

## MINI REVIEW

# The microbial landscape in bioturbated mangrove sediment: A resource for promoting nature-based solutions for mangroves

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### Abstract

Globally, soils and sediments are affected by the bioturbation activities of benthic species. The consequences of these activities are particularly impactful in intertidal sediment, which is generally anoxic and nutrient-poor. Mangrove intertidal sediments are of particular interest because, as the most productive forests and one of the most important stores of blue carbon, they provide global-scale ecosystem services. The mangrove sediment microbiome is fundamental for ecosystem functioning, influencing the efficiency of nutrient cycling and the abundance and distribution of key biological elements. Redox reactions in bioturbated sediment can be extremely complex, with one reaction creating a cascade effect on the succession of respiration pathways. This facilitates the overlap of different respiratory metabolisms important in the element cycles of the mangrove sediment, including carbon, nitrogen, sulphur and iron cycles, among others. Considering that all ecological functions and services provided by mangrove environments involve microorganisms, this work reviews the microbial roles in nutrient cycling in relation to bioturbation by animals and plants, the main mangrove ecosystem engineers. We highlight the diversity of bioturbating organisms and explore the diversity, dynamics and functions of the sediment microbiome, considering both the impacts of bioturbation. Finally, we review the growing evidence that bioturbation, through altering the sediment microbiome and environment, determining a 'halo effect', can ameliorate conditions for plant growth, highlighting the potential of the mangrove microbiome as a nature-based solution to sustain mangrove development and support the role of this ecosystem to deliver essential ecological services.

## BACKGROUND

Bioturbation is a process that affects soils and sediments in marine and terrestrial environments across the world through the creation of biogenic structures and redistribution of soil or sediment particles and elemental components (Meysman et al., 2006). Bioturbating organisms are also known as 'ecosystem engineers' because they create

and maintain habitats (Jones et al., 1994), introduce biogeochemical heterogeneity (through modulation of carbon and nutrient availability) and alter oxygen availability, redox potential, pH and temperature in sediment, thereby affecting soil or sediment microbial communities (Booth, Fusi, Marasco, Mboobo, et al., 2019; Fusi et al., 2022).

In intertidal ecosystems (e.g. salt marshes, mangroves, mudflats), which are generally characterized

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by anoxic and nutrient-poor sediment, bioturbation increases the oxygenation of the sediment, thus triggering cascades of biogeochemical reactions. Intertidal systems harbour an abundant and diverse community of bioturbating animals, feeding on or in the sediment, reworking the substrate and constructing burrow networks. Of those systems that are vegetated in the intertidal zone, mangrove forests are the most productive, even rivalling tropical forests with a global gross primary production of approximately  $4.6 \times 10^{13} \text{ mol C year}^{-1}$  (Alongi, 2014; Donato et al., 2011), which is partly exported as organic matter to the open seas and partly sunk as blue carbon (McLeod et al., 2011; S awstr om et al., 2016), defined here as the carbon stored within the plants and in the sediments in aquatic ecosystems such as mangroves (Lovelock & Duarte, 2019). Thus, the importance of mangrove forests, despite their relatively small global coverage of approximately 152,000 km<sup>2</sup> (Giri et al., 2011), extends from the local scale ecosystem services they provide (e.g. as nursery grounds for fish and coastal marine animals or physical barriers protecting the coasts from erosion) to the global scale mitigating the effects of climate change (Barbier et al., 2011; Siikamaki et al., 2012).

The sediment microbiome is fundamental for mangrove ecosystem functioning, influencing the efficiency of nutrient cycling and the abundance and distribution of key biological elements such as carbon, oxygen, nitrogen, sulphur and phosphorus (Boto et al., 1989; Bouillon et al., 2008; Holguin et al., 2001; Kristensen et al., 2008). Microorganisms comprise around 30% of mangrove sediment carbon (Alongi, 2005) and provide important ecosystem services, including organic matter decomposition, which occurs slowly due to its high tannin, polyphenol, cellulose and lignin content (Lee, 1998), and modification and removal of potentially toxic compounds (e.g. sulphide, ammonia; Palumbi et al., 2009). The synergistic actions of a complex network of bacteria, archaea and fungi have a dominant role in driving fluxes of carbon (Booth, Fusi, Marasco, Mbobbo, et al., 2019; Booth, Fusi, Marasco, Michoud, et al., 2019; Boto et al., 1989; Holguin et al., 2001) and conserving nitrogen and phosphorous within intertidal systems (Laverock et al., 2011). Fungi, in particular, are known to have a highly plastic metabolism and are able to dissolve and consume lignocellulose and other polyphenols, positively facilitating the bacterial/archaeal community (De Boer et al., 2005; Newell, 1996; Sul et al., 2013; Zhou & Chen, 2010). Methanogenic archaea and sulphate-reducing bacteria also cooperate in the degradation of organic matter (Plugge et al., 2011), and bacteria and fungi have evolved a mutual co-existence; for example, bacteria thriving on fungal exudates and fungi using substrates ameliorated by bacteria cellulose production (De Boer et al., 2005; Warmink et al., 2011).

In mangrove sediment, bioturbation is a source of heterogeneity acting as a driving force of 'microbial engines' (Falkowski et al., 2008), increasing microbial metabolic plasticity, redundancy and vicariance under changing environmental conditions (Konhauser, 2007). Enhanced oxygen availability is the main selective force driven by burrowing and sediment reworking and this oxygen is rapidly consumed at oxic/anoxic boundaries (Gundersen & Jorgensen, 1990; Michaels & Ziemann, 2013). Although oxygen penetrates only a few millimetres, this is sufficient to induce changes in sediment redox status at a depth of tens of centimetres, determining a cascade of effects influencing overall sediment biogeochemistry, microorganism abundance and community composition (Bertics & Ziebis, 2009; Dunn et al., 2012; Laverock et al., 2011). Ultimately, by affecting oxygen, carbon and nutrient availability (Bertics & Ziebis, 2009; Booth, Fusi, Marasco, Mbobbo, et al., 2019), bioturbation promotes the development of new functional niches for microorganisms and organic matter decomposition pathways. Since ecosystem resilience, the capacity to adapt under changing conditions, relies on functional diversity, bioturbation can boost resilience and have far-reaching effects on the mangrove ecosystem.

There is also evidence that bioturbation can attenuate environmental stress for other biotic components of ecosystems (Bertness & Callaway, 1993; Jones et al., 1994), which may be more important in structuring microbial communities in challenging physicochemical environments, such as those in the intertidal zone (Passarelli et al., 2014). Habitat amelioration by ecosystem engineers can also have notable effects on the ability of plants to inhabit extreme mangrove environments exposed to severe environmental stresses (Daleo et al., 2007; Fusi et al., 2022).

## AIM OF THE REVIEW

All ecological functions and services provided by mangrove environments involve, directly or indirectly, microorganisms (Allard et al., 2020). The role of microorganisms in mangroves was comprehensively reviewed by Holguin et al. (2001). Since then, advances in molecular techniques have allowed the further discovery of the diversity and functions of the mangrove sediment microbiome. New microorganisms (among others, Sefrji et al., 2021, 2022) and microbial roles in nutrient cycling have been recognized to determine profound effects (Volland et al., 2022), which will be reviewed here, on sediment microbial communities and overall ecosystem functioning. In this review, we first introduce the main groups of bioturbating macrofaunal species and their ecology and then, reviewing the more recent literature, explore the diversity, dynamics and function of the sediment microbiome considering the

impact of animal bioturbation, particularly the 'halo effect', as well as the effect of other ecosystem engineers, namely plant roots, on reconditioning of sediments. We propose future directions for studies considering ecosystem engineers, plants and animals, and microbial communities as integrated components that can shape the resilience and functionality of mangrove forests and explain their huge productivity.

## BEHAVIOUR AND ECOLOGY OF MACROBENTHIC BIOTURBATATORS

The activities of benthic macrofauna that bioturbate the sediment in intertidal ecosystems include burrowing, sediment reworking and grazing (detritivorous organisms), sediment transport and deposition of faecal material (Allard et al., 2020; Lee, 2008). Consequently, the effects of bioturbation occur over a range of horizontal and vertical distances in accordance with the size and ecology of the animal in question. We must also consider that these species rarely exist alone, and any given area may be subject to bioturbation by a range of animals of different sizes and ecology, thus the overall impact can be large and complex. In mangroves, bioturbation is performed by diverse animal groups, including crabs, ants, shrimps, worms, bivalves, fishes, mudskippers and gastropods (reviewed in Meysman et al., 2006). This review focuses predominantly on crustaceans (crabs and shrimps) and molluscs (gastropods and bivalves), which are some of the best-studied groups.

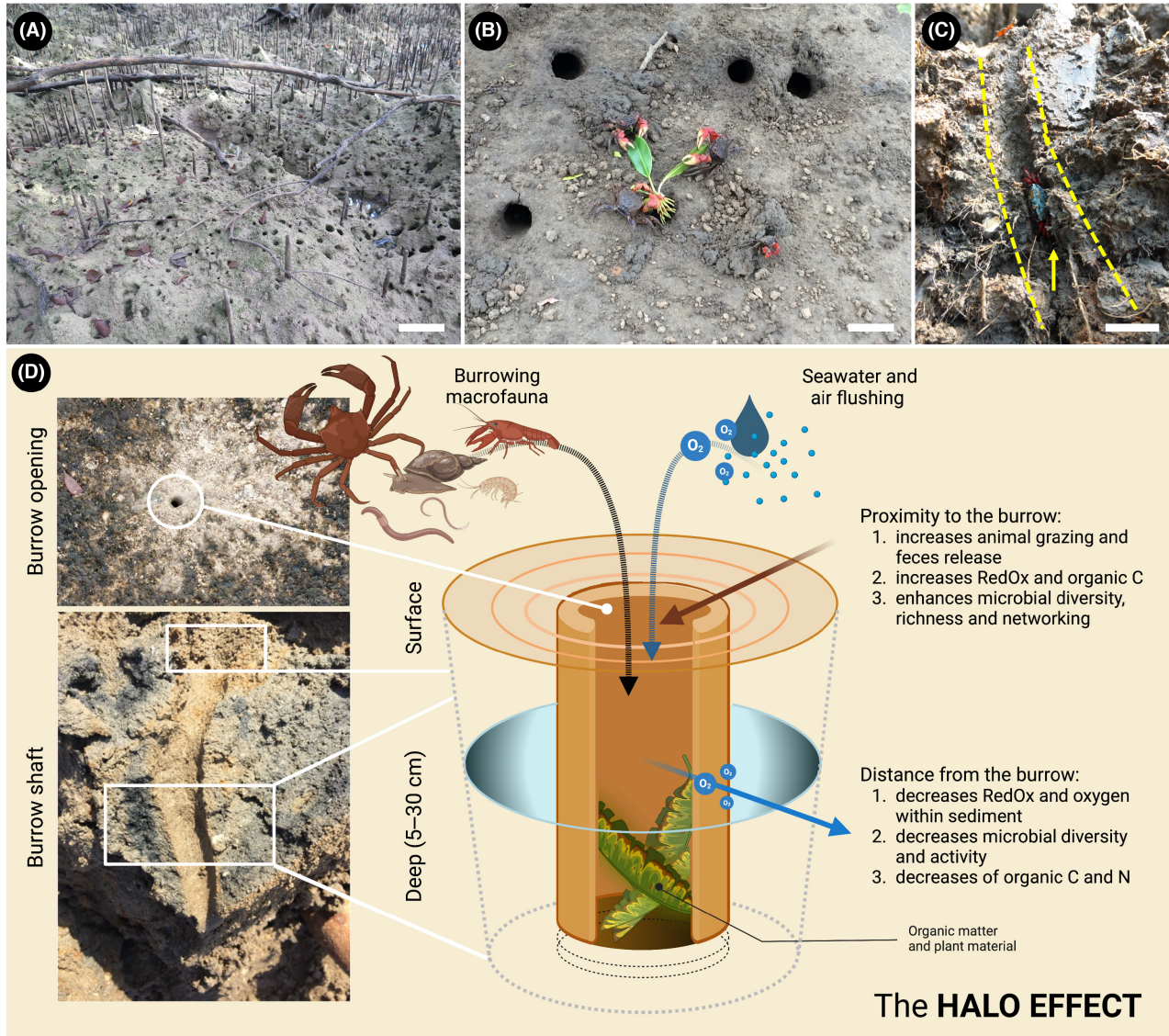
### Burrowing and sediment reworking

The greatest influence of macrofauna on sediment is undoubtedly burrow construction and irrigation, allowing oxygen to be transported to anoxic sediment and increasing solute transport for redox reactions (Aller, 2001). Burrows are unique in intertidal environments; the three-dimensional structure extends oxic/anoxic boundaries allowing enhanced oxygen diffusion from air or water (Fenchel, 1996; Kristensen & Kostka, 2005). Burrowing is one of the main driving forces mediating the structure and activity of the intertidal sediment microbiome because it affects sediment hydrology and enhances biogeochemical processes (Bertics & Ziebis, 2009; Dunn et al., 2012; Laverock et al., 2011). Biogeochemical gradients in and around macrofauna burrows are temporally and spatially dependent on the ecology of the burrow system, such as the burrow morphology and sediment characteristics (Bertics & Ziebis, 2009; Kristensen & Kostka, 2005; Nielsen et al., 2003). Diffusion of oxygen into sediment from air or water does not occur equally at the sediment surface and along burrow walls due to the

curved shape of the burrow (Fenchel, 1996). Oxygen, therefore, penetrates radially in addition to vertically, as it does at the surface (Figure 1), affecting a larger volume of sediment in a shorter diffusion distance (Fenchel, 1996). While this oxic/anoxic boundary also exists at the sediment surface, burrows are unique because their wall microbiome consumes oxygen rapidly, resulting in a very thin oxic sediment layer (Michaels & Zieman, 2013).

