherisan and Bingham, 2001). More than 50% of carbon sequestered by mangrove vegetation is unaccounted for, predominantly due to the underestimation of mineralized carbon. Most mineralized carbon is transferred from mangroves to marine environments as dissolved inorganic carbon (Bouillon et al., 2008).

When mangals are converted to aquaculture ponds, the disturbed sediment releases sequestered carbon for atmospheric uptake. Mangrove deforestation accounts for about 10% of deforestation emissions globally, despite covering only 0.7% of tropical forested areas. Carbon fixed in coastal vegetated habitats is 180 times greater in magnitude than that of deep-sea sediment, and accounts for 50% of the organic carbon buried in marine sediments, even though these habitats only occupy 0.2% of coastal cover (Katherisan and Bingham, 2001). The disturbance of the immense carbon sinks may provide some explanation to this seemingly disproportionate difference in greenhouse gas emissions from deforestation of mangals as opposed to other forest types (Katherisan and Bingham, 2001; Donato et al., 2011)

Ecology and Biology of Mangroves

Mangroves occur between 30° north and 30° south, distributed circumtropically throughout 112 countries. They prefer loose, alluvial soil rich in humus and thrive in locations where freshwater inflow supplies nutrients and silt, (Katherisan and Bingham, 2001). Mangroves are regularly subjected to extreme stressors, such as high salinity, high temperatures, intense UV radiation, strong winds, variable tides and anaerobic soils. To adapt to these challenges, mangroves have evolved morphological and physiological adaptations unlike those seen in any other plants (Katherisan and Bingham, 2001; Miryeganeh and Saze, 2021).

Morphologically, mangroves have several different types of “roots”: the trees employ lateral roots to anchor themselves in the fine, muddy sediment and exposed, aerial roots known as pneumatophores to participate in gas exchange and to produce viviparous propagules (Katherisan and Bingham, 2001; Miryeganeh and Saze, 2021). While the anatomical details of root structure and function vary between species and habitats, the general structure of mangrove roots is consistent. Rather than sending deep roots to penetrate loose, anaerobic soils, mangrove roots disperse a broad network of lateral roots for stability according to Emilio et al. (1997), as cited by Katherisan and Bingham (2001). Miryeganeh and Saze (2021) conducted a study on mangroves in Japan seeking to correlate phenotypic expression of structural traits to environmental conditions and found morphologically distinct populations of the same species, with shrub-like morphology on the oceanside and tree-like structures on the riverside.

Physiological adaptations to stressors are multi-faceted, and can be traced to the existence and expression of specific stress-response genes (Miryeganeh and Saze, 2021). The efficiency of mangrove stress response to both biotic and abiotic stressors may be affected by microbial community composition on the given mangrove (D’Souza, 2016; Soldan, 2019). Among abiotic stressors, high salinity is one of the most challenging for plants to accommodate—there are approximately 10,000 tree species adapted to the transitional ecosystems between non-saline water and land, compared to only 80 tree species inhabiting saline intertidal zones (Miryeganeh and Saze, 2021). Salinity can fluctuate wildly in the intertidal regions that mangroves inhabit, both seasonally and daily from variations in rainfall, temperature, and sea level oscillation (Miryeganeh and Saze, 2021). To survive high variability in salinity, mangroves have special features that allow them to uptake water against great osmotic pressure. They then excrete excess salts through their leaves to maintain internal osmotic homeostasis (Katherisan and Bingham, 2001).

The molecular mechanisms behind salt-tolerance are not fully understood due to a lack of reference genomes for mangroves, but de novo RNA-Seq assembly provides a feasible understanding through an extensive search of transcriptomes to identify expressed genes (Miryeganeh and Saze, 2021). The phenotypic expression of stress-resistance genes fluctuates based on species, location, and conditions: structural changes in biomass, height, and root configuration can be traced to DNA methylation patterns and fluctuating conditions (Katherisan and Bingham, 2001; Miryeganeh and Saze, 2021).

