The Global Mangrove Microbiome

Dad, look at those trees growing in the sea!

Photo Credit: Marco Fusi

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Storyline

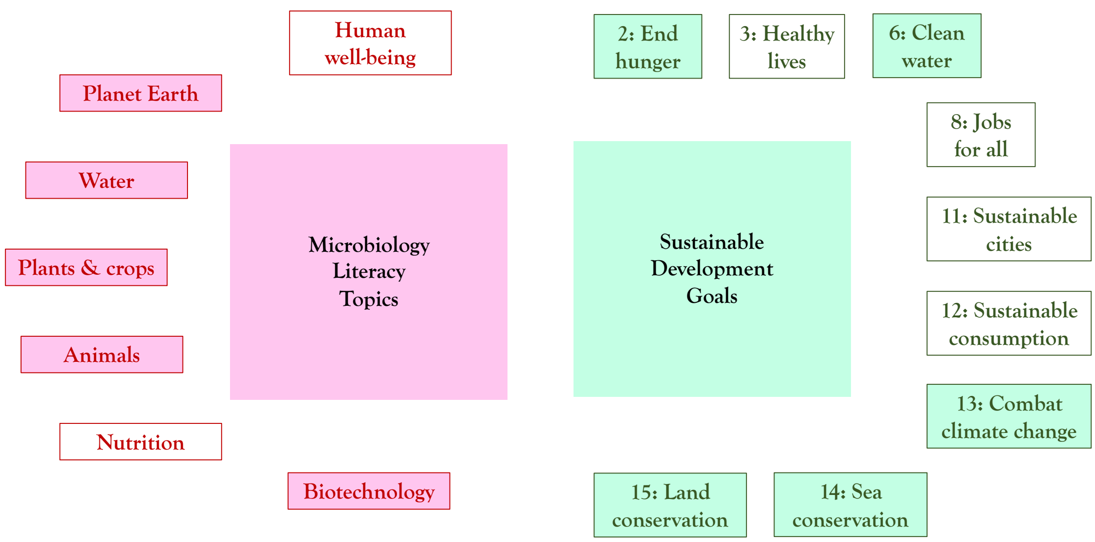
Imagine walking through a tropical forest, and suddenly you can see trees dipping their roots into the ocean's salty waters. They are mangroves! These resilient trees stand tall in the intertidal zone, covering more than half of the coastline of tropical regions. Unlike any other typical trees that live on land, mangroves have mastered the art of thriving in marine water, creating a magical ecosystem where terrestrial trees host aquatic animals, and the ebb and flow of the tides shape their distinctive habitats. They have evolved specialised features to face saline conditions and frequent tidal influences. One essential adaptation and distinctive feature is a unique network of roots, which include prop roots that anchor the trees in the shifting sands of intertidal zones. These intricate root structures not only provide stability but also enable the trees to absorb oxygen directly from the air, compensating for the low-oxygen conditions prevalent in waterlogged soils/sediments. Additionally, many mangrove species have evolved several physiological modifications to embrace the challenges of salty marine environments, allowing them to extract freshwater from the surrounding saline environment and offering a sustainable solution to their water needs.

As we delve deeper into our journey into the mangroves, let's explore and unravel the mysteries of the adaptation and resilience of these terrestrial trees in marine water and the support their associated microbes offer them to counteract the challenges posed by global climate changes, much like in other complex ecosystems of our planet.

The Microbiology and Societal Context

The microbiology: mangrove ecosystem; intertidal microbial mats; sediment microbial community; bioturbation from intertidal invertebrates; microbes-crabs associations for terrestrial adaptation; plant-promoting microorganisms. *Sustainability issues*: sustainability of coastal ecosystems, economy and employment; environmental stability; marine biodiversity.