In intertidal sediments, at low tide, burrows enhance the downward vertical transfer of gases and act to increase the surface area for gaseous exchange and redox reactions (Kristensen, 2008), whereas at high tide, they provide sites with steep geochemical gradients since they form boundaries between anoxic sediment (rich in reduced chemical species and metabolites) and water (enriched in oxygen) (Furukawa, 2005). Uptake of dissolved oxygen by sediments via diffusion occurs at these oxic/anoxic interfaces (Furukawa, 2005), and burrows influence the rates and extent of organic matter mineralization in addition to fluxes in nutrient cycling (Aller, 2001). They allow carbon substrates and oxygen to be transported deeper into the sediment, while toxic metabolites (e.g. gaseous sulphide) can be oxidized aerobically by microbial metabolisms (Kristensen & Kostka, 2005).

Due to their abundance, burrowing crabs belonging to the families Ocypodidae, Sesarmidae and Geocarcinidae are the major and most widely distributed macrofaunal bioturbators in mangrove forests around the world (Cannicci et al., 2008; Kristensen et al., 2008; Lee, 1998, 2008). In mangrove sediment, Stieglitz et al. (2000) estimated crustacean burrows alone to increase the sediment surface area by a factor of seven. Although the general function of burrows is similar, acting as refuges from predators (Wilson, 1989), breeding sites (Mautz et al., 2011) and facilitating thermoregulation during low tide and shelter during high tides (Crane, 1975), burrow construction and maintenance by different crabs are diverse. Ocypodid crabs, a pantropical group, display little inter-specific variation in burrow construction; burrows can be cylindrical, L- or J-shaped, and penetrate up to 40 cm deep (Kristensen, 2008; Nielsen et al., 2003). Instead, those belonging to large members of the families Sesarmidae, Geocarcinidae and Ucididae are more complex and reach depths of 2 m or more (Berti et al., 2008). For instance, ocypodid crabs actively plug their burrows to trap oxygenated air inside for air-breathing at high tide (Fusi et al., 2015), while other mangrove crabs either remain in their flooded burrows or shelter on mangrove roots or mangrove litter (Cannicci et al., 2008; Lee, 2008). Population densities of different crabs differ in mangroves, and ocypodid crabs are usually much more abundant than sesarmid crabs (10–500 and 0.2–10 m<sup>-2</sup>, respectively, e.g. Andretta et al., 2014). However, as sesarmid crabs



**FIGURE 1** The halo effect. Bioturbators, by reworking sediments, allow penetration of oxygen-rich air and water in waterlogged anoxic soil. The change in redox and chemical conditions drives a change in microbiome assemblage and nutrient cycling, creating a halo effect that amplifies the impact of the bioturbation. (a) The high density of burrows (up to 80/100 per m<sup>2</sup>; see Video S1) determines a high density of burrows, with a profound impact on sediment ecology. At such a density, almost 90% of mangrove sediment is reconditioned by the bioturbators (bar = 10 cm). (B) Bioturbators (*Neosarmatium africanum* is shown) often graze leaves or other organic material and store this in their burrows, where degradation occurs and organic matter in the burrow shaft is enriched, with consequences on oxygen, redox and geochemical changes that drive specific microbial assemblages (bar = 5 cm). (C) Section of burrow shaft of *Paraleptuca chlorophthalmus* (indicated by the yellow arrow) delimited by the yellow dashed line. Along the burrow shaft, there is a large presence of mangrove root that further bioturbates the sediment (bar = 2 cm). (D) The 'halo effect': the effect that bioturbation creates around the burrow in the deep anoxic sediment and the burrow opening on the surface. The grazed light sediment and the dark un-grazed sediment full of cyanobacteria are shown. In the shaft, the sediment colour becomes darker (more anoxic) away from the burrow. The burrow shaft, instead, is light brown that shows the presence of oxidized sediment.

act to increase the sediment and water/air interface by 150%–380% compared to only 1% by ocypodid crabs, due to their larger size and deeper burrow systems, the overall effect of the two groups is thought to be similar (Kristensen, 2008). Another large burrowing sesarimid crab, *Parasesarma bidens*, was recently found to increase the air-sediment surface below ground through its burrowing activity by ~190% in Hong Kong mangroves (Agusto et al., 2021).

Bivalves are another important group that dwells in mangrove sediment; the lucinid family, in particular, has closely evolved with mangroves over the last 400 million years (Stanley, 2014). Although this group does not create a true 3D burrow structure in the sediment, they bury themselves at a depth of up to around 20 cm and, through a symbiotic association with sulphur-oxidizing bacteria in the gills (van der Heide et al., 2012), they can survive in anoxic and sulphur-rich environments.

Animals rework sediment when they construct and maintain their burrows, which causes the mixing of sediment from the surface and deep layers (Booth, Fusi, Marasco, Mboho, et al., 2019). The animal movement also reworks sediment. Molluscs are a well-represented group in mangroves (Kathiresan & Bingham, 2001), and the gastropod *Terebralia palustris* (mud whelk, family Potamididae) has been extensively studied because it is a widespread and abundant species on the Indo-Pacific coastline. This snail is large with a shell diameter of up to 15 cm and displaces sediment as it travels, leaving a trail approximately 5 mm deep (Carlen & Olafsson, 2002; Penha-Lopes et al., 2010). Another abundant gastropod, *Cerethidea decollata*, migrates daily up and down mangrove trees to graze on sediment and then avoid being submerged by the tide, reworking the sediment surface as they move (Vannini et al., 2008).

## Grazing and herbivory

Mangrove macrofaunal groups have a diverse diet and can be detritivores, herbivores, predators or omnivores (Sousa & Dangremond, 2011), with different consequential effects on the sediment environment. Most macrofauna feed on mangrove litter (Lee, 1998) colonized by a complex and diverse microbial community (Behera et al., 2019). This feeding behaviour reduces organic carbon on the surface and deeper layers into which this carbon would leach (Joly et al., 2020). Feeding on microalgae and bacteria in surface sediment has a strong impact on the structure of the surface microbial community; in addition to affecting the abundance of certain groups, the complex interactions of bacteria, archaea and fungi are also affected (Booth, Fusi, Marasco, Michoud, et al., 2019). Ocypodid crabs are detritivores that feed on surface sediment (Icely & Jones, 1978), extracting bacteria, microalgae and meiofauna from the top sediment layer and depositing pellets, thus inducing biochemical changes and oxidation in the upper 2 cm of sediment (Botto & Iribarne, 2000; Kristensen & Alongi, 2006). Like gastropods, their bioturbation activities involve sediment grazing, litter degradation and displacement of sediment as they move across the mangrove floor. Sesamid and grapsid crabs are predominantly leaf and litter consumers, although they supplement their diets with nitrogen-enriched components, such as mud and bacteria (Kristensen, 2008; Skov & Hartnoll, 2002). These crabs often store mangrove leaves and propagules in their burrows (Andretta et al., 2014; Smith et al., 1991). In fact, via consumption or burial, sesamid crabs are estimated to remove up to 79% of annual leaf-litter fall (Robertson & Daniel, 1989), trapping organic carbon inside their burrows (Kristensen, 2008; Lee, 2008). They increase the surface area for degradation by shredding

litter, and microbial communities proliferate on stored litter in burrows, contributing to the heterogeneous microbial landscape in the deep mangrove sediment (Fusi et al., 2022).

## THE EFFECTS OF ANIMAL BIOTURBATION ON MICROBIAL ACTIVITY, ABUNDANCE, RICHNESS AND DIVERSITY

Bioturbation is a strong force in structuring microbial community characteristics. Early investigations of sediment around macrofauna burrows in intertidal zones have revealed changes in composition and activity (active bacterial biomass, measured as ATP or phospholipid fatty acids) of microbial communities (Bird et al., 2000; Hansen et al., 1996; Reichardt, 1988). Sediment filter-feeding macrofauna that shows a high burrow fidelity (such as ocypodid crabs) tend to deplete microbial abundance and activity around burrows by selectively feeding on bacteria. Fiddler crabs have been widely reported to reduce bacterial abundance, richness and activity in surface sediment around their burrows, varying significantly on a small spatial scale (i.e. millimetres, Booth et al., 2019). In a mesocosm study conducted in Mexico on the fiddler crab *Minuca thayeri*, Cuellar-Gempeler and Munguia (2013) found increased surface sediment bacterial richness and abundance in the absence of crabs. The reduction of microbial activity, abundance, richness and diversity on surface sediment is largely due to grazing on the bacterial biomass thriving on the surface of the sediments, mainly composed of cyanobacteria. Other macrofaunal species, such as gastropods, may also graze on prokaryote biomass on the sediment surface and they contribute to prevent the build-up of thick cyanobacterial mats due to frequent bioturbation of the surface (Carlen & Olafsson, 2002; Levinton et al., 1984). In Guianese mangroves, Aschenbroich et al. (2016) estimated sedimentary dynamics to be modified by crab reworking on a scale of  $11.7 \pm 9.7 \text{ g of dw m}^{-2} \text{ day}^{-1}$  in pioneer and  $6.8 \pm 3.0 \text{ g of dw m}^{-2} \text{ day}^{-1}$  in young mangroves.

Bertics and Ziebis (2009) used geochemical analyses and whole-microbial assemblage fingerprinting to determine the effect of the bioturbation activity of the ghost shrimp *Neotrypaea californiensis* and fiddler crab *Leptuca crenulata*, with different burrow characteristics, on microbial diversity along geochemical gradients in coastal lagoon sediment microniches. The authors found microbial communities in the sediment surface to be similar to those in burrow wall sediment when geochemical parameters were similar, identifying the availability of oxidants as a key determining factor in microbial presence, abundance and community structure. Animals themselves are also colonized by sediment microorganisms, for example

the guts and carapaces of crabs are colonized by sediment microorganisms from both the burrow and the surface, and the burrow sediment was found to be the main colonist pool for the carapace, but bacteria can move between colonist pools (Cuellar-Gempeler & Leibold, 2018).

## ANIMAL BIOTURBATION MODIFIES OXYGEN AND REDOX IN THE MICROBIAL NICHE ENVIRONMENT: THE HALO EFFECT

Oxygen is the most energetically favourable electron acceptor in the oxidation of carbon and is consumed quickly in mangrove sediments (Gundersen & Jorgensen, 1990). Early studies demonstrated that redox potential is higher at burrow walls than surrounding sediment due to the oxidizing effect of burrowing (e.g. Ocy podid burrows, Howes et al., 1981; Katz, 1980). Therefore, oxygen presence strongly affects microbial communities, segregating aerobes and anaerobes (Bertics & Ziebis, 2009). The penetration of oxygen into sediment is affected by organic carbon content, with sediments less enriched in organic carbon displaying reduced oxygen consumption and greater penetration depths of oxygen (Cai & Sayles, 1996). In a saltmarsh, Dollhopf et al. (2005) examined the microbial communities in fiddler crab burrow walls using quantitative 16S rRNA gene-based profiling, targeting specific sulphate-reducing and iron-reducing anaerobic bacteria; they found those microorganisms to be active within 1 cm of the burrow wall, highlighting the short penetration distance of oxygen. In another study of salt marshes, Michaels and Zieman (2013) found oxygen present until depths of only 1 cm and oxic zones to extend 0.5 mm through fiddler crab burrow walls (though this is expected to be greater in well-drained sediment). Kristensen et al. (2000) also showed that oxygen penetration depths in mangrove sediment positively correlate with the bioturbation level, with oxygen penetrating further in sediment heavily bioturbated by crabs. In a study in a Japanese mangrove, Mchenga and Tsuchiya (2008) investigated the burrowing crab *Helice formosensis* and found their presence to significantly affect the redox potential of sediment in the burrow opening shaft due to the increase in sediment oxygenation. Around *Ucides cordatus* burrows in Brazil, Pülmanns et al. (2014) found sediment redox potential to be higher around burrows, noting that this likely increases aerobic decomposition processes. Booth et al. (2019) also found mangrove sediment oxygen content to drop to zero within the first 5 mm of unbioturbated sediment and an mm scale penetration of oxygen through fiddler crab burrow walls in bioturbated areas despite the behaviour of fiddler crabs to plug their burrows, trapping oxygenated air, during high tide.

Although sediment was anoxic around burrows, pulses of oxygen were recorded that were likely due to infrequent burrowing, and this may contribute to an increase in the level of redox potential as far as 5 cm from the burrow wall to depths of 5 cm compared to the unbioturbated sediment. This redox potential shift is significant because it determines the microbial-driven biogeochemical processes in bioturbated sediment. In a study of sesamid crab burrows, a large and predominantly herbivorous group, Booth et al. (2019) showed that burrow walls were enriched in anaerobic taxa. While the increased microbial activity found at the burrow walls of fiddler crabs is likely due to increased oxygen, in litter-trapping crab burrows it may be also due to the enhanced organic matter in burrows and taxa involved in organic matter decomposition.

The overall effect of sediment engineering by bioturbators has been defined as a 'halo effect' (Booth et al., 2019). The burrow 'halo effect' can be extensive in a mangrove forest and it has been estimated to affect up to the 85% of the mangrove sediments, with important consequences on sediment biogeochemistry, the hospitability for the mangrove plants and positively increase their growth and biomass accumulation (Fusi et al., 2022).

