



Plant-Microbial Symbioses in Coastal Systems: Their Ecological Importance and Role in Coastal Restoration

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Received: 9 August 2021 / Revised: 20 January 2022 / Accepted: 24 January 2022
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Abstract

Coastal systems are immensely valuable to humans. They contain unique ecosystems that are biodiversity reservoirs and provide key ecosystem services as well as a wealth of cultural heritage. Despite their importance to humans, many coastal systems are experiencing degradation that threatens their integrity and provisioning of services. While much is known about the plant communities and associated wildlife in coastal areas, the importance of microorganisms represents a large knowledge gap. Here we review the ecology of plant-microbial symbioses in coastal systems, including mycorrhizae, nitrogen fixers, endophytes, rhizosphere microbes, and pathogens. We focus on four common coastal communities: sand dunes, marshes, mangroves, and forests/shrublands. We also assess recent research and the potential for using microbes in coastal restoration efforts to mitigate anthropogenic impacts. We find that microbial symbionts are largely responsible for the health of plants constituting the foundation of coastal communities by affecting plant establishment, growth, competitive ability, and stress tolerance, as well as modulating biogeochemical cycling in these stressful coastal systems. Current use of microbial symbionts to augment restoration of stressful and degraded coastal systems is still very much in its infancy; however, it holds great promise for increasing restoration success on the coast. Much research is still needed to test and develop microbial inocula for facilitating restoration of different coastal systems. This is an excellent opportunity for collaboration between restoration practitioners and microbial ecologists to work toward a common goal of enhancing resilience of our coastal ecosystems at a time when these systems are vulnerable to an increasing number of threats.

Keywords Coastal forests · Coastal shrublands · Sand dunes · Mangroves · Marshes · Plant-soil interactions

Introduction

Coastal areas provide immense value to humans. They represent 22% of the land area worldwide while providing home to 38% of the human population and 50% of the world's largest cities (Kummu et al. 2016). Coastal areas contain unique ecosystems that are biodiversity reservoirs, and they provide key ecosystem services including food production, storm surge protection, filtration of pollutants, carbon storage, recreation, and cultural heritage (UNEP 2006). Despite their importance to humans, many coastal systems are experiencing degradation from a number of stressors that threaten

their integrity and provisioning of ecosystem services (Millennium Ecosystem Assessment 2005).

Previous reviews on coastal ecosystems have investigated the current status of coastal systems (Burke et al. 2001; UNEP 2006), climate change impacts (Field et al. 2001; Scavia et al. 2002), resilience to climate change (Bernhardt and Leslie 2013; Duarte et al. 2015), and management approaches (Powell et al. 2019; Spalding et al. 2014). These reviews have well documented that anthropogenic global change has a major impact on coastal systems. Climate warming is causing sea level rise and inundation and degradation of coastal ecosystems such as salt marshes (Jankowski et al. 2017; Kirwan and Megonigal 2013) and sand dunes (Feagin et al. 2005). Warming is also linked to increased intensity and frequency of storms making landfall in coastal areas (Knutson et al. 2010). Pollution from industry, agriculture, and oil spills has caused marsh and mangrove degradation and erosion (Kingsford et al. 2016; Silliman et al. 2012). Previous reviews have stressed the difficulties and

Communicated by Kenneth L. Heck

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idiosyncratic nature of restoration and recovery of coastal systems, with partial rather than full recovery prevailing and the existence of feedbacks that maintain coastal systems in degraded states (Duarte et al. 2015). Past work further highlights the importance of biodiversity and connectivity in sustaining the resilience of coastal systems (Bernhardt and Leslie 2013; Duarte et al. 2015).

The purpose of this review with a plant-microbial focus is twofold. First, despite much research on coastal systems, one identified knowledge gap is the ecology and importance of microorganisms (UNEP 2006). We aim to take a first step by reviewing literature on the ecology of plant-microbial symbioses in coastal ecosystems. A baseline understanding of these microscopic components of ecosystems is important for land managers and restoration ecologists, because microbes too are shifting with climate change and have important consequences for the functioning of coastal systems (Cavicchioli et al. 2019). Second, it is clear that there is an overwhelming sense of urgency to act expeditiously to reverse degradation from climate change in coastal areas because of our reliance on coastal ecosystems (UNEP 2006). While many general and specific solutions have been put forth to enhance restoration and management success (Bernhardt and Leslie 2013; Perrow and Davy 2002), the potential for plant-microbial interactions to improve restoration success of degraded coastal ecosystems has rarely been considered and not previously reviewed.

We focus on four main types of coastal ecosystems: sand dunes, marshes, mangroves, and forests/shrublands (Fig. 1). We chose these terrestrial systems, because they are dominated by plants (rather than algae) and have commonalities in how plant-microbe symbioses manifest. For a review of plant-microbe interactions in aquatic systems, see Srivastava et al. (2017). While sand dunes, marshes, mangroves, and forests/shrublands differ in notable ways (abiotic conditions, proximity to land-water interface, biotic communities), they are similar in that they are all stressful environments, as a result of low nutrients, high salt, or drought conditions. It is generally thought that stressful environments have more positive plant-microbe interactions (Bertness and Callaway 1994; Lekberg et al. 2018) and that stressful systems, in particular, would benefit from microbial mutualists to aide in successful establishment and persistence of plants during restoration (Valliere et al. 2020).

The Role of Plant-Microbe Symbioses in Ecosystems

Symbiosis (from Greek, “living together”) is a close and long-term biological interaction between two different species. Symbioses can be mutualistic (+/+), commensalistic (+/0), or parasitic/pathogenic (+/–). Microbes are important symbionts of plants that play key roles in ecosystems

Fig. 1 The four coastal community types addressed in this review: **A** sand dunes (photo credit: Keith Clay), **B** marshes (photo credit: Emily Farrer), **C** mangroves (photo credit: Sunshine Van Bael), and **D** forests/shrublands (photo credit: Loralee Larios)

A) Sand dunes



B) Marshes



C) Mangroves



D) Forests/shrublands



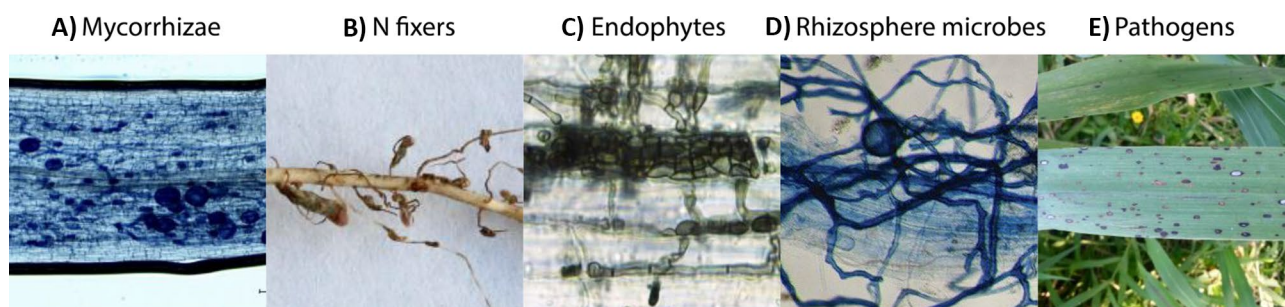
by affecting plant performance (as mutualists and pathogens) and by mediating nutrient cycling.