Box 1 – Microbiology theme and SDGs treated in this chapter

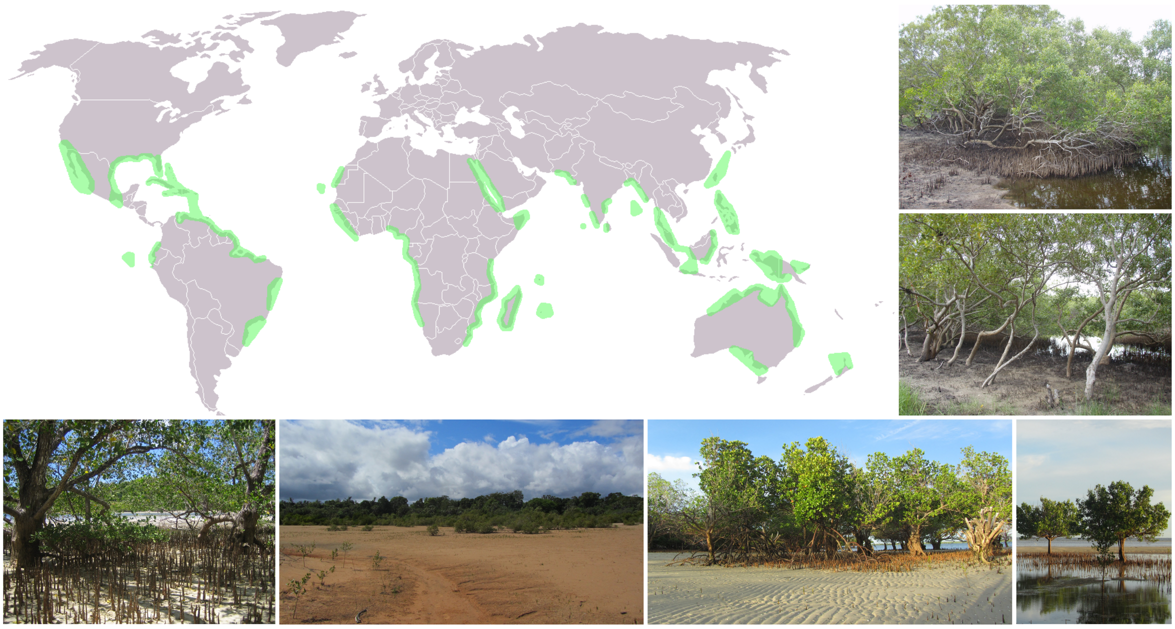


Mangroves are a vital component of coastal ecosystems. Their robust and intricate root systems provide shoreline stability as a natural buffer against erosion and storm surges. Moreover, these coastal forests serve as essential nurseries for various forms of marine life, offering a sheltered and safe environment for juvenile fish, crustaceans, and other aquatic organisms to thrive. All these services, which have multiple consequences for Sustainable Developmental Goals [Box 1], are assembled with the irreplaceable and invaluable assistance of microorganisms.

Mangrove Ecosystems: the Microbiology

1. What are mangroves? Mangrove ecosystems and their inhabitants. Mangroves are forests that thrive in tropical and sub-tropical sheltered coasts worldwide [map in Box 2]. They are formed by an extraordinary diversity of terrestrial trees and shrubs that evolved to live back in the sea. These forests can host different species of mangroves or just a single species, as in most Red Sea mangroves, where *Avicennia marina* is the only species in many coastline areas [pictures in Box 2].

Box 2 – Mangrove distribution and diversity at global scale



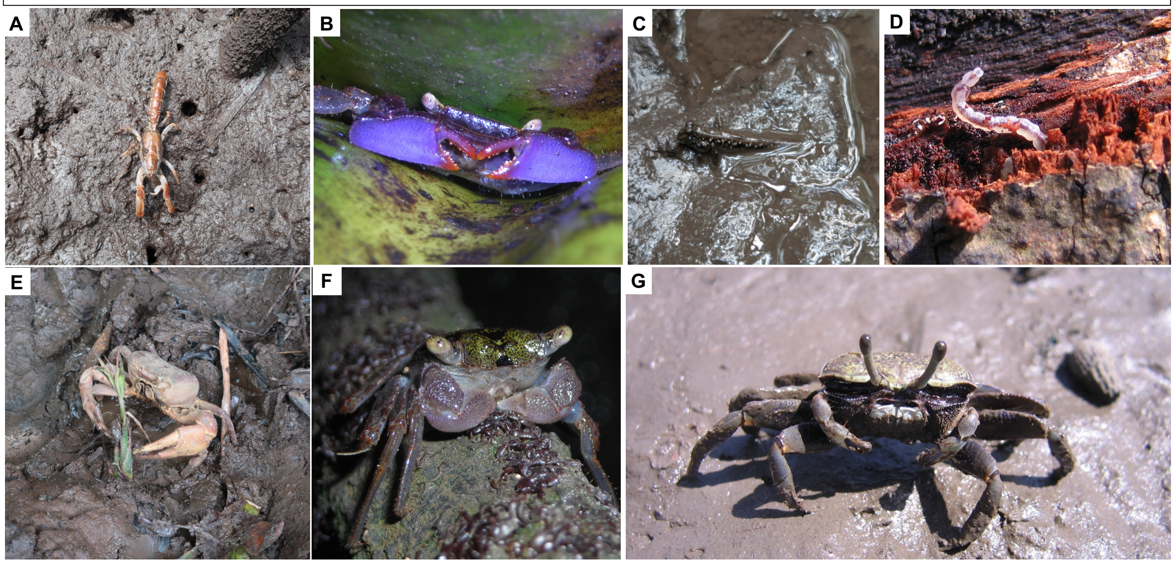
World Mangrove Distribution map (Author: Pinpin, Wiki Commons). Mangrove forest occur in different settings and are composed by different species of trees whose root morphology, adapted to live in the water form spatially complex ecosystems. (Photo Credit: Marco Fusi)

Mangrove plants likely emerged during the late Cretaceous period, around 150 million years ago, as terrestrial plants adapted to coastal habitats, where they coexisted with numerous species of dinosaurs. Belonging to the Magnoliopsida class, and distributed between Rhizophoraceae, Avicenniaceae, and Acanthaceae families, mangroves gradually evolved specialised adaptations to thrive in intertidal zones and brackish water environments.

With their intricate aerial roots, mangroves trap massive quantities of debris transported by the sea, building up sediment layers. Sediment is one of the most important parts of the mangrove ecosystem. Despite its inhospitable appearance derived from its muddy and salty nature, mangrove sediment hosts a huge amount of marine life. An astonishing number of bacterial, archaeal and fungal species, as well as algae and animals, have evolved to cope with the conditions imposed by the tidal fluctuations.

When we walk through the mangrove, we do not just walk on top of salty mud but also top of invisible layers of microorganisms, plant roots, and little animals. Larger animals, like crabs, snails and clams that live in the sediment, become burrowers, meaning they build their own houses by excavating burrows in the ground, as earthworms do in our gardens. There are many burrowing animals in mangrove forests. There are tiny, wingless beetles that are able to dig their houses up to 10 cm deep. There are pink worms that make complex networks of tunnels. There are pink shrimps that fishermen search for to use as bait to catch large fish. Giant clams dwell in the sediment and use a long syphon to reach the ground surface to feed and breathe during high tide. There are giant crabs that dig two-meter-deep holes to shelter away from herons and cranes that want to catch them, and are able to store large quantities of mangrove leaves that have fallen on the ground. There are enormous mud lobsters that, by digging their homes, make mountains of mud up to 3 meters tall that, in relation to the size of their inhabitants, look like skyscrapers in large cities [Picture in Box 3].