## ANIMAL BIOTURBATION DRIVES MANGROVE SEDIMENT MICROBIOME NUTRIENT CYCLING

Initial studies of mangrove sediment microorganisms were limited to estimates of broad taxonomic group abundance, but advances in molecular methods have rapidly improved our understanding of the mangrove sediment microbiome, highlighting their functional diversity and importance in nutrient cycling. Heterotrophic prokaryotes dominate mangrove sediments (Alongi, 2005) and sulphate-reducing, methanogenic, nitrogen-fixing, denitrifying and iron- and manganese-reducing prokaryotes are ubiquitous. Sediment redox status can range from more than 300 mV at the surface to -200 mV at 1 m depth (Alongi, 2005), providing a wide range of redox conditions able to harbour different microbial functional groups (Falkowski et al., 2008; Faulwetter et al., 2009; Finlay et al., 1997). Bacteria show great metabolic plasticity, switching terminal electron acceptors in response to the availability of their preferred substrates and environmental conditions; for example, several nitrates- and sulphate-reducing bacteria can switch to Fe(III) reduction (Konhauser, 2007). Redox reactions in burrow-surrounding sediment can be extremely complex, with one reaction creating a cascade effect on the succession of respiration pathways and micro-niches, which likely facilitates the overlap of different respiration pathways (Konhauser, 2007).

## Carbon

Mangrove forests globally boast organic carbon accumulation levels of approximately  $26.1 \text{ Tg year}^{-1}$  (Breithaupt et al., 2012). Organic matter deposited on the mangrove floor is colonized by sediment fungi and bacteria capable of degrading lignocellulose (Boto et al., 1989; Holguin et al., 2001). While mangroves are large exporters of coastal carbon, accounting for an estimated 10% of dissolved organic carbon transported to oceans (Dittmar et al., 2006), studies suggest that the sediment microbiome consumes most of the carbon dissolved in interstitial water in mangrove sediment (Holguin et al., 2001), supporting high retention of this element within the system.

Many studies have investigated the role of microorganisms in the degradation of above-ground organic matter in mangroves (Alongi, 1998, 2012); however, their role in sediment is less well known (Holguin et al., 2001). Bioturbation has a spatially modifying effect on organic matter accumulation and degradation. As mentioned, many crab species actively remove litter from the mangrove surface to store in their burrows. Two of the largest species, *Neosarmatium africanum* in East African mangrove systems and *Ucides cordatus* in Brazil, can remove up to almost 80% of mangrove ground litter, respectively (Nordhaus et al., 2006). Fungi proliferate on this litter, increasing the palatability for the crabs and, correspondingly, studies have found burrow walls of these large herbivores to be enriched in POC and a higher abundance of bacteria, archaea and fungi (Booth et al., 2019). This enrichment of organic matter in burrow sediment extends no further than 1 cm horizontally (Gillis et al., 2019). In a study of *N. africanum* burrows, Booth et al. (2019) found saprotrophic fungi to be the key components of microbial networks throughout burrow sediment, likely enriched in sediment from leaf litter in the burrow. Interestingly, the experimental design of Gillis et al. (2019) included the study of artificial burrows and the authors found that organic matter breakdown in the sediment was unrelated to the presence of crabs or leaves in burrows, indicating it is the burrow structure itself and increased oxygen penetration which is important for promoting organic matter breakdown and altering microbial community function. Functional changes in mangrove sediment microbial community structure have also been shown to be related to the aerobic degradation of complex carbohydrates (Palit et al., 2022).

## Nitrogen

Mangrove sediments are a sink for nitrogen derived from nitrogen fixation, litterfall and tidal input (Ray et al., 2014) and microorganisms mediate its bioavailability through several processes, such as nitrification and denitrification (Holguin et al., 2001). High nitrogen fixation rates have been associated with all components

of mangrove ecosystems, including pneumatophores, decomposing litter and cyanobacterial mats that cover the sediment surface and also within the sediment (see refs in Holguin et al., 2001). Nitrogen-retaining microbial processes were identified in early studies of mangrove sediment, for example, the possible role of dissimilatory nitrate reduction in ammonium (Tiedje, 1988) and anaerobic oxidation of ammonium (Jetten et al., 2005).

Bioturbated surface sediment, although typically depleted in POC, is enriched in PON resulting from the deposition of nitrogen-rich faecal pellets, and burrow walls are also hotspots of organic nitrogen (Booth et al., 2019). Through their various bioturbation activities, macrofauna stimulate nitrification–denitrification processes by extending oxic-anoxic surfaces and increasing the passage of nutrients (Laverock et al., 2011). Bioturbation has implications for nutrient flux rates because the extension of the oxic sediment surface has an immediate increasing effect on coupled nitrification–denitrification reactions which occur across the oxic/anoxic boundaries (Aller, 2001), resulting in overall nitrogen loss from sediments (Gilbert et al., 1995). Dissolved organic nitrogen flux across the sediment/water interface can be 2.5–3.5 times higher in bioturbated compared to unbioturbated mangrove sediment (Kristensen, 2000).

A study of key genes involved in nitrogen cycling demonstrated that microniches within burrow environments indirectly affect fluxes in the nitrogen cycle by modifying anaerobic respiration pathways within the sediment, for example by inhibitory effects of increased sulphate reduction on nitrification (Laverock et al., 2011). The expansion of oxidized zones allows aerobic taxa to proliferate in abundance and diversity. In a study of the sesarmin crab *Parasesarma bidens* in Hong Kong mangroves, Chen and Gu (2017) found  $\text{NH}_4$  and ammonia-oxidizing archaeal diversity, richness and abundance to be higher in bioturbated sediments. Burrowing fauna typically enhance sediment nitrification and denitrification rates due to the increased availability of nitrate (Bertics et al., 2010; Howe et al., 2004). Laverock et al. (2014) highlighted the importance of macrofaunal bioturbation in affecting the temporal variation in coastal sediment nitrogen cycling, finding mud shrimp burrows to provide a unique environment, with abundances of bacterial genes belonging to different functional guilds involved in nitrogen cycling to differ compared to surface sediment. Diazotrophs in burrow walls fix nitrogen and release ammonium from the anoxic sediment into the burrow water to be removed by tidal flow (Bertics et al., 2010). Mud crab (*Helice crassa*) burrow walls are important niches for nitrogen-cycling bacteria in New Zealand mangroves (Vopel & Hancock, 2005). In Australian mangroves, bioturbation by the marine yabby (*Trypaea australiensis*) stimulates benthic metabolism and nitrification due to the removal of anoxic sediment micro-patches (Jordan et al., 2009).

*T. australiensis* excavates complex burrows up to 1 m deep and buries organic matter (in this case, *Avicennia marina* leaves), and the authors of this study attributed increased microbial metabolism, nitrification, total nitrate reduction and denitrification to the increase in oxic sediment zones created by burrow walls.

In sesarmid crab burrows in South African mangroves, Booth et al. (2019) found nitrate availability, a significant driver of bacterial community composition, to increase further from the burrow wall and, thus, it is likely rapidly consumed in the burrow wall sediment by microorganisms and/or flushed out at high tide. Nutrient limitation in arid mangroves with minimal external inputs, such as those in the Red Sea, results in stunted plant growth (Almahasheer et al., 2016). In these systems, atmospheric nitrogen fixation can be an important nitrogen input. Crab bioturbation, measured as crab burrow density, has been found to negatively impact  $N_2$  fixation rates, possibly linked to grazing by crabs on cyanobacteria (Qashqari et al., 2020).

## Sulphur and iron

Sulphur is abundant in mangrove sediment and the transformation of sulphur species is a highly active process (Lyimo et al., 2009). In mangroves with highly anaerobic sediment, sulphate-reduction is a major respiration pathway accounting for almost 100% of sediment  $CO_2$  emissions (Kristensen et al., 1991). The high abundance of organic matter and low availability of oxygen favour the growth of sulphate-reducing bacteria that play a significant role in the decomposition of organic matter through dissimilatory sulphate reduction (Jørgensen, 1982). In Brazilian mangrove sediment, *Betaproteobacteria* (sulphur oxidizers), *Gammaproteobacteria* (sulphur oxidizers) and *Deltaproteobacteria* (sulphate reducers) are the most abundant groups associated with sulphur cycling (Andreote et al., 2012; Varon-lopez et al., 2013).

In mangroves rich in iron, iron respiration may be equally if not more important than sulphur respiration if processes which allow iron oxidation are present, since  $Fe^{3+}$  is a more favourable electron acceptor (Kristensen et al., 2000; Kristensen & Alongi, 2006). This process generates pyrite (iron sulfide) due to the reaction of sulfide with detrital iron-bearing minerals (Ferreira et al., 2007; Raiswell & Canfield, 1998). Bioturbation introduces oxygen into sediments, altering reactive sulphur and iron forms and affecting which electron acceptors are used in carbon oxidation (Kristensen & Kostka, 2005). The mediating effect of bioturbation on sulphate and iron respiration rates has been highlighted in various studies (reviewed in Kristensen & Alongi, 2006). Iron-reducing bacteria were found to be more abundant in sediment rich in

$Fe(III)$  and bioturbated by fiddler crabs than in unbioturbated sediment (Dollhopf et al., 2005). By maintaining suitable redox conditions for  $Fe^{3+}$  reduction, bioturbation reduces the accumulation of toxic sulphide by suppressing sulphate reduction and reducing sulphide precipitation as pyrite (Kristensen & Kostka, 2005). The dominance of iron reduction as a respiration pathway and the almost complete suppression of sulphate reduction due to bioturbation by *Uca* spp. has also been observed in intertidal salt marshes, with the converse pattern observed in adjacent unbioturbated sediment (Gribsholt et al., 2003).

The unsteady-state redox of mangrove sediment was highlighted in a recent study of mangrove sediment cores, which revealed evidence of sudden oxygen input causing sudden and significant reoxidation of reduced sulphur (Ding et al., 2014). Nielsen et al. (2003) remarked on the importance of fiddler crab burrows in effectively preventing sulfide accumulation in mangrove sediment due to sulfide reoxidation. Furthermore, in a study of ocypodid crabs (*Ucides cordatus* and *Uca maracoani*) in mangroves, Araújo et al. (2011) noted the higher redox potential and a higher degree of pyrite oxidation associated with bioturbated sediment compared to sediment unaffected by bioturbation. In this study, species with larger and deeper burrows determined a more pronounced oxidizing effect on iron sulphides (Araújo et al., 2011). While ocypodid crabs generally forage in the upper few millimetres of mangrove sediment, their effective mixing depth extends much deeper than this. Kristensen and Alongi (2006) found *Gelasimus vocans* to affect the presence of forms of iron and sulphur to depths of 2 cm, observing a higher content of  $Fe(III)$  (i.e. oxidized forms) and lower content of  $Fe(II)$  and  $Fe^{2+}$ ,  $H_2S$ ,  $FeS$ , elemental sulphur and  $FeS_2$  –pyrite (i.e. reduced forms), due to presumed oxidation of surface and subsurface sediments through feeding activities and burrow construction. Fiddler crabs have been shown to stimulate the reoxidation of sulphide, reducing accumulation in mangrove sediment. In a study of fiddler crabs, Booth et al. (2019) found sulphate-reducing bacteria to be more abundant and diverse away from crab burrows in accordance with lower redox status. However, burrows do not always have the same effect; in a study of a large burrowing sesarmid (*N. africanum*), Booth et al. (2019) found abundant sulphur-reducing bacteria in burrow wall sediment. This species excavates in the range of  $80\text{--}210\text{ cm}^3\text{ m}^{-2}\text{ day}^{-1}$  (Kristensen, 2008), and this is unidirectional from the deep to the surface, so highly anoxic sediment from deep below the surface is spread along the burrow walls.

In reducing intertidal sediments, obligate symbiotic associations between bacteria and animals are common (Duperron et al., 2013; Hill et al., 2006; Laurent et al., 2009). By hosting sulphide-oxidizing bacteria, bivalves can have an important role in cycling buried organic material and ecosystem productivity



(Johnson et al., 2002). Chemosymbiotic relationships between bacteria and bivalves of the families *Lucinidae* and *Solemyidae* have been well studied in highly sulfidic anoxic shallow-water marine sediments, providing examples of most types of association (reviewed in Roeselers & Newton, 2012). Bivalve symbionts are typically associated with the gills, either intracellularly within bacteriocytes or extracellularly within the gill tissue, or epibiotically attaching to the gill surface (Roeselers & Newton, 2012). However, symbionts are also involved in processing metabolic waste and nutrient acquisition and chemical defence (Lee et al., 2009), such as the nitrogen-fixing bacteria *Teredinibacter turnerae* living in symbiosis on the gills of the bivalve *Neoteredo reynei* (Distel et al., 2002). Lucinid bivalves have received attention due to their supposed obligate symbiosis with sulphide-oxidizing bacteria in their gills (Gros et al., 2003). These bivalves inhabit the boundaries of oxic/suboxic sediment of mangrove fringes (Lebata, 2001); bioturbating the sediment and tunnelling with the foot provides access to interstitial water which passes into the mantle cavity (Dando et al., 1986).

## Methane

Methane respiration is a major respiration pathway in mangrove sediment (Mohanraju & Natarajan, 1992), and its magnitude is related to freshwater input, sea level and organic input (Call et al., 2015; Sea et al., 2019). More recently, the importance of archaea in carbon transformation, using methanol as a substrate, by the process of methanogenesis has been observed (Lyimo et al., 2009; Taketani et al., 2010), and the discovery of highly diverse methanogenic archaea in mangroves in Saudi Arabia, Brazil and India suggest that methane metabolism is globally important (Imchen et al., 2017). Cyanobacterial mats also significantly contribute to methane production in mangroves (Bižić et al., 2020). The formation of methane by cyanobacteria contributes to methane accumulation in oxygen-saturated marine and limnic surface waters. In these environments, frequent cyanobacterial blooms are predicted to increase further because of global warming potentially having direct positive feedback on climate change (Bižić et al., 2020).