Fungi and prokaryotes (bacteria and archaea) play direct roles in plant establishment, growth, competitive ability, and stress tolerance. Essentially, all plants host microbes within and on every plant organ and tissue: leaves, stems, rhizomes, roots, flowers, and seeds (Partida-Martinez and Heil 2011). These microbiomes are so essential to the plant that a plant's characteristics are a manifestation of highly coordinated and co-regulated plant and microbial genes. Microbial endophytes in plant seeds can increase germination rate (Berg and Raaijmakers 2018; Billingsley Tobias et al. 2017), and soil and root microbes such as arbuscular mycorrhizal fungi, ectomycorrhizal fungi, and actinorhizae can increase plant establishment (Kozioł et al. 2018), especially in stressful habitats (Roy et al. 2007; Shemesh et al. 2020). Microbes also dictate plant competitive ability; for example, when fungicide is used to suppress fungal symbionts, dominant grasses no longer suppress subdominant plants to the same degree (Hartnett and Wilson 1999; O'Connor et al. 2002). Plant growth promoting rhizobacteria can enhance plant growth through mechanisms including nitrogen fixation, nutrient uptake, and production of plant growth hormones (Backer et al. 2018; van Loon 2007). Plant pathogens can have strong negative effects on plant growth and survival, as exemplified by the success of many invasive plant species who have escaped their pathogens in their native range (i.e., the enemy release hypothesis, Keane and Crawley 2002), as well as by exotic pathogen epidemics that have virtually wiped out native plant species (i.e., the chestnut blight, Anagnostakis 1987). Some endophytic fungi have been found to increase stress tolerance of plants; for example, inoculating plants with endophytes, especially endophytes isolated from saline areas, can substantially increase the growth of plants subjected to salt stress (Rodríguez et al. 2008; Soares et al. 2016). Because microbes benefit plants in stressful conditions, microbes will be key in helping plants tolerate stresses (e.g., heat, drought, salinity) due to climate change (Porter et al. 2019).

Microbial communities associated with plants play critical roles in biogeochemical cycling in ecosystems (Beinart 2019). Because symbionts are often protected by hosts and supported by host substrates, they can obtain large population sizes and high activity levels (Beinart 2019). Ectomycorrhizae and dark septate endophytes are plant symbionts that play important roles in decomposition, particularly of recalcitrant organic matter, through the production of extracellular degradative enzymes (Moreau et al. 2019). In the rhizosphere, plant roots produce exudates (labile

carbon compounds) that stimulate symbiotic bacterial and fungal activity, called “priming the soil”. This rhizosphere priming typically enhances carbon (C) and importantly nitrogen (N) mineralization, which can then be used to meet microbial and plant N demands (Henneron et al. 2020; Moreau et al. 2019). Arbuscular mycorrhizal fungi (AMF), obligate plant symbionts whose hyphae extend in a complex network throughout the soil environment, play an important role in ecosystem carbon sequestration by promoting soil aggregate formation which physically protects soil organic matter (SOM) from degradation (Rillig 2004). Furthermore, ectomycorrhizal- and AMF-derived carbon is a significant component of SOM and contains recalcitrant compounds (e.g., glomalin, chitin) that resist decomposition (Parihar et al. 2020; Rillig 2004; Soudzilovskaia et al. 2015; Wilson et al. 2009). Plant-associated symbionts are also key players in the nitrogen cycle. Nitrogen fixation (conversion of N₂ gas to biologically available ammonium) is often performed by internal root bacteria, such as *Rhizobium* (in legumes) and *Frankia* (in actinorhizal plants), or bacteria in the rhizosphere of plants (Moreau et al. 2019). Particularly in flooded, anaerobic, and wetland sediments, bacterial symbionts in the rhizosphere perform the vast amount of nitrification (oxidation of ammonium to nitrate that can be leached, taken up by plants, or denitrified), because it is an aerobic process that can be fueled by oxygen flux through plant roots (Penton et al. 2013; Reddy et al. 1989). Denitrification (nitrate and nitrite reduced to NO, N₂O, and N₂ gases and returned to the atmosphere) is often coupled to nitrification and can be stimulated by rhizodeposition under more anaerobic conditions (Penton et al. 2013; Reddy et al. 1989).

Plant symbionts also influence biogeochemical cycling in indirect ways via their effects on plant growth, plant species composition, and soil microbial composition (Beinart 2019; Rillig 2004). Both beneficial and disease-causing microbes influence plant growth and tissue quality, which in turn influence carbon and nutrient cycling via biomass, litter, and exudate production (Rillig 2004). Numerous studies have shown that symbiont community composition, for example, AMF composition, can alter plant community composition (Johnson et al. 2003; van der Heijden et al. 1998), which can thereby influence primary production and nutrient cycling via traits of the component plant species (Rillig 2004). Ectomycorrhizae and AMF can also affect soil fungal and bacterial composition (i.e., saprotrophs, nitrogen transformers, phosphate solubilizing bacteria), which in turn influence decomposition, carbon storage, and nutrient cycling (Nuccio et al. 2013; Rillig 2004; Soudzilovskaia et al. 2015).



Box 1 Definitions and descriptions: common microbial symbionts of plants. **A** AMF structures (vesicles, hyphae, and arbuscules) in mangrove roots (photo credit: Mareli Sanchez Julia). **B** N fixers in root nodules of a legume (photo credit: Emily Farrer). **C** Dark septate endophytes in *Spartina alterniflora* roots (photo credit: Sunshine Van Bael). **D** Rhizosphere microbes (photo credit: Andrea Porras-Alfaro). **E** Leaf spot pathogen (could be from a number of different fungal taxa) in *Phragmites australis* (photo credit: Warwick Allen). **Mycorrhizae:** A symbiotic relationship between plants and fungi. The relationship is typically mutualistic, but can be parasitic. The fungi colonize the roots of the host plant providing nutrients and water to the plant in exchange for carbohydrates (photosynthate). Two major types are ectomycorrhizae and endomycorrhizae. Ectomycorrhizae ensheath the root but usually do not penetrate the root cells. Endomycorrhizae penetrate the root cells; the most widespread group of endomycorrhizae is the arbuscular mycorrhizal fungi (AMF). Less common are orchid and ericoid mycorrhizae. **Nitrogen fixers (diazotrophs):** Nitrogen-fixing bacteria and archaea capable of transforming nitrogen gas (N_2) from the atmosphere into ammonia (NH_4). Nitrogenase, the enzyme that catalyzes the reaction is degraded by

oxygen; thus, nitrogen fixation often occurs in anaerobic conditions. Nitrogen fixers can be free-living, or they can live within a host plant's roots like the *Rhizobia* that colonize legumes and the *Frankia* that colonize actinorhizal plants. **Endophytes:** Bacteria or fungi that live within a host plant without causing symptoms of disease. Endophytes can be mutualistic or have neutral impacts on hosts. Endophytes can increase host nitrogen acquisition, reduce abiotic stressors like drought or salinity, and can inhibit or facilitate plant pathogens (Busby et al. 2016; Porras-Alfaro and Bayman 2011). **Rhizosphere microbes:** The rhizosphere is the narrow zone surrounding and influenced by plant roots. Rhizosphere microorganisms include fungi, bacteria, archaea, and algae. Many of these organisms are so-called plant growth promoting microbes which improve plant nutrient acquisition, protect against pathogen attack, facilitate plant growth, and help plants tolerate abiotic stress. However, pathogens can also populate the rhizosphere. **Pathogens:** Microorganisms that cause disease. Pathogens include fungi, bacteria, oomycetes ("water molds", a group of filamentous protists), viruses, and nematodes (roundworms). Interestingly, archaea have not been found to be pathogens (Cavicchioli et al. 2003); however, it may be that they have not yet been discovered.

