Terrestrialization: How plants and animals emerged from the water to conquer land

Mom, Dad, I read that all plants and animals were in the ocean before living on land. What happened to them? How do they come out?

Photo credit: Marco Fusi

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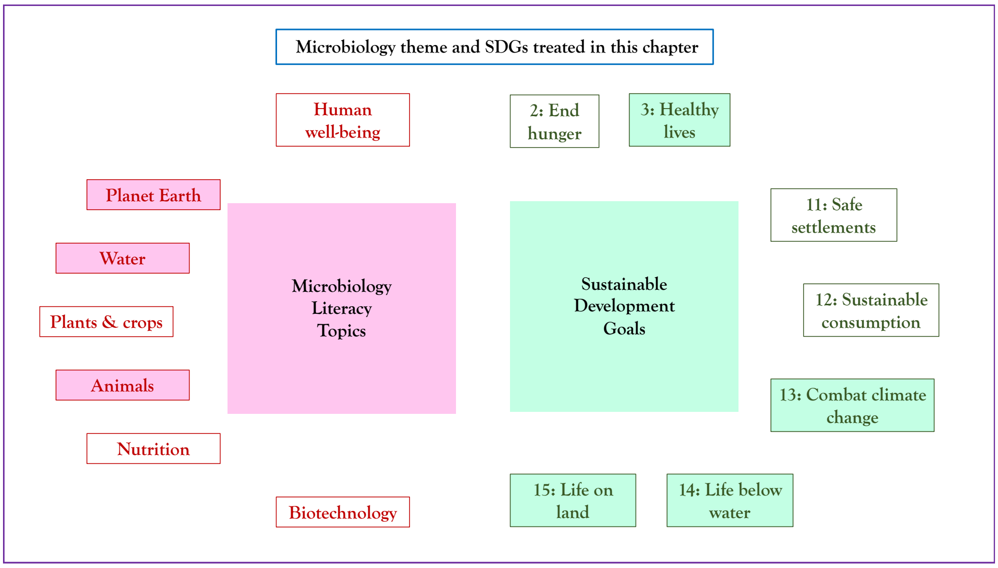
Terrestrialization: How plants and animals emerged from the water to conquer land

Storyline

Long before forests, insects, or animals filled the land, all life lived in the oceans. Terrestrialization is the name we give to the incredible process that changed everything, during which some life forms learned how to breathe, move, and survive on land. In fact, billions of years ago, Earth was almost entirely covered by oceans—the cradle where life first appeared in the form of tiny microorganisms (or microbes) like bacteria. As time passed, around 500 million years ago, continents slowly rose from the sea, creating rocky coastlines, sandy beaches, and river deltas. At first, these lands were harsh and barren, too dry and unstable for most life, but tiny pioneers, such as cyanobacteria, algae, and fungi living in the oceans, began to colonise the rocks. They formed microbial mats and biological crusts that trapped dust, broke down minerals, and created the first thin soil layers. Gradually, plants followed, spreading across damp areas and bringing shade, oxygen, and food to the new landscape. As the land became greener and more prosperous, some marine species began to evolve features that helped them survive in shallow or temporary waters: stronger fins for pushing, tougher skins to prevent drying, and lungs or air sacs to breathe when oxygen levels were low. These adaptations were the first steps toward life on land. Then, about 200 million years later, some "brave" organisms began their journey to fully explore life beyond water by evolving new body parts and behaviours that enabled them to breathe air, move on solid ground, eat new foods, and reproduce on land. This transition from water to land is one of the most important steps in the history of life on Earth, and microorganisms played a significant role in it. Yet even after plants and animals arrived, microorganisms continued to play vital roles by forming microbe-host partnerships.

The Microbiology and Societal Context

The microbiology: plant and animal microbial symbiont (or symbiome); plant/animal metaorganism (or holobiont); plant-growth-promoting microorganisms; microbe-mediated adaptation. *Sustainability issues*: terrestrial and marine biodiversity; ecosystem functioning.