## MANGROVE PLANT BIOTURBATION AND ITS EFFECT ON THE SEDIMENT MICROBIOME

As shown in several studies, plants have developed a tight partnership with the edaphic microbial communities, mainly bacteria, fungi and archaea, that together form the plant microbiome (Marasco, Ramond, et al., 2023). These associated microorganisms

accomplish essential functions and ecological services complementary to those encoded by the host plant, having a crucial role in sustaining plant fitness and growth (Bulgarelli et al., 2013; Trivedi et al., 2020). Some of these microorganisms have been part of a co-evolutive process with the plant hosts, developing strong associations that vary from mutualism to commensalism and parasitism (Berg et al., 2014; Sánchez-Cañizares et al., 2017). Mangroves are not an exception and—like all plants—they cannot be understood as isolated entities but as an association between the host plant and its associated microbiome (Allard et al., 2020; Soldan et al., 2019). The microbial recruitment process mediated by the mangrove root system starts in the sediment (Alzubaidy et al., 2016; Andreote et al., 2012). Mangrove plants are also important ecosystem engineers and root growth deeply modifies sediment physical characteristics, biochemistry, and microbial communities (Pii et al., 2015; Zhalnina et al., 2018; Zhao et al., 2019). Plants, as primary producers, develop the roots in the soil to obtain water and nutrients. This belowground portion of the plant represents between 20% and 85% of a plant's biomass (Jackson et al., 1996). During the growth of the root system, the plant roots passively penetrate through multiple layers of soil/sediment/substrate (i.e. pushing aside the soil rather than excavating it) with increasing pressure. Bioturbation by roots has a profound impact on the soil by disturbing and/or mixing events mainly driven by root growth and decay. There is evidence that roots can penetrate deep into the soil and initiate intrusion in rock/mineral substrates through mineral weathering and dissolution (Stothoff et al., 1999). The entire bioturbation process results in a network of channels/macropores that promote water infiltration, soil transport and gas exchange and stimulates microbiological activity (Sarker et al., 2021). For instance, in mangrove ecosystems, plant roots perturb the sediment and the associated microbial communities by permeating the substrate with oxygen and a vast array of compounds during growth and root exudation, respectively (Bashan & Holguin, 2002; Kuzyakov & Domanski, 2000; Preece & Peñuelas, 2020). In this way, the sediment, which tends to be anoxic, is oxidized and enriched in nutrients, such as sugars, amino acids, organic acids, vitamins and sterols, forming the so-called rhizosphere (Hartmann et al., 2009; Kristensen et al., 2012). This portion of the soil, in contact with the root and consistently enriched in nutrients, is a 'hot spot' for microorganisms (in terms of abundance), their activity and interactions (Preece & Peñuelas, 2020; Trivedi et al., 2020). Regardless of their beneficial or pathogenic nature, edaphic microorganisms living in the sediment are highly prone to colonize such nutrient-rich regions (Bulgarelli et al., 2013). However, not all sediment microorganisms are able to form part of the plant-associated microbiome, because a series of plant-mediated processes drive the selection and

recruitment of a limited pool of such microorganisms (Van Der Heijden & Schlaeppi, 2015).

Studies conducted on mangroves have shown that microorganisms can reach up to  $10^9$  cells  $g^{-1}$  (range,  $10^6$ – $10^9$ ) in the rhizosphere compared with the lower microbial cell abundance in the bulk soil (range,  $10^5$ – $10^7$ ) (Zuberer & Silver, 1978). Along with cell abundance, mangrove roots also influence bacterial composition in the rhizosphere (Gomes et al., 2010). For example, a study conducted on *Rhizophora mangle* in Brazil revealed that bacteria belonging to *Rhizobiales*, *Campylobacterales* (mainly *Sulfurovum*), *Methylococcales* (mainly aerobic methanotrophs of *Methylomonas* genus) and *Vibrionales* (mainly *Vibrio* and diazotrophic *Listonella*) tend to be more abundant in the rhizosphere than in the bulk sediment (Gomes et al., 2010). Diazotrophic bacteria capable of fixing atmospheric nitrogen into an assimilable form (i.e. ammonia) contribute to plant productivity by providing organic nitrogen (Flores-Mireles et al., 2007). Also, photosynthetic anoxygenic (mainly belonging to class *Alphaproteobacteria*) and methanotrophic bacteria can meliorate mangrove productivity through carbon fixation and reduction of methane emissions, respectively (Bashan & Holguin, 2002; Shiau et al., 2018). Considering the fungal components of the mangrove microbiome, *Aspergillus* and *Schizosaccharomyces* are the most dominant fungal genera in the rhizosphere (Simoes et al., 2015). Members of these groups are important for mangrove ecosystems due to their capacity to induce Indole-3-acetic acid (IAA) synthesis, thus leading to the regulation of plant growth and development (Arfi et al., 2012; Simoes et al., 2015). The information present in the literature clearly shows how the microbial diversity and composition of the plant microbiome influence plant growth and health (Trivedi et al., 2020).

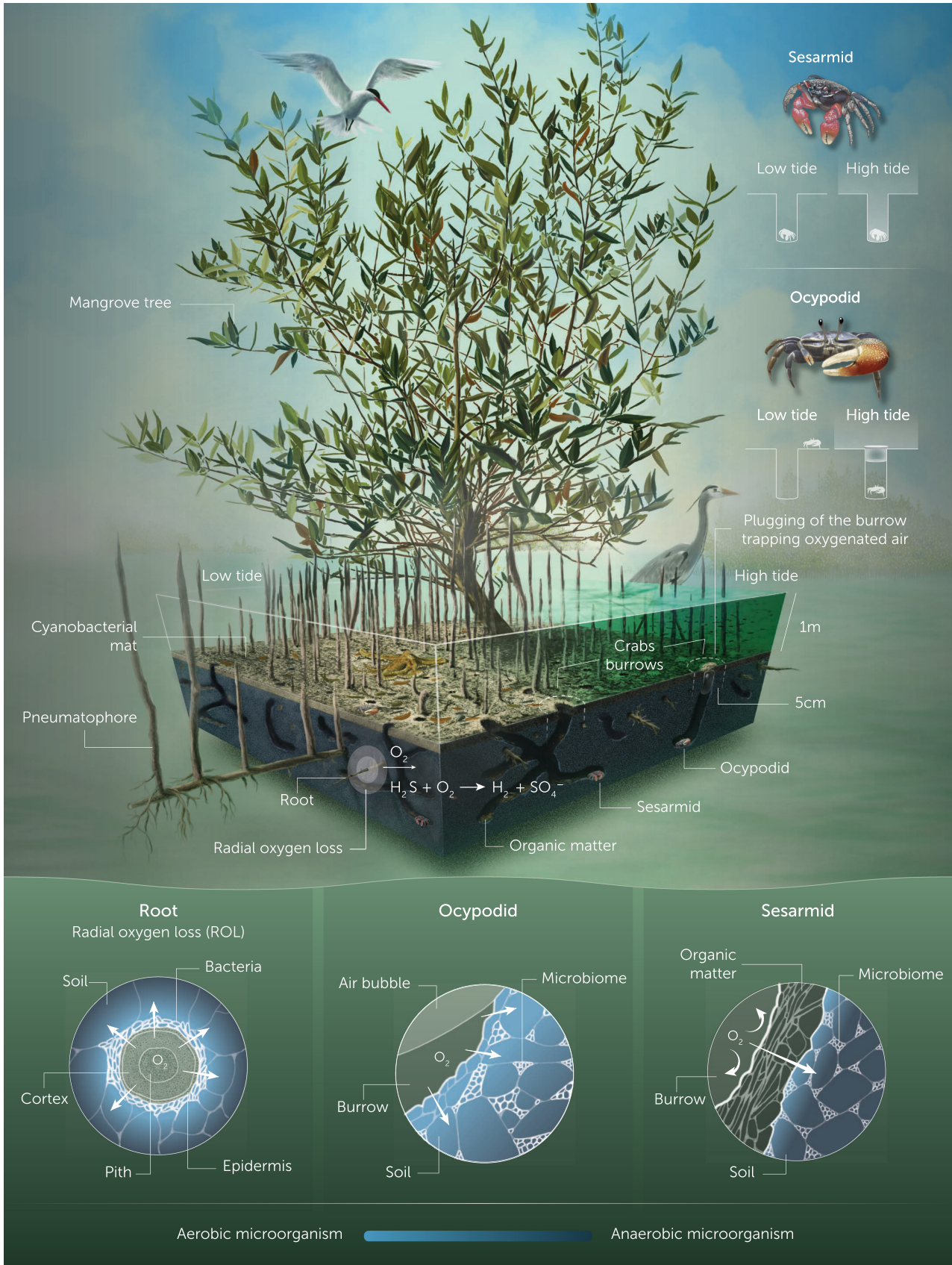
A further impact of plant roots is through oxygen diffusion occurring within roots, which is termed radial oxygen loss (Armstrong & Beckett, 1987; Xu et al., 2013). The result is an aerobic microenvironment around which there can be particular consequences for the formation of  $NO_3^-$  in the rhizosphere, as the microenvironment promotes the growth of aerobic organisms such as bacteria and archaea that oxidize ammonia (Cheng et al., 2020; Li et al., 2008). This may have a significant impact particularly anoxic waterlogged mangrove

sediment. Cheng et al. (2020) highlighted that their finding of greater N acquisition by seaward pioneer *Avicennia marina* trees compared to other more landward mangrove species being strongly linked to radial oxygen loss (ROL), and the associated regulation on N transformation in the rhizosphere, may contribute to our understanding of mangrove zonation.

## BIOTURBATION AND THE SEDIMENT MICROBIOME: A MISSING LINK IN THE PLANT PRODUCTIVITY PARADOX

Mangrove productivity rivals that of tropical rainforests (Donato et al., 2011). Yet, these ecosystems are characterized by stresses such as sediment nutrient deficiency, salinity, high levels of toxic compounds and anoxic conditions. Mangrove plants are perfectly adapted, both physically and physiologically, to cope with these stresses (Cheng et al., 2015). However, positive interactions between plants and animals may also be of particular importance in harsh environments, whereby one or both groups may buffer environmental stresses, directly or indirectly, for the other (Bertness & Callaway, 1993; Fusi et al., 2022). In mangroves, there is evidence that suggests burrowing by macrofauna may be an important factor affecting plant growth and sustaining mangrove productivity (Figure 2). The ecological effects of ocypodid crabs on mangrove plants were described by Smith et al. (2009), who investigated the effect of burrowing on white mangrove (*Laguncularia racemosa*) growth and productivity in a restored Florida coastal area. The authors found that crab burrowing had a positive impact on the growth of trees (height and diameter) and leaf production compared to areas with crab exclusion zones, with a positive relationship between growth and productivity and burrow density. The same study also found that sediment with crab exclusion had reduced redox potential and higher interstitial water salinity and that young mangrove growth was higher in areas with reduced salinity. Salinity is an important stress factor for mangrove growth, and increasing water flow through sediment burrowing can reduce interstitial water salinity (Montague, 1982). An earlier crab exclusion experiment by Smith et al. (1991) in Australian mangroves also measured increased forest

**FIGURE 2** Mangrove microbiome landscape. Bioturbation by animals and plants contributes to diversify and enrich the microbial community in mangrove sediment. Burrowing and grazing species alter the physico-chemical properties of the sediment in different ways by allowing oxygen to penetrate water-logged anoxic soil or by storing organic material along the burrow wall. Plant roots modify the condition of the sediment by oxidizing the surrounding sediment and changing the environmental conditions, allowing beneficial microorganisms to colonize the rhizosphere and the root, providing essential nutritional and protection support to the plant facing the stressful conditions of the intertidal habitat. Sediment engineering by burrowers increases the redox potential of the sediments by determining a 'burrow halo effect' (Booth et al., 2019) that ameliorates sediment conditions for plant growth. As a result, the plant can increase its biomass and productivity (Fusi et al., 2022). This indicates that manipulation of bioturbation may represent a Nature-Based Solution to sustain mangrove forests under the challenging conditions of climate change.



productivity (stipule fall) in control plots with mangrove crabs compared to exclusion plots. In a mesocosm experiment, Kristensen and Alongi (2006) recorded the

positive impact of fiddler crabs (*Gelasimus vocans*) on the growth of *Avicennia marina* seedlings, in terms of leaf and pneumatophore growth. While mesocosm

experiments have their merits and provide an ideal situation for experimental manipulation and testing broad-scale mechanisms, studies of sediment biochemistry and the sediment microbiome (essential components to understand and incorporate in any study of plant productivity) require minimal to no disturbance to sediment structure. This can only be achieved under natural conditions. Fusi et al. (2022) provided experimental evidence that in a natural arid mangrove setting bioturbation improves the performance of mature mangrove plants, specifically in terms of tree height, branch diameter and the number of pneumatophores. The mechanism of this positive interaction suggests that bioturbation boosts plant growth by reducing plant stressors, such as salinity, and cycling important nutrients. Hydrogen sulphide is known to inhibit plant growth and nitrogen uptake by plants (Bradley & Morris, 1990). Mangrove plants possess their own mechanisms to cope with this stress, oxidizing the compound within their rhizospheres (Smith et al., 2009), but macrofauna burrows in proximity to roots can also facilitate the oxidation of hydrogen sulfide by increasing oxygen availability in sediment. Zhao et al. (2014) reported increased hydrogen sulphide emission in salt marshes with crab burrows, thus reducing sediment hydrogen sulphide levels and promoting its oxidation.