Box 3 – Burrower animal in mangrove sediment

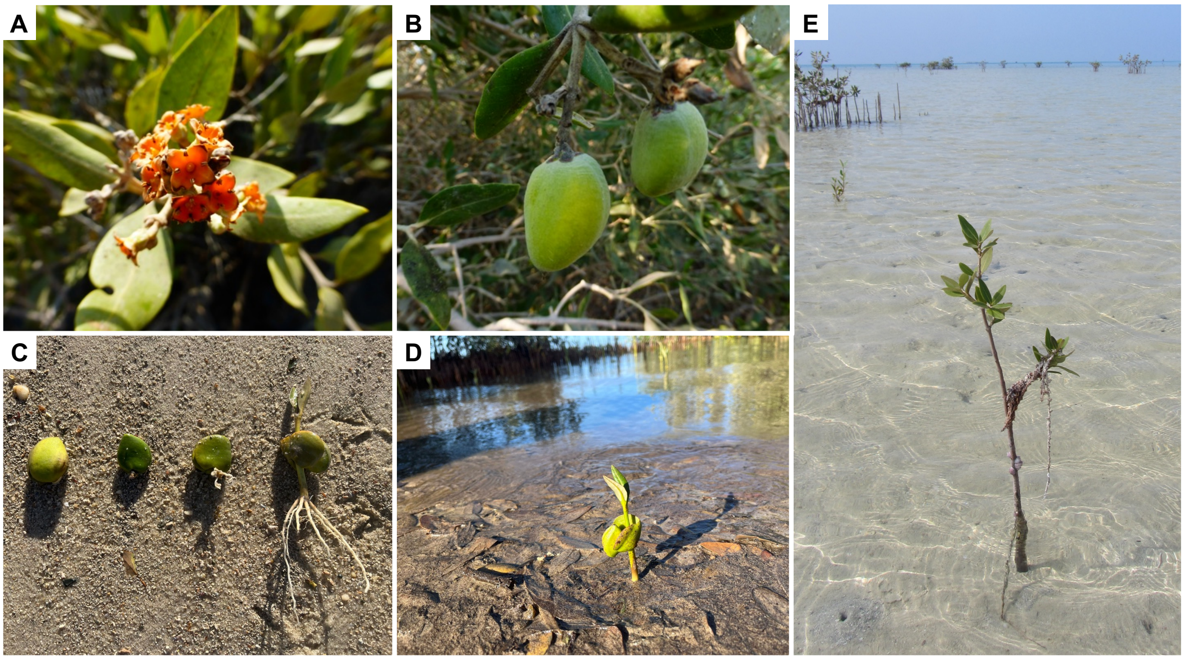


A. The mud lobster *Thalassina anomala*; B) The flat claws mangrove crabs *Chiromantes buetttikoferi*; C) the mudskipper; D) Worm living rotting wood on mangrove sediment; E) One of the largest crab and burrower in mangrove, *Cardisoma carnifex*; F) The climbing crab *Armases elegans*; G) the fiddler crabs *Afruca tangeri* (Photo credit: Marco Fusi)

The floor of the mangrove is submerged by seawater when the tide is high. This makes the ground salty and also reduces the presence of oxygen because the water slows down the diffusion of this gas into the sediment. Oxygen is essential for life on Earth and the most important gas in the atmosphere, allowing us, animals and plants to breathe and live. But how do mangrove flora and fauna cope? How can such a harsh environment host so much life? The answer to this question lies in the different strategies that plants and the associated animals evolved to cope with this challenging lifestyle, and in which microbes play a vital role.

2. Mangrove plants connect microorganisms between the sea and the land: how microorganisms travel up to the canopy of the mangrove forests. It's time to delve into the microscopic wonders that hold the secrets of mangrove resilience. For a terrestrial plant to survive in such unconventional conditions, mangroves have evolved several physiological and morphological adaptations, like an effective salt filtration system in the roots that prevents the transport of the salt present in the water into the plant, and salt glands in their leaves to expel excess salt. They also developed an efficient reproductive method consisting of propagules containing enough nutrients to develop a healthy plant [Box 4]. However, like all plants, mangroves depend heavily on their association with microorganisms: beneath the water and sediment, around the mangrove roots, live tiny superheroes, mainly bacteria and fungi, that all together are named microbiome.

Box 4 – Adaptation of mangrove tree: the vivipary and quick germination



(A) Mangrove Flower (*Avicennia marina*). Once pollinated, the flowers develop the fruit that contains the seed that germinates on the plant (vivipary), forming the propagules (B). After maturation, the "ready" propagule drops and is transported by ocean currents for months until it stops on sediments and starts to produce roots (C) and forms in a few days seedlings (D) that develop into a little tree in a few months (E). This process is supported and boosted by sediment and seawater microorganisms. (Photo credit: Marco Fusi and Ramona Marasco)

The plant-associated microbiome is a fundamental part of the plant metaorganism (i.e., host and microorganisms) that promotes plant fitness, productivity, and growth, especially for those species living in adverse environments. Plant-associated microorganisms are mainly recruited by the root system (root tissues and rhizosphere) in a complex process of attraction and selection mediated by the plant. The colonisation process starts with the release of root exudates rich in organic compounds; this "food" source is sensed by the surrounding microorganisms that are thereby attracted to the rhizosphere zone. The root surface (rhizoplane) then selects those microorganisms that can enter the tissues as endophytes. However, microorganisms recruited belowground not remain only in the root system but enter and use the plant transport systems (sap and xylem) to migrate toward the shoots, leaves and reproductive organs.

Along with sediments, other environmental sources like dust, air, rain, and insects can contribute to the diversity of the plant microbiome. For instance, microorganisms associated with pollinator insects (e.g., bees) and herbivores (among others, coleopterans, lepidopterans, and orthopterans) can be redistributed on the plant surface and internal tissues during insect activities, such as sucking and chewing plant tissues.