The Microbial Role in Nutrient Cycling

The importance of nutrient cycling in coastal ecosystems (or any ecosystem, for that matter) cannot be understated: mangroves are essential in transforming nitrogen and phosphorus, as well as supplying organic matter to complex marine food webs (Allard et al., 2020; Holguin et al., 2001).

The composition of a microbial community suggests a great deal about an ecosystem, particularly in relation to soil and fungal-bacterial ratios. Arbuscular mycorrhizal fungi (AMF) are notable factors in the development and direction of microbial community structure (D’Souza, 2016). The composition of these communities fluctuates in accordance with traceable spatiotemporal patterns that correlate to several abiotic and biotic factors, such as seasonality, tide, salinity and vegetation (Cheung et al., 2018). A study sampling the Mai Po wetlands in Hong Kong found the dominant fungal phylum during the dry season to be Ascomycota, while Basidiomycota dominated during the wet season; bacterial communities were dominated by the phyla Bacillota (former name: Proteobacteria) and Bacteroides, regardless of season (Cheung et al., 2018). Bacteria demonstrated greater richness and beta diversity during the wet season, much of which can be explained either by temperature, archaeal diversity, or fungal diversity (Cheung et al., 2018). Fungi followed similar patterns as bacteria and were also most heavily influenced by temperature and microbial diversity. In terms of composition, archaea contrast against bacteria and fungi in their ability to resist the abiotic stress of temperature fluctuation, as their diversity distribution was unaffected by these fluctuations (Cheung et al., 2018).

Vegetative material from mangroves is decomposed by myriad microorganisms and converted to detritus before the enclosed nutrients become bioavailable for other organisms, from plants to filter-feeding invertebrates. The decomposition begins as soon as the fungi and bacteria residing in the sediment are able to colonize the leaf-litter, with each kingdom playing distinct roles based on their enzymatic capacities (Holguin et al., 2001). The result is detritus, organic matter rich in energy that is actively undergoing decomposition. This detritus serves as a direct food source for roughly one-third of coastal organisms and an indirect food source for many more species important to coastal fisheries (Holguin et al., 2001).

Bacteria are essential to this process of nutrient transformation: they fix nitrogen, make phosphorus available to plants (a common limiting factor), decompose organic matter through sulfate-reduction in anaerobic soils, and fix carbon through photosynthesis. High rates of nitrogen fixation are correlated to the detritus produced from mangrove vegetation (Holguin et al., 2001).

Fungi are essential in these processes, facilitating bi-directional transport of nutrients through hyphal networks. Carbon fixed by the host through primary production is assimilated into the mycelial network, while soil-derived nutrients are transported to the host (Willis et al., 2013). Mangrove-associated fungal communities, particularly AMF, have an enhanced ability to capture and store carbon as biomass, producing more carbon per unit than their bacterial counterparts (Strickland and Rousk, 2010).

While many fungal species have been detected in the decomposition of mangrove detritus, little is known about their role and function in the ecosystem, outside of taxonomic placement. It is clear that they play an important role in the early stages of decomposition, breaking down lignin and cellulose which prepares the detritus for secondary colonization by bacteria and yeasts to further the process of decomposition (Holguin et al., 2001). The fungal participation in early-stage decomposition may be due to a high tolerance of phenolic compounds that inhibit the growth of secondary colonizers. Beyond decomposing cellulose and lignin, these fungi have demonstrated proteolytic, pectinolytic and amylolytic activity, according to Raghukumar et al. (1994), as cited in Holguin et al. (2001). Identified species in this role belong to the phylum Ascomycota and appear to predominantly colonize this detritus at or below tide-level, although they are predominantly limited to the outer layers of detritus due to their high oxygen consumption (Holguin et al., 2001). The impact of microbial location and diversity on interactions between kingdoms leads to the question, “What types of interactions are ongoing between these communities, and how do those interactions impact the ecosystem at-large?” Interaction between microbes can be traced through co-occurrence networks, among other analyses, to delineate the ecologically meaningful interactions between members of the represented microbial kingdoms (Cheung et al., 2018). These analyses also provide information about the functional roles or potential ecological niches of the relative communities. For example, a study by Warmink et al. (2010) conducted a series of tests on a group of bacterial species in concert with saprotrophic fungi, discovering that select fungal hyphae play a role in transporting bacterial species to novel environments for colonization. Many of these novel environments were deep layers of anoxic sediment that bacteria had limited access to; thus, bacterial migration facilitated by fungi is a key piece of information when it comes to determining the ecological success in the given species of soil bacteria (Warmink et al., 2010).

