



Global Diversity and Distribution of Rhizosphere and Root-Associated Fungi in Coastal Wetlands: A Systematic Review

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Abstract

Coastal wetlands have been long recognized for their importance to biodiversity and many biogeochemical processes including carbon sequestration; however, our understanding of plant-microbe interactions that govern many processes in these ecosystems remains elusive. Fungal communities are known to play critical roles in coastal wetlands, particularly due to their close relationships with plants, yet, systematic understanding of their distributional patterns and the factors shaping these patterns in natural coastal wetland environments has been rarely assessed. We synthesized existing published literature from fifty-one studies spanning 60 years to examine global fungal distributional patterns in coastal wetlands, draw linkages between fungi, the plant communities, and their environment, and identify gaps in fungal research and suggest future research directions. We focused on studies that reported root-associated fungi and fungi from the plant rhizosphere (i.e., soil surrounding roots) in coastal dunes, intertidal flats, salt marshes, and tidal wetlands. Our synthesis has revealed that (1) 203 fungal species were reported from salt marshes, 59 fungal species from coastal dunes, 32 from tidal wetlands, and ten from intertidal flats; (2) rhizosphere fungal communities were more species-rich and reported more often for all ecosystems except in salt marshes; and (3) nineteen different fungal guilds, which are predominantly arbuscular mycorrhizal fungi. We conclude that more research is needed to better understand root-associated fungal diversity in less studied ecosystems reviewed here. We have identified knowledge gaps in reported data and outlined suggestions to facilitate future plant-fungal research in these declining, but important, coastal ecosystems.

Keywords Rhizosphere and endosphere fungi · Synthesis · Global patterns · Coastal ecosystems

Introduction

Coastal wetlands, considered as ecological ecotones between terrestrial and ocean environments, play an indispensable role in the global ecosystems (Kirwan and Megonigal 2013).

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While they only account for 5–8% of the global land surface (Mitsch et al. 2013), coastal wetlands are hotspots for productivity, performing critical functions including nutrient and biogeochemical cycling and providing important ecosystem services such as water quality improvement, biodiversity, and carbon sequestration (Baustian et al. 2012). Globally, tidal wetlands accumulate 53.65 gigatons of carbon (C) a year, serving as an important carbon sink (i.e., “blue” Carbon) (Wang et al. 2021) and thus considerably contributing to the global C budget (Howard et al. 2017). Many of the coastal ecosystem processes and functions are regulated or mediated by their constitutive biota such as plants and microbial communities in the soil (Emerson et al. 1999; Weiss et al. 2004; Yarwood 2018). Due to a greater focus on anaerobic processes in the generally anoxic wetland soils, bacteria are often considered the primary mediators of many coastal ecosystem processes, with fungi historically being relegated to having minor importance relative to bacteria (Khan 2004). Fungal communities are thus overlooked in

coastal ecosystems and studies on their diversity, function and distribution lags that of bacterial studies.

There is a growing recognition, however, that fungi can also be critical players in coastal ecosystem processes such as decomposition, largely due to their tight associations or symbiotic relationships with plant communities (Onufrak et al. 2020; Bahram and Netherway 2022; Wang et al. 2022). For example, arbuscular mycorrhizal fungi (AMF) have largely been shown to be ubiquitous and critical in wetland ecosystems (Wolfe et al. 2007; Xu et al. 2016). Other types of fungi such as endophytes (fungi that live inside plant tissues) and fungi in the rhizosphere soil zone (i.e., soil that is in contact with plant roots) are beginning to be explored as well, unmasking rich and diverse communities whose ecology and functions are critical for wetland plants and to coastal wetland ecosystems (Farrer et al. 2022). However, there is still a lack of systematic understanding of patterns related to their distribution and diversity globally and the different factors shaping these processes in coastal wetlands in space and time. Basic understanding of these dynamics is necessary in order to fully assess the magnitude of their roles in coastal wetland ecosystem functioning.

The diversity and distribution of fungi in coastal wetlands are influenced by interplay of both biotic and abiotic factors depending on the substrate, i.e., inside plants tissues or soil. For example, rhizosphere soil fungi and those living inside plant roots (e.g., mycorrhiza and endophytes) can display varying and sometimes opposite diversity patterns, likely due to different underlying mechanisms shaping their patterns (Lumibao et al. 2021). Host factors are likely to have stronger influence on endosphere fungi than on rhizosphere fungal communities, acting as selective filters for fungi colonizing their roots. However, these patterns might be contingent upon the intrinsic abiotic and biotic factors of their local environment and would thus differ when larger spatial scales, i.e., across continents, are considered. A recent review of arbuscular mycorrhizal fungi (AMF), for example, suggests that they have global distribution in coastal wetlands though they are limited by flooding, hypoxia, soil pH, salinity, and the host plant's identity or genotype (Wang et al. 2022). Across coastal wetland habitats, pronounced variations in local environmental conditions (e.g., anoxic saltmarsh soils vs. oxygenated mangrove swamp soils) can also drive differences in fungal communities (Alzarhani et al. 2019).

In this review, we focus on belowground fungal communities that are in close associations with coastal wetland plants for a number of reasons. First, as coastal wetlands like marshes are often dominated by only a few plant species (e.g., *Spartina alterniflora*), functional shifts in plant-fungal associations of dominant vegetation can lead to considerable ecosystem-level outcomes. Second, plant-fungal interactions encompass a feedback mechanism. Plants influence fungal communities in the rhizosphere soil (i.e., soil in contact with their roots) and those living inside their roots

(Lumibao et al. 2020). In turn, fungi can influence physiology and tolerance of the plants under an environmental stressor (Torres-Martínez et al. 2020; Lumibao et al. 2022) and help in nutrient acquisition (e.g., Schultz et al. 2001; Bowles et al. 2018; Moreau et al. 2019). The dynamics of these associations can potentially regulate coastal ecosystem processes. Third, the diversity and composition of rhizosphere soil fungi and endophytic fungal communities are subject to the competing and/or synergistic influences of both biotic, i.e., plants, and abiotic, i.e., local environment, that are likely to vary across spatial and temporal scales.

We address the patterns of fungal diversity associated with plants in naturally occurring wetland habitats across the globe. We synthesized literature that focused on rhizosphere soil and root endosphere fungal communities (including mycorrhizae) across four wetland habitat types: coastal dunes, intertidal flats, salt marshes, and tidal wetlands. Our aims were to (1) synthesize literature/data on rhizosphere and root endosphere fungi across different coastal wetland habitats, (2) determine the commonalities, if any, in fungal research across global coastal wetland habitats, and (3) identify research gaps in fungal studies in coastal wetlands.

Materials and Methods

We performed a systematic quantitative literature review by searching Scopus (Elsevier, Atlanta, U.S.A) and ISI Web of Knowledge (Core collection; Thomson Reuters, NY, U.S.A.). These databases were searched through article title, abstract, and keywords using the search string: (fung* OR microb*) AND (“saltmarsh” OR “salt marsh” OR “coastal ecosystem” OR “tidal wetland” OR “freshwater swamp” OR “tidal marsh”) AND (“rhizosphere” OR “rhizo*” OR “root” OR “endosphere” OR “endoph*”). Available literature until December 2021 was included. This search returned 382 and 145 papers in Scopus and ISI Web of Knowledge, respectively. All papers were imported into COVIDENCE (Covidence systematic review software, Veritas Health Innovation, Melbourne) for screening. Covidence removed automatically duplicates resulting in 527 papers that were included in title and abstract screening. Further screening of the 527 studies based on our criteria ultimately resulted in 51 studies that were used for the synthesis (Table S1, Online Resources 1).

We defined coastal ecosystems as types of habitats at the transition zone between terrestrial and aquatic or ocean environments. This encompasses coastal dunes, restinga forest, intertidal flats, tidal wetlands (including mangroves), forested wetlands (including freshwater wetlands), and salt marshes (Table 1). Where applicable further (i.e., more specific), categorization was carried out based on how it was defined in the papers used in this synthesis and/or Ramsar Convention (2016) as described in Tables 1 and S1 (Online Resources 1).