Following such relocation events, microbes differentially colonise the plant compartments. This is because each plant compartment provides a unique niche in which the physio-chemical properties, nutrients and metabolites drive the selection of specific microorganisms able to survive best in these conditions, thereby determining a microbial-tissue specificity. Once selected, these microscopic buddies form partnerships with the trees to keep the mangroves healthy. It is a masterpiece of teamwork orchestrated by nature.

These tiny organisms help mangroves in various ways. First, they break down dead leaves and other organic matter, turning them into nutrients that mangrove trees can use for food. They also contribute to controlling pathogen infection, stimulating growth, improving resistance to abiotic stresses (e.g., drought and high salinity), and filtering and degrading harmful substances from the water. These processes keep the soil and plants healthy and allow the mangroves to grow better. One example is given by the bacteria *Bacillus amyloliquefaciens* isolated from the roots of mangroves growing in the arid ecosystems of Mexico; it is capable of solubilising the phosphate present in the sediment, resulting in improved fertility of soils and, as a consequence, promotion of plant growth. Another study of the rhizosphere of mangrove plants in Brazil found several bacterial genera (i.e., *Azospirillum*, *Vibrio*, *Listonella*, *Azotobacter*, *Rhizobium*, *Pseudomonas*) capable of offering nutrients, such as nitrogen, phosphorous, potassium and iron, to the plant. These bacteria can also help propagules to grow faster and create a robust root system to keep them anchored during high tide, thereby favouring their development and persistence [Box 4].

All these functional services mediated by microorganisms contribute to the balance and health of the mangrove ecosystem, making it more robust and able to withstand challenges like climate change or pollution. So, these tiny microorganisms act as invisible helpers that keep mangroves strong and resilient.

3. If terrestrial plants go to the sea, the marine animals colonise the land: How mangroves and microbes help marine animals to conquer terrestrial ecosystems. The microscopic magic doesn't stop with mangrove trees. Diving into the world of creatures that call the mangroves home, like crabs, shrimps, worms, clams and many other groups, it is possible to discover how these creatures also get help from microbes.

Acting as bridges between the land and the sea, mangrove forests represent a unique ecosystem for terrestrial evolution, where many organisms, from bacteria to plants and animals, are gradually adapting from water to terrestrial environments. For example, within mangrove forests, we can find the amphibious fish known as mudskipper (Oxudercidae family), which can spend up to three-quarters of its time in the moistened intertidal mud outside the water. To achieve this, mudskippers have developed a method of air-breathing known as cutaneous respiration and evolved articulated fins functioning as walking joints.

Cyclically flooded by water due to tides, mangrove forests are characterised by large environmental fluctuations that require the animals to be capable of coping with these variable conditions. For example, some crabs belonging to S*copimera* species have evolved lungs in their legs for air-breathing, in addition to gills for underwater breathing. Other species of crabs have modified the shape of their body to avoid desiccation during low tide and exposure to air [Box 5].

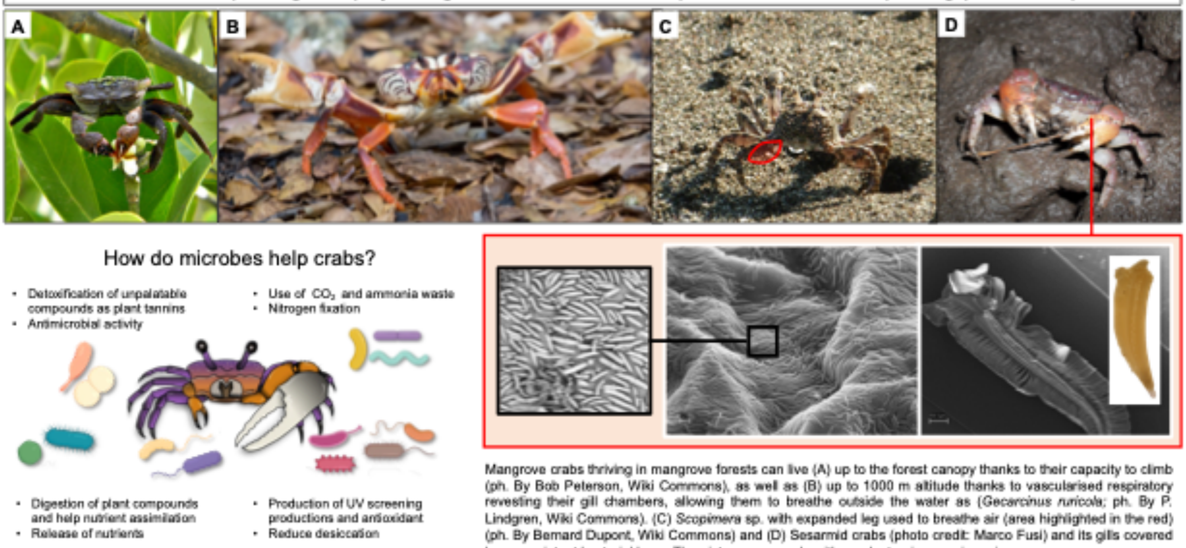
The conquest of land by marine organisms, termed "*terrestrialisation*", represents one of the most important evolutionary processes in the history of life on Earth. For aquatic animals that live underwater, adaptation to the terrestrial environment is a very challenging task that requires changes in several body parts and in many aspects of their lives.

Terrestrial plants evolved from marine algae to colonise terrestrial environments, exploiting a stable association with specific microorganisms such as mycorrhizal fungi. These microbial partners acted as root extensions, providing the ancestral terrestrial plant anchorage to the sediment, drought tolerance and enhanced mineral uptake. In return, the fungi obtained shelter and nutrients from the algae. This mutual collaboration led to a coevolutionary process where both partners, through reciprocal adaptations, gained new evolutionary advantages, allowing them to thrive in areas they alone wouldn't be able to colonise.