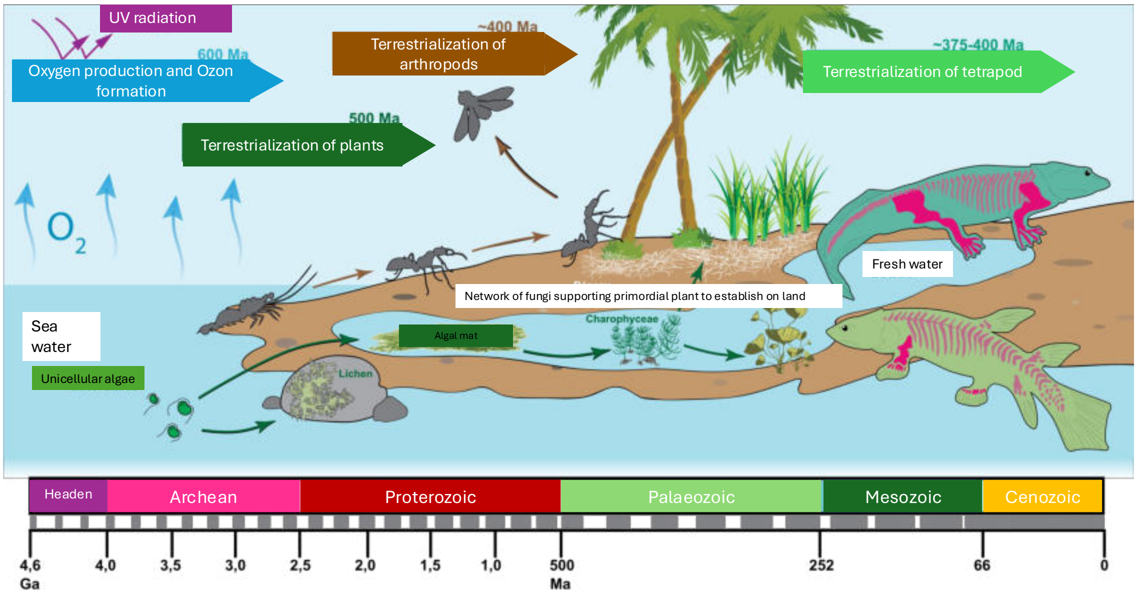


1. The terrestrialization process: the timeline of events in a nutshell.

Terrestrialization is the name scientists give to the big evolutionary shift when living things moved from water to land. This incredible journey began hundreds of millions of years ago and completely changed life on Earth.

Before animals and plants took their first "steps" on land, tiny organisms like bacteria, fungi, algae, and lichens were already there. These microscopic pioneers lived on rocks and soil, forming crusts that helped hold the ground together. Some of them, like cyanobacteria, have the capacity to synthesise oxygen, a gas that would later be essential for animals to breathe. Later, around 480 million years ago, small plants began to grow on land. They not only made the landscape greener but also created shade, food, and shelter, setting the stage for animals to follow. The earliest land animals were arthropods, creatures with jointed legs and hard outer shells, such as millipedes and ancient insect relatives. One fossil millipede, *Pneumodesmus newmani*, is about 428 million years old and shows tiny breathing holes called spiracles, proving it could breathe air. Other animals, like snails and slugs (called molluscs), adapted by developing air-breathing lungs to survive on land.

From sea to land: the journey of microbes, plants, and animals



Life's transition from aquatic to terrestrial environments occurred in multiple stages over hundreds of millions of years. Oxygenic photosynthesis by cyanobacteria and algae enriched the atmosphere and led to ozone formation, reducing harmful UV radiation. Microbial mats and lichens were among the first to colonize land, stabilizing surfaces and initiating soil formation. Green algae (*Charophyceae*) adapted to fluctuating wet–dry conditions, giving rise to early land plants. These plants transformed landscapes, enabling the later terrestrialization of arthropods (~400 Ma) and vertebrates (~375–400 Ma), culminating in fully developed terrestrial ecosystems.

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Much later in evolutionary history, some fish developed air-breathing lungs, this time derived from their swim bladders, along with stronger, limb-like fins that could support their bodies. One famous example is the Coelacanth, often called a "living fossil", which still inhabits the deep waters of the Indian Ocean. Unlike typical ray-finned fish, the Coelacanth has robust, lobed fins with a bone-like structure, an essential step toward the evolution of limbs capable of supporting terrestrial movement.