Table 1 Coastal wetland category description adopted from Ramsar Convention on Wetlands (2016), key representative vegetation type, the reported region they occur, and published studies used in this synthesis. The full list of host plant species/vegetation can be found in Online Resources 1

Type	Definition	Representative vegetation	Region	Study
Coastal dune	Eolian landforms/habitat formed from deposition of sand and gravel within a marine beach	<i>Brachiaria</i>	Global	Estrada et al. 2013; da Silva et al. 2015 (sand dune)
Restinga forest	Coastal tropical sand forests growing on ancient dune formations; porous sandy soil	Undefined	Eastern coast of Brazil; northern Uruguay	da Silva et al. 2017
Intertidal flats	Muddy and sandy areas exposed regularly between tide levels <i>ca</i> twice a day	<i>Zygophyllum</i> , <i>Limoniastrum</i>	Global	El-Morsy 1999
Tidal wetlands (including mangroves in this study)	Flat, vegetated areas that are subject to regular flooding by the tides (<i>excluding all categories defined here</i>)	<i>Tamarix</i> , <i>Avicennia</i> , <i>Calligonum</i>	Global	Sengupta and Chaudhuri 2002; Bohrer et al. 2004; Medina et al. 2015; J. Wang et al. 2021; da Silva et al. 2017; Gaonkar and Rodrigues 2021
Forested wetlands (including freshwater wetlands)	Forest swamp where soils are saturated or flooded for at least a portion of the growing season, and vegetation, dominated by trees, is adapted to tolerate flooded conditions (<i>excludes mangroves in this study</i>)	<i>Salix</i> , <i>Leersia</i> , <i>Typha</i>	Temperate, subtropical and tropical regions of the world	Cooke and Lefor 1998; Bauer et al. 2003
Saltmarsh	Coastal wetlands that are flooded and drained by salt water brought in by the tides; soil composed of deep mud and peat	<i>Spartina</i> , <i>Phragmites</i> , <i>Suaeda</i>	Global	Pugh 1961; Hendrarto and Dickinson 1984; A. Sengupta and Chaudhuri 1990; Hoefnagels et al. 1993; Brown and Bledsoe 1996; El-Morsy 2000; Carvalho et al. 2001; Burke et al. 2003; Carvalho et al. 2004; Caravaca et al. 2005; Daleo et al. 2007; Maciá-Vicente et al. 2008; Roda et al. 2008; Schloss et al. 2009; Wilde et al. 2009; Kandalepas et al. 2010; Welsh et al. 2010; Elmer and Marra 2011; Elmer et al. 2012; Estrada et al. 2013; Kannan et al. 2014; H. Li et al. 2014; Khalmuratova et al. 2015; Liang et al. 2016; Chaudhary et al. 2017; Chaudhary et al. 2018; D'Entremont et al. 2018; Alzarhani et al. 2019; Hernández et al. 2020; Kolton et al. 2020; d'Entremont et al. 2021; Gonçalves et al. 2021; Khalmuratova et al. 2021; Park et al. 2021; Elmer et al. 2016; Ding et al. 2021

Study Inclusion Criteria

Relevant studies were imported and screened using COVidence. Selection was based on the following criteria to

be included in the systematic review: study must be (1) conducted in a natural/pristine coastal ecosystem, i.e., no environmental disturbances reported; (2) conducted in field conditions without field manipulative experiments or lab

experiments; and (3) focused on fungi inside roots (root endophytes or mycorrhizae) and/or rhizosphere soil. All studies not meeting the criteria were excluded in the final screening. Data extraction was conducted manually within COVIDENCE, which included information on author, publication year, geographic location of the study, habitat type, substrate, and host plant (Table S1, Online Resources 1). We did not make any distinction on whether the host plant species is native or foreign to the specific area or geographic location; thus, they are included as long as studies meet the criteria. Non-target ecosystem types that were captured during the keyword search but do not pertain to this study were removed (i.e., three seagrass studies). Mangrove studies were merged with the tidal wetland category as we did not include “mangroves” in key word searches.

Analyses

We conducted all analyses and created graphs in R (R Core Team 2020) and Microsoft Excel 365 (Version 2208, Microsoft Corporation) where applicable. To assess plant and fungal richness patterns, we counted the number of either phyla, genera, or species reported across all studies

from each coastal wetland type. Functional guilds were assigned to taxa using FUNGuild (Nguyen et al. 2016). All assignments that were “highly probable” and “probable” were kept as recommended by Nguyen et al. (2016).

Results

The studies included in our review were published between 1961 and 2021 (Fig. 1a). The total mean number of studies published on root and rhizosphere communities in coastal ecosystems between 1961 and 2021 was 2 per year (Fig. 1a). Since 2019, there has been an increase in the number of studies published (6) suggesting an increasing interest in the fungal microbial communities in coastal ecosystems. Majority of studies were conducted in the USA (i.e., 21%, Fig. 1b), followed by Spain (12%), China, and India, both 8% (Fig. 1b).

Fungal Communities in the Roots and Rhizosphere of Coastal Plant Communities

Our results showed that 73% of studies reported fungal communities from salt marshes, followed by 16% from tidal

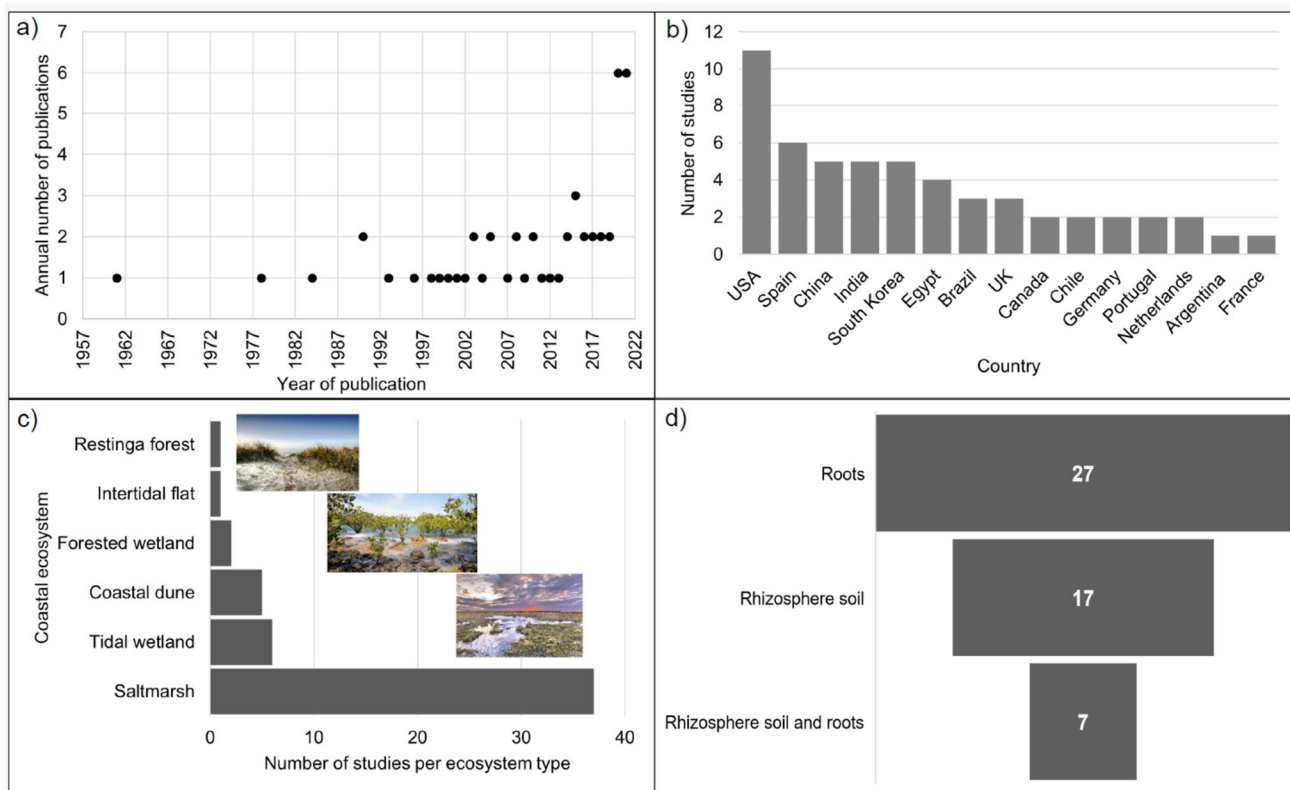


Fig. 1 **a** Global annual number of publications on root and rhizosphere fungal communities in coastal ecosystems. **b** Number of publications per country. **c** Number of studies per ecosystem type. Photos

from left to right illustrate reported coastal ecosystems: coastal dune, tidal wetland, and saltmarsh. **d** Number of studies per substrate

wetlands, 10% from coastal dunes, and other coastal ecosystems (Fig. 1c). Over half of the studies (53%) assessed fungal communities from roots, followed by rhizosphere soil (33% of studies) and 14% from both roots and rhizosphere soil (Fig. 1d). Culture and root staining methods were the most reported assessment techniques, i.e., 37% and 31%, respectively, of fungal communities in the roots and rhizosphere of coastal plant communities. High-throughput sequencing (HTS) methods were used in 8% of studies, but yielded the highest number of fungal species identified (Fig. S1, Online Resources 2). Other studies assessed fungal communities with a combination of methods, e.g., phospholipid fatty acid analysis (PLFA) and enzyme activity assessment or direct fungal spore counting (Fig. S1, Online Resources 2).