While the role of microbial symbiosis in the terrestrialisation of plants is documented, little is known about this in animals. Only recently have scientists begun to explore the role of the animal microbiota in terrestrialisation, with noteworthy findings emerging from studies conducted in mangrove forests, particularly those focused on mangrove crabs.

Terrestrialisation is far from being a single, completed process: it has occurred multiple times in the past and can still be observed today in specific environments and groups of organisms. In such circumstances, the metabolic plasticity of microbial partners can be helpful for the survival of their animal hosts. Bacteria can quickly adapt to the fast-changing conditions. Similarly to plants, symbiotic relationships between microorganisms and marine animals could have an essential role in helping animals transition toward a terrestrial lifestyle [Box 5].

Box 5 – Morphological, physiological and microbe-adaptation: A land-conquering partnership



Mangrove crabs thriving in mangrove forests can live (A) up to the forest canopy thanks to their capacity to climb (ph. By Bob Peterson, Wiki Commons), as well as (B) up to 1000 m altitude thanks to vascularised respiratory revesting their gill chambers, allowing them to breathe outside the water as (*Gecarcinus ruricola*; ph. By P. Lindgren, Wiki Commons). (C) *Scopimera* sp. with expanded leg used to breathe air (area highlighted in the red) (ph. By Bernard Dupont, Wiki Commons) and (D) Sesarmid crabs (photo credit: Marco Fusi) and its gills covered by a consistent bacterial layer. The pictures are made with an electronic scanning microscope.

Among the mangrove fauna, brachyuran crabs have successfully colonised different terrestrial niches and are suggested by scientists as a model animal group for terrestrialisation studies. In these arthropods, the gill is central to terrestrial adaptation, supporting important physiological functions, such as respiration and excretion. Under a microscope, crab gills are covered by a thick layer of bacteria that colonise its surface. But why would an animal cover its breathing organ with a layer of microorganisms? The answer is that the ‘cost’ of hosting microbial associates on their gills is compensated by an even greater benefit, namely a specific ‘cleaning’ function they provide. Researchers discovered that the gills of fiddler crab species originating from mangrove forests on different continents (Africa and Asia) consistently harbour a particular bacterial genus, *Ilumatobacter*, that helps the crabs eliminate harmful substances, such as ammonia (this is the equivalent of urine in the crab). Because it is not washed away by the seawater, ammonia can accumulate on the gill surface during periods out of the water, reaching toxic levels for the crab. The gill microbes have the ability to consume and transform the hazardous waste generated by their crab host (detoxification), thereby preventing the build-up to toxic levels and enhancing the survival of the crabs outside of their original marine environment. Other possible functional roles of gill-associated microorganisms in the process of Brachyuran crab terrestrialisation include protection from desiccation and other toxic compounds, such as sulfides and phenolic molecules, along with the production of bioactive compounds against pathogens.

The microorganisms inhabiting the gut of crabs also help their host in their daily nutrition and their transition from water to land. They support crabs in switching digestive processes from feeding on algae or other food resources found underwater to those found above water. For example, many crabs living in mangroves feed on mangrove leaves. Microbes in the gut help the crab to digest the mangrove leaves and assimilate the nutrients, in an analogous fashion ot the microbes in the rumens of cows and sheep that enable the hosts able to feed on grass. This adaptation and cooperation with the microbes allowed mangrove crabs to exploit new terrestrial food resources.

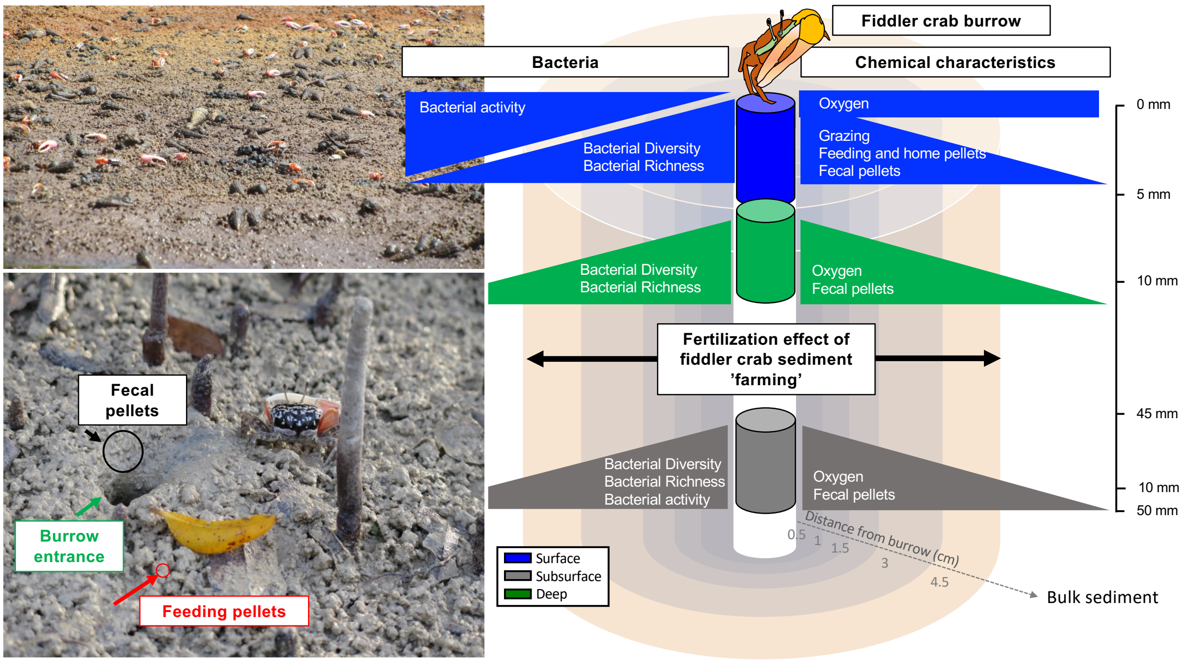
The knowledge we are building on these animals and the role of their gill and gut microbiota in their terrestrial adaptation represents a pivotal step in comprehending how bacteria can help animal evolution.