Fossils such as Tiktaalik, Acanthostega, and Ichthyostega reveal how vertebrates (animals with backbones) gradually adapted to life on land. These transitional species show a mix of aquatic and terrestrial features, including limbs with digits and lungs for breathing air. By around 395 million years ago, fossilised footprints with distinct toes were discovered in rocks in Poland, providing evidence that tetrapods, i.e., four-limbed vertebrates, were already venturing onto dry land.

2. Why terrestrialization matters in Earth's evolution

Terrestrialization stands as one of the most profound evolutionary shifts in Earth's history. When life ventured from water onto land, it didn't merely change its surroundings, but it redefined the architecture of ecosystems and the trajectory of biodiversity. This transition sparked the rise of land plants, which anchored soils, enriched the atmosphere with oxygen, and led to the formation of expansive forests. These new landscapes became the scaffolding for intricate food webs and ecological niches. From arthropods to amphibians, reptiles to mammals—including ourselves—every terrestrial creature owes its existence to this ancient leap.

3. How terrestrialisation unfolded

Let's take a closer look at the key stages of terrestrialization, focusing on the colonisation of land by (i) microorganisms, (ii) plants, and (iii) animals:

a. ***Microorganisms, the invisible allies of life on land.*** Microorganisms were the first great engineers of our planet's transformation. Around 3.5 billion years ago, simple microbial life already existed in Earth's oceans, but it was the rise of cyanobacteria—microscopic organisms capable of oxygenic photosynthesis that changed everything. Before them, the atmosphere contained almost no oxygen. Cyanobacteria used sunlight, carbon dioxide (CO_2), and water (H_2O) to produce energy, releasing oxygen as a waste product (the photosynthesis reaction: CO_2+H_2O+light energy → sugars + O_2). About 2.4 billion years ago, over a period of hundreds of millions of years, this process triggered the Great Oxidation Event, one of the most important turning points in Earth's history. The oxygen released by these microbes slowly accumulated in the oceans and atmosphere, reacting with dissolved iron to form vast bands of rust-colored rock (the banded iron formations we still find today). As oxygen levels rose, the ozone layer (O_3) formed in the upper atmosphere, protecting Earth's surface from harmful ultraviolet radiation. This protection was essential because it allowed living organisms to survive and thrive on land. Meanwhile, microalgae and algae, which evolved later in the oceans, joined this global photosynthetic revolution. They expanded oxygen production and formed the foundation of marine food webs, feeding animals and shaping the chemistry of coastal ecosystems.

These photosynthetic microorganisms, along with other bacteria, fungi, and lichens (formed by fungi and algae), formed the first microbial mats and biological crusts by growing on bare rock surfaces. These living films trapped dust, broke down minerals, and created the first thin, nutrient-rich soils. They stabilised sediments against erosion and helped retain moisture—conditions that allowed mosses, liverworts, and other early plants to take root. Moreover, when these microorganisms died, they added organic matter to the soil, enriching it with nutrients and making it more conducive to plant growth.

In short, microorganisms were responsible for oxygenating Earth's atmosphere and preparing the land for colonisation. They transformed a lifeless, rocky surface into a dynamic and habitable environment, paving the way for plants, animals, and eventually humans. Without their ancient work, the story of terrestrialization—and indeed the story of life on Earth—would never have been possible.