Plant-Microbial Symbioses on Coasts

We focus on five major types of microbial symbionts: mycorrhizae, nitrogen fixers (also called diazotrophs), endophytes, rhizosphere microbial communities, and pathogens (see Box 1; Fig. 2). Some categories may overlap (for example, nitrogen fixers can be rhizosphere microbes), but these are common categories of symbionts discussed in microbiology and restoration.

Mycorrhizae

Mycorrhizal fungi form mutualistic associations with plant roots in most habitats, including coastal areas such as salt marshes (d'Entremont et al. 2018), estuaries (Carvalho et al. 2001), mangroves (Sengupta and Chaudhuri 2002), sand dunes (Koske et al. 2008), and heaths (Botnen et al. 2015). The symbiosis between mycorrhizae and plants is especially key for plants in stressful environments (e.g., primary succession in dunes), since mycorrhizae facilitate plants through uptake of nutrients as well as increase tolerance to drought and salt stress (Koske et al. 2008). Arbuscular mycorrhizal fungi are found in association with 74% of

plant species (Brundrett 2009), including many trees, shrubs, and grasses that grow on coasts. However, some plant families/taxa that are abundant on coasts are non-mycorrhizal (e.g., the Chenopodiaceae which includes *Salicornia*, pickleweed) or have low or variable mycorrhizal colonization (e.g., the Cyperaceae, which includes *Carex*, sedges) (Muthukumar et al. 2004). There is some debate on whether high levels of salinity – like those found in coastal waters and soils – inhibit arbuscular mycorrhizae (Evelin et al. 2009). Moreover, whether arbuscular mycorrhizae act as facilitators or antagonists of plant growth in saline environments may be context and host-species dependent (Evelin et al. 2009; Johnson-Green et al. 2001). Arbuscular mycorrhizal fungi are well known to be important to primary succession on sand dunes as they facilitate grasses, forbs, and creepers in this phosphorus deficient and droughty environment (Beena et al. 2000, 2001; Koske et al. 2008). Ectomycorrhizal fungi are associated with approximately 9% of shrub and tree species (Brundrett 2009). Coastal forests are particularly reliant on associations with ectomycorrhizal fungi in temperate (Obase et al. 2009) and tropical regions (Séne et al. 2015), and primary succession in sand dune systems colonized by *Salix*, *Pinus*, and other woody species depends on a high

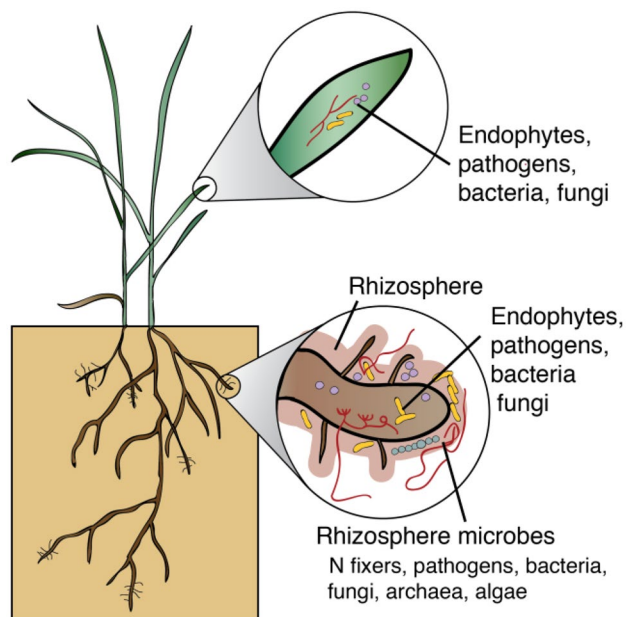


Fig. 2 The leaf and root microbiome, illustrating the many microbial players and the complexity of plant microbiomes

diversity of ectomycorrhizal fungi (Ashkannejhad and Horton 2006; Roy-Bolduc et al. 2015; van der Heijden et al. 2000). There are many gaps in knowledge that exist with respect to mycorrhizal fungi – both for all terrestrial plants and for those along coasts. For example, via nutrient uptake and increased coastal plant growth, mycorrhizae could contribute to carbon sequestration along coasts. Mangroves have pan-tropical distribution, and a few studies have showed that their roots associate with arbuscular mycorrhizal fungi (e.g. Kumar and Ghose 2008), yet no studies have estimated the contribution of mycorrhizae to mangrove nutrient budgets and/or performance. Further study is warranted on the role of mycorrhizae in coastal plants, to better understand their benefits to plants and their contributions to soil formation and a resilient coastal ecosystem.

N-Fixers

Primary production and decomposition are N limited in mangroves (Bashan and Holguin 2002), marshes (Lovell et al. 2000), and sand dunes (Dalton et al. 2004; Wahab and Wareing 1980), and coastal systems are highly dependent on N inputs from plant-associated diazotrophs (Lovell 2005; Morris 1991). For example, in mangrove systems, it is estimated that N fixers supply 40% (Van Der Valk and Attiwill 1984) to 60% (Zuberer and Silver 1978) of the nitrogen requirement of plants. Because N fixation is carbon limited, N fixers are very active in the root, rhizosphere, and litter layers of the soil, and N fixation rates are tightly coupled

with plant photosynthesis and decomposition (Whiting et al. 1986). N fixation is an anaerobic reaction; thus, saturated anoxic environments like wetlands and mangroves are prime habitats for N fixation; however, many adaptations exist for fixing N in variable or high oxygen environments, like the rhizosphere or dry soils (Mitsch and Gosselink 2007; Mus et al. 2016).