4. Farmers of the mangroves: How crabs and mangrove sediment microbes help trees to grow. Understanding the delicate balance that keeps the mangrove ecosystem in harmony involves considering all the components of such a complex ecosystem, including plants, animals and microorganisms. For instance, by excavating burrows, fiddler crabs (and all the other burrowing animals inhabiting the mangroves) have a fundamental function: they allow air and oxygen to penetrate the anoxic sediment. Fiddler crabs are one of the most important crab groups living on tropical coasts all over the world, and are filter-feeder animals, meaning they obtain all the nutritive substances they need by extracting them from the sediments. The surfaces of sediment grains are coated with organic matter, including bacteria, fungi and tiny organisms like little worms and algae. In the feeding process, the crab grasps a bit of sediment from the ground with its claws and brings it to the mouth, where the nutrients are removed from each grain [Box 6]. By feeding, fiddler crabs, every day, graze the area surrounding their burrow, generating numerous pellets of 'cleaned sediment', but at the same time, they also produce 'faecal pellet' (crab poo) containing very high concentrations of indigested bacteria, fungi, diatoms and microalgae. So, if they filter the sediment by feeding, they also release faecal pellets that contain live microbes that re-enrich the sediment. They also produce 'home pellets', big sediment balls from burrow maintenance. This is particularly important because they avoid damage or collapse of the burrow wall induced by the tide. Similarly to earthworms, fiddler crabs constantly rework the mangrove sediment. By doing this, the anoxic sediment (usually very dark in colour) is brought to the ground, and all the bacteria, fungi and algae in the deep are exposed to the oxygen. This mixing favours the proliferation of beneficial microorganisms that help mangrove trees thrive by fertilising the surrounding sediment. For example, some bacteria selected by the farming process deliver particular nutrients to the plant that would otherwise be lost with the tide.

Like actual farmers, fiddler crabs also increase sediment stability, helping to prevent erosion in mangrove areas. At the same time, the high density of the burrows creates a network of channels that trap sediments, reducing the impact of tidal forces and preventing the loss of soil. Fiddler crab burrows also provide microhabitats for various tiny organisms, including invertebrates and juvenile fish, and they can serve as refuge and breeding sites, contributing to the overall biodiversity of mangrove ecosystems. In some instances, fiddler crabs play a role in seed dispersal by moving seeds within and between different parts of the mangrove habitat, and the movement of seeds within the crab's burrow systems can aid in plant recruitment, contributing to the regeneration of mangrove vegetation.

Therefore, these restless mangrove farmers have a central role in keeping this important ecosystem healthy and productive by harnessing the sediment microorganism while contributing to fighting climate change and addressing the great challenge global warming poses to us.

Box 6 – Crabs bioturbation: An innovative way of "farming" mangrove ecosystem



Fiddler crabs are hard-working farmers in mangrove ecosystems. Due to their high density (up to 100 crabs can be found per square metre), the impacts of their sediment reworking have massive consequences for mangrove ecosystems. Crabs rework sediment to search for food and repair their burrows, but at the same time, disperse faecal pellets on the sediment. Their ceaseless work means that they can 'farm', on average, 78% of the mangrove forest floor worldwide, highlighting the significant ecological importance of fiddler crabs. In doing so, these crabs control the microorganisms in the sediment and select beneficial bacteria that support mangrove mangrove tree growth and health. (Photo Credit: Marco Fusi).

Relevance for Sustainable Development Goals and Grand Challenges

The microbial role in mangrove ecosystems relates to several SDGs, including:

Goal 2. Zero hunger. The mangrove microbiome indirectly influences SDG 2 by contributing to the overall health and mangrove ecosystem productivity, which, in turn, can positively affect local communities and food security. The microbiome within mangrove ecosystems plays a role in nutrient cycling, soil fertility and water quality, which are essential for the growth and health of these aquatic plants and inhabitants. Since mangroves serve as critical habitats for many fish and shellfish species, sustainable fisheries and aquaculture can be supported by healthy mangrove ecosystems and contribute to food security. Well-developed mangroves can also provide resources and livelihood opportunities for local communities, such as beekeeping and charcoal production. Income generated from such activities contributes to poverty reduction and supports the goal of zero hunger.

Goal 6. Clean water and sanitation. While the mangrove microbiome does not directly address freshwater and clean water issues, its contribution to support the mangrove ecosystem is crucial to the broader environmental goals of SDG 6. Bacteria and other microorganisms break down organic matter and recycle nutrients, preventing the accumulation of pollutants and excess nutrients. Also, association with beneficial bacteria promotes root system growth and development, favouring the development of an intricate root network that is able to stabilise coastlines to avoid soil erosion and trap sediments to prevent their entering land freshwater bodies.

Goal 13. Take urgent action to combat climate change and its impacts. Mangroves, along with the associated microbiome, significantly contribute to climate action by sequestering carbon and providing other ecosystem services. Mangrove microbiomes contribute to various ecological processes, including nutrient cycling, carbon sequestration, and ecosystem services. The microbiome within the mangrove soil contributes to carbon sequestration by participating in organic matter decomposition processes and stable soil organic carbon formation. Diverse mangrove microbial communities enhance the resilience of mangrove ecosystems to climate change impacts, such as rising sea levels and extreme weather events, by increasing the adaptability of mangrove ecosystems.