Photosynthetic bacteria and (micro)algae oxygenating our planet

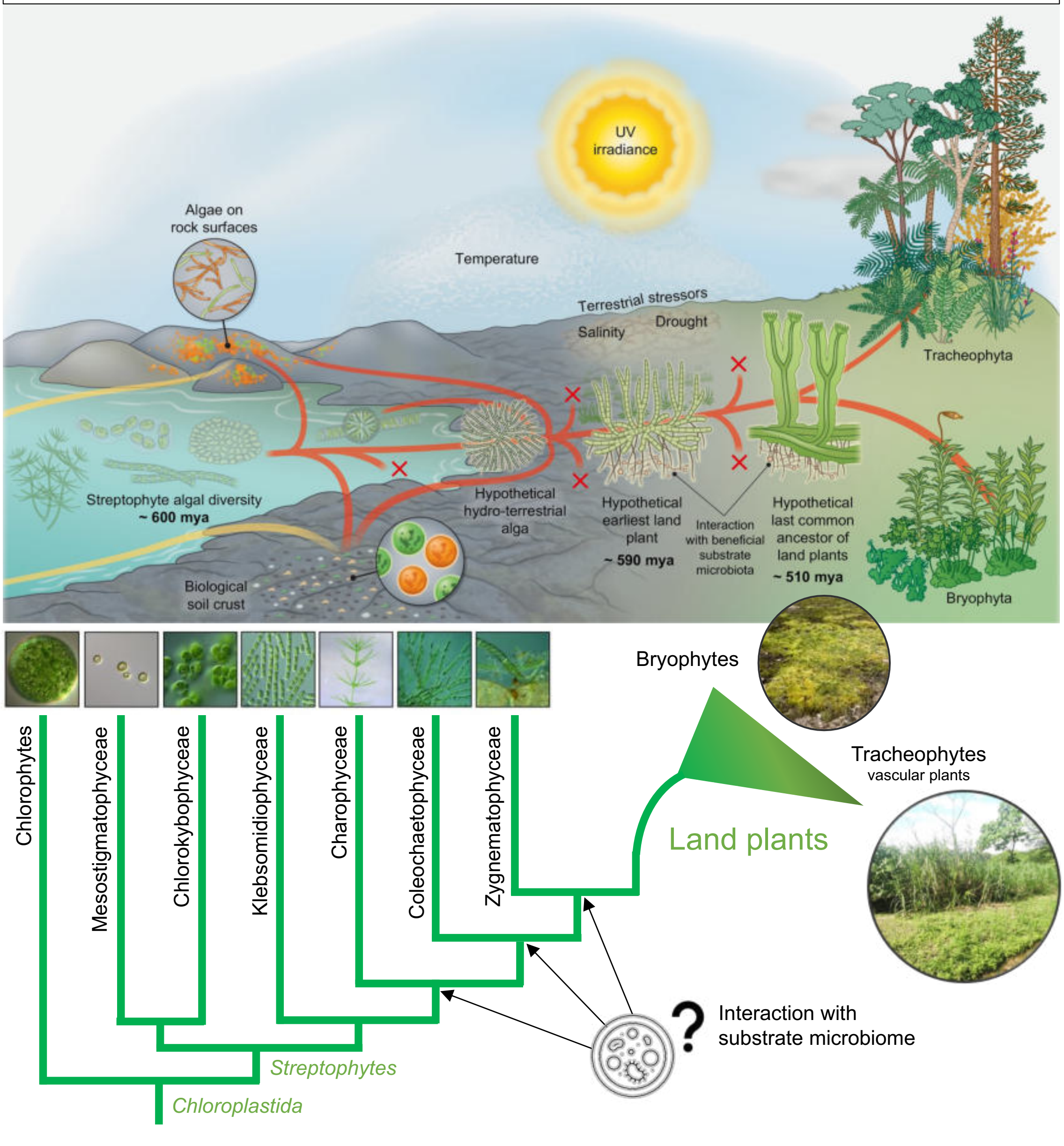
Cyanobacteria and microalgae are key drivers of oxygen production on Earth. Through photosynthesis, they capture sunlight and release oxygen, supporting ecosystems in aquatic and coastal environments. These microbial mats and biofilms, found in tidal flats and shallow waters, represent modern analogues of the ancient communities that first oxygenated our planet and made terrestrial life possible.

Image credits: photographs by Ramona Marasco and Khaoula Lassoued.

b. ***Plants, the green pioneers.*** Plants were the first complex organisms to colonise the land after microorganisms. When the first moss-like plants appeared on land about 480 million years ago, they began to cover bare rocks and soils. These plants trapped water, added organic matter, and produced additional oxygen. As plants grew taller and developed stems, roots, and leaves, they created shade, food, and shelter. Forests of giant ferns and trees soon covered large areas, shaping the landscape and providing new habitats for insects, amphibians, and reptiles. During this transition, plants evolved notable physiological and morphological modifications to survive. First, they developed waxy leaves and stems to prevent water loss. They also formed stomata, tiny pores that can open and close to control breathing and water loss. To stand tall and reach sunlight, plants evolved lignin, a strong material in their cell walls, which allowed them to grow upright and form stems and trunks. Roots and root hairs appeared, helping them anchor to the soil and absorb water and nutrients. Finally, plants developed spores and later seeds with protective coats, allowing them to reproduce without staying in water.