Both symbiotic and free-living diazotrophs are abundant in coastal ecosystems. In coastal sand dunes and heathlands, symbiotic rhizobial associations (*Rhizobium* or *Bradyrhizobium*) are common in woody and herbaceous legumes (Rodríguez-Echeverría 2010; Sridhar et al. 2005) and actinorhizal (*Frankia*) associations are widespread in a number of important shrub species, especially in higher latitudes (Dudley et al. 1996; Swensen 1996). Legumes such as *Lathyrus japonicus* are often the very first colonizers of dunes and beaches (Brightmore and White 1963). Dune grasses have also been shown to be colonized by other endophytic N fixing taxa (*Burkholderia*) (Dalton et al. 2004) and also rely on N fixers in the rhizosphere to cope with low soil nutrients (Abdel Wahab 1975; Wahab and Wareing 1980). In mangrove systems, high rates of N fixation are associated with roots, the pneumatophore (aerial root) surface, the rhizosphere, tree bark, decomposing leaves, and the soil and comprise a diversity of organisms including cyanobacteria and many other phyla (Alfaro-Espinoza and Ullrich 2015; Holguin et al. 2001). In coastal systems, N fixation by free-living microbes contributes significantly to ecosystem N cycling, especially in systems like salt marshes and coastal forests that do not contain many symbiotic N fixing plants. In forest communities developing on lava flows in Hawai'i, N fixers on leaf litter are important in successional development (Crews et al. 2001). Diazotrophs are very active in the rhizoplane and rhizosphere of salt marsh plants and come from diverse and novel bacterial and archaeal lineages (Davis et al. 2018; Lovell and Davis 2012). Much applied work on N fixers in coastal sand dunes/beaches (Potgieter et al. 2014; Rodríguez-Echeverría et al. 2009) and forests (Vitousek and Walker 1989) has addressed the impacts of invasive N fixing species, as N fixation ability can allow species like Casuarinas (sheoak), Acacias, and *Myrica faya* to successfully colonize and invade low nutrient coastal habitats. Research is needed to link how the soil legacy effects of N fixers (e.g., elevated N, altered microbial communities) present barriers to restoration and how to overcome these barriers (Nsikani et al. 2018). In other coastal systems, such as marshes and mangroves, the use or promotion of N fixing microorganisms to enhance restoration of plant communities has long been suggested (Bashan and Holguin 2002; Holguin et al. 2001), and current research is examining the best practices for inoculation and soil amendments (Murphy et al. 2018).

Endophytes

Endophytic fungi and bacteria live inside of roots, stems, leaves, and inflorescences of coastal grasses, sedges, forbs, and trees. Although not well studied, coastal plants have been found to host high diversities of endophytes (David et al. 2016; Lumibao et al. 2018), including bacteria and fungi that have been previously described from marine, soil, and freshwater habitats (Ananda and Sridhar 2002). By definition, endophytes live asymptotically within plant tissues, with functions that include antagonism or facilitation of plant disease (Busby et al. 2016) and increased stress resilience to host plants (Ali et al. 2014; Rodriguez et al. 2008). Much research on endophyte function *in planta*, however, has been restricted to agricultural plants (Busby et al. 2016), with less attention to coastal plants. Work in coastal sand dune systems suggests that the presence of an *Epichloë* sp. fungal leaf endophyte greatly increases *Ammophila breviligulata* (American beachgrass) survival (Emery and Rudgers 2013), belowground biomass (Bell-Dereske et al. 2017), vegetative growth, and sand accumulation (Emery et al. 2015), which has important implications for dune succession and stabilization. A similar fungal endophyte (*Periglandula* sp.) in *Ipomoea pes-caprae* (beach morning glory) was present in 100% of populations sampled on Florida coasts, USA, suggesting strong benefit (Beaulieu et al. 2021). Other studies on coastal plant endophytes have mostly focused on the compounds produced by endophytes *in vitro*, such as searching within mangrove endophytes for enzymes (Castro et al. 2014; Ravindran et al. 2012) and for medicinally active compounds (Gayathri et al. 2010). Since introducing endophytes from one host species to another is feasible, endophytes may be useful in biotechnology. For example, several recent studies have demonstrated the potential of using endophytes to attenuate pollutants in coastal wetlands (e.g., bioremediation, Rehman et al. 2018; Saleem et al. 2019; Zheng et al. 2018). Another compelling example is the use of endophytes that were isolated from a mangrove species to inoculate and improve the growth of a tree species used for restoration in Brazil (Castro et al. 2018). Thus, the stress of living in a coastal area has led to adaptations for both hosts and their internal symbionts, so endophyte studies in the coastal environment hold promise for understanding stress resilience and symbioses.

Rhizosphere Microbes

As in other terrestrial systems, the rhizosphere microbial communities in coastal systems are significantly different than bulk soil with elevated abundances of taxa known to be endophytes (Sanka Loganathachetti et al. 2017), mycorrhizae (Estrada et al. 2013; Johansen et al. 2015), and plant growth promoting bacteria (Park et al. 2005). In sand dunes,

plant roots are important sources of carbon for microbial communities in a matrix that is otherwise characterized by resource limitation and high physical stress (Rajaniemi and Allison 2009). In inundated coastal systems, too, roots provide an important source of carbon for fueling microbial processes important to plants (N fixation) and decomposition (sulfate reduction, an anaerobic process that reduces sulfates to hydrogen sulfide). Sulfate reducing bacteria are responsible for more than half of the total decomposition of organic matter in salt marshes (Howarth and Hobbie 1982) and have been found to tolerate environments like the rhizosphere with rapidly changing redox conditions (Rooney-Varga et al. 1997). In fact, rates of N fixation and sulfate reduction, sometimes performed by the same organism, are considerably higher in the rhizosphere than in bulk soil (Nielsen et al. 2001). Many wetland plants also have structural adaptations (aerenchyma and pneumatophores) that oxidize the soil, at least in the immediate vicinity of the root or root tip (Andersen and Kristensen 1988; Koop-Jakobsen et al. 2017), which ameliorates the detrimental effects of hydrogen sulfide, stimulates microbial heterotrophic activity, and affects CO₂ emission (Hester et al. 2018). Several rhizosphere bacteria in marshes (Gong et al. 2018; Halda-Alija 2003; Mavrodi et al. 2018), mangroves (Bashan and Holguin 2002), and sand dunes (Godinho 2015; Jayaprakashvel et al. 2014) have plant growth promoting capabilities, including IAA (indole acetic acid, i.e., auxin) production, siderophores, and phosphate solubilization. Much current and future work in this area is in the context of bioprospecting saline rhizosphere habitats for microorganisms that can facilitate agricultural plants under conditions of soil salinization (Godinho 2015; Gong et al. 2018). Another important future direction is understanding the impacts of current restoration techniques and timescales necessary for restoring microbial function (Mavrodi et al. 2018), as well as the application of rhizosphere microbial communities for aiding restoration (Bashan and Holguin 2002).

Pathogens

Pathogens are important in shaping the natural community dynamics in coastal systems. In coastal sand dunes, soil pathogens (pathogenic fungi and parasitic nematodes) can promote plant species replacement and facilitate ecological succession (Van der Putten and Peters 1997). Fungal pathogens are also natural components of coastal forests causing winter seedbank mortality in coastal sage scrub communities (Mordecai 2012). Ergot (*Claviceps purpurea*) epidemics have been observed in *Spartina anglica* marshes in the UK (Raybould et al. 1998) and *Spartina alterniflora* marshes in the East and Gulf Coasts of North America (Eleuterius 1970; Eleuterius and Meyers 1974), where ergot infection during epidemics greatly reduces seed fecundity of these dominant

grasses. In mangrove systems, a survey found abundant plant pathogens (*Eutypella*, *Phaeophleospora*, *Phaeosphaeria*, *Phaeoramularia*, *Mycosphaerella*), root pathogens (*Gaeumannomyces*, *Cytospora*, *Magnaporthe*, *Pyricularia*), and leaf pathogens (*Diaporthe*, *Ramulispora*) in above- and belowground mangrove tissues (Arfi et al. 2012). A number of fungal diseases in mangroves have been identified, and some mangrove diebacks in Gambia, Australia, and Hawai'i have been attributed to fungal pathogens (Osorio et al. 2016). However, much more work on the importance of pathogens to mangrove growth and forest dynamics is needed.