Goal 14. Life below water. The mangrove contributes significantly to the objectives of SDG 14 by promoting biodiversity and sustainable resource management in coastal and marine environments. This ecosystem serves as a nursery habitat for fishes, crustaceans, cephalopods, etc. It also indirectly supports coral reefs, seagrass, and seaweed meadows by means of the connectivity mediated by mass transfers and animal movements between these habitats. Bacterial partnership with mangrove plants and marine animals can boost their adaptability and help maintain the outstanding richness of species inhabiting this ecosystem and those associated with it.

Goal 15. Life on land. While associated with coastal ecosystems, the mangrove microbiome plays a role in the broader context of terrestrial and marine interfaces, contributing to several aspects of SDG 15. Mangroves, with their microbiome, contribute to preventing land degradation along coastlines. The root systems of mangrove trees, along with microbial processes, stabilise soil and prevent erosion, restore degraded land, and strive to achieve a land-degradation-neutral world. Mangroves are also crucial for terrestrial species like the Bengal tiger in Sunderbans or migratory birds that use these ecosystems for hunting and nesting.

Potential Implications for Decisions

1. Individual behaviours and initiatives for mangrove preservation. Combined and cumulative actions of individuals, over time and at a sufficient scale, can bring about change in governments' attitudes, policies and actions. Commuity-led projects promoted by community leaders have so far demonstrated the best success in implementing restoration practices for mangrove ecosystems. Community-led projects also significantly increased the awareness of the importance of mangrove ecosystems up to the national level, like the project Mkoko Pamoja in Kenya, where the Gazi village community self-organised to restore mangroves affected by coastal development. Mkoko Pamoja is now one of the leading projects in the country to promote the best restoration practices and best conservation strategy, ultimately contributing to the control of atmospheric carbon dioxide levels and global temperatures.

2. Community policies for mangrove preservation. Preserving mangrove biomes is strictly linked to protecting the coastline from extensive development, fishing, and resource overexploitation, such as timber recruitment or intensive aquaculture farming. Educational programs should be undertaken to alert people of the delicate nature of the mangrove ecosystems and biomes and their potential for contributing to preserving a healthy planet. To protect and minimise disturbance and disruption of mangroves, it is fundamental to increase the protection of coastlines where mangroves thrive and the inland use to avoid contaminants being discharged in mangroves. For example, regulations could be implemented to limit access by creating protected areas requiring the acquisition of specific permits to exploit resources within mangrove ecosystems.

3. National policies for mangrove preservation. The future of mangroves and their biomes are linked to the future of the climate scenarios. National and international initiatives to limit greenhouse gas emissions, global warming and climate change are essential for preserving mangroves. Their capacity to stock carbon and provide essential ecosystem services promotes their afforestation worldwide, promising new scenarios for mangrove expansion.

Pupil participation

1. Class discussion on the mangrove ecosystems and their preservation

2. Pupil awareness

Mangrove areas close to cities and tourist resorts are frequently threatened by coastal development, which disturbs the ecosystems. Can you think of any initiatives individuals may take to preserve mangrove forests on tropical coastlines?

The evidence base, further reading and teaching aids

Conquest Of The Land. https://www.youtube.com/watch?v=It9jQFPj8vE
How the Evolution of Land Plants Helped to Shape Earth. https://www.youtube.com/watch?v=vZDkRbpC2sw
The intertidal zone: https://education.nationalgeographic.org/resource/intertidal-zone/
The mangrove ecosystem: https://education.nationalgeographic.org/resource/the-mangrove-ecosystem/
Tides: https://education.nationalgeographic.org/resource/tide/
Why Crabs Keep Leaving the Sea for the Land. https://www.youtube.com/watch?v=2qYPVUBlXE4
Fiddle crabs burrow closing: https://www.youtube.com/watch?v=mizplWHsMG8
Crabs feeding: https://www.youtube.com/watch?v=6XJtq2d_lFs
Fiddler crab behaviour: https://www.britannica.com/video/180351/fiddler-crabs-mudskippers

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Glossary

Adaptation: the ability of organisms to develop special traits (modifying their behaviour, physiology or morphology) to better fit their surrounding environment. For example, animals might grow thicker fur in cold places, or plants might develop deep roots to find water.

Arthropods: a group of invertebrate animals with exoskeletons, segmented bodies, and jointed appendages. Insects, spiders, crustaceans, and centipedes are examples of arthropods.

C pool defines a system (or reservoir) which can store or release Carbon.

Carbon mineralisation is a **carbon sequestration** process by which carbon dioxide (CO_2) is immobilised in minerals such as carbonates (e.g., calcium carbonate [$CaCO_3$]).

Carbon sequestration encompasses all the natural and industrial processes that remove carbon dioxide (CO_2) from the atmosphere.

Climate change refers to all the modifications in the chemical composition of the Earth's atmosphere, such as the increase of greenhouse gases like carbon dioxide (CO_2), nitrous oxides (N_2O) and methane (CH_4), that are driven by human activity since the Industrial Revolution. These modifications have led/are leading to global and regional modifications of climate (temperature and precipitation patterns). For example, with climate change, it is expected that drylands will experience hotter temperatures globally and regional modification in their precipitation patterns (less, more, or no).

Coevolutionary process: the reciprocal evolutionary influence between two or more interacting species, where changes in one species may drive adaptations in the other, leading to a joint evolutionary path.

Cutaneous respiration: a form of breathing that occurs through the skin. Some organisms, particularly amphibians, rely on cutaneous respiration in addition to or instead of respiratory organs like lungs or gills.

Detoxification: the process of removing or neutralising (transformation to an unharmful form) toxins or harmful substances from an organism or its environment.

Ecosystem: a community of living organisms (plants, animals, and microorganisms) interacting with each other and their physical environment (like soil, water, and air).

Ecosystem productivity: how well an ecosystem can produce and maintain living organisms (biomass), such as microorganisms, plants and animals. It's the ecosystem's ability to grow and support life.