These adaptations allowed plants to spread across land, create forests, and shape the environment that animals—including us—depend on today. However, these traits didn’t evolve in a single way; instead, they followed different evolutionary paths depending on the environment, driving the incredible diversity we see across Earth’s landscapes today. From damp riverbanks and shaded forests to deserts and high mountains, plants evolved distinct strategies to cope with temperature, light, and water availability. For example, desert plants evolved thick stems and tiny leaves to conserve water, mountain plants developed compact forms to resist cold and wind, and coastal species adapted to salty soils and shifting tides. Notably, *Klebsormidium* (often shortened to Klebs) belongs to the streptophyte algae, which represent the ancestral lineage from which land plants evolved. The genus *Klebsormidium* is among the best-known and most widely studied members of this group and is considered one of the closest living relatives of early land plants. It can still be found today in terrestrial and freshwater ecosystems across a wide range of climates, from polar to tropical regions. Its remarkable ability to withstand desiccation, intense light, and fluctuating water availability makes it a valuable modern analogue for studying the molecular, structural, and physiological traits that facilitated the terrestrialization of plants—see for more details *EvolutionaryStar: Klebs (Klebsormidium flaccidum)* in the *Evolutionary Route Marker Star Microbes, Portrait Gallery*.

Plant terrestrialization: from green algae to vascular plants



From aquatic algae to early land plants, evolution involved major innovations such as rhizoids, cuticles, stomata, and partnerships with fungi that allowed survival outside water. These adaptations transformed Earth's surface, enabling the rise of terrestrial ecosystems.

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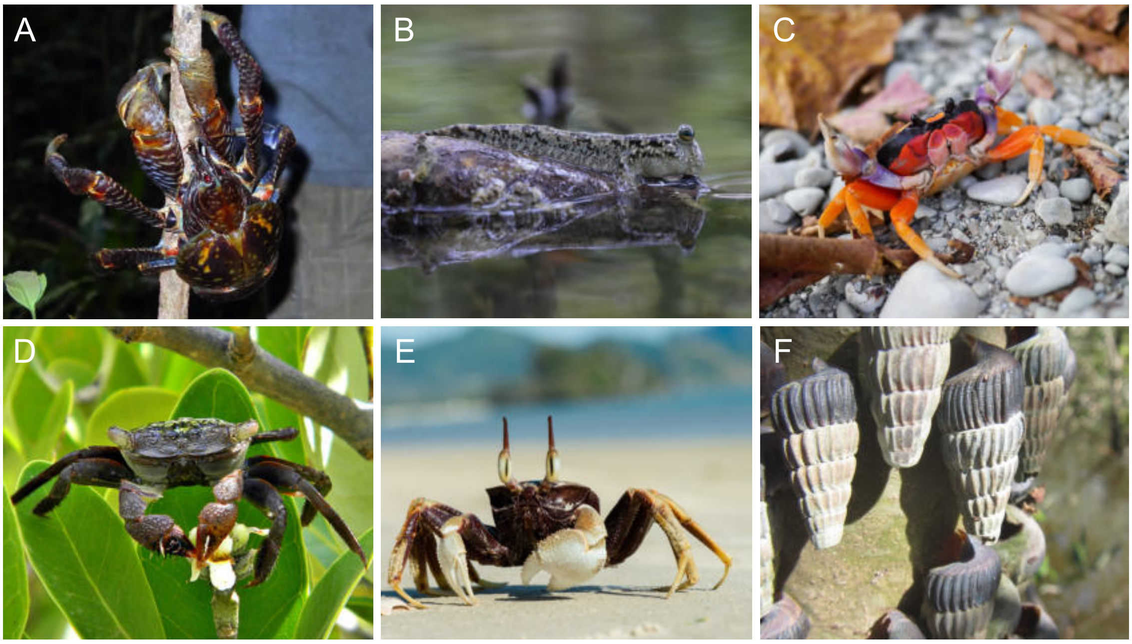
c. ***Animals followed.*** The arrival of animals on land was only possible thanks to the groundwork laid by microorganisms and plants, which transformed barren terrain into habitable ecosystems. Without these early pioneers stabilising soils, producing oxygen, and creating food sources, animals would have had neither the opportunity nor the means to leave the water.