Pathogens have been notable for their (potential) involvement in two high profile die-off events in coastal systems in recent history. Sudden vegetation dieback describes large die-offs of *Spartina alterniflora* that occurred in the late 1990s and 2000s in the USA, during which time over 1000 km² in the Gulf Coast and 10% of Cape Cod's marshes turned brown and died over the course of a few months (Elmer et al. 2013). The underlying cause of sudden vegetation dieback is still not known for certain, and some hypotheses do not invoke pathogens; however, two hypotheses posit that pathogens played a role: (1) *Fusarium* spp., which were isolated and abundant in many dieback areas, were believed to cause plant death particularly in combination with drought stress that marshes experienced at that time (Elmer et al. 2013), and (2) the periwinkle snail which promotes growth of a facultative plant pathogen (*Phaeosphaeria spartinicola*) was also thought to cause high *Spartina* mortality during periods of drought (Silliman et al. 2005). Sudden oak death is an ongoing epidemic caused by *Phytophthora ramorum*, a recently emerged generalist water mold pathogen which has decimated oak and tanoak populations in California and Oregon affecting over 2000 km² of coastal forest (Grünwald et al. 2019; Rizzo and Garbelotto 2003). The pathogen also causes a similar disease with high mortality in Japanese larch trees in UK plantations. The wide host range of *P. ramorum* (over 100 plant species in 40 genera) is particularly problematic, as it can survive and sporulate on many forest understory species (Grünwald et al. 2012, 2019). Sudden oak death has also severely affected the horticulture industry because of quarantine regulations on the wide range of nursery plants that host the disease (Grünwald et al. 2019).

Pathogens play a key role in influencing plant invasions in coastal habitats. On the West coast of North America, ergot epidemics can facilitate invasive *Spartina* species and cause decline of native *Spartina foliosa* since outbreaks only occur in the native species and greatly reduce seed set (Fisher et al. 2007). Pathogens are also implicated in *Spartina alterniflora* invasion in China, as pathogen spillover of *Fusarium palustre* from *Spartina* has caused dieback in native *Phragmites australis* stands in coastal marshes (Li et al. 2014). In coastal sand dunes in California, invasive

Ammophila arenaria promotes its own invasion by accumulating local pathogens which have larger negative effects on native plants (Eppinga et al. 2006). In South African coastal sand dunes, invasion intensity of *Ammophila arenaria* is a balance between enemy release from parasitic nematodes and biotic resistance imparted by native soil pathogens, which inhibit its invasion (Knevel et al. 2004). Similarly, native pathogens may somewhat limit *Bromus diandrus* invasion into the Californian coastal sage scrub (Hilbig and Allen 2015). Overall, pathogens play a major role in the ecology of coastal habitats, and future work to understand and control pathogens responsible for die-off events, manage the pathogens involved in species invasions, and understand how changing environmental conditions influence disease dynamics will be essential for maintaining the integrity of coastal communities.

Microbes in Coastal Restoration

Many coastal systems are experiencing severe degradation from global environmental change including sea level rise, warming, oil spills and other pollutants, drought, hurricane frequency, and invasive species. Because degradation threatens the provisioning of ecosystem services critical to humans, including food production, storm surge protection, filtration of pollutants, and carbon storage, the restoration of coastal systems has become a huge focus of conservation groups and governmental entities alike. Because sand dunes, marshes, mangroves, and forests/shrublands are all stressful systems, microbial mutualists that assist plants in tolerating low nutrients, drought, and salinity stress will likely be beneficial in restoration (Table 1). Below we review research on how microbial symbionts of plants may be specifically used to enhance coastal restoration and identify important considerations when implementing restorations using microbes.

Review of the Literature

There is growing recognition from inland systems that microbiota can be leveraged to enhance restoration success (Eviner and Hawkes 2008; Maltz and Treseder 2015). To do this, one typically applies inoculum, material containing spores, fungal hyphae, or bacterial cells, to seeds or plantings at the restoration site or to potted nursery plants that will be outplanted. Inocula can be sourced from whole soil or roots collected from a reference ecosystem, or specific microbial taxa can be cultured and multiplied in the laboratory (for fungal endophytes/bacteria) or greenhouse (for AMF). Generic commercial inocula are becoming readily available for use in restoration practice (Fisher 2012; Perkins and Hatfield 2016); however, locally sourced microbes have

Table 1 Potential uses of microbes in the restoration of coastal systems

Microbe/inoculum	Systems where the microbes have been studied for restoration use	Citations for restoration use	Systems which likely will benefit from the microbes	Benefits for restoration	Caveats
Arbuscular mycorrhizal fungi (AMF)	Sand dunes Forests/shrublands	Miller and Jastrow (1992), Sylvia et al. (1993), Gemma and Koske (1997), Al Agely and Sylvia (2008), de Souza et al. (2010), Bashan et al. (2012), Aprahamian et al. (2016)	Sand dunes Forests/shrublands Marshes Mangroves	Assist plants with nutrient uptake, confer drought and salinity tolerance, protect from pathogens	Culturable on living plants only, not on traditional media
Ectomycorrhizal fungi	Forests/shrublands	Caravaca et al. (2005)	Forests/shrublands	Assist plants with nutrient uptake, confer drought tolerance, protect from pathogens	Only associate with limited (typically woody) plant species, need to collect/process spores
Rhizosphere bacteria/fungi	Forests/shrublands Mangroves Marshes	Caravaca et al. (2005) Bashan et al. (1998), Bashan and Holguin (2002), do Carmo et al. (2011), Bledsoe and Boopathy (2016), Mavrodi et al. (2018)	Forests/shrublands Mangroves Marshes Sand dunes	Solubilize phosphorus, fix nitrogen, produce plant growth hormones, enhance plant stress tolerance, degrade oil	Need to be cultured
Endophytes	Sand dunes Marshes Forests/shrublands	Emery and Rudgers (2013), Emery et al. (2015), Bell-Dereske et al. (2017), Zheng et al. (2018), Egan et al. (2021)	Sand dunes Marshes Forests/shrublands Mangroves	Confer drought tolerance, increase nutrient acquisition, protect from pathogens, produce plant growth hormones, degrade oil	Need to be cultured
Whole soil inoculum	Sand dunes Forests/shrublands	Gemma and Koske (1997), de Souza et al. (2010), Emery and Rudgers (2011), Bozzolo and Lipson (2013), Aprahamian et al. (2016), Phillips et al. (2020)	Sand dunes Forests/shrublands	Contains unculturable microbes (including AMF), no need of laboratory equipment or materials for culturing	May contain pathogens, need to collect it from a reference site, may be difficult in flooded systems

proven to be a superior source of mutualistic partners (Emam 2015; Maltz and Treseder 2015; Middleton and Bever 2012; Wubs et al. 2016). The use of microbial inocula in restoration can increase survival, growth, and establishment of target species (Richter and Stutz 2002; Thrall et al. 2005) and can increase plant diversity in restored sites (Koziol and Bever 2017), providing benefits for up to several years in the field (Maltz and Treseder 2015).