Furthermore, bioturbation may engineer an altered sediment microbiome, mainly through the increased availability of oxygen and consequent effects on biochemistry, beneficial for plant growth (Fusi et al., 2022). The role of arbuscular mycorrhizal fungi in providing nutrition to plants (Bertness, 1985) is a well-known symbiotic association that has evolved over the last 400 million years in terrestrial ecosystems (recently reviewed in Puginier et al., 2022). As fungi are obligate aerobes, this relationship has largely been ignored in waterlogged anoxic sediment where spores are thought to be unable to develop (Carvalho et al., 2004). However, recent findings show that plant growth in 'anoxic' wetlands is known to be ameliorated by crab (*Chasmagnathus granulatus*) burrowing which allows mycorrhizal fungi to colonize plant roots in salt marshes (Daleo et al., 2007). In this example, crabs regulate abiotic factors, increasing oxygen availability and redox potential of sediment, facilitating arbuscular mycorrhizal growth (Daleo et al., 2007). The plugging behaviour of fiddler crabs maintains aerobic conditions within the burrow even during high tide (Fusi et al., 2015), which could also facilitate the development of mycorrhizae. Furthermore, Booth et al. (2019) recently highlighted the pivotal role of fungi in sediment microbial networks in mangrove sediment both around macrofaunal burrows and in unbioturbated sediment.

Mangrove environments can be particularly interesting sites for investigations of fungi taxonomy (Bahram & Netherway, 2022) because they are bridges between the land and the sea and many colonization events

have occurred in the evolution of fungi from both marine-to-terrestrial and terrestrial-to-marine environments. Mangrove fungi are the second largest component of the marine fungal world, and yet they are still poorly studied (as highlighted by Thatoi et al., 2013). Fungi in mangrove ecosystems comprise marine and terrestrial groups, referred to as manglicolous fungi, and are highly biodiverse, encompassing saprophytic, parasitic and symbiotic forms (Shearer et al., 2007). Most mangrove fungi are saprophytic with an important intermediary role in nutrient cycling, being capable of breaking down organic matter prior to colonization and further decomposition by other microorganisms (Holguin et al., 2001). Similar to other microorganisms, fungal diversity is dependent on physico-chemical characteristics of the environment, such as salinity, tidal range and temperature (Jones, 2000).

Mangrove leaves are highly resistant to degradation by most microorganisms due to the high content of lignocellulose, tannins and other recalcitrant compounds (Robertson, 1988). Hyde et al. (1998) identified a number of phylogenetically diverse marine fungi capable of degrading lignocellulose. Fungi can tolerate low oxygen conditions, and thus mangroves are likely one of the dominant degraders of lignocellulose and other plant material. Although several systematic studies exist, the role of fungi in sediment, except for the primary degradation of organic matter, is largely unknown. As mentioned, arbuscular mycorrhizal fungi are prevalent in mangroves (Sengupta & Chaudhuri, 2002; Wang et al., 2010). In fact, Wang et al. (2011) reported arbuscular mycorrhizal fungal diversity associated with mangrove roots to be equal to that associated with terrestrial plant roots, although areas affected by intensive flooding were associated with reduced diversity and root colonization, likely inhibited by lack of oxygen outside the rhizosphere. In a study of sesarmid crabs in a South African mangrove, Booth et al. (2019) found saprotrophic fungi to be a pivotal component of microbial community networks when exploring interactions between bacteria, archaea and fungi in burrow sediment and unbioturbated sediment. Fungi were the major structuring component and keystone species of microbial networks in all sediment niches examined. The authors underlined the suggested importance of the fungal microbiome in mangrove sediment, and that studies of microbial networks should be a focus moving forwards. In an intertidal marsh system in China, Wu et al. (2021) found soil microbial community composition to be altered by crab bioturbation; for fungi, bioturbation was found to reduce the modularity of fungal networks and fungal diversity was reduced in bioturbated sediment (the latter being consistent with Booth et al., 2019, and possibly because crabs mechanically break up hyphal networks).

Undoubtedly, bioturbating fauna increase habitat heterogeneity through their various activities including

burrowing, sediment mixing and trapping organic matter. This heterogeneity in the sediment environment promotes functional redundancy in microbial communities, which can increase the ecological resilience of the entire ecosystem. Studies of sediment and soil microbial communities are increasingly addressing all microbial components as a synergistic unit capable of sustaining the persistence and resistance of mangrove ecosystems to global change (Palit et al., 2022).

## THE MANGROVE MICROBIOME AS NATURAL CAPITAL TO BE LEVERAGED BY MANIPULATIVE SEDIMENT BIOTURBATION

Mangrove forests are under a series of threats affecting their health and ecosystem functioning. This review has highlighted the importance of the sediment microbiome in the functioning of the mangrove ecosystem, and thus studies of the processes affecting the sediment microbiome and nutrient cycling are critical in assessing their functioning and resilience to threats. Since we know that many organisms responsible for bioturbation are sensitive to environmental changes (Sunday et al., 2019), such as temperature and pH, the effect of ongoing ocean warming on bioturbating organisms will undoubtedly have consequential effects on nutrient cycling by sediment microorganisms. Mangroves are no exception. As highlighted by Booth et al. (2019), sesamid crabs may be extremely important mediators of the sediment microbiome due to their role in trapping organic matter. Furthermore, bioturbation by the crab *Ucides cordatus* in semiarid Brazilian mangroves has been found to reduce nitrous oxide ( $N_2O$ ) emissions from sediment, identifying an important ecological service reducing emissions of greenhouse gas (Otero et al., 2020). A warming climate affecting the geographic distribution of mangrove macrofauna will likely have important consequential effects on the sediment microbiome and thus on the overall functioning of mangrove ecosystems.

Putting the mangrove sediment microbiome into action to enhance the resilience of the system to stress is becoming a concrete possibility in light of improved understanding. The current literature review has revealed that bioturbation favours the oxygen balance in the first tens of centimetres of the sediment (Figures 1 and 2). Such changes in the redox conditions of sediment favour the nutrient turnover and detoxification of the mangrove ecosystem from natural toxic compounds like sulphides and wood-derived polyphenols. This, in turn, enhances plant growth and wood accumulation with a potential benefit for carbon storage. Hence, the mangrove sediment microbiomes can be seen as a natural capital to reinforce the mangrove forests' resilience,

which in many countries represents an important and growing economic asset. Different studies propose components of the mangrove sediment microbiome as probiotic tools for favouring mangrove growth and resilience. For instance, Soldan and colleagues have identified a bacterial mangrove endophyte isolated from *A. marina* propagules from the Red Sea as capable of enhancing root development from the early plantlets from propagules, concluding that such root growth promotion may favour the establishment of new mangrove plants challenging the dispersal effect that currents and tides may have (Soldan et al., 2019). If the current evidence is confirmed by further quantitative studies, manipulating bioturbation may become a concrete nature-based solution that can be leveraged to alleviate the increasing stresses that mangrove forests are exposed to and improve their role as efficient carbon sinks.

New technologies for studying the culturable and the whole microbiome of mangrove sediment and the other compartments of the ecosystem suggest that many microorganisms are yet to be discovered and may represent potentially invaluable resources for the sustainability of tropical coastal ecosystems (Allard et al., 2020; Demain & Vaishnav, 2011; Sefrji et al., 2022). For example, three novel bacteria have been isolated from bioturbated sediments from arid mangroves of the central Red Sea: *Kaustia mangrove* (Sefrji et al., 2021), *Mangrovibacillus cuniculi* (Sefrji et al., 2022) and *Mangrovivirga cuniculi* (Sefrji et al., 2022). The importance of these findings is highlighted by the biotechnology potential of these strains, which carry genes for salt resistance and nutrient recycling, for sulphur and nitrogen reuse, which make them interesting in assisting mangrove plants in thriving under stressful conditions (Fusi et al., 2022). Other studies that describe the isolation of important enzymes for biotechnology have confirmed this untapped microbial potential. For example, epoxide hydrolases and haloalkane dehalogenases have been found in microbial communities of mangroves contaminated with crude oil (Jiménez et al., 2015), showing the extreme plasticity of the microbial community in response to an environmental emergency. Similarly, a recent paper describes a new bacterial species isolated in contaminated areas of mangroves along the Red Sea, which carries genes for hydrocarbon degradation (Marasco, Michoud, et al., 2023). Also, the mangrove fungal community have high biotechnological potential. Antifungal, antibacterial, cytotoxic and anticancer compounds, along with acetylcholine esterase inhibitors, antioxidants, insecticidal molecules and enzyme inhibitors, have all been described in fungi isolated from mangrove sediments (Thatoi et al., 2013). This reveals mangrove sediment as a potentially valuable resource, especially when impacted by bioturbators, to find molecules to tackle

human challenges and contribute to enrich knowledge on the natural capital of mangroves (Cziesielski et al., 2021).

Bioturbation-controlled microbial functionality can therefore also be considered in multidisciplinary management approaches targeting the Sustainable Development Goals (SDGs) foreseen by the Agenda 2021 of the United Nations to tackle the most important challenges of our time. By sustaining mangrove microbiomes and, consequently, ecosystem functionality, at least five SDGs are included. Functional mangroves can help to fight poverty (SDG 1), provide food (SDG 2) (zu Ermgassen et al., 2020) and provide clean water (SDG 6) due to the microbial capacity to filter pollutants and contaminants (Iturbe-Espinoza et al., 2022). Microbial exploration in mangroves can have a deep impact on biotechnological innovation (SDG 9), for example the potential for heavy metals cleanup (Muñoz-García et al., 2022). By promoting plant growth and productivity, microbial communities shaped by bioturbation can have a fundamental role in climate action (SDG 13) by promoting the accumulation of blue carbon in the sediment (Hurtado-McCormick et al., 2022) and promoting the biogeochemical conditions for life (Fusi et al., 2022) to thrive in these intertidal ecosystems SDG 14 (Friess et al., 2019).

## AUTHOR CONTRIBUTIONS

**Marco Fusi:** Conceptualization (equal); data curation (equal); investigation (equal); project administration (equal); writing – original draft (equal). **Jenny M. Booth:** Conceptualization (equal); data curation (equal); investigation (equal); project administration (equal); writing – original draft (equal). **Ramona Marasco:** Data curation (equal); visualization (equal); writing – original draft (equal); writing – review and editing (equal). **Daniele Daffonchio:** Conceptualization (equal); funding acquisition (equal); writing – review and editing (equal).

## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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## REFERENCES

- Agusto, L., Fratini, S., Jimenez, P.J., Quadros, A. & Cannicci, S. (2021) Structural characteristics of crab burrows in Hong Kong mangrove forests and their role in ecosystem engineering. *Estuarine, Coastal and Shelf Science*, 248, 106973.
- Allard, S.M., Costa, M.T., Bulseco, A.N., Helfer, V., Wilkins, L.G.E., Hassenrück, C. et al. (2020) Introducing the mangrove microbiome initiative: identifying microbial research priorities and approaches to better understand, protect, and rehabilitate mangrove ecosystems. *mSystems*, 5, e00658-20.
- Aller, C. (2001) *The benthic boundary layer*. Oxford: Oxford University Press.
- Almahasheer, H., Duarte, C.M. & Irigoien, X. (2016) Nutrient limitation in central Red Sea mangroves. *Frontiers in Marine Science*, 3, 1–14.
- Alongi, D.M. (1998) *Coastal ecosystem processes*. Boca Raton: CRC Press.
- Alongi, D.M. (2005) Mangrove-microbe-soil relations. In: E. Kristensen, R.R. Haese & J.E. Kostka (Eds.) *Interact between macro- and microorganisms in marine sediments*, pp. 85–103. Washington: American Geophysical Union.
- Alongi, D.M. (2012) Carbon sequestration in mangrove forests. *Carbon Management*, 3, 313–322.
- Alongi, D.M. (2014) Carbon cycling and storage in mangrove forests. *Annual Review of Marine Science*, 6, 195–219.
- Alzubaidy, H., Essack, M., Malas, T.B., Bokhari, A., Motwalli, O., Kamanu, F.K., Jamhor, S.A., Mokhtar, N.A., Antunes, A., Simões, M.F. & Alam, I. (2016) Rhizosphere microbiome metagenomics of gray mangroves (*Avicennia marina*) in the Red Sea. *Gene*, 576(2), 626–636.
- Andreetta, A., Fusi, M., Cameldi, I., Cimò, F., Carnicelli, S. & Cannicci, S. (2014) Mangrove carbon sink. Do burrowing crabs contribute to sediment carbon storage? Evidence from a Kenyan mangrove system. *Journal of Sea Research*, 85, 524–533.
- Andreote, F.D., Jiménez, D.J., Chaves, D., Dias, A.C.F., Luvizotto, D.M., Dini-Andreote, F. et al. (2012) The microbiome of Brazilian mangrove sediments as revealed by metagenomics. *PLoS One*, 7, e38600.
- Araújo, J.M.C., Otero, X.L., Marques, A.G.B., Nóbrega, G.N., Silva, J.R.F. & Ferreira, T.O. (2011) Selective geochemistry of iron in mangrove soils in a semiarid tropical climate: effects of the burrowing activity of the crabs *Ucides cordatus* and *Uca maracoani*. *Geo-Marine Letters*, 32, 289–300.
- Arfi, Y., Marchand, C., Wartel, M. & Record, E. (2012) Fungal diversity in anoxic-sulfidic sediments in a mangrove soil. *Fungal Ecology*, 5, 2–5.
- Armstrong, W. & Beckett, P.M. (1987) Internal aeration and the development of stelar anoxia in submerged roots: a multishelled mathematical model combining axial diffusion of oxygen in the cortex with radial losses to the stele, the wall layers and the rhizosphere. *The New Phytologist*, 105, 221–24510.
- Aschenbroich, A., Michaud, E., Stieglitz, T., Fromard, F., Gardel, A., Tavares, M. et al. (2016) Brachyuran crab community structure and associated sediment reworking activities in pioneer and young mangroves of French Guiana, South America. *Estuarine, Coastal and Shelf Science*, 182, 60–71.
- Bahram, M. & Netherway, T. (2022) Fungi as mediators linking organisms and ecosystems. *FEMS Microbiology Reviews*, 46, fuab058.
- Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C. & Silliman, B.R. (2011) The value of estuarine and coastal ecosystem services. *Ecological Monographs*, 81, 169–193.
- Bashan, Y. & Holguin, G. (2002) Plant growth-promoting bacteria: a potential tool for arid mangrove reforestation. *Trees*, 16, 159–166.
- Behera, P., Mohapatra, M., Kim, J.Y., Adhya, T.K., Pattnaik, A.K. & Rastogi, G. (2019) Spatial and temporal heterogeneity in the structure and function of sediment bacterial communities of a tropical mangrove forest. *Environmental Science and Pollution Research*, 26, 3893–3908.
- Berg, G., Grube, M., Schlöter, M. & Smalla, K. (2014) Unraveling the plant microbiome: looking back and future perspectives. *Frontiers in Microbiology*, 5.
- Berti, R., Cannicci, S., Fabbri, S. & Innocenti, G. (2008) Notes on the structure and the use of *Neosarmatium meinerti* and *Cardisoma carnifex* burrows in a Kenyan mangrove swamp