Across 51 studies we reviewed, 69 plant species' fungal communities were reported to at least genus level. Of those, the ten most studied host species reflected saltmarsh and tidal wetland communities. They were *Spartina alterniflora* (12 studies), *Phragmites australis* (10 studies), *Suaeda maritima* (6 studies), *Spartina patens* (5 studies), *Arthrocnemum macrostachyum* (4 studies), *Avicennia marina* (4 studies), *Carpobrotus edulis* (3 studies), and *Limonium tetragonum* (3 studies). A few studies assessed fungal communities associated with succulent marsh plants (*Salicornia* and *Batis*).

Overall, salt marsh plant fungal communities have been reported the most, followed by tidal wetland and coastal dune plant communities (Fig. 2a). Some plant host species, e.g., *P. australis* and *S. alterniflora*, were reported from multiple coastal ecosystems, e.g., saltmarsh and tidal wetland, respectively (Appendix 1, Online Resources 3). Other plant species were more restricted, e.g., *Calligonum polygonoides* (Polygonaceae) was only reported from coastal dune, *Tamarix chinensis* (Tamaricaceae) from tidal wetland and *Zygo-phylla coccineum* (Zygophyllaceae) from intertidal flat. Fungal genera and species richness varied considerably between the ecosystems, with overall highest fungal species richness reported within the roots of saltmarsh plants, followed by coastal dune plants and tidal wetland plants (Fig. 2b, Online Resources 3). Root-associated fungal communities were not reported from intertidal flats (Fig. 2b). Fungal species richness in the rhizosphere was the highest around saltmarsh plants, followed by coastal dune and tidal wetland plants (Fig. 2b, Online Resources 3). At the phylum level, Ascomycota was described only from intertidal flats. Basidiomycota was reported only from salt marshes while Glomeromycota was investigated in coastal dunes, salt marshes, and tidal wetlands. Mucoromycota was only reported from salt marshes. Fungal genera varied between the coastal ecosystems with 98 genera reported from salt marshes, 39 from coastal dunes, 21 from tidal wetlands, and 5 from intertidal flats. Most reported fungal genera from coastal dunes included *Acaulospora*, *Glomus*, and *Funneliformis* (Fig. 3). Most reported fungal genera from intertidal flats included *Aspergillus*, *Penicillium*, and *Cladosporium*

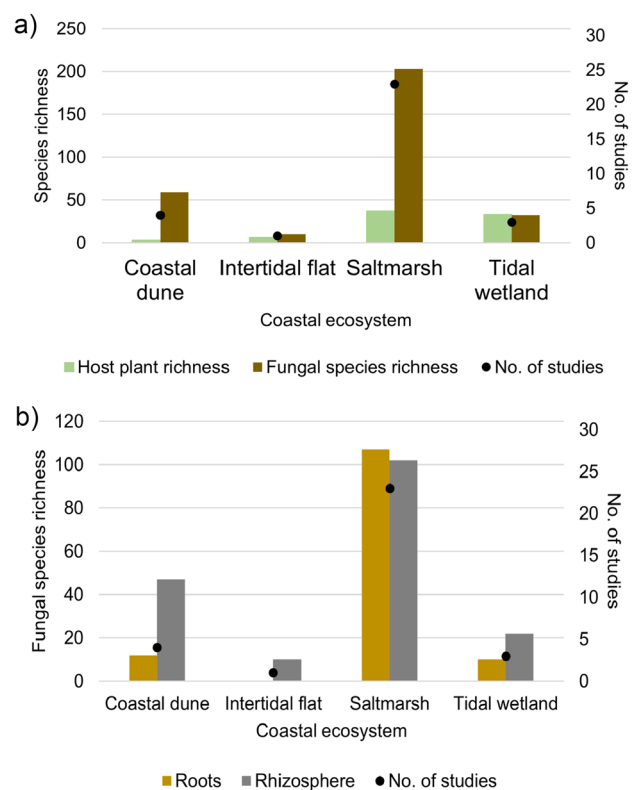


Fig. 2 **a** Host plant and fungal species richness in the rhizosphere and plant roots from reviewed coastal ecosystems; **b** fungal species richness across the rhizosphere and the roots of coastal plants (Online Resources 3). Note that figure does not include plant and fungal richness reported in Alzarhani (2019)

(Fig. 3). In salt marshes, it was *Glomus*, *Fusarium*, and *Aspergillus* (Fig. 3). In tidal wetlands, *Acaulospora*, *Rhizophagus*, and *Funneliformis* (Fig. 3).

In terms of functional guilds, nineteen guilds were reported across all studies reviewed here, with predominantly arbuscular mycorrhizal fungi (AMF) reported with an exception of intertidal flats and freshwater wetlands, where AMF were not reported (Fig. 4). Across all reported fungal taxa in both roots and rhizosphere soil, FUNGuild analyses revealed that 39% were AMF, 11% belong to the Plant Pathogen-Dung-Undefined-Wood Saprotroph complex, 6% plant pathogen, 2% animal pathogen, and 33% as cannot be assigned confidently to any known functional guild (Fig. 4). The rest of the assigned guilds were low in abundance and mostly occurred in salt marshes. Tidal wetlands contain primarily AMF with one identified saprotroph while intertidal flats only harbor different types of saprotrophs.

Discussion

It is increasingly recognized that fungi may play critical roles in coastal wetland processes (Bahram and Netherway 2022), driving soil multifunctionality (Li et al. 2022).

Fungal genus	Coastal dune	Intertidal flat	Saltmarsh	Tidal wetland
<i>Acaulospora</i>				
<i>Acremonium</i>				
<i>Alternaria</i>				
<i>Ambispora</i>				
<i>Archaeospora</i>				
<i>Aspergillus</i>				
<i>Cetraspora</i>				
<i>Cladosporium</i>				
<i>Claroideoglossum</i>				
<i>Corymbioglomus</i>				
<i>Entrophora</i>				
<i>Funneliformis</i>				
<i>Fusarium</i>				
<i>Gigaspora</i>				
<i>Glomus</i>				
<i>Lecanicillium</i>				
<i>Monodictys</i>				
<i>Penicillium</i>				
<i>Phoma</i>				
<i>Pleospora</i>				
<i>Racocetra</i>				
<i>Rhizophagus</i>				
<i>Septoglossum</i>				
<i>Stachybotrys</i>				
<i>Trichoderma</i>				

Fig. 3 Twenty-five most abundant fungal genera across coastal dunes, intertidal flats, salt marshes, and tidal wetlands (full list found in Online Resources 3)

However, fungi in these ecosystems remain underexplored; thus, a systematic understanding of their diversity and distribution is still elusive. Here, we focused on

root-associated and rhizosphere soil fungal communities as they form close relationships with plants (e.g., mycorrhizal symbioses), and the dynamics of these associations can potentially influence ecosystem processes (e.g., carbon sequestration, provisioning of biodiversity).

Our synthesis provides insights into the current state of fungal research in coastal ecosystems globally, revealing an increasing number of publications over the past decade. Our analysis revealed that fungal research in coastal systems is geographically biased and skewed towards the USA with a large proportion of studies focusing on saltmarsh fungal communities. Outside the USA, the majority of studies were conducted in China, South Korea, and India. Notably, China contains Asia’s largest wetlands, accounting for about 10% of the global wetland area (Xiao et al. 2019). Tropical coastal wetlands in Southeast Asia were greatly underrepresented in this region, indicating the need for better representation of these regions globally in future coastal wetland fungal research. Moreover, our analysis revealed that coastal ecosystems have unique plant and fungal assemblages with salt marshes reported to have the highest richness of fungal taxa in their roots.