But how did animals adapt to life on land? This transition demanded a suite of evolutionary innovations, both behavioural and anatomical. From breathing air and moving without the buoyancy of water to sensing new environmental cues, animals had to reengineer their bodies and behaviours to survive in the air-exposed, gravity-bound world of terrestrial life.

Animal terrestrialization: Modern analogue and associated behaviors



A – Coconut crabs, *Birgus latro*; B- Mudskipper, *Periophthalmus barbarus,* C- Land crabs, *Geocarcinus lateralis*; D – Climbing crabs, *Aratus pisonii*; E – Ghost crabs, *Ocypode macropthalmus*; E – Climbing snail , *Cerethidea decollate.* All these animals are undergoing multiple adaptation to survive out of the water. Some, like the coconut crabs and the climbing crabs did so well that they live on the canopy of trees at several meters of height, feeding in fresh leaves. Although not visible with our eyes, microbes are their best allies to made this happen. For examples, they help the digestion of fresh leaves, much more difficult to digest compared to algae, they help with breathing and weeing, and also, they will help them to protect from the ultraviolet rays of the sun by producing carotenoids on the surface of their carapace!

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Below are some of the most essential evolutionary upgrades that made this leap possible:

- ***Breathe air:*** gills worked well underwater, but on land, lungs were essential. Some fish evolved lung-like organs, allowing them to draw oxygen directly from the atmosphere.
- ***Motility:*** fins transformed into limbs with elbows, wrists, and digits, seen in fossils like Tiktaalik, giving early tetrapods the ability to push, crawl, and eventually walk. But movement required strength, so animals evolved reinforced skeletons, including strong backbones, hips, and limb girdles, to support their body weight without the buoyancy of water.
- ***Weeing:*** marine animals release ammonia directly into water, but land animals need kidneys and specialised excretory systems to conserve water and safely remove nitrogenous waste. This led to the production of concentrated urine, often aided by microbial partners that helped detoxify and recycle nutrients.
- ***Dryness:*** on land, animals needed protective barriers—such as thicker skin, shells, or other coverings—to prevent dehydration and defend against both UV and new predators and microbes.

- ***Reproduction:*** eggs laid in water were vulnerable on land, so animals developed hard shells, nesting behaviours, and other strategies to protect their offspring.
- ***Sensing the new environment:*** eyes and ears adapted to air rather than water, and brains evolved to process new kinds of information—from navigating terrain to spotting predators in open landscapes.

Each of these adaptations was a solution to the unique challenges of life on land that fish, millipedes, centipedes, spiders, insects, and even snails overcame in their own distinct ways. Through countless evolutionary experiments, these pioneers laid the foundation for the rich and diverse ecosystems we see today. From tiny insects to towering mammals, every land-dwelling animal carries the imprint of this ancient transformation, a legacy written in bones, lungs, limbs, and instincts.