Anthropogenic Degradation of the Mangal

The destruction of mangrove forests is widespread and occurring at an alarming rate: the main processes contributing to this degradation are coastal development, pollution and climate change (Allard et al., 2020; D’Souza, 2016). While mangroves have evolved spectacular adaptations to deal with their stressful environments, they often live at the edge of their tolerance, leaving them particularly susceptible to disturbances such as those created by anthropogenic activity (Katherisan and Bingham, 2001; Wee et al., 2019). These ecosystems are among the most vulnerable to climate change, particularly to the challenges presented by sea-level rise, as the pressures of development and pollution pose additional stressors and constraints on their habitat and range (Donato et al., 2011; D’Souza, 2016). Over the past five decades, up to half of global mangrove cover has declined due to development and aquaculture (Donato et al., 2011). Efforts are underway to reforest mangroves, restore degraded ecosystems, convert fisheries and aquacultures to sustainable practices, regulate coastal development, and involve local communities with conservation (Holguin et al., 2001; Allard et al., 2020).

Land-use change is one of the greatest contributors to anthropogenic carbon dioxide emissions, second only to fossil-fuel combustion (Donato et al., 2011). Land-use change can take many forms, ranging from development of urban areas for residential use or tourism to industrial uses, such as conversion from mangal to aquaculture ponds. Mangroves mediate acidity changes in the soil and, when they are deforested, bacterial colony diversity has been shown to decline as the primary source of carbon from mangrove vegetation is removed (Holguin et al., 2001). Even the extent of mangrove coverage can be maintained while quality continues to degrade, as has been the case in the Sundarbans. In response, Bangladesh has adopted and innovated mangrove management strategies to account for the conservation and enhancement of biodiversity (Iftekhar and Islam, 2004).

Inoculation & Nursery Strategies

Selecting the proper species' of bacteria or fungi to inoculate a mangrove seedling is a process not yet well-understood, as the ideal inoculants will depend on a slew of abiotic factors, such as geographic location or salinity stress (Soldan et al., 2019). Biotic factors will also play a role, as microbial community composition vary by mangrove species. Plants and microorganisms have evolved together since time immemorial, and plants discharge root exudates to attract the proper endophytic organisms—these organisms are often transmittable to the plant's progeny, demonstrated through their presence in seeds and seed coats (Holguin et al., 2001; Soldan et al., 2019). In some mangroves, inoculation has been linked to drastic increases in photosynthetically derived carbon exudates and nitrogen fixation (Holguin et al., 2001). This process is important to plant development as many of these are plant growth promoting (PGP) organisms, and particularly important for mangroves due to the extreme environments they inhabit—they host halotolerant and halophilic bacteria by necessity, to support them through the relative abiotic stressors (Soldan et al., 2019). AMF specifically have been shown to influence response to climatic fluctuations, increase tolerance of plants and increase plant productivity (D'Souza, 2016). As soil constituents, AMF are integral to the cycling of carbon and nitrogen and promote selective uptake in plants to reduce phytotoxic heavy metals (D'Souza, 2016). They also assist mangrove pneumatophores in supplying oxygen to the sediment (Holguin et al., 2001). Inoculation is an integral step since PGP bacterial endophytes support root establishment by enhancing root length, exerting positive effects under salt-stress and increasing biomass during developmental periods (Soldan et al., 2019).