Status of Global Fungal Research in Coastal Wetlands

Coastal wetlands account for 5–8% of the global land surface (Mitsch et al. 2013; Gardner and Finlayson 2018) and are responsible for many climate-soil feedback processes including greenhouse gas fluxes, biodiversity, and carbon sequestration. Overall, the number of publications of fungal research in natural coastal wetlands showed

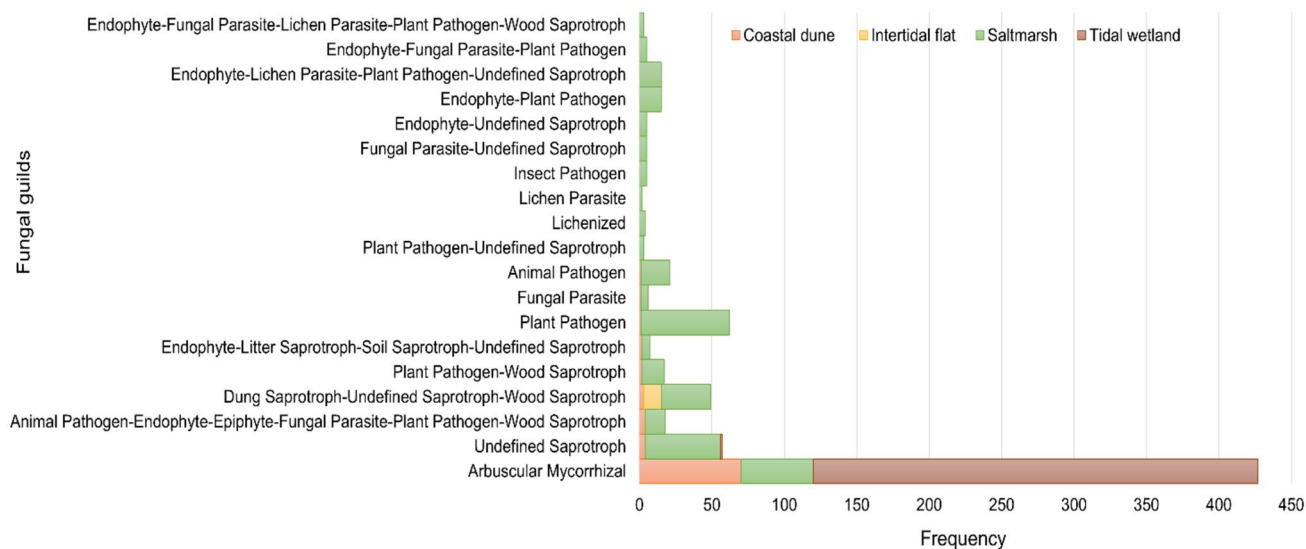


Fig. 4 Frequency of reported fungal functional guilds across coastal dunes, intertidal flats, salt marshes, and tidal wetlands

marginal increase since 2019. Despite the wide availability of high-throughput sequencing technology over the past 10 years, which allows for in-depth and more comprehensive characterization of rhizosphere and endosphere fungi, plant root-associated and soil fungal research in coastal systems has been sporadic compared to higher number of studies focusing on bacterial or fungal diversity in terrestrial ecosystems (e.g., Tedersoo et al. 2022). Notably, our study only included studies reporting fungal communities from natural or pristine environments conducted up to 2021; hence, we did not review fungal research conducted in restored, managed, or disturbed wetlands over the past decades (e.g., Carrasco et al. 2006; Lumibao et al. 2018). For instance, there have been growing interests in the functional role of fungi in metal and oil-contaminated sites in coastal and marine environments due to their potential use for bioremediation (Zhao et al. 2022).

Fungal Diversity Across Coastal Wetlands

Coastal wetlands support diverse but unique assemblages of fungi according to wetland types. Despite salt marshes harboring naturally depauperate plant assemblages dominated by ecosystem engineers like *Spartina alterniflora*, they contain the highest number of root-associated and rhizosphere fungal taxa, with *Glomus* and *Penicillium* as the two most dominant genera. In general, wetland habitats with lower (reported) plant richness can still harbor a high number of root-associated and rhizosphere soil fungal taxa. For example, coastal dune habitat showed similar fungal richness (59 fungal species) despite lower plant richness (only three reported plant species) compared to tidal wetland (32 fungal species; 33 plant species) habitats. These patterns are in contrast with studies demonstrating strong correlation between high plant diversity and belowground fungal communities in terrestrial communities (e.g., Roy-Bolduc et al. 2016; Onufrak et al. 2020). Thus, our analysis revealed that low plant richness in coastal ecosystems does not translate into lower reported fungal richness in roots and/or rhizosphere.

Salt marshes also harbor diverse functional guilds—from mycorrhizae and endophytes to saprotrophs and pathogens. On the other hand, coastal dunes and tidal wetlands were almost completely composed of mycorrhizae while only saprotrophs (with a few undefined) were identified in intertidal flats. This reflects the potential influence of habitat type in promoting growth of certain fungal taxa that performs specific functions. For example, the high abundance of saprotrophs in the rhizosphere soils associated with a few plant species (e.g., *Zygophyllum*, *Limoniastrum*) in the intertidal flat as reported by El-Morsy (1999) might indicate that a large number of saprophytic fungi play a significant role in the organic matter decomposition in these habitats as found in other studies (e.g., Li et al. 2016; Lin et al. 2023). While

intertidal flats are generally considered unproductive and poorly vegetated, they can still support certain plants as found in the reported study (El-Morsy 1999). Notably, as salt marshes were heavily studied in the literature, marsh fungal communities are, thus, better characterized compared to the other habitats, which explains the presence of diverse fungal guilds.

The unique assemblages—different fungal genera and species—found in each wetland habitat type could be due to different abiotic conditions, i.e., the environment supporting different plant species that in turn support unique fungal taxa. For instance, several *Aspergillus* species are known to thrive in the soils of semi-arid regions and Mediterranean coasts (Abdel-Azeem et al. 2020). Here, *Aspergillus* was reported only in salt marshes and intertidal flats (in Egypt), where it is the most common fungal genera in the latter. On the other hand, the genus *Glomus* was reported across all coastal wetland habitats globally except in intertidal flats and was most dominant in the salt marshes. Fungal species belonging to *Glomus* are exclusively mycorrhizal fungi, which are cosmopolitan and form symbiotic associations with different (host) plant species (Schwarzott et al. 2001). Thus, the ability of fungi to associate with plants might have contributed to the widespread distribution of *Glomus* (as well as the other mycorrhizal genera like *Acaulospora*) across coastal wetland habitats.

Known plant, insect, and animal pathogens such as those belonging to the genera *Fusarium* were reported from salt marshes (though other *Fusarium* species are capable of switching to necrotrophs, i.e., kill host then feed on dead host cells (Summerell 2019). Different species of *Fusarium* that are known plant pathogens (e.g., *F. palustre*) were reported in plant roots, mostly those in salt marshes across the globe (Elmer et al. 2016). *F. palustre* has been associated with the dieback of the saltmarsh grass, *S. alterniflora*, in its native North American salt marshes (Elmer 2014; Li et al. 2014).

Notably, the majority of the reported fungal species were mycorrhizal fungi (arbuscular mycorrhiza) as they were the focus of more than 40% of the studies included in our synthesis. Plant-mycorrhizal symbioses represent the oldest symbiotic relationships between plants and fungi, having co-evolved *ca.* 200–400 M years ago, with mycorrhiza colonizing about 85% of vascular plants (Brundrett 2002). Fungi supply nutrients to plants, and plants provide carbon substrate as food to fungi, and this symbiosis has been widely studied in terrestrial ecosystems (e.g., Kivlin et al. 2011; Soudzilovskaia et al. 2019). Based on our synthesis, mycorrhizae in natural coastal wetland plants were first reported only in 1990 (Cooke and Lefor 1990), though it became the main focus of fungal research in coastal wetlands in the following decades (e.g., D'Entremont et al. 2018; Kandalepas et al. 2010). In part, this might be driven by the potential of mycorrhiza

in mediating ecosystem functions as observed in terrestrial systems. Arbuscular and ectomycorrhizal vegetation in terrestrial ecosystems store between 241 ± 15 and 100 ± 17 GT carbon, respectively, in aboveground biomass compared to non-mycorrhizal vegetation (29 ± 5.5 GT carbon) (Soudzilovskaia et al. 2019), suggesting that mycorrhizal fungi contribute significantly to carbon sequestration. High frequency of reported mycorrhizal fungi found in reviewed studies may also reflect the availability and relatively low cost of assessing mycorrhizal colonization in plant roots. Specifically, AMF characterization is a considerably less expensive approach requiring standard laboratory consumables and materials to assess root colonization—which involves root washing, staining, and counting presence of fungi under microscope—compared to more technically complex and expensive analyses such as high-throughput sequencing.