4. The microbial side of the story: how microorganisms contribute to plant and animal terrestrialization

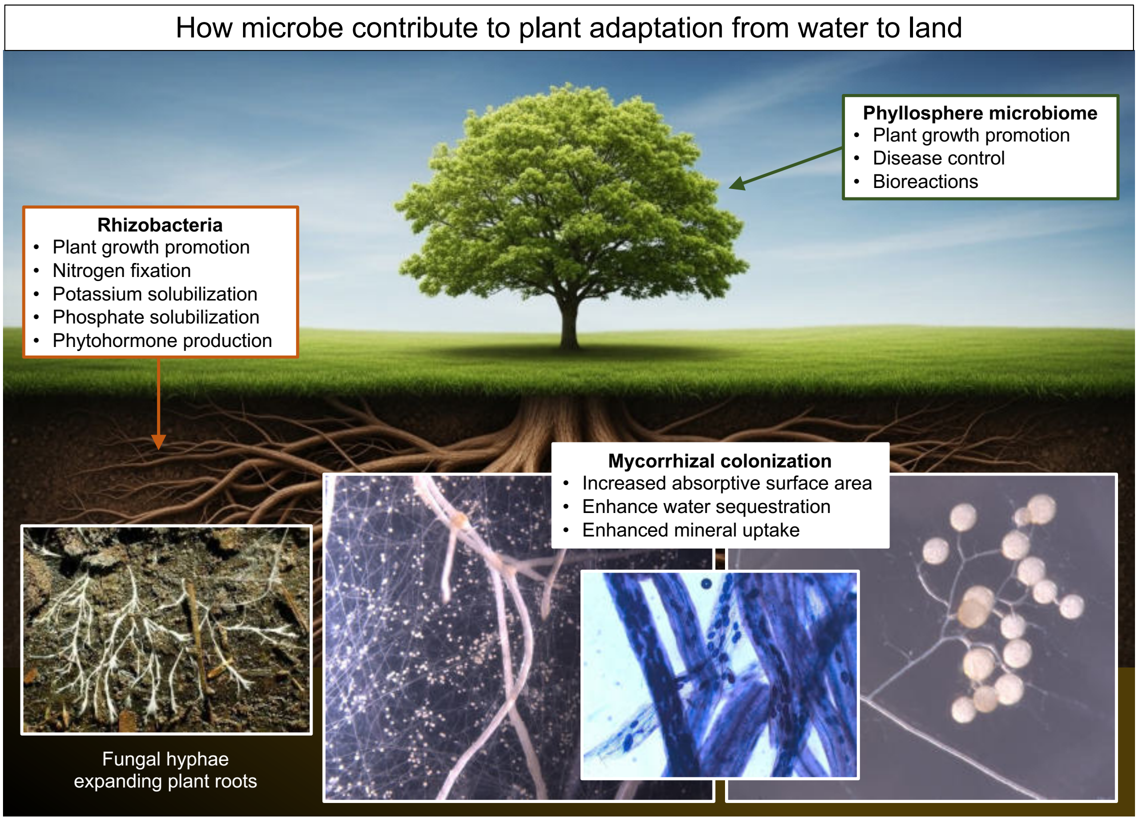
Which role did bacteria play in the terrestrialization of plants and animals? Microorganisms were the quiet engineers of terrestrialization, preparing the land, supporting the newcomers, and still sustaining ecosystem functionality and stability on Earth today. Besides their role in reshaping terrestrial ecosystems, microorganisms also helped plants and animals adapt out of water.

a. Plant-microbe interaction. Interactions between plants and microbes were among the most crucial partnerships in Earth's history, and fungi played a leading role in helping plants make the move from water to land. For the first moss-like organisms, the presence of mycorrhizal fungi—fungi forming close associations with plant tissues. These fungi, which were connected to the primitive rhizoids or root-like structures of early plants, formed a mutualistic relationship known as mycorrhiza, in which both partners benefited. The fungi's fine, branching filaments (hyphae) spread through the soil, greatly expanding the plant's ability to absorb water and essential minerals, especially phosphorus and nitrogen, from nutrient-poor environments. In exchange, plants supplied the fungi with sugars and organic compounds produced during photosynthesis, delivered through root exudates.

This collaboration went far beyond nutrient exchange—it fundamentally shaped terrestrial ecosystems. Mycorrhizal fungi acted as biological extensions of the root system, exploring tiny soil spaces that plant cells could not reach. They also protected plants from pathogens and environmental stresses such as drought or salinity by improving water balance and enhancing resistance. Remarkably, scientists believe that these fungi began helping plants before true roots even evolved. Early land plants, small and simple in structure, lacked the deep roots of modern vegetation, yet fungal hyphae functioned like temporary roots, anchoring plants and facilitating mineral uptake from raw, rocky surfaces.

Over time, these interactions drove co-evolution: as plants developed true roots and vascular systems, mycorrhizal fungi evolved alongside them, diversifying into arbuscular, ectomycorrhizal, and ericoid forms. This symbiosis not only enabled plants to colonise new habitats but also transformed barren land into fertile soil, stabilising sediments and fostering the establishment of larger plant communities. In essence, the partnership between plants and fungi was the biological bridge between the aquatic world and the terrestrial biosphere, laying the foundation for the prosperous and stable ecosystems that cover Earth today.