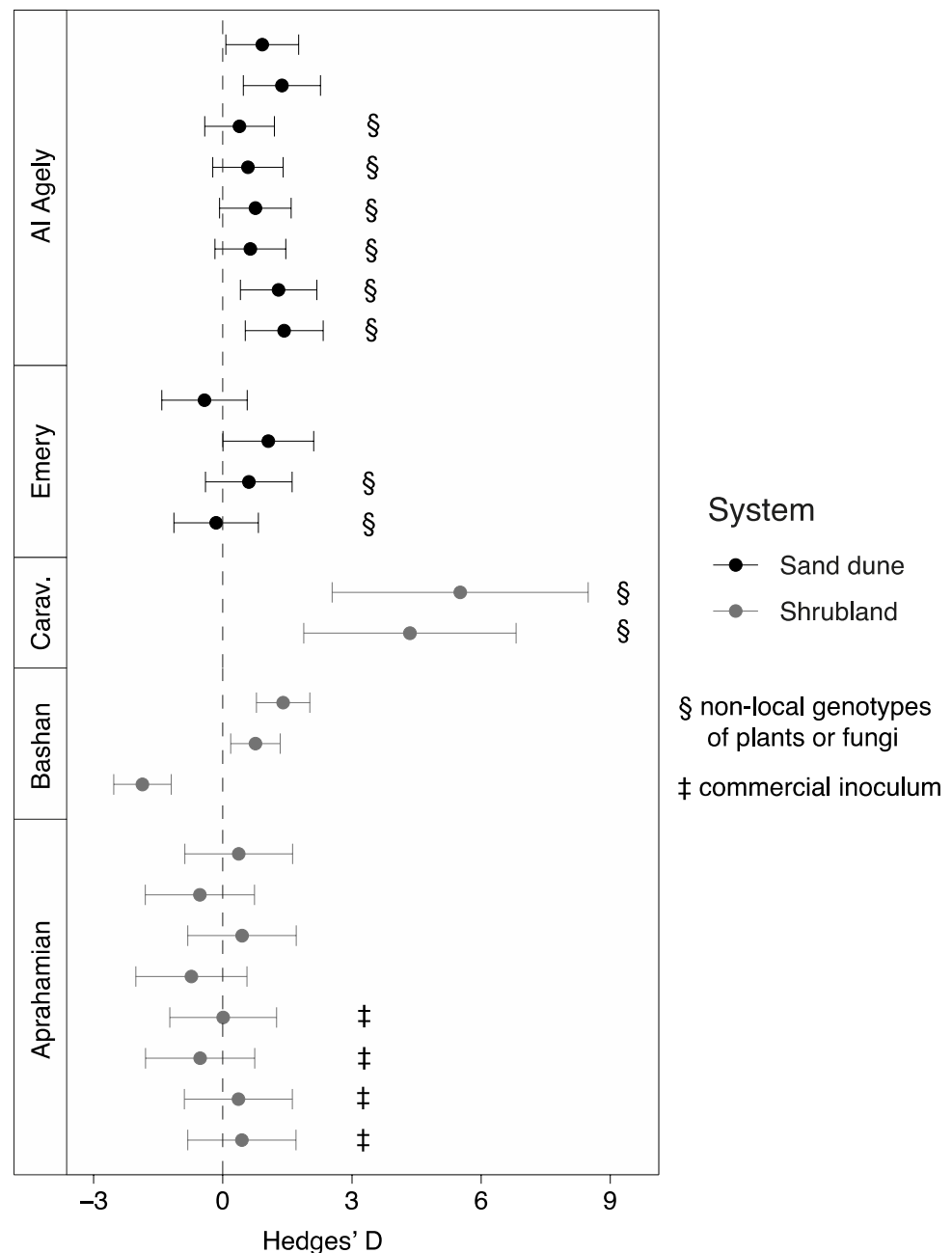
Sand dunes are one coastal system in which the use of AMF microbial inocula in restoration has received a lot of attention. Sand dunes are low nutrient, low organic matter systems, and most dune plants rely on mycorrhizae for nutrient acquisition as well as for drought and salt tolerance (Sigren et al. 2014). Studies have generally shown that inoculation with AMF prior to outplanting can increase survivorship (Emery and Rudgers 2011), growth (Al Agely and Sylvia 2008; de Souza et al. 2010; Emery and Rudgers 2011; Gemma and Koske 1997; Sylvia et al. 1993), flowering (Gemma and Koske 1997), and phosphorus content (Al Agely and Sylvia 2008) of dune grasses and trees. We quantified how AMF affected the growth of dune species across those restoration experiments above that reported sufficient information using Hedges' *D* (Nakagawa and Cuthill 2007) and found there was a positive effect of AMF in 42% of the cases (5/12) and no significant effect in the rest (7/12; Fig. 3). Indeed, many studies find that AMF responses are site specific, i.e., an increase in performance from AMF inoculation does not occur at all sites (Al Agely and Sylvia 2008; Emery and Rudgers 2011; Sylvia et al. 1993), which may depend on the abundance of the mycorrhizal community prior to restoration. Interestingly, even in cases in which plant growth was not increased, root colonization and soil hyphae were elevated with the AMF inoculum treatment, which has benefits for dune stabilization (de Souza et al. 2010; Sylvia et al. 1993). Similarly, even if the effects of AMF inoculation are short lived (e.g., an increase in plant growth for only 1–2 years), there is still value to temporarily increasing growth if the restoration goal is dune stabilization (Miller and Jastrow 1992). Two studies also noted that different varieties of dune grasses responded differently to inocula, suggesting the choice of plant variety is key to successful use of inoculum in restoration (Al Agely and Sylvia 2008; Emery and Rudgers 2011). And, as found in other systems, local AMF inocula typically were more beneficial (Al Agely and Sylvia 2008; Sylvia et al. 1993).

Coastal shrubland systems are another area in which restoration success may be limited by a lack of mycorrhizal fungi at restoration sites (Bowler 2000). A greenhouse study in coastal sage scrub suggested that field inoculum may improve restoration outcomes, because native species benefitted more from inoculum than invasive plants (Bozzolo and Lipson 2013). Another greenhouse

experiment showed that both invasive and native inoculum increased native shrub seedling biomass, but native inoculum resulted in higher colonization and diversity of AMF and non-AMF fungi (Phillips et al. 2020). However, a field study found that applying live native soil and commercial AMF inoculum prior to seeding had no effect on plant root colonization, growth, or flower production, and commercial inoculum actually had negative effects on plant height (Aprahamian et al. 2016). In Baja California, inoculation of plant growth promoting bacteria and mycorrhizae at planting had short-term (but not long-term) positive effects on growth of two out of three leguminous trees (Bashan et al. 2012). In the Mediterranean, there was a large positive growth effect of mycorrhizal spore inoculation to pots prior to outplanting two native shrub species (Caravaca et al. 2005). When we summarized the effect of mycorrhizae on shrub growth across these field restoration experiments using Hedges' *D*, we found that the effect of mycorrhizae was positive in four cases, neutral in eight cases, and negative in one case (Fig. 3). Overall, results of these meta-analyses suggest that there is potential that microbes can enhance restoration success in coastal shrublands, but more work in these systems is warranted.