Recent studies reviewed in our synthesis have illustrated that mycorrhiza, particularly, AMF (belonging to genus *Glomus*), are globally ubiquitous across different coastal wetlands. For example, AMF have been reported from tidal wetlands in the US and Egypt (e.g., Bauer et al. 2003; Abd-Elgawad et al. 2020; others), mangrove-dominated habitats in India (e.g., Gaonkar and Rodrigues 2021), and from salt marshes in North America, Europe and Asia (Wang et al. 2022; Daleo et al. 2007; others). They appear to be associated with almost all the wetland plants studied, supporting previous AM findings from wetlands (e.g., Xu et al. 2016). This suggests that AMF plays an equally important functional role in coastal systems as in terrestrial systems via provisioning of critical ecosystem processes (e.g., nutrient acquisition, mediation of stress tolerance of plants), warranting further in-depth study.

Notably, our synthesis did not capture other coastal habitats such as seagrasses and mangroves. Recent studies suggest that seagrasses might also be an important reservoir of fungal diversity (Vohnik et al. 2015; Ettinger and Eisen 2019; Poli et al. 2022) as are mangrove-dominated habitats (e.g., de Souza Sebastianes et al. 2013). These findings highlight the increasing recognition of the importance of fungi in coastal ecosystems.

Our review includes studies that were published between 1961 and 2021. We acknowledge that since 2021, seminal papers have been published reviewing microbial community diversity, including fungi, in coastal ecosystems. For example, Crump and Bowen (2024) synthesized recent research on microbial habitats in estuaries. Farrer et al. (2022) reviewed the ecology of plant-microbial symbioses in coastal systems including mycorrhizae.

Key Knowledge Gaps and Future Research

While the fungal research in coastal ecosystems is slowly on the rise, there are still many research gaps that need

to be addressed. Below, we outline three main research gaps resulting from our synthesis analyzing reported root-associated and rhizosphere fungal communities from coastal ecosystems.

First, increased representation of the different coastal wetland habitats, regionally and/or globally, is needed. More research is needed to better understand the diversity and functional importance of fungal communities associated with plants from restinga forests, intertidal flats, and forested wetlands. Second, the geographic bias in global fungal research can limit our inferences on the global diversity and distribution patterns of fungi in coastal wetlands. We found that the majority of studies reporting root or rhizosphere fungal communities were from the USA, Spain, and China, collectively accounting for 41% of reviewed studies. Increasing the reporting of fungal research from underrepresented countries is critical for global biodiversity assessments.

Third, we found that 68% of studies reviewed here analyzed root and rhizosphere fungal communities using exclusively culture-based or root-staining methods and only 8% of studies used sequencing methodologies. Fungal analysis using cultures is very valuable; however, only a small fraction of fungi is culturable, and thus, the true diversity of fungal communities using culture-dependent methods will be underestimated. For instance, only 10–30% of fungi are culturable by using traditional microbiological methods (Magnuson and Lasure 2002). High-throughput sequencing (HTS) offers high-quality, cutting-edge alternatives for analyzing microbiome structure and functioning from complex environmental DNA samples (Tedersoo et al. 2021). High costs associated with HTS may be a significant impediment as the total cost of sampling, extraction of DNA, PCR, and sequencing of fungal DNA at a commercial lab is AU\$/US\$50–120/sample with the total costs of a one-off analysis quickly escalating depending on the number of samples and thus may be inaccessible to many researchers and practitioners (Birnbaum and Trevathan-Tackett 2022). Therefore, more collaboration to advance the study of plant-associated fungal diversity in underrepresented coastal regions is warranted using the latest cutting-edge molecular tools.

We suggest that further research should focus on addressing the knowledge gaps highlighted above as well as assess the functional roles of fungal communities across coastal wetlands. Currently, majority of the reported studies were descriptive, and most are focused on single fungal guild e.g., mycorrhizae. While studies on mycorrhizae provide important insights into their ecosystem role, especially with respect to plant physiology in coastal systems, systematic community level characterization of fungi is needed—at the levels of taxonomic, functional, and metabolic diversity.

Conclusion

The need for fungal research in natural coastal wetlands cannot be understated. As increasing pressures from anthropogenic-driven changes to the coastal wetland environment impact these ecosystems, generating baseline data of fungal communities—their distribution, diversity, and functional roles—in natural, pre-disturbed environment is critical for a better predictive capacity to anticipate organismal and ecosystem-system level impacts of such disturbances. It can also provide important insights that can aid global coastal restoration and management efforts (Birnbaum and Trevathan-Tackett 2022; Farrer et al. 2022).

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Author Contribution CB and CL conceived the idea; CB, CL, and GH are responsible for the data extraction; CB led the data analysis with assistance from CL; CL wrote the first draft; and CB and GH significantly contributed to manuscript editing.

Data Availability All data is included in the Supplementary material.

Declarations

Competing Interest The authors declare no competing interests.

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References

- Abdel-Azeem, A., A. Abu-Elsaoud, A. Darwish, B. Balbool, F. Abo Nough, H. Abo Nahas, M. Abd El-Azeem, N. Ali, and P. Kirk. 2020. The Egyptian Ascomycota I: genus *Aspergillus*. *Microbial Biosystems* 5: 61–99. <https://doi.org/10.21608/mb.2020.100044>.
- Abd-Elgawad, A.M., Y.M. Rashad, A.M. Abdel-Azeem, S.A. Al-Barati, A.M. Assaeed, and A.M. Mowafy. 2020. Calligonum polygonoides I. Shrubs provide species-specific facilitation for the understory plants in coastal ecosystem. *Biology* 9: 1–22. <https://doi.org/10.3390/biology9080232>.
- Alzarhani, A.K., D.R. Clark, G.J.C. Underwood, H. Ford, T.E.A. Cotton, and A.J. Dumbrell. 2019. Are drivers of root-associated fungal community structure context specific? *ISME Journal* 13: 1330–1344. <https://doi.org/10.1038/s41396-019-0350-y>.
- Bahram, M., and T. Netherway. 2022. Fungi as mediators linking organisms and ecosystems. *FEMS Microbiology Reviews* 46: 1–16. <https://doi.org/10.1093/femsre/fuab058>.
- Bauer, C.R., C.H. Kellogg, S.D. Bridgham, and G.A. Lamberti. 2003. Mycorrhizal colonization across hydrologic gradients in restored and reference freshwater wetlands. *Wetlands* 23: 961–968. [https://doi.org/10.1672/0277-5212\(2003\)023\[0961:MCAHGJ\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2003)023[0961:MCAHGJ]2.0.CO;2).
- Baustian, J.J., I.A. Mendelssohn, and M.W. Hester. 2012. Vegetation's importance in regulating surface elevation in a coastal salt marsh facing elevated rates of sea level rise. *Global Change Biology* 18: 3377–3382. <https://doi.org/10.1111/j.1365-2486.2012.02792.x>.
- Birnbaum, C., and S.M. Trevathan-Tackett. 2022. Aiding coastal wetland restoration via the belowground soil microbiome: An overview. *Restoration Ecology*. <https://doi.org/10.1111/rec.13824>.
- Bohrer, K.E., C.F. Friese, and J.P. Amon. 2004. Seasonal dynamics of arbuscular mycorrhizal fungi in differing wetland habitats. *Mycorrhiza* 14: 329–337. <https://doi.org/10.1007/s00572-004-0292-7>.
- Bowles, T.M., L.E. Jackson, and T.R. Cavagnaro. 2018. Mycorrhizal fungi enhance plant nutrient acquisition and modulate nitrogen loss with variable water regimes. *Global Change Biology* 24: e171–e182. <https://doi.org/10.1111/gcb.13884>.
- Brown, A.M., and C. Bledsoe. 1996. Spatial and temporal dynamics of mycorrhizas in *Jaumea carnosa*, a tidal saltmarsh halophyte. *Journal of Ecology* 84: 703–715. <https://doi.org/10.2307/2261333>.
- Brundrett, M.C. 2002. Coevolution of roots and mycorrhizas of land plants. *New Phytologist* 154: 275–304. <https://doi.org/10.1046/j.1469-8137.2002.00397.x>.
- Burke, D.J., E.P. Hamerlynck, and D. Hahn. 2003. Interactions between the salt marsh grass *Spartina patens*, arbuscular mycorrhizal fungi and sediment bacteria during the growing season. *Soil Biology and Biochemistry* 35: 501–511. [https://doi.org/10.1016/S0038-0717\(03\)00004-X](https://doi.org/10.1016/S0038-0717(03)00004-X).
- Caravaca, F., M. Del Mar Alguacil, P. Torres, and A. Roldán. 2005. Microbial activities and arbuscular mycorrhizal fungi colonization in the rhizosphere of the salt marsh plant *Inula crithmoides* L. Along a Spatial Salinity Gradient. *Wetlands* 25: 350–355. <https://doi.org/10.1672/11>.
- Carrasco, L., F. Caravaca, J. Álvarez-Rogel, and A. Roldán. 2006. Microbial processes in the rhizosphere soil of a heavy metals-contaminated Mediterranean salt marsh: A facilitating role of AM fungi. *Chemosphere* 64: 104–111. <https://doi.org/10.1016/j.chemosphere.2005.11.038>.
- Carvalho, L.M., I. Caçador, and M. Martins-Loução. 2001. Temporal and spatial variation of arbuscular mycorrhizas in salt marsh plants of the Tagus estuary (Portugal). *Mycorrhiza* 11: 303–309. <https://doi.org/10.1007/s00572-001-0137-6>.
- Carvalho, L.M., P.M. Correia, and M.A. Martins-Loução. 2004. Arbuscular mycorrhizal fungal propagules in a salt marsh. *Mycorrhiza* 14: 165–170. <https://doi.org/10.1007/s00572-003-0247-4>.
- Chaudhary, D.R., A.P. Rathore, R. Kumar, and B. Jha. 2017. Spatial and halophyte-associated microbial communities in intertidal coastal region of India. *International Journal of Phytoremediation* 19: 478–489. <https://doi.org/10.1080/15226514.2016.1244168>.
- Chaudhary, D.R., J. Kim, and H. Kang. 2018. Influences of different halophyte vegetation on soil microbial community at temperate salt marsh. *Microbial Ecology* 75: 729–738. <https://doi.org/10.1007/s00248-017-1083-y>.
- Cooke, J.C., and M.W. Lefor. 1990. Comparison of vesicular-arbuscular mycorrhizae in plants from disturbed and adjacent undisturbed regions of a coastal salt marsh in Clinton, Connecticut, USA. *Environmental Management* 14: 131–137. <https://doi.org/10.1007/BF02394027>.