- (Decapoda Brachyura). *Ethology Ecology and Evolution*, 20, 101–113.
- Bertics, V.J., Sohm, J.A., Treude, T., Chow, C.E.T., Capone, D.G., Fuhrman, J.A. et al. (2010) Burrowing deeper into benthic nitrogen cycling: the impact of bioturbation on nitrogen fixation coupled to sulfate reduction. *Marine Ecology Progress Series*, 409, 1–15.
- Bertics, V.J. & Ziebis, W. (2009) Biodiversity of benthic microbial communities in bioturbated coastal sediments is controlled by geochemical microniches. *The ISME Journal*, 3, 1269–1285.
- Bertness, M.D. (1985) Fiddler crab regulation of *Spartina alterniflora* production on a New England salt marsh. *Ecology*, 66, 1042–1055.
- Bertness, M.D. & Callaway, R. (1993) Positive interactions in communities. *Trends in Ecology & Evolution*, 9, 27–29.
- Bird, F.L., Boon, P.I. & Nichols, P.D. (2000) Physicochemical and microbial properties of burrows of the deposit-feeding thalassinidean ghost shrimp *Biffarius arenosus* (Decapoda: Callianassidae). *Estuarine, Coastal and Shelf Science*, 51, 279–291.
- Bižić, M., Klintzsch, T., Ionescu, D., Hindiyeh, M.Y., Günthel, M., Muro-Pastor, A.M. et al. (2020) Aquatic and terrestrial cyanobacteria produce methane. *Science Advances*, 6, 1–10.
- Booth, J.M., Fusi, M., Marasco, R., Mbobo, T. & Daffonchio, D. (2019) Fiddler crab bioturbation determines consistent changes in bacterial communities across contrasting environmental conditions. *Scientific Reports*, 9, 3749.
- Booth, J.M., Fusi, M., Marasco, R., Michoud, G., Fodelianakis, S., Merlino, G. et al. (2019) The role of fungi in heterogeneous sediment microbial networks. *Scientific Reports*, 9, 1–14.
- Boto, K., Alongi, D. & Nott, A. (1989) Dissolved organic carbon-bacteria interactions at sediment-water interface in a tropical mangrove system. *Marine Ecology Progress Series*, 51, 243–251.
- Botto, F. & Iribarne, O. (2000) Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. *Estuarine, Coastal and Shelf Science*, 51, 141–151.
- Bouillon, S., Borges, A.V., Castañeda-Moya, E., Diele, K., Dittmar, T., Duke, N.C. et al. (2008) Mangrove production and carbon sinks: a revision of global budget estimates. *Global Biogeochem Cycles*, 22, GB2013.
- Bradley, P.M. & Morris, J.T. (1990) Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in *Spartina alterniflora*. *Ecology*, 71, 282–287.
- Breithaupt, J.L., Smoak, J.M., Smith, T.J., III, Sanders, C.J. & Hoare, A. (2012) Organic carbon burial rates in mangrove sediments: strengthening the global budget. *Global Biogeochem Cycles*, 26, 1–11.
- Bulgarelli, D., Schlaeppli, K., Spaepen, S., van Themaat, E.V.L., Schulze-Lefert, P., Loren, V. et al. (2013) Structure and functions of the bacterial microbiota of plants. *Annual Review of Plant Biology*, 64, 807–838.
- Cai, W.-J. & Sayles, F.L. (1996) Oxygen penetration depths and fluxes in marine sediments. *Marine Chemistry*, 52, 123–131.
- Call, M., Maher, D.T., Santos, I.R., Mangion, P., Sanders, C.J., Erler, D.V. et al. (2015) Spatial and temporal variability of carbon dioxide and methane fluxes over semi-diurnal and spring-neap-spring timescales in a mangrove creek. *Geochimica et Cosmochimica Acta*, 150, 211–225.
- Cannicci, S., Burrows, D., Fratini, S., Smith, T.J., Offenberg, J. & Dahdouh-Guebas, F. (2008) Faunal impact on vegetation structure and ecosystem function in mangrove forests: a review. *Aquatic Botany*, 89, 186–200.
- Carlen, A. & Olafsson, E. (2002) The effects of the gastropod *Terebralia palustris* on infaunal communities in a tropical tidal mud-flat in East Africa. *Wetlands Ecology and Management*, 10, 303–311.
- Carvalho, L.M., Correia, P.M. & Martins-Loução, M.A. (2004) Arbuscular mycorrhizal fungal propagules in a salt marsh. *Mycorrhiza*, 14, 165–170.
- Chen, J. & Gu, J. (2017) Faunal burrows alter the diversity, abundance, and structure of AOA, AOB, anammox and n-damo communities in coastal mangrove sediments. *Microbial Ecology*, 74, 140–156.
- Cheng, H., Liu, Y., Jiang, Z. & Wang, Y. (2020) Radial oxygen loss is correlated with nitrogen. *Tree Physiology*, 44, 1548–1560.
- Cheng, H., Wang, Y.S., Fei, J., Jiang, Z.Y. & Ye, Z.H. (2015) Differences in root aeration, iron plaque formation and water-logging tolerance in six mangroves along a continuous tidal gradient. *Ecotoxicology*, 24, 1659–1667.
- Crane, J. (1975) *Fiddler crabs of the world (Ocypodidae, genus: Uca)*. Princeton, NJ: Princeton University Press.
- Cuellar-Gempeler, C. & Leibold, M.A. (2018) Multiple colonist pools shape fiddler crab-associated bacterial communities. *The ISME Journal*, 12, 1–13.
- Cuellar-Gempeler, C. & Munguia, P. (2013) Fiddler crabs (*Uca thayeri*, Brachyura: Ocypodidae) affect bacterial assemblages in mangrove forest sediments. *Community Ecology*, 14, 59–66.
- Cziesielski, M.J., Duarte, C.M., Aalismail, N., Al-Hafedh, Y., Anton, A., Baalkhuyur, F. et al. (2021) Investing in blue natural capital to secure a future for the Red Sea ecosystems. *Frontiers in Marine Science*, 7, 1183.
- Daleo, P., Fanjul, E., Mendez Casariego, A., Silliman, B.R., Bertness, M.D. & Iribarne, O. (2007) Ecosystem engineers activate mycorrhizal mutualism in salt marshes. *Ecology Letters*, 10, 902–908.
- Dando, P., Southward, A. & Southward, E.C. (1986) Chemoautotrophic symbionts in the gills of the bivalve mollusc *Lucinoma borealis* and the sediment chemistry of its habitat. *Proceedings of the Royal Society B: Biological Sciences*, 227, 227–247.
- De Boer, W., Folman, L.B., Summerbell, R.C. & Boddy, L. (2005) Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiology Reviews*, 29, 795–811.
- Demain, A.L. & Vaishnav, P. (2011) Natural products for cancer chemotherapy. *Microbial Biotechnology*, 4, 687–699.
- Ding, H., Yao, S. & Chen, J. (2014) Authigenic pyrite formation and re-oxidation as an indicator of an unsteady-state redox sedimentary environment: evidence from the intertidal mangrove sediments of Hainan Island, China. *Continental Shelf Research*, 78, 85–99.
- Distel, D.L., Morrill, W., MacLaren-Toussaint, N., Franks, D. & Waterbury, J. (2002) *Teredinibacter turnerae* gen. nov., sp. nov., a dinitrogen-fixing, cellulolytic, endosymbiotic gamma-proteobacterium isolated from the gills of wood-boring molluscs (Bivalvia: Teredinidae). *International Journal of Systematic and Evolutionary Microbiology*, 52, 2261–2269.
- Dittmar, T., Hertkorn, N., Kattner, G. & Lara, R.J. (2006) Mangroves, a major source of dissolved organic carbon to the oceans. *Global Biogeochem Cycles*, 20, 1–7.
- Dollhopf, S.L., Hyun, J., Smith, A.C., Harold, J., Brien, S.O., Kostka, J.E. et al. (2005) Quantification of ammonia-oxidizing bacteria and factors controlling nitrification in salt marsh sediments: quantification of ammonia-oxidizing bacteria and factors controlling nitrification in salt marsh sediments. *Applied and Environmental Microbiology*, 71(1), 240–246.
- Donato, D.C., Kauffman, J.B., Murdiyarso, D., Kurnianto, S., Stidham, M. & Kanninen, M. (2011) Mangroves among the most carbon-rich forests in the tropics. *Nature Geoscience*, 4, 293–297.
- Dunn, R.J.K., Welsh, D.T., Jordan, M.A., Arthur, J.M., Lemckert, C.J. & Teasdale, P.R. (2012) Interactive influences of the marine yabby (*Trypaea australiensis*) and mangrove (*Avicennia marina*) leaf litter on benthic metabolism and nitrogen cycling in sandy estuarine sediment. *Hydrobiologia*, 693, 117–129.
- Duperron, S., Pottier, M.-A., Léger, N., Gaudron, S.M., Puillandre, N., Le Prieur, S. et al. (2013) A tale of two chitons: is habitat