The use of microbes in restoration of wetland systems, such as coastal marshes and mangroves, is much less studied. However, many of these wetland systems are low in nutrients, suggesting that adding growth-promoting microbes responsible for nutrient cycling could increase planting success (Bashan and Holguin 2002). Many taxa of growth promoting bacteria and fungi have been isolated from coastal marshes (Bledsoe and Boopathy 2016; Mavrodi et al. 2018; Smith and Farrer, unpublished data) and mangroves (Bashan and Holguin 2002; do Carmo et al. 2011; Vazquez et al. 2000), providing a starting point for research aimed at using microbes in restoration. For example, in one study, a high percentage (4–60%) of fungal taxa isolated from marsh plant roots had the capability of inhibiting pathogens, solubilizing phosphate, or producing plant growth hormones (Fig. 4; Smith and Farrer, unpublished data). A number of isolated rhizosphere wetland bacteria from mangroves (do Carmo et al. 2011; Piedad Díaz et al. 2000) and marshes (Zheng et al. 2018) also degrade oil and could be used to enhance remediation and restoration after oil spills. Initial greenhouse experiments in the saltmarsh grass *Spartina alterniflora* suggest that inoculation with growth promoting bacterial consortia can increase growth and nutrient uptake in plants over the short-term (2 months) (Bledsoe and Boopathy 2016). In mangroves, inoculation of seedlings with diazotrophic (N fixing) cyanobacteria increased nitrogen content in leaves (Bashan et al. 1998). Overall, these findings suggest that more research into using microbial communities in wetland restoration may be fruitful.

Fig. 3 The effect of AMF fungi or local field soil inoculum on growth (biomass, tiller production, height) of coastal sand dune and shrubland species outplanted in field restoration experiments. Data were extracted from the figures of available published papers using Plot Digitizer 2.6.9. Data shown below are the calculated Hedges' *D* values with 95% confidence intervals (Nakagawa and Cuthill 2007); a positive number indicates that microbes positively affected growth. Labels indicate the study from which the data came: Al Agely and Sylvia (2008), Emery and Rudgers (2011), Caravaca et al. (2005), Bashan et al. (2012), and Aprahamian et al. (2016). The multiple points for each study indicate multiple sites, species, or genotypes tested. We only display results from low density treatments and first sampling dates. The species tested in each study were the following: Al Agely (*Uniola paniculata*), Emery (*Ammophila breviligulata*), Caravaca (*Cistus albidus*, *Quercus coccifera*), Bashan (*Prosopis articulata*, *Parkinsonia microphylla*, *Parkinsonia florida*), Aprahamian (*Deinandra fasciculata*, *Mirabilis laevis*, *Salvia columbariae*, *Salvia mellifera*). A number of studies mentioned in the text could not be analyzed here, because they did not report error bars



While the vast majority of microbially minded coastal restoration is focused on belowground microbial associates, leaf endophytes deserve a brief mention. First, some plant species harbor a special type of aboveground, systemic fungal endophyte that is vertically transmitted via seeds (Panaccione et al. 2014). The dune grass *Ammophila breviligulata* is colonized by such *Epichloë* endophytes, which can greatly increase plant growth and can enhance dune stabilization and restoration (Bell-Dereske et al. 2017; Emery et al. 2015; Emery and Rudgers 2013). Because they are vertically transmitted, endophyte manipulation may involve introducing endophytes to the seed/seedling with a

needle (Emery et al. 2015) or purchase of endophyte positive nursery stock (Emery et al. 2010). However, care must be taken because not all natural populations of *Ammophila* host the endophyte (Emery et al. 2010), and it may be detrimental to introduce endophyte-infected plants into areas where they are not native as they may displace locally adapted genotypes (Slaymaker et al. 2015). Second, foliar spraying of (non-vertically transmitted) leaf endophytes is a technique that has proven useful in agricultural settings (Vimal and Singh 2020). In a greenhouse trial, Egan et al. (2021) found that foliar application of an endophytic yeast reduced disease incidence from invasive powdery mildew

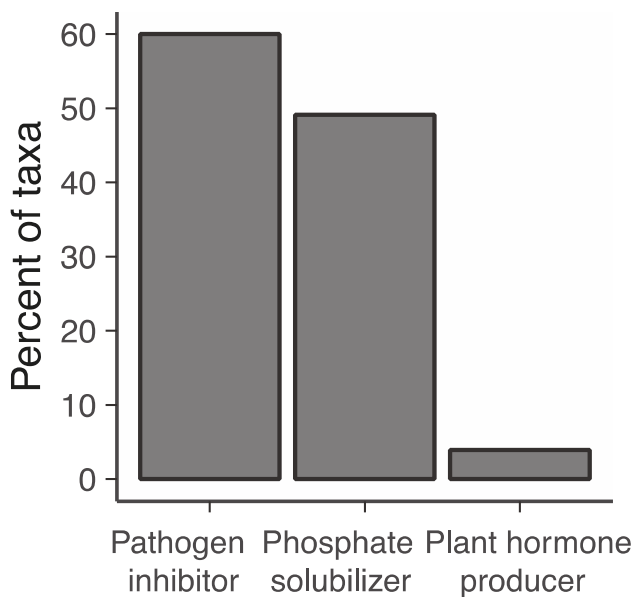


Fig. 4 Percent of fungal taxa isolated from the roots of coastal marsh plants in Louisiana that have different plant growth promotion abilities: inhibiting pathogens, solubilizing phosphate, and producing plant growth hormones (auxin). Fungi were isolated from roots of common fresh, brackish, and saline marsh plants (*Sagittaria lancifolia*, *Spartina patens*, *Phragmites australis*, *Spartina alterniflora*, *Juncus roemerianus*) and tested for their ability to inhibit growth of a common pathogen (*Fusarium palustre*), solubilize phosphorus, and produce auxin (IAA) (Smith and Farrer, unpublished data). Percentages are out of 40, 57, and 51 taxa screened, respectively. This suggests a large proportion of culturable fungi may be useful in restoration

on a critically endangered mint species endemic to coastal forests of O‘ahu. Overall, despite relatively little research on leaf endophytes in coastal systems, these studies suggest that they warrant more consideration and research into what they can bring to restoration.

Considerations for Using Microbes in Coastal Restoration

The potential for using microbes to enhance restoration in coastal systems will depend on three things: (1) the reliance of plants on microbes (including site conditions and degradation), (2) the type of inoculum used, and (3) the type of restoration employed (outplanting live plants or seeding).