In an attempt to discover the most effective method for discerning and isolating the proper bacterial strains, Soldan et al. (2019) sampled various mangrove populations, testing multiple parts of the plant and sediment for community composition. The most populous phyla of bacterial endophytes discovered in the root propagules included Bacillota, Firmicutes, Actinobacteria and Bacteroidetes. These phyla are known to associate with the seeds of multiple plant species, were widespread in mangrove tissues throughout the plant, and dominate in both soil and marine ecosystems (Soldan et al., 2019). They speculate that mangroves recruit bacterial endophytes from sediment environments rather than the water, and demonstrated through high-throughput sequencing that these associations were mutually beneficial, supporting mangroves in light of abiotic stressors including osmotic stress, high temperatures, and high salinity (Soldan et al., 2019).

Nurseries & Reforestation

While selecting the proper inoculant is crucial, there are several other factors that impact transplantation success rates. The selection of proper mangrove species, transplantation site, and microbial inoculation strategies are essential to ensure the success of mangrove seedlings and bolster reforestation efforts (Allard et al., 2020). The general, long-term survival rate of mangrove transplantation is low, between 10 – 20%—the greatest successes have arisen from strategies that engage local community members in conservation and upkeep of the mangrove forests (Primavera and Esteban, 2008). Intentional inclusion of genetic diversity in the species selected for transplantation is crucial—*Rhizophora*, the current “flagship” species for reforestation efforts, is ideal for a few locations but doesn’t possess the phenotypic plasticity necessary to succeed in all coastal regions (Primavera and Esteban, 2008; Wee et al., 2019). Thus, a variation of species and hybrids, tailored to the conditions of a given location, will be integral to widespread success in mangrove reforestation.

As many hybrids are indistinguishable from the parent species at face value, molecular techniques that provide genetic identification are invaluable in distinguishing the best species for a given location (Wee et al., 2019). These molecular screenings would be best conducted by large nurseries supplying seedlings, or by outsourcing the sequencing work for verification before embarking on a transplantation project (Wee et al., 2019). Transplantation techniques must be interactive and adaptive to their geographic location if these practices are to be successful (Dahdouh-Guebas et al., 2020).

While the mobilization of sequestered carbon isn’t clearly understood, current evidence suggests the conversion of mangroves to clearings, aquaculture, drainage, or coastal development decreases the soil’s carbon-content significantly (Donato et al., 2011). The sheer amount of carbon sequestered in mangrove soils and ecosystems provides ample motivation for the conservation of mangroves, outside of their ecological, economic, and intrinsic value, and they have been increasingly attracting attention in international policy (Cameron et al., 2019). Wee et al. (2019) has suggested ecologically meaningful, defined, conservation units as a contributing solution to the degradation of mangroves. These conservation units could be based on genetic connectivity, or declared by creating new Ramsar sites or marine protected areas based on mangrove density, which may prove useful in stifling their rapid degradation. Either way, in order for this level of conservation to be successful, a widespread phylogeographic analysis of mangrove species and hybrids would need to be completed, entailing large-scale genotyping achieved through international collaboration (Wee et al., 2019).

Research Findings

Mangroves act as unique nurseries to many ecologically and economically important species by providing physical protection, nesting grounds and accessible food sources. They protect communities from natural disasters and stabilize coastlines against erosion; mangroves filter seawater contaminated by terrestrial runoff, pollution, effluent, and industrial waste. The mangrove microbiome cycles nutrients such as nitrogen and phosphorus by converting leaf-litter into detritus, supplying organic matter to large and complex marine food webs. The microbiome also sequesters carbon in biomass and soils, and supports mangroves in light of biotic and abiotic stressors. Mangrove ecosystems are under acute stress and are increasingly threatened by anthropogenic activities, namely, land-use changes to aquaculture and palm oil plantations, coastal development and pollution.

There are a number of reforestation initiatives taking place across the globe, with varying success levels. The most successful strategies incorporate community partners who live in close proximity to mangroves and can assist in their maintenance. Additionally, studies show that mangrove seedlings grow faster, larger, and are more resistant to stressors when inoculated with select fungal and bacterial species. Some of these microbes, notably AM fungi, are transmitted to progeny through seeds, alluding to evolutionary links between plants and fungi and affirming the notion that their relationship is mutually beneficial. As most species are particularly vulnerable in early life stages, and mangroves are particularly susceptible to stressors, the support that inoculation confers is significant when seeking to increase the success rate during transplantation of seedlings from nurseries to mangrove habitats. Thus, further investigation into specific inoculant species pairing (between mangrove, fungi and bacteria) will illuminate best practices for mangrove reforestation going forward.