- specialisation linked to distinct associated bacterial communities? *FEMS Microbiology Ecology*, 83, 552–567.
- Falkowski, P.G., Fenchel, T. & Delong, E.F. (2008) The microbial engines that drive Earth's biogeochemical cycles. *Science*, 320, 1034–1039.
- Faulwetter, J.L., Gagnon, V., Sundberg, C., Chazarenc, F., Burr, M.D., Brisson, J. et al. (2009) Microbial processes influencing performance of treatment wetlands: a review. *Ecological Engineering*, 35, 987–1004.
- Fenchel, T. (1996) Worm burrows and oxic microniches in marine sediments. 1. Spatial and temporal scales. *Marine Biology*, 127, 289–295.
- Ferreira, T.O., Otero, X.L., Vidal-Torrado, P. & Macías, F. (2007) Effects of bioturbation by root and crab activity on iron and sulfur biogeochemistry in mangrove substrate. *Geoderma*, 142, 36–46.
- Finlay, B.J., Maberly, S.C. & Cooper, J.I. (1997) Microbial diversity and ecosystem function. *Oikos*, 80, 209.
- Flores-Mireles, A.L., Winans, S.C. & Holguin, G. (2007) Molecular characterization of diazotrophic and denitrifying bacteria associated with mangrove roots. *Applied and environmental microbiology*, 73(22), 7308–7321.
- Friess, D.A., Aung, T.T., Huxham, M., Lovelock, C., Mukherjee, N. & Sasmito, S. (2019) SDG 14: life below water—impacts on mangroves. In: P. Katila, C.J. Pierce Colfer, W. de Jong, G. Galloway, P. Pacheco & G. Winkel (Eds.) *Sustainable development goals: their impacts on forests and people*. Cambridge: Cambridge University Press, pp. 445–481.
- Furukawa, Y. (2005) Macro and microorganisms in marine sediments: coastal and estuarine studies. *Coastal and Estuarine Studies*, 60, 159–177.
- Fusi, M., Booth, J.M., Marasco, R., Merlino, G., Garcias-bonet, N., Barozzi, A. et al. (2022) Bioturbation intensity modifies the sediment microbiome and biochemistry and supports plant growth in an arid mangrove. *Microbiology Spectrum*, 10, 1–15.
- Fusi, M., Giomi, F., Babbini, S., Daffonchio, D., McQuaid, C.D., Porri, F. et al. (2015) Thermal specialization across large geographical scales predicts the resilience of mangrove crab populations to global warming. *Oikos*, 124, 784–795.
- Gilbert, F., Bonin, P. & Stora, G. (1995) Effect of bioturbation on denitrification in a marine sediment from the West Mediterranean littoral. *Hydrobiologia*, 304, 49–58.
- Gillis, L.G., Snavely, E., Lovelock, C. & Zimmer, M. (2019) Effects of crab burrows on sediment characteristics in a *Cerriops australis*-dominated mangrove forest. *Estuarine, Coastal and Shelf Science*, 218, 334–339.
- Giri, C., Ochieng, E., Tieszen, L.L., Zhu, Z., Singh, A., Loveland, T. et al. (2011) Status and distribution of mangrove forests of the world using earth observation satellite data. *Global Ecology and Biogeography*, 20, 154–159.
- Gomes, N.C.M., Cleary, D.F.R., Pinto, F.N., Egas, C., Almeida, A., Cunha, A. et al. (2010) Taking root: enduring effect of rhizosphere bacterial colonization in mangroves. *PLoS One*, 5, 1–10.
- Gribsholt, B., Kostka, J.E. & Kristensen, E. (2003) Impact of fiddler crabs and plant roots on sediment biogeochemistry in a Georgia saltmarsh. *Marine Ecology Progress Series*, 259, 237–251.
- Gros, O., Liberge, M., Heddi, A. & Felbeck, H. (2003) Detection of the free-living forms of sulfide-oxidizing gill endosymbionts in the lucinid habitat (*Thalassia testudinum* environment). *Applied and Environmental Microbiology*, 69, 6264–6267.
- Gundersen, J.K. & Jorgensen, B.B. (1990) Microstructure of diffusive boundary layers and the oxygen uptake of the sea floor. *Nature*, 345, 604–607.
- Hansen, K., King, G.M. & Kristensen, E. (1996) Impact of the soft-shell clam *Mya arenaria* on sulfate reduction in an intertidal sediment. *Aquatic Microbial Ecology*, 10, 181–194.
- Hartmann, A., Schmid, M., van Tuinen, D. & Berg, G. (2009) Plant-driven selection of microbes. *Plant and Soil*, 321, 235–257.
- Hill, M., Hill, A., Lopez, N. & Harriott, O. (2006) Sponge-specific bacterial symbionts in the Caribbean sponge, *Chondrilla nucula* (Demospongiae, Chondrosida). *Marine Biology*, 148, 1221–1230.
- Holguin, G., Vazquez, P. & Bashan, Y. (2001) The role of sediment microorganisms in the productivity, conservation, and rehabilitation of mangrove ecosystems: an overview. *Biology and Fertility of Soils*, 33, 265–278.
- Howe, R.L., Rees, A.P. & Widdicombe, S. (2004) The impact of two species of bioturbating shrimp (*Callinassa subterranea* and *Upogebia deltaura*) on sediment denitrification. *Journal of the Marine Biological Association of the UK*, 84, 629–632.
- Howes, B.L., Howarth, R.W., Teal, J.M. & Valiela, I. (1981) Oxidation-reduction potentials in a salt marsh: spatial patterns and interactions with primary production. *Limnology and Oceanography*, 26, 350–360.
- Hurtado-McCormick, V., Trevathan-Tackett, S.M., Bowen, J.L., Connolly, R.M., Duarte, C.M. & Macreadie, P.I. (2022) Pathways for understanding blue carbon microbiomes with amplicon sequencing. *Microorganisms*, 10, 2121.
- Hyde, K.D., Jones, E.B.G., Leaño, E., Pointing, S.B., Poonyth, A.D. & Vrijmoed, L.L.P. (1998) Role of fungi in marine ecosystems. *Biodiversity and Conservation*, 7, 1147–1161.
- Icely, J. & Jones, D. (1978) Factors affecting the distribution of the genus *Uca* (Crustacea: Ocypodidae) on an East African shore. *Estuarine and Coastal Marine Science*, 6, 315–325.
- Imchen, M., Kumavath, R., Barh, D., Avezedo, V., Ghosh, P., Viana, M. et al. (2017) Searching for signatures across microbial communities: metagenomic analysis of soil samples from mangrove and other ecosystems. *Scientific Reports*, 7, 1–13.
- Iturbe-Espinoza, P., Bonte, M., Gundlach, E., Brandt, B.W., Braster, M. & van Spanning, R.J.M. (2022) Adaptive changes of sediment microbial communities associated with cleanup of oil spills in Nigerian mangrove forests. *Marine Pollution Bulletin*, 176, 113406.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108, 389–411.
- Jetten, M.S.M., Cirpus, I., Kartal, B., van Niftrik, L., van de Pas-Schoonen, K.T., Sliemers, O. et al. (2005) 1994–2004: 10 Years of research on the anaerobic oxidation of ammonium. *Biochemical Society Transactions*, 33, 119–123.
- Jiménez, D.J., Dini-Andreote, F., Ottoni, J.R., de Oliveira, V.M., van Elsas, J.D. & Andreote, F.D. (2015) Compositional profile of  $\alpha/\beta$ -hydrolase fold proteins in mangrove soil metagenomes: prevalence of epoxide hydrolases and haloalkane dehalogenases in oil-contaminated sites. *Microbial Biotechnology*, 8, 604–613.
- Johnson, M.A., Fernandez, C. & Pergent, G. (2002) The ecological importance of an invertebrate chemoautotrophic symbiosis to phanerogam seagrass beds. *Bulletin of Marine Science*, 71, 1343–1351.
- Joly, F., Coq, S., Coulis, M., David, J., Hättenschwiler, S., Mueller, C. et al. (2020) Detritivore conversion of litter into faeces accelerates organic matter turnover. *Communications Biology*, 3, 1–9.
- Jones, C., Lawton, J. & Shachak, M. (1994) Organisms as ecosystem engineers. In: Samson, F. & Knopf, F. (Eds.) *Ecosystem management*. Berlin: Springer, pp. 130–147.
- Jones, E.B.G. (2000) Marine fungi: some factors influencing biodiversity. *Fungal Diversity*, 193, 53–73.
- Jordan, M.A., Welsh, D.T., Dunn, R.J.K. & Teasdale, P.R. (2009) Influence of *Trypaea australiensis* population density on benthic metabolism and nitrogen dynamics in sandy estuarine sediment: a mesocosm simulation. *Journal of Sea Research*, 61, 144–152.



- Jørgensen, B.B. (1982) Mineralization of organic matter in the sea bed – the role of sulphate reduction. *Nature*, 296, 643–645.
- Kathiresan, K. & Bingham, B.L. (2001) *Biology of mangroves and mangrove ecosystems*. Amsterdam: Elsevier.
- Katz, L.C. (1980) Effects of burrowing by the fiddler crab, *Uca pugnax* (Smith). *Estuarine and Coastal Marine Science*, 11, 233–237.
- Konhäuser, K. (2007) *Introduction to geomicrobiology*. Oxford: Blackwell Publishing.
- Kristensen, E. (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia*, 426, 1–24.
- Kristensen, E. (2008) Mangrove crabs as ecosystem engineers; with emphasis on sediment processes. *Journal of Sea Research*, 59, 30–43.
- Kristensen, E. & Alongi, D.M. (2006) Control by fiddler crabs (*Uca vocans*) and plant roots (*Avicennia marina*) on carbon, iron, and sulfur biogeochemistry in mangrove sediment. *Limnology and Oceanography*, 51, 1557–1571.
- Kristensen, E., Andersen, F.Ø., Holmboe, N., Holmer, M. & Thongtham, N. (2000) Carbon and nitrogen mineralization in sediments of the Bangrong mangrove area, Phuket, Thailand. *Aquatic Microbial Ecology*, 22, 199–213.
- Kristensen, E., Bouillon, S., Dittmar, T. & Marchand, C. (2008) Organic carbon dynamics in mangrove ecosystems: a review. *Aquatic Botany*, 89, 201–219.
- Kristensen, E., Holmer, M. & Bussawarit, N. (1991) Benthic metabolism and sulfate reduction in a southeast Asian mangrove swamp. *Marine Ecology Progress Series*, 73, 93–103.
- Kristensen, E. & Kostka, J.E. (2005) Macrofaunal burrows and irrigation in marine sediment: microbiological and biogeochemical interactions. In: E. Kristensen, R.R. Haese & J.E. Kostka (Eds.) *Interact between macro- and microorganisms in marine sediments*. Washington, D.C., United States: American Geophysical Union, pp. 125–157.
- Kristensen, E., Penha-lobes, G., Delefosse, M., Valdemarsen, T., Quintana, C.O. & Banta, G.T. (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, 446, 285–302.
- Kuzyakov, Y. & Domanski, G. (2000) Carbon input by plants to soil. Review. *Journal of Plant Nutrition and Soil Science*, 163, 421–431.
- Laurent, M.C.Z., Gros, O., Brulport, J.P., Gaill, F. & Bris, N.L. (2009) Sunken wood habitat for thiotrophic symbiosis in mangrove swamps. *Marine Environmental Research*, 67, 83–88.
- Laverock, B., Gilbert, J.A., Tait, K., Osborn, A.M. & Widdicombe, S. (2011) Bioturbation: impact on the marine nitrogen cycle. *Biochemical Society Transactions*, 39, 315–320.
- Laverock, B., Tait, K., Gilbert, J.A., Osborn, A.M. & Widdicombe, S. (2014) Impacts of bioturbation on temporal variation in bacterial and archaeal nitrogen-cycling gene abundance in coastal sediments. *Environmental Microbiology Reports*, 6, 113–121.
- Lebata, M.J. (2001) Oxygen, sulphide and nutrient uptake of the mangrove mud clam *Anodonta edentula* (Family: Lucinidae). *Marine Pollution Bulletin*, 42, 1133–1138.
- Lee, O.O., Chui, P.Y., Wong, Y.H., Pawlik, J.R. & Qian, P.-Y. (2009) Evidence for vertical transmission of bacterial symbionts from adult to embryo in the Caribbean sponge *Svenzea zeai*. *Applied and Environmental Microbiology*, 75, 6147–6156.
- Lee, S.Y. (1998) Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research*, 49, 335–434.
- Lee, S.Y. (2008) Mangrove macrobenthos: assemblages, services, and linkages. *Journal of Sea Research*, 59, 16–29.
- Levinton, J.S., Bianchi, T.S. & Stewart, S. (1984) What is the role of particulate organic matter in benthic invertebrate nutrition? *Bulletin of Marine Science*, 35, 270–282.
- Li, Y., Fan, X. & Shen, Q. (2008) The relationship between rhizosphere nitrification and nitrogen-use efficiency in rice plants. *Plant, Cell and Environment*, 31, 73–85.
- Lovelock, C.E. & Duarte, C.M. (2019) Dimensions of blue carbon and emerging perspectives. *Biology Letters*, 15, 1–5.
- Lyimo, T.J., Pol, A., Jetten, M.S.M. & den Camp, H.J.M.O. (2009) Diversity of methanogenic archaea in a mangrove sediment and isolation of a new *Methanococoides* strain. *FEMS Microbiology Letters*, 291, 247–253.
- Marasco, R., Michoud, G., Sefrji, F.O., Fusi, M., Antony, C.P., Seferji, K.A. et al. (2023) The identification of the new species *Nitratireductor thuwali* sp. nov. reveals the untapped diversity of hydrocarbon-degrading culturable bacteria from the arid mangrove sediments of the Red Sea. *Frontiers in Microbiology*, 14, 1155381. <https://doi.org/10.3389/fmicb.2023.1155381>
- Marasco, R., Ramond, J.-B., Van Goethem, M.W., Rossi, F. & Daffonchio, D. (2023) Diamonds in the rough: dryland microorganisms are ecological engineers to restore degraded land and mitigate desertification. *Microbial Biotechnology*, 1–8. <https://doi.org/10.1111/1751-7915.14216>
- Mautz, B., Detto, T., Wong, B.B.M., Kokko, H., Jennions, M.D. & Backwell, P.R.Y. (2011) Male fiddler crabs defend multiple burrows to attract additional females. *Behavioral Ecology*, 22, 261–267.
- Mchenga, I.S.S. & Tsuchiya, M. (2008) Nutrient dynamics in mangrove crab burrow sediments subjected to anthropogenic input. *Journal of Sea Research*, 59, 103–113.
- McLeod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M. et al. (2011) A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO<sub>2</sub>. *Frontiers in Ecology and the Environment*, 9, 552–560.
- Meysman, F.J.R., Middelburg, J.J. & Heip, C.H.R. (2006) Bioturbation: a fresh look at Darwin's last idea. *Trends in Ecology & Evolution*, 21, 688–695.
- Michaels, R.E. & Zieman, J.C. (2013) Fiddler crab (*Uca* spp.) burrows have little effect on surrounding sediment oxygen concentrations. *Journal of Experimental Marine Biology and Ecology*, 448, 104–113.
- Mohanraju, R. & Natarajan, R. (1992) Methanogenic bacteria in mangrove sediments. *Hydrobiologia*, 247, 187–193. <https://doi.org/10.1007/BF00008218>
- Montague, C. (1982) The influence of fiddler crab burrows on metabolic processes in salt marsh sediments. *Estuarine Comparisons*, 37, 283–301.
- Muñoz-García, A., Arbeli, Z., Boyacá-Vásquez, V. & Vanegas, J. (2022) Metagenomic and genomic characterization of heavy metal tolerance and resistance genes in the rhizosphere microbiome of *Avicennia germinans* in a semi-arid mangrove forest in the tropics. *Marine Pollution Bulletin*, 184, 114204.
- Newell, S.Y. (1996) Established and potential impacts of eukaryotic mycelial decomposers in marine/terrestrial ecotones. *Journal of Experimental Marine Biology and Ecology*, 200, 187–206.
- Nielsen, O.I., Kristensen, E. & Macintosh, D.J. (2003) Impact of fiddler crabs (*Uca* spp.) on rates and pathways of benthic mineralization in deposited mangrove shrimp pond waste. *Journal of Experimental Marine Biology and Ecology*, 289, 59–81.
- Nordhaus, I., Wolff, M. & Diele, K. (2006) Litter processing and population food intake of the mangrove crab *Ucides cordatus* in a high intertidal forest in northern Brazil. *Estuarine, Coastal and Shelf Science*, 67, 239–250.
- Otero, X.L., Jr., Araújo, J.M.C., Barcellos, D., Queiroz, H.M., Romero, D.J., Gabriel, N.N. et al. (2020) Crab bioturbation and seasonality control nitrous oxide emissions in semiarid