Endophytes: tiny organisms like bacteria or fungi that live inside plants without causing harm. They can help plants grow better or protect them from diseases.

Environmental fluctuations: changes in environmental features (e.g., in temperature, rainfall, or amount of nutrients) that spontaneously take place in natural habitats.

Erosion is a natural geological process leading to the terrestrial loss of material through the action of wind and/or water.

Evolutionary processes: biological processes relating to the way in which living things develop over millions of years, generation after generation, involving a gradual transition of change and development.

Fauna: all the animals that live in a specific region or ecosystem. This includes mammals, birds, reptiles, amphibians, fish, insects, and any other types of animals.

Flora: all the plants that grow in a specific region or ecosystem. This includes trees, flowers, shrubs, grasses, ferns, and any other types of plants.

Food security, as defined by the United Nations' Committee on World Food Security, is the principle that all people must have access to sufficient, safe, and nutritious food for an active and healthy life.

Functional services: the benefits or useful functions that ecosystems provide to humans and other living organisms. These services can include things like clean air and water, pollination of plants, and regulation of climate.

Harsh environment: a natural area where it is difficult for living things to survive and thrive due to extreme conditions such as high temperatures, low water availability, strong winds, or limited food resources.

Intertidal ecosystem/zone: those ecosystems collocated above the water level at low tide and underwater at high tide: in other words, the part of the littoral zone within the tidal range. These ecosystems are characterised by fluctuating environmental conditions and support a variety of marine and terrestrial life.

Metabolic plasticity refers to the ability of an organism's metabolism to adapt to different environmental conditions. It allows organisms to adjust their metabolic processes in response to changes in their surroundings.

Metaorganism: a host organism and its associated microorganisms (such as bacteria, fungi, and viruses), considered all together and functioning as a sole collective organism.

Microbial mats: layered communities of microorganisms, including bacteria, algae, and other microbes, that grow on abiotic surfaces like sediments and rocks. They are often found in aquatic environments.

Microbiome/Microbiota: the community of microorganisms and their genomes, including bacteria, fungi, viruses, and other microbes, that inhabit a particular ecological niche, such as the plant or animal organs, soil, or other specific environments. All together, these microorganisms play a crucial role in various biological processes and can have significant effects on the health and functioning of the host organism or system.

Model animal: organisms, often specific species, used in scientific research to understand biological processes. They are chosen for their suitability in providing insights that can be applied to a broader context.

Morphology: the physical form, building structure, or appearance of an organism (how it looks or is shaped).

Mycorrhizal fungi: microbial fungi forming a symbiotic relationship with the roots of plants. These fungi assist in nutrient absorption by the plant roots, especially minerals like phosphorus, in exchange for carbohydrates from the plant.

(Ecological) niche: the role and position that a species has in its environment, including how it interacts with other organisms and the physical surroundings. It encompasses the species' habitat, food sources, behaviour, and other factors that contribute to its survival and reproduction.

Nitrogen fixation generally refers to the fixation of atmospheric nitrogen by diazotrophic microorganisms into a more assimilable form of nitrogen, such as ammonia.

Phosphate solubilisation is the process that transforms inorganic/insoluble phosphorus compounds into soluble forms assimilable by plants and other organisms. This process is mainly mediated by phosphate-solubilizing bacteria living in the soil.

Physiological refers to processes and functions related to the normal functioning of living organisms and their parts, including biochemical and physical activities.

Plant growth promoters are microorganisms (mainly bacteria and fungi) that favour the growth, health and development of plants, especially during stresses such as drought and salinity.

Primary production is the production of biomass (organic compounds) from inorganic molecules such as carbon dioxide (CO_2) and gaseous dinitrogen (N_2).

Productivity in (microbial) ecology refers to the production of biomass in an environment.

Prop roots are special roots that grow above the ground or water to support tall plants like mangroves. They help the plant stay stable in soft or flooded soil.

Propagules are small parts of plants, like seeds or cuttings, that can grow into new plants. They are like plant babies that can start a new plant.

Resilient: being able to quickly recover from damages, difficult situations or adaptational challenges.

Rhizoplane: the surface of a plant's roots where helpful bacteria and other tiny organisms live. They can benefit the plant by helping it absorb nutrients from the soil.

Rhizosphere: the narrow portion of soil (a few millimetres) that is in contact with the roots; it is directly influenced by plant-root secretions (root exudates) and is rich in nutrients, such as sugars and proteins.

Salt-exclusion strategies: ways that plants use to keep salt out of their tissues. For example, some plants have special cells or structures that prevent salt from entering, allowing them to grow in salty environments like marine coastal areas.

Shoreline stability: how well the land along the shore (like beaches or cliffs) holds together and resists erosion caused by waves, tides, and other forces. Plants with strong roots and protective features can help maintain shoreline stability by preventing soil erosion.

Soil microbiome represents the totality of microorganisms (bacteria, archaea, fungi, protozoa and viruses) living within the soil.

Sustainable Developmental Goals are a collection of 17 global goals designed to be a "blueprint to achieve a better and more sustainable future for all"; these were set in 2015 by the United Nations General Assembly and are intended to be achieved by the year 2030.

Symbiotic relationship: a close and often long-term interaction between two different species living in direct contact with each other. It can be mutually beneficial (mutualism), one-sided benefit (commensalism), or detrimental to one of the species (parasitism).

Terrestrialisation: the process by which an organism undergoes a transition from being primarily aquatic (spending its life in water) to terrestrial (spending its life on land). It involves the colonisation and adaptation of organisms to terrestrial habitats.

Tides: the regular rise and fall of sea levels caused by the gravitational pull of the moon and the sun on Earth's water masses. They create cyclic patterns of high and low water levels (called high and low tides) along coastlines.