- Cooke, J.C., and M.W. Lefor. 1998. The mycorrhizal status of selected plant species from Connecticut wetlands and transition zones. *Restoration Ecology* 6: 214–222. <https://doi.org/10.1046/j.1526-100X.1998.00628.x>.
- Crump, B.C., and J.L. Bowen. 2024. The microbial ecology of estuarine ecosystems. *Annual Review of Marine Science* 16: 335–360. <https://doi.org/10.1146/annurev-marine-022123-101845>.
- D'Entremont, T.W., J.C. López-Gutiérrez, and A.K. Walker. 2018. Examining arbuscular mycorrhizal fungi in saltmarsh hay (*Spartina patens*) and smooth cordgrass (*Spartina alterniflora*) in the Minas Basin, Nova Scotia. *Northeastern Naturalist* 25: 72–86. <https://doi.org/10.1656/045.025.0107>.
- d'Entremont, T.W., Z. Migicovsky, J.C. López-Gutiérrez, and A.K. Walker. 2021. Saltmarsh rhizosphere fungal communities vary by sediment type and dominant plant species cover in Nova Scotia, Canada. *Environmental Microbiology Reports* 13: 458–463. <https://doi.org/10.1111/1758-2229.12904>.
- da Silva, I.R., D.K.A. da Silva, F.A. de Souza, F. Oehl, and L.C. Maia. 2017. Changes in arbuscular mycorrhizal fungal communities along a river delta island in northeastern Brazil. *Acta Oecologica* 79: 8–17. <https://doi.org/10.1016/j.actao.2016.12.011>.
- da Silva, D.K.A., R.G. de Souza, and B. A. de A. Velez, G. A. da Silva, F. Oehl, and L. C. Maia. 2015. Communities of arbuscular mycorrhizal fungi on a vegetation gradient in tropical coastal dunes. *Applied Soil Ecology* 96: 7–17. <https://doi.org/10.1016/j.apsoil.2015.06.009>.
- Daleo, P., E. Fanjul, A.M. Casariego, B.R. Silliman, M.D. Bertness, and O. Iribarne. 2007. Ecosystem engineers activate mycorrhizal mutualism in salt marshes. *Ecology Letters* 10: 902–908. <https://doi.org/10.1111/j.1461-0248.2007.01082.x>.
- de Souza Sebastião, F.L., A.S. Romão-Dumaresq, P.T. Lacava, R. Harakava, J.L. Azevedo, I.S. de Melo, and A.A. Pizzirani-Kleiner. 2013. Species diversity of curable endophytic fungi from Brazilian mangrove forests. *Current Genetics* 59: 153–166. <https://doi.org/10.1007/s00294-013-0396-8>.
- Ding, M.Y., W. Chen, X.C. Ma, B.W. Lv, S.Q. Jiang, Y.N. Yu, M.J. Rahimi, et al. 2021. Emerging salt marshes as a source of *Trichoderma arenarium* sp. nov. and other fungal bioeffectors for biosaline agriculture. *Journal of Applied Microbiology* 130: 179–195. <https://doi.org/10.1111/jam.14751>.
- Elmer, W.H. 2014. A Tripartite interaction between *Spartina alterniflora*, *Fusarium palustre*, and the purple marsh crab (*Sesarma reticulatum*) contributes to sudden vegetation dieback of salt marshes in New England. *Phytopathology* 104: 1070–1077. <https://doi.org/10.1094/PHYTO-08-13-0219-R>.
- Elmer, W.H., and R.E. Marra. 2011. New species of *Fusarium* associated with dieback of *Spartina alterniflora* in Atlantic salt marshes. *Mycologia* 103: 806–819. <https://doi.org/10.3852/10-155>.
- Elmer, W.H., J.A. LaMondia, and F.L. Caruso. 2012. Association between *Fusarium* spp. on *Spartina alterniflora* and dieback sites in Connecticut and Massachusetts. *Estuaries and Coasts* 35: 436–444. <https://doi.org/10.1007/s12237-011-9448-9>.
- Elmer, W.H., R.E. Marra, H. Li, and B. Li. 2016. Incidence of *Fusarium* spp. on the invasive *Spartina alterniflora* on Chongming Island, Shanghai. *China. Biological Invasions* 18: 2221–2227. <https://doi.org/10.1007/s10530-015-1012-2>.
- El-Morsy, E.S.M. 1999. Microfungi from the ectorhizosphere-rhizoplane zone of different halophytic plants from the Red Sea Coast of Egypt. *Mycologia* 91: 228–236.
- El-Morsy, E.S.M. 2000. Fungi isolated from the endorhizosphere of halophytic plants from the Red Sea Coast of Egypt. *Fungal Diversity* 5: 43–54.
- Emerson, D., J.V. Weiss, and J.P. Megonigal. 1999. Iron-oxidizing bacteria are associated with ferric hydroxide precipitates (Fe-plaque) on the roots of wetland plants. *Applied and Environmental Microbiology* 65: 2758–2761. <https://doi.org/10.1128/aem.65.6.2758-2761.1999>.
- Estrada, B., M. Beltrán-Hermoso, J. Palenzuela, K. Iwase, J.M. Ruiz-Lozano, J.M. Barea, and F. Oehl. 2013. Diversity of arbuscular mycorrhizal fungi in the rhizosphere of *Asteriscus maritimus* (L.) Less., a representative plant species in arid and saline Mediterranean ecosystems. *Journal of Arid Environments* 97: 170–175. <https://doi.org/10.1016/j.jaridenv.2013.05.019>.
- Ettinger, C.L., and J.A. Eisen. 2019. Characterization of the mycobiome of the seagrass, *Zostera marina*, reveals putative associations with marine chytrids. *Frontiers in Microbiology* 10: 1–13. <https://doi.org/10.3389/fmicb.2019.02476>.
- Farrer, E.C., S.A. Van Bael, K. Clay, and M.K.K.H. Smith. 2022. Plant-microbial symbioses in coastal systems: their ecological importance and role in coastal restoration. *Estuaries and Coasts* 45: 1805–1822. <https://doi.org/10.1007/s12237-022-01052-2>.
- Gardner, R.C., and C. Finlayson. 2018. Global wetland outlook: state of the world's wetlands and their services to people. *Ramsar convention secretariat* 2020–2025.
- Gaonkar, S., and B.F. Rodrigues. 2021. Arbuscular mycorrhizal fungal status in mangroves of Pichavaram Forest, Tamil Nadu, India. *Tropical Ecology* 62: 538–548. <https://doi.org/10.1007/s42965-021-00167-0>.
- Gonçalves, D.R., R. Pena, G. Zotz, and D.C. Albach. 2021. Effects of fungal inoculation on the growth of *Salicornia* (Amaranthaceae) under different salinity conditions. *Symbiosis* 84: 195–208. <https://doi.org/10.1007/s13199-021-00783-3>.
- Hendrarito, I.B., and C.H. Dickinson. 1984. Soil and root microorganisms in four salt marsh communities. *Transactions - British Mycological Society* 83: 615–620. [https://doi.org/10.1016/S0007-1536\(84\)80181-3](https://doi.org/10.1016/S0007-1536(84)80181-3).
- Hernández, E.G., E. Baraza, C. Smit, M.P. Berg, and J.F. Salles. 2020. Salt marsh elevation drives root microbial composition of the native invasive grass *Elytrigia atherica*. *Microorganisms* 8: 1–19. <https://doi.org/10.3390/microorganisms8101619>.
- Hoefnagels, M.H., S.W. Broome, and S.R. Shafer. 1993. Vesicular-arbuscular mycorrhizae in salt marshes in North Carolina. *Estuaries* 16: 851–858. <https://doi.org/10.2307/1352444>.
- Howard, J., A. Sutton-Grier, D. Herr, J. Kleypas, E. Landis, E. Mcleod, E. Pidgeon, and S. Simpson. 2017. Clarifying the role of coastal and marine systems in climate mitigation. *Frontiers in Ecology and the Environment* 15: 42–50. <https://doi.org/10.1002/fee.1451>.
- Kandalepas, D., K.J. Stevens, G.P. Shaffer, and W.J. Platt. 2010. How abundant are root-colonizing fungi in Southeastern Louisiana's degraded marshes? *Wetlands* 30: 189–199. <https://doi.org/10.1007/s13157-010-0017-y>.
- Kannan, K.P., D. Madhan Kumar, P.R. Ramya, S. Madhu Nika, G. Meenatchi, A.N. Sowmya, and S. Bhuvanewari. 2014. Diversity of endophytic fungi from salt tolerant plants. *International Journal of ChemTech Research* 6: 4084–4088.
- Khalmuratova, I., H. Kim, Y.J. Nam, Y. Oh, M.J. Jeong, H.R. Choi, Y.H. You, et al. 2015. Diversity and plant growth promoting capacity of endophytic fungi associated with halophytic plants from the west coast of Korea. *Mycobiology* 43: 373–383. <https://doi.org/10.5941/MYCO.2015.43.4.373>.
- Khalmuratova, I., D.H. Choi, H.J. Yoon, T.M. Yoon, and J.G. Kim. 2021. Diversity and plant growth promotion of fungal endophytes in five halophytes from the Buan salt marsh. *Journal of Microbiology and Biotechnology* 31: 408–418. <https://doi.org/10.4014/JMB.2012.12041>.
- Khan, A. G. 2004. Mycotrophy and its significance in wetland ecology and wetland management. In *Wetlands Ecosystems in Asia*, ed. M.H. Wong pp. 95–114. Amsterdam: Elsevier.
- Kirwan, M.L., and J.P. Megonigal. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature* 504: 53–60. <https://doi.org/10.1038/nature12856>.
- Kivlin, S.N., C.V. Hawkes, and K.K. Treseder. 2011. Global diversity and distribution of arbuscular mycorrhizal fungi. *Soil Biology and*