Reliance of Plants on Microbes

Both plant characteristics and site conditions influence the dependence of plants on microbial symbionts. While most plants benefit from rhizosphere symbionts (Vacheron et al. 2013) and mycorrhizae, it is well known that some plant families are non-mycorrhizal (*Brassicaceae*: mustards, *Caryophyllaceae*: pinks, *Chenopodioideae*: chenopods,

Proteaceae: proteas) (Cosme et al. 2018) or less dependent on mycorrhizae (annuals are less dependent than perennials) (Collier et al. 2003) and thus would not benefit from mycorrhizal inoculation prior to restoration. Site conditions and the degree of land degradation have long been known to influence restoration success (Bakker and Berendse 1999), and we propose that they also impact the degree to which microbes will be useful in improving restoration. For example, in sand dunes, many plants are thought to be reliant on AMF due to the low nutrient content and low moisture in dune soils (Koske et al. 2008), and, as seen above, these systems often benefit from AMF inoculation during restoration (Al Agely and Sylvia 2008; de Souza et al. 2010; Emery and Rudgers 2011; Gemma and Koske 1997; Sylvia et al. 1993). In coastal shrublands, it has been found that a legacy of fungal pathogens limits restoration of former citrus fields (Hilbig and Allen 2019); thus, restoration success may be increased by inoculating with symbionts that promote pathogen resistance. Site degradation by invasive species has also been found to dramatically reduce mycorrhizal abundance and alter the composition of mycorrhizal communities (Grove et al. 2017); thus, previously invaded sites in coastal areas would likely benefit from mycorrhizal inoculation during restoration. Another example of an area that may lack microbial associates of plants are coastal marshes created using dredged sediment for restoration purposes; these created marshes may benefit from microbial inoculation during outplanting, even though inoculation is not common practice in marshes at this time. Lastly, despite the old microbial adage “everything is everywhere, but the environment selects” (Becking 1934), it is well known that microbes can be dispersal limited (Peay et al. 2010) particularly in restoration settings (Chen et al. 2020; Murphy and Foster 2014); therefore, sites such as impounded wetlands (with little water flow) or sites far from other natural areas (surrounded by agriculture or human habitation) may especially benefit from microbial inoculation.

Type of Inoculum

Many types of inocula are used in restoration projects including whole soil, single taxon, consortia of taxa, and commercial inoculum, with microbial taxa ranging from mycorrhizae to rhizosphere bacteria to endophytes to all of the above. Current research is in agreement that the type and source of inoculum used in restoration are of utmost importance to maximize success (Al Agely and Sylvia 2008; Aprahamian et al. 2016; Bashan et al. 2014; Sylvia et al. 1993) – the wrong inoculum can actually hinder plant growth and limit restoration (Aprahamian et al. 2016). It is important to understand the ecology of the focal species when selecting inoculum. For example, some plant species are purely ectomycorrhizal (pines, oaks, birches, eucalyptus) (Bruns et al. 2002). And

while many plants associate with AMF, plants can be locally adapted to their particular AMF community, performing best with local AMF assemblages (Rúa et al. 2016). Similarly, plant growth promoting rhizobacteria are thought to be highly generalist, but the growth promotion effects of these microbes can depend on plant genotype and the particular bacterial strain (Droge et al. 2012; Vacheron et al. 2013). This suggests that whole soil inoculum taken from underneath focal plants in similar reference habitats or microbial taxa isolated or propagated from focal species or genotypes may be best to use in restoration compared to externally sourced or commercial inoculum, a finding which has been confirmed by manipulative experiments (Emam 2015; Maltz and Treseder 2015; Middleton and Bever 2012; Wubs et al. 2016). There are costs and benefits to using whole soil inoculum vs. cultured microbes and this decision will depend on access to reference sites for soil collection, laboratory/greenhouse equipment and expertise in isolating and culturing microbial taxa, and financial costs of laboratory/greenhouse work. It is also important to note that the vast majority (>99%) of microbes are non-culturable (Schloss and Handelsman 2005); thus, whole soil will contain a broader array of mutualists but may also contain parasites and pathogens. As an aside, AMF are not culturable in agar but can be propagated using host plants in soil (see Koziol et al. 2017 for more discussion of practical aspects of using AMF in restoration). While most restoration research has focused on root-associated microbial symbionts, leaf endophytes can also impart drought tolerance and disease resistance, and cultured leaf endophytes have been applied in agriculture to increase crop performance (Canellas et al. 2015; Wu et al. 2013). Partnerships among restoration practitioners and microbial ecologists will be particularly fruitful in researching and selecting the best inoculum for a given restoration project or system.

Type of Restoration

In coastal systems, such as sand dunes, forests/shrublands, marshes, and mangroves, outplanting live plants or saplings is the typical method of active restoration. This is in contrast to more commonly studied grassland systems in which restorations rely heavily on seeding (although seeding is sometimes used in coastal shrubland communities (Allen et al. 2013)). Interestingly, outplanting makes it much easier to ensure microbial inoculation of the plant, because this can be done prior to restoration. It can be accomplished by using a fraction (often 10% volume) of whole soil or AMF infected soil in the potting media (Koziol et al. 2017), by adding inoculum pellets (Bashan et al. 2012) or liquid culture to the potting media (Tiepo et al. 2018), or by soaking plants in microbial suspensions prior to outplanting (Yuan et al. 2016). Some restorations, particularly in sand dune systems, inoculate the soil during outplanting by adding whole soil

from reference sites or AMF infected soil to the holes just before planting (de Souza et al. 2010; Emery and Rudgers 2011; Gemma and Koske 1997). For leaf endophytes, plants could be sprayed with inoculant prior to outplanting or after planting. Foliar spraying of leaf endophytes also opens up the interesting possibility of applying endophytes at a large scale to enhance plant growth in mature, existing restoration sites, as large-scale application of *belowground* mutualists is typically not successful (Canellas et al. 2015). However, it is generally thought that smaller-scale nursery application is more effective at transmitting symbionts and more cost-effective (Bashan et al. 2014).

Restorations using seeding have a much harder time dispersing microbes and ensuring subsequent microbial survival and colonization of roots (Koziol et al. 2017). Dispersing microbes with seeds has, however, been well studied in agriculture for which there is much interest in using microbial symbionts to boost yield and stress tolerance of crops. Coating the seed with inoculum prior to seeding and drilling granular inoculants in seedbed furrows with the seed at sowing time are two main methods currently used in agriculture (Bashan et al. 2014), and these methods are just beginning to be adapted for restoration (Koziol et al. 2017). Overall, the type of restoration used, outplanting or seeding (which often depends on the type of plant), is an important consideration when assessing the ease of incorporating microbial symbionts in a restoration project.

Conclusions

Mycorrhizae, nitrogen fixers, endophytes, rhizosphere microbes, and pathogens play key roles in the functioning of coastal ecosystems. They are responsible, in large part, for the health (or lack thereof) of the plants that make up the foundation of coastal communities, on which a large web of wildlife, fisheries, and humans rely. These microscopic symbionts affect plant establishment, growth, competitive ability, and stress tolerance and regulate biogeochemical cycling in coastal systems. Current use of microbial symbionts to augment restoration of stressful and/or degraded coastal systems is still very much in its infancy; however, it holds great promise for increasing success of restoration on the coast. Much research is warranted to address the utility of microbes in different coastal systems and will be necessary for the development of local, effective inocula for use in restoration sites across the globe. This is an excellent opportunity for collaboration between restoration practitioners and microbial ecologists to work toward a common goal of increasing resilience of our coastal ecosystems. Such collaborations are especially relevant at a time when these systems are increasingly vulnerable to a great number of threats and as their ecosystem services become more valuable with global climate change.

Funding Funding was provided by the Louisiana State Board of Regents (LEQSF(2017–20)-RD-A-14), the Coypu Foundation, the National Science Foundation (DEB-2027920), and the US Department of Agriculture's National Institute of Food and Agriculture (2020–67014-31922) to EF and the National Science Foundation (DEB-2116358) to SV.

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