Research Limitations & Future Recommendations

There were several factors that limited the findings of this research, one of them being a lack of time sufficient to delve into the literature. Another is a mere lack of information surrounding the nuanced role of the microbial community in the health and viability of the mangal. Fungi are understudied and poorly understood, and particularly so in marine environments. The various types of fungi present in this system, from yeasts to mycorrhizae, may play more or less significant roles than our estimates and studies can account for—further research must address these concerns. The lack of information on fungal communities partially extends to bacterial communities, although bacteria are more broadly documented and understood (Lee et al., 2020). Thus, part of the information presented on fungal-bacterial interactions is speculation.

Further research would benefit from sampling plans that span and compare geographically diverse mangrove ecosystems, sampling microbial communities across mangrove structures in a variety of climatic conditions including varying tides, seasons, and disturbances. This combination of biotic and abiotic data will constitute a more holistic picture, and may account for some confounding factors that currently blur the nuance in microbial interactions. Beyond a sampling plan, bioinformatic pipelines can delineate the molecular data to discern and compare fungal and bacterial presence and construct phylogenetic data for both the mangroves and the microbial communities. This genomic information could be further used to determine common motifs for predictive protein modeling that may present useful information about secondary metabolites and, thus, potential ecological niches.

Conclusion & Originality

In order to prevent the complete degradation of mangroves, and to begin restoration of the millions of hectares of deforested mangroves, we must employ targeted and strategic practices for cultivating the appropriate mangrove seedlings in nurseries, inoculated with the appropriate microbes, and involving the correct community partners. The appropriate seedling species will depend upon the abiotic conditions present, and will account for genetic diversity and phenotypic plasticity, avoiding hybrids that struggle with fertility. The appropriate microbe inoculation strategy will be both species- and location-dependent, as varying species have varying nutrient requirements that are further affected by abiotic, environmental conditions. Finally, the correct community partners will include scientists, investors and conservationists, but it will also include local community members who live in proximity to these ecosystems, understand their importance, and are willing to contribute to the upkeep and maintenance.

The complexity of mangrove ecosystems is not well-understood, including the multi-faceted roles they play by providing and facilitating a multiplicity of integral ecosystem processes. In large part, the lack of knowledge surrounding mangrove ecology stems from a lack of knowledge about the coastal microbiome, from community assembly to composition to microbial interactions (Allard et al., 2020). However, we have many pieces of the puzzle and scientists, activists, farmers, locals and others are collaborating to discover sustainable, successful, interdisciplinary methods that can protect and restore these vital ecosystems.

It has been shown that microbial diversity supports mangrove seedlings during development by assisting in root stabilization, increased biomass, increased plant productivity, increased resistance to stressors, and decreased uptake of toxic compounds (D’Souza, 2016; Holguin et al., 2001; Soldan et al., 2019). There is also ample evidence to suggest that microbial interactions work synergistically to support mangrove health, process nutrients in various stages, facilitate transport to new microhabitats for colonization, and ward off disease (Cheung et al., 2018; Katherisan, 2012). The key to bolstering transplantation success rates lies in fabricating specific strategies based on geographical locations and abiotic conditions of the target environment, then tailoring the inoculant and development strategy to those parameters (Holguin et al., 2001).

This research provides significant insight into the functioning of the mangal and the role of the mangrove microbiome, integrating this information with the end goal of conservation and ecosystem restoration. The conservation of mangroves will be essential to meeting Sustainable Development Goals 13, 14 and 15 as mangroves are integral stakeholders in the global carbon budget, and provide myriad resources and functions to support life both below water and on land. Mangrove conservation also falls in line with the goals of the UN Decade of Ocean Science for

Sustainable Development and the UN Decade on Ecosystem Restoration, and can provide integral insight into the management and rehabilitation of coastal ecosystems worldwide.

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