- Biochemistry* 43: 2294–2303. <https://doi.org/10.1016/j.soilbio.2011.07.012>.
- Kolton, M., J.L. Rolando, and J.E. Kostka. 2020. Elucidation of the rhizosphere microbiome linked to *Spartina alterniflora* phenotype in a salt marsh on Skidaway Island, Georgia, USA. *FEMS Microbiology Ecology* 96: 1–19. <https://doi.org/10.1093/FEMSEC/FIAA026>.
- Li, H., X. Zhang, R. Zheng, X. Li, W.H. Elmer, L.M. Wolfe, and B. Li. 2014. Indirect effects of non-native *Spartina alterniflora* and its fungal pathogen (*Fusarium palustre*) on native saltmarsh plants in China. *Journal of Ecology* 102: 1112–1119. <https://doi.org/10.1111/1365-2745.12285>.
- Li, W., M. Wang, X. Bian, J. Guo, and L. Cai. 2016. A high-level fungal diversity in the intertidal sediment of Chinese seas presents the spatial variation of community composition. *Frontiers in Microbiology* 7: 2098.
- Li, J., L. Cui, M. Delgado-Baquerizo, J. Wang, Y. Zhu, R. Wang, W. Li, et al. 2022. Fungi drive soil multifunctionality in the coastal salt marsh ecosystem. *Science of the Total Environment* 818: 151673. <https://doi.org/10.1016/j.scitotenv.2021.151673>.
- Liang, X., C. He, X. Zhu, X. Chen, Y. Lei, H. Zhang, Z. Qin, and X. Qi. 2016. Effect of exotic *Spartina alterniflora* on fungal symbiosis with native plants *Phragmites australis* and *Scirpus mariqueter*, and model plants *Lolium perenne* L. and *Trifolium repens*. *Aquatic Botany* 130: 50–58. <https://doi.org/10.1016/j.aquabot.2015.10.003>.
- Lin, W., X. Liu, L. Gong, R. Liu, M. Ling, C. Guo, H. Meng, et al. 2023. Impact of environmental factors on diversity of fungi in sediments from the Shenzhen River Estuary. *Archives of Microbiology* 205: 1–15. <https://doi.org/10.1007/s00203-023-03438-7>.
- Lumibao, C.Y., B.M. Bernik, S.K. Formel, D. Kandalepas, K.L. Mighell, J. Pardue, S.A. Van Bael, and M.J. Blum. 2020. Rhizosphere microbial communities reflect genotypic and trait variation in a salt marsh ecosystem engineer. *American Journal of Botany* 107: 941–949. <https://doi.org/10.1002/ajb2.1497>.
- Lumibao, C.Y., E.R. Kimbrough, R.H. Day, W.H. Conner, K.W. Krauss, and S.A. van Bael. 2021. Divergent biotic and abiotic filtering of root endosphere and rhizosphere soil fungal communities along ecological gradients. *FEMS Microbiology Ecology* 96: 1–10. <https://doi.org/10.1093/FEMSEC/FIAA124>.
- Lumibao, C.Y., L. Torres Martínez, J.P. Megonigal, S.A. Van Bael, and M.J. Blum. 2022. Microbial mediation of salinity stress response varies by plant genotype and provenance over time. *Molecular Ecology* 31: 4571–4585. <https://doi.org/10.1111/mec.16603>.
- Lumibao, C.Y., S. Formel, V. Elango, J.H. Pardue, M. Blum, and S.A. Van Bael. 2018. Persisting responses of salt marsh fungal communities to the Deepwater Horizon oil spill. *Science of the Total Environment* 642: 904–913. <https://doi.org/10.1016/j.scitotenv.2018.06.077>.
- Maciá-Vicente, J.G., H.B. Jansson, S.K. Abdullah, E. Descals, J. Salinas, and L.V. Lopez-Llorca. 2008. Fungal root endophytes from natural vegetation in Mediterranean environments with special reference to *Fusarium* spp. *FEMS Microbiology Ecology* 64: 90–105. <https://doi.org/10.1111/j.1574-6941.2007.00443.x>.
- Magnuson, J.K., and L. Lasure. 2002. Fungal diversity in soils as assessed by direct culture and molecular techniques. *Abstracts from the 102nd General Meeting of the American Society for Microbiology* 19–23. http://www.pnnl.gov/biobased/docs/fungal_diversity.pdf. Accessed July 2023
- Medina, J., S. Meier, R. Rubio, G. Curaqueo, F. Borie, P. Aguilera, F. Oehl, and P. Cornejo. 2015. Arbuscular mycorrhizal status of pioneer plants from the mouth of lake Budi, Araucanía Region, Chile. *Journal of Soil Science and Plant Nutrition* 15: 142–152. <https://doi.org/10.4067/S0718-95162015005000012>.
- Mitsch, W.J., B. Bernal, A.M. Nahlik, Ü. Mander, L. Zhang, C.J. Anderson, S.E. Jørgensen, and H. Brix. 2013. Wetlands, carbon, and climate change. *Landscape Ecology* 28: 583–597. <https://doi.org/10.1007/s10980-012-9758-8>.
- Moreau, D., R.D. Bardgett, R.D. Finlay, D.L. Jones, and L. Philippot. 2019. A plant perspective on nitrogen cycling in the rhizosphere. *Functional Ecology* 33: 540–552. <https://doi.org/10.1111/1365-2435.13303>.
- Nguyen, N.H., Z. Song, S.T. Bates, S. Branco, L. Tedersoo, J. Menke, J.S. Schilling, and P.G. Kennedy. 2016. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. *Fungal Ecology* 20: 241–248.
- Onufrak, A., M.A. Rúa, and K. Hossler. 2020. The missing metric: An evaluation of fungal importance in wetland assessments. *Wetlands* 40: 825–838. <https://doi.org/10.1007/s13157-019-01228-w>.
- Park, J.M., J.W. Hong, Y.H. You, and J.G. Kim. 2021. Endophytic fungi of emerged halophytes in river deltas and tidal flats of the Korean Ramsar wetlands. *Journal of Marine Science and Engineering* 9. <https://doi.org/10.3390/jmse9040430>.
- Poli, A., G.C. Varese, L. Garzoli, and V. Prigione. 2022. Seagrasses, seaweeds and plant debris: An extraordinary reservoir of fungal diversity in the Mediterranean Sea. *Fungal Ecology* 60: 101156. <https://doi.org/10.1016/j.funeco.2022.101156>.
- Pugh, G.J.F. 1961. Fungal colonization of a developing salt marsh. *Nature* 190: 1032–1033. <https://doi.org/10.1038/1901032a0>.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ramsar Convention on Wetlands. 2016. *An introduction to the Ramsar Convention on Wetlands*, 7th ed. Gland, Switzerland: Ramsar Convention Secretariat.
- Roda, J.J., G. Díaz, and P. Torres. 2008. Spatial distribution of arbuscular mycorrhizal fungi in the rhizosphere of the salt marsh plant *Inula crithmoides* L. along a salinity gradient. *Arid Land Research and Management* 22: 310–319. <https://doi.org/10.1080/15324980802388199>.
- Roy-Bolduc, A., E. Laliberté, S. Boudreau, and M. Hijri. 2016. Strong linkage between plant and soil fungal communities along a successional coastal dune system. *FEMS Microbiology Ecology* 92: 1–10. <https://doi.org/10.1093/femsec/fiw156>.
- Schloss, P.D., S.L. Westcott, T. Ryabin, J.R. Hall, M. Hartmann, E.B. Hollister, R.A. Lesniewski, et al. 2009. Introducing mothur: Open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Applied and Environmental Microbiology* 75: 7537–7541. <https://doi.org/10.1128/AEM.01541-09>.
- Schultz, P.A., R.M. Miller, J.D. Jastrow, C.V. Rivetta, and J.D. Bever. 2001. Evidence of a mycorrhizal mechanism for the adaptation of *Andropogon gerardii* (Poaceae) to high- and low-nutrient prairies. *American Journal of Botany* 88: 1650–1656.
- Schwarzott, D., C. Walker, and A. Schüßler. 2001. Glomus, the largest genus of the arbuscular mycorrhizal fungi (*Glomales*), is nonmonophyletic. *Molecular Phylogenetics and Evolution* 21: 190–197. <https://doi.org/10.1006/mpev.2001.1007>.
- Sengupta, A., and S. Chaudhuri. 1990. Vesicular arbuscular mycorrhiza (VAM) in pioneer salt marsh plants of the Ganges river delta in West Bengal (India). *Plant and Soil* 122: 111–113. <https://doi.org/10.1007/BF02851917>.
- Sengupta, Anjan, and S. Chaudhuri. 2002. Arbuscular mycorrhizal relations of mangrove plant community at the Ganges river estuary in India. *Mycorrhiza* 12: 169–174. <https://doi.org/10.1007/s00572-002-0164-y>.
- Soudzilovskaia, N.A., P.M. van Bodegom, C. Terrer, and M. van't Zelfde, I. McCallum, M. Luke McCormack, J. B. Fisher, M. C. Brundrett, N. C. de Sá, and L. Tedersoo. 2019. Global mycorrhizal plant distribution linked to terrestrial carbon stocks. *Nature Communications* 10: 1–10. <https://doi.org/10.1038/s41467-019-13019-2>.