- mangrove forests (Ceará, Brazil). *Applied Sciences*, 10, 1–16.
- Palit, K., Rath, S., Chatterjee, S. & Das, S. (2022) *Microbial diversity and ecological interactions of microorganisms in the mangrove ecosystem: threats, vulnerability, and adaptations*. Berlin, Heidelberg: Springer.
- Palumbi, S.R., Sandifer, P.A., Allan, J.D., Beck, M.W., Fautin, D.G., Fogarty, M.J. et al. (2009) Managing for ocean biodiversity to sustain marine ecosystem services. *Frontiers in Ecology and the Environment*, 7, 204–211.
- Passarelli, C., Olivier, F., Paterson, D.M., Meziane, T. & Hubas, C. (2014) Organisms as cooperative ecosystem engineers in intertidal flats. *Journal of Sea Research*, 92, 92–101.
- Penha-Lopes, G., Bartolini, F., Limbu, S., Cannicci, S., Mgaya, Y., Kristensen, E. et al. (2010) Ecosystem engineering potential of the gastropod *Terebralia palustris* (Linnaeus, 1767) in mangrove wastewater wetlands – a controlled mesocosm experiment. *Environmental Pollution*, 158, 258–266.
- Pii, Y., Mimmo, T., Tomasi, N., Terzano, R., Cesco, S. & Crecchio, C. (2015) Microbial interactions in the rhizosphere: beneficial influences of plant growth-promoting rhizobacteria on nutrient acquisition process. A review. *Biology and Fertility of Soils*, 51, 403–415.
- Plugge, C.M., Zhang, W., Scholten, J.C.M. & Stams, A.J.M. (2011) Metabolic flexibility of sulfate-reducing bacteria. *Frontiers in Microbiology*, 2, 1–8.
- Preece, C. & Peñuelas, J. (2020) A return to the wild: root exudates and food security. *Trends in Plant Science*, 25, 14–21.
- Puginier, C., Keller, J. & Delaux, P. (2022) Plant–microbe interactions that have impacted plant terrestrializations. *Plant Physiology*, 190, 72–84.
- Pülmanns, N., Diele, K., Mehlig, U. & Nordhaus, I. (2014) Burrows of the semi-terrestrial crab *Ucides cordatus* enhance CO<sub>2</sub> release in a North Brazilian mangrove forest. *PLoS One*, 9, e109532.
- Qashqari, M.S., Garcias-Bonet, N., Fusi, M., Booth, J.M., Daffonchio, D. & Duarte, C.M. (2020) High temperature and crab density reduce atmospheric nitrogen fixation in Red Sea mangrove sediments. *Estuarine, Coastal and Shelf Science*, 232, 106487.
- Raiswell, R. & Canfield, D.E. (1998) Sources of iron for pyrite formation in marine sediments. *American Journal of Science*, 298, 219–245.
- Ray, R., Majumder, N., Das, S., Chowdhury, C. & Jana, T.K. (2014) Biogeochemical cycle of nitrogen in a tropical mangrove ecosystem, east coast of India. *Marine Chemistry*, 167, 1–11.
- Reichardt, W. (1988) Impact of bioturbation by *Arenicola marina* on microbiological parameters in intertidal sediments. *Marine Ecology Progress Series*, 44, 149–158.
- Robertson, A.I. (1988) Decomposition of mangrove leaf litter in tropical Australia. *Journal of Experimental Marine Biology and Ecology*, 116, 235–247.
- Robertson, A.I. & Daniel, P.A. (1989) The influence of crabs on litter processing in high intertidal mangrove forests in tropical Australia. *Oecologia*, 78, 191–198.
- Roeselers, G. & Newton, I.L.G. (2012) On the evolutionary ecology of symbioses between chemosynthetic bacteria and bivalves. *Applied Microbiology and Biotechnology*, 94, 1–10.
- Sánchez-Cañizares, C., Jorrín, B., Poole, P.S. & Tkacz, A. (2017) Understanding the holobiont: the interdependence of plants and their microbiome. *Current Opinion in Microbiology*, 38, 188–196.
- Sarker, S., Masud-Ul-Alam, M., Shahadat Hossein, M., Rahman Chowdhury, S. & Sharifuzzaman, S. (2021) A review of bioturbation and sediment organic geochemistry in mangroves. *Geological Journal*, 56, 2439–2450.
- Sävström, C., Hyndes, G.A., Eyre, B.D., Huggett, M.J., Fraser, M.W., Lavery, P.S. et al. (2016) Coastal connectivity and spatial subsidy from a microbial perspective. *Ecology and Evolution*, 6, 6662–6671.
- Sea, M.A., Garcias-bonet, N., Saderne, V. & Duarte, C.M. (2019) Carbon dioxide and methane fluxes at the air–sea interface of Red Sea mangroves. *Biogeosciences*, 15, 5365–5375.
- Sefrji, F.O., Marasco, R., Michoud, G., Seferji, K.A., Merlino, G. & Daffonchio, D. (2021) *Kaustia mangrovi* gen. nov., sp. nov. isolated from red sea mangrove sediments belongs to the recently proposed parvibaculaceae family within the order rhizobiales. *International Journal of Systematic and Evolutionary Microbiology*, 71, 004806.
- Sefrji, F.O., Marasco, R., Michoud, G., Seferji, K.A., Merlino, G. & Daffonchio, D. (2022) Insights into the cultivable bacterial fraction of sediments from the Red Sea mangroves and physiological, chemotaxonomic, and genomic characterization of *Mangrovibacillus cuniculi* gen. nov., sp. nov., a novel member of the Bacillaceae family. *Frontiers in Microbiology*, 13, 1–13.
- Sengupta, A. & Chaudhuri, S. (2002) Arbuscular mycorrhizal relations of mangrove plant community at the Ganges river estuary in India. *Mycorrhiza*, 12, 169–174.
- Shearer, C.A., Descals, E., Kohlmeyer, B., Kohlmeyer, J., Marvanová, L., Padgett, D. et al. (2007) Fungal biodiversity in aquatic habitats. *Biodiversity and Conservation*, 16, 49–67.
- Shiau, Y., Cai, Y., Lin, Y., Jia, Z. & Chiu, C. (2018) Community structure of active aerobic methanotrophs in red mangrove (*Kandelia obovata*) soils under different frequency of tides. *Microbial Ecology*, 75, 761–770.
- Siikamaki, J., Sanchirico, J.N. & Jardine, S.L. (2012) Global economic potential for reducing carbon dioxide emissions from mangrove loss. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 14369–14374.
- Simoës, M., Antunes, A., Ottoni, C.A., Amini, M.S., Alam, I., Alzubaidy, H. et al. (2015) Soil and rhizosphere associated fungi in gray mangroves (*Avicennia marina*) from the Red Sea—A metagenomic approach. *Genomics, Proteomics & Bioinformatics*, 13, 310–320.
- Skov, M.W. & Hartnoll, R.G. (2002) Paradoxical selective feeding on a low-nutrient diet: why do mangrove crabs eat leaves? *Oecologia*, 131, 1–7.
- Smith, N.F., Wilcox, C. & Lessmann, J.M. (2009) Fiddler crab burrowing affects growth and production of the white mangrove (*Laguncularia racemosa*) in a restored Florida coastal marsh. *Marine Biology*, 156, 2255–2266.
- Smith, T.J., Boto, K.G., Frusher, S.D. & Giddins, R.L. (1991) Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science*, 33, 419–432.
- Soldan, R., Mapelli, F., Crotti, E., Schnell, S., Daffonchio, D., Marasco, R. et al. (2019) Bacterial endophytes of mangrove propagules elicit early establishment of the natural host and promote growth of cereal crops under salt stress. *Microbiological Research*, 223–225, 33–43.
- Sousa, W.P. & Dangremond, E.M. (2011) Trophic interactions in coastal and estuarine mangrove forest ecosystems. In: E. Wolanski & D. McLusky (Eds.) *Treatise on estuarine and coastal science*. Academic: Waltham, MA; London, pp. 43–93.
- Stanley, S.M. (2014) Evolutionary radiation of shallow-water Lucinidae (Bivalvia with endosymbionts) as a result of the rise of seagrasses and mangroves. *Geology*, 42, 803–806.
- Stieglitz, T., Ridd, P. & Müller, P. (2000) Passive irrigation and functional morphology of crustacean burrows in a tropical mangrove swamp. *Hydrobiologia*, 421, 69–76.
- Stothoff, S.A., Or, D., Groeneveld, D.P. & Jones, S.B. (1999) The effect of vegetation on infiltration in shallow soils underlain by fissured bedrock. *Journal of Hydrology*, 218, 169–190.
- Sul, W.J., Asuming-Brempong, S., Wang, Q., Tourlousse, D.M., Penton, C.R., Deng, Y. et al. (2013) Tropical agricultural land management influences on soil microbial communities through its effect on soil organic carbon. *Soil Biology and Biochemistry*, 65, 33–38.

- Sunday, J., Bennett, J.M., Calosi, P., Clusella, S., Leiva, P., Gravel, S. et al. (2019) Thermal tolerance patterns across latitude and elevation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 374, 20190036.
- Taketani, R.G., Yoshiura, C.A., Dias, A.C.F., Andreote, F.D. & Tsai, S.M. (2010) Diversity and identification of methanogenic archaea and sulphate-reducing bacteria in sediments from a pristine tropical mangrove. *Antonie Van Leeuwenhoek*, 97, 401–411.
- Thatoi, H., Behera, B.C. & Mishra, R.R. (2013) Ecological role and biotechnological potential of mangrove fungi: a review. *Mycology*, 4, 54–71.
- Tiedje, J. (1988) Ecology of denitrification and dissimilatory nitrate reduction to ammonium. In: A.J.B. Zehnder (Ed.) *Biology of anaerobic microorganisms*. John Wiley & Sons, pp. 179–244.
- Trivedi, P., Leach, J.E., Tringe, S.G., Sa, T. & Singh, B.K. (2020) Plant–microbiome interactions: from community assembly to plant health. *Nature Reviews. Microbiology*, 18, 607–621.
- van der Heide, T., Govers, L., de Fouw, J., Olf, H., van der Geest, M., van Katwijk, M. et al. (2012) A three-stage symbiosis forms the foundation of seagrass ecosystems. *Science*, 336, 1432–1434.
- Van Der Heijden, M.G.A.A. & Schlaeppi, K. (2015) Root surface as a frontier for plant microbiome research. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 2299–2300.
- Vannini, M., Lori, E., Coffa, C. & Fratini, S. (2008) *Cerithidea decollata*: a snail that can foresee the future? *Animal Behaviour*, 76, 983–992.
- Varon-lopez, M., Cavalcante, A., Dias, F., Fasanella, C.C., Durrer, A., Melo, I.S. et al. (2013) Sulphur-oxidizing and sulphate-reducing communities in Brazilian mangrove sediments. *Environmental Microbiology*, 16, 845–855.
- Volland, J., Gonzalez-rizzo, S., Gros, O., Tymb, T., Ivanova, N., Schulz, F. et al. (2022) A centimeter-long bacterium with DNA contained in metabolically active, membrane-bound organelles. *Science*, 1458, 1453–1458.
- Vopel, K. & Hancock, N. (2005) More than just a crab hole. *Water & Atmosphere*, 13, 18–19.
- Wang, Y., Huang, Y., Qiu, Q., Xin, G., Yang, Z. & Shi, S. (2011) Flooding greatly affects the diversity of arbuscular mycorrhizal fungi communities in the roots of wetland plants. *PLoS One*, 6, e24512.
- Wang, Y., Qiu, Q., Yang, Z., Hu, Z., Tam, N.F.Y. & Xin, G. (2010) Arbuscular mycorrhizal fungi in two mangroves in South China. *Plant and Soil*, 331, 181–191.
- Warmink, J.A., Nazir, R., Corten, B. & Van Elsas, J.D. (2011) Hitchhikers on the fungal highway: the helper effect for bacterial migration via fungal hyphae. *Soil Biology and Biochemistry*, 43, 760–765.
- Wilson, K.A. (1989) Ecology of mangrove crabs: predation, physical factors and refuges. *Bulletin of Marine Science*, 44, 263–273.
- Wu, C., Wu, H., Liu, D., Han, G., Zhao, P. & Kang, Y. (2021) Crab bioturbation significantly alters sediment microbial composition and function in an intertidal marsh. *Estuarine, Coastal and Shelf Science*, 249, 107116.
- Xu, Q., Yang, L., Zhou, Z., Mei, F., Qu, L. & Zhou, G. (2013) Process of aerenchyma formation and reactive oxygen species induced by waterlogging in wheat seminal roots. *Planta*, 238, 969–982.
- Zhalnina, K., Louie, K.B., Hao, Z., Mansoori, N., da Rocha, U.N., Shi, S. et al. (2018) Dynamic root exudate chemistry and microbial substrate preferences drive patterns in rhizosphere microbial community assembly. *Nature Microbiology*, 3, 470–480.
- Zhao, H., Yang, W., Fang, C., Qiao, Y., Xiao, Y., Cheng, X. et al. (2014) Effects of tidewater and crab burrowing on H<sub>2</sub>S emission and sulfur storage in *Spartina alterniflora* Marsh. *Clean – Soil, Air, Water*, 42, 1682–1688.
- Zhao, M., Yuan, J., Shen, Z., Dong, M., Liu, H., Wen, T. et al. (2019) Predominance of soil vs root effect in rhizosphere microbiota reassembly. *FEMS Microbiology Ecology*, 95, 7308–7321.
- Zhou, W. & Chen, D. (2011) Entangled chemosensory emotion and identity: Familiarity enhances detection of chemosensorily encoded emotion. *Social Neuroscience*, 6(3), 270–276.
- zu Ermgassen, P.S.E., Mukherjee, N., Worthington, T.A., Acosta, A., da Rocha Araujo, A.R., Beittl, C.M. et al. (2020) Fishers who rely on mangroves: modelling and mapping the global intensity of mangrove-associated fisheries. *Estuarine, Coastal and Shelf Science*, 247, 106975.
- Zuberer, D. & Silver, W. (1978) Biological dinitrogen fixation (acetylene reduction) associated with Florida mangroves. *Applied and Environmental Microbiology*, 35, 567–575.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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