- Summerell, B.A. 2019. Resolving *Fusarium*: Current status of the genus. *Annual Review of Phytopathology* 57: 323–339. <https://doi.org/10.1146/annurev-phyto-082718-100204>.
- Tedersoo, L., M. Albertsen, and S. Anslan. 2021. Perspectives and benefits of high-throughput long-read. *Applied Environmental Microbiology* 87: 1–19.
- Tedersoo, L., V. Mikryukov, A. Zizka, M. Bahram, N. Hagh-Doust, S. Anslan, O. Prylutskyi, et al. 2022. Global patterns in endemicity and vulnerability of soil fungi. *Global Change Biology* 28: 6696–6710. <https://doi.org/10.1111/gcb.16398>.
- Torres-Martínez, L., M. Sánchez-Julia, E. Kimbrough, T.C. Hendrix, M. Hendrix, R.H. Day, K.W. Krauss, and S.A. Van Bael. 2020. Influence of soil microbiota on *Taxodium distichum* seedling performance during extreme flooding events. *Plant Ecology* 221: 773–793. <https://doi.org/10.1007/s11258-020-01059-4>.
- Vohník, M., O. Borovec, I. Župan, D. Vondrášek, M. Petrtýl, and R. Sudová. 2015. Anatomically and morphologically unique dark septate endophytic association in the roots of the Mediterranean endemic seagrass *Posidonia oceanica*. *Mycorrhiza* 25: 663–672. <https://doi.org/10.1007/s00572-015-0642-7>.
- Wang, J., S. Ma, G.G. Wang, L. Xu, Z. Fu, J. Song, and J. Zhang. 2021. Arbuscular mycorrhizal fungi communities associated with wild plants in a coastal ecosystem. *Journal of Forestry Research* 32: 683–695. <https://doi.org/10.1007/s11676-020-01127-5>.
- Wang, X.Q., Y.H. Wang, Y. Bin Song, and M. Dong. 2022. Formation and functions of arbuscular mycorrhizae in coastal wetland ecosystems: a review. *Ecosystem Health and Sustainability* 8: 2144465. <https://doi.org/10.1080/20964129.2022.2144465>.
- Weiss, J.V., D. Emerson, and J.P. Megonigal. 2004. Geochemical control of microbial Fe(III) reduction potential in wetlands: Comparison of the rhizosphere to non-rhizosphere soil. *FEMS Microbiology Ecology* 48: 89–100. <https://doi.org/10.1016/j.femsec.2003.12.014>.
- Welsh, A.K., D.J. Burke, E.P. Hamerlynck, and D. Hahn. 2010. Seasonal analyses of arbuscular mycorrhizae, nitrogen-fixing bacteria and growth performance of the salt marsh grass *Spartina patens*. *Plant and Soil* 330: 251–266. <https://doi.org/10.1007/s11104-009-0197-5>.
- Wilde, P., A. Manal, M. Stodden, E. Sieverding, U. Hildebrandt, and H. Bothe. 2009. Biodiversity of arbuscular mycorrhizal fungi in roots and soils of two salt marshes. *Environmental Microbiology* 11: 1548–1561. <https://doi.org/10.1111/j.1462-2920.2009.01882.x>.
- Wolfe, B.E., D.L. Mummey, M.C. Rillig, and J.N. Klironomos. 2007. Small-scale spatial heterogeneity of arbuscular mycorrhizal fungal abundance and community composition in a wetland plant community. *Mycorrhiza* 17: 175–183. <https://doi.org/10.1007/s00572-006-0089-y>.
- Xiao, D., L. Deng, D.G. Kim, C. Huang, and K. Tian. 2019. Carbon budgets of wetland ecosystems in China. *Global Change Biology* 25: 2061–2076. <https://doi.org/10.1111/gcb.14621>.
- Xu, Z., Y. Ban, Y. Jiang, X. Zhang, and X. Liu. 2016. Arbuscular mycorrhizal fungi in wetland habitats and their application in constructed wetland: a review. *Pedosphere* 26: 592–617. [https://doi.org/10.1016/S1002-0160\(15\)60067-4](https://doi.org/10.1016/S1002-0160(15)60067-4).
- Yarwood, S.A. 2018. The role of wetland microorganisms in plant-litter decomposition and soil organic matter formation: A critical review. *FEMS Microbiology Ecology* 94: 1–17. <https://doi.org/10.1093/femsec/fiy175>.
- Zhao, Z., H. Li, Y. Sun, A. Zhan, W. Lan, S.P. Woo, A.T. Shau-Hwai, and J. Fan. 2022. Bacteria versus fungi for predicting anthropogenic pollution in subtropical coastal sediments: Assembly process and environmental response. *Ecological Indicators* 134: 108484. <https://doi.org/10.1016/j.ecolind.2021.108484>.