Subsequently, other soil and root-associated microbes joined this alliance, giving rise to the plant microbiome—the complex community of bacteria, fungi, and archaea living in and around plant tissues. Some bacteria, such as rhizobia, formed nitrogen-fixing nodules in roots, providing essential nutrients in exchange for carbon. Others, like plant-growth-promoting rhizobacteria, released hormones that stimulated root elongation or protected against pathogens. Together, these microbial partners created a protective, nutrient-recycling network that continues to sustain plant life today, showing that terrestrialization was not just a story of plants conquering land, but of entire microbial communities working together to make it possible.



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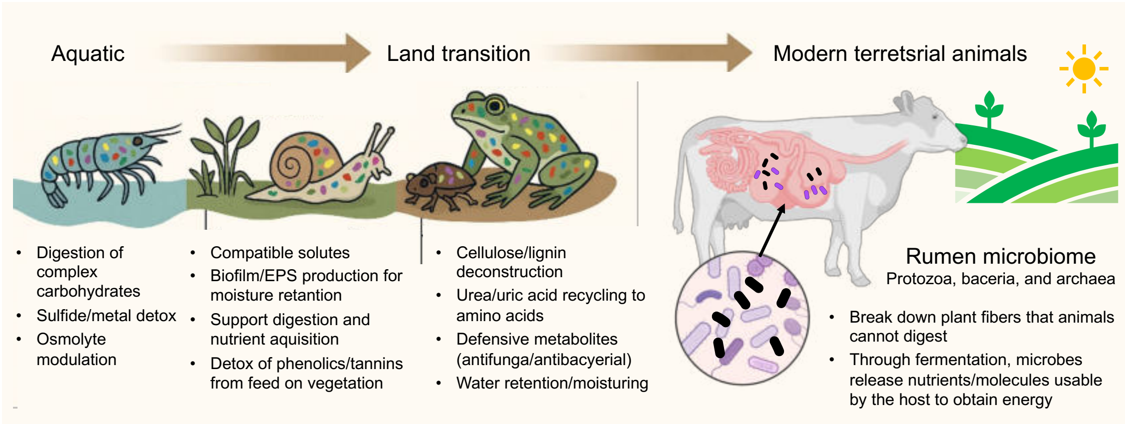
b. Animal-microbe interaction. Microbes also played a crucial role in helping animals adapt to new environments. As animals began to be exposed to new (and challenging) conditions, including dry air, sunlight, and fluctuating temperatures, their interactions with microbes became crucial. Based on current research on frogs and salamanders, scientists have shown that skin microbes have become increasingly critical during terrestrialization. Skin stays naturally moist in water, but on land it dries quickly. Whereas some bacteria can form protective biofilms—natural shields that help prevent infections and dehydration—others secrete antimicrobial compounds that stop harmful fungi or viruses from growing, a defence strategy that persists today. Even reproductive success may have depended on microbes. When early animals began to lay eggs on land, soil bacteria and fungi likely helped recycle nutrients, keep the ground oxygen-rich, and prevent rotting processes or invasion by other microbes. They supported embryo development in drier conditions and, in some cases, facilitated the transmission of certain microbes to newborns that consume egg remnants after hatching.

Besides these microbe-interactions, one of the most important is the one that evolved to help digest new complex materials and types of food on land, such as fibrous plants, tough leaves, and insects with hard shells. At first, the microbial colonisation of the stomach and/or gut probably occurred as microbes entered the digestive tracts passively through food, water, or sediment. Over time, certain microbial species formed stable symbiotic relationships with their animal hosts, colonising specialised areas of the intestine where conditions were ideal for growth. Once established, these gut microbes provided essential services: they broke down cellulose and chitin that the animals could not digest on their own, produced vitamins, and helped release energy from food that would otherwise be unavailable. In return, the animals provided the microbes with a safe, nutrient-rich habitat. This mutualistic relationship became a key evolutionary advantage and remains the key to survival for animals. For example, modern herbivores like cows, goats, deer, and sheep host specialised bacteria living in their stomachs (the rumen) that break down low-quality, fibrous plant materials like grass and hay into energy-rich compounds and proteins. This transformation turns plant matter into high-quality, protein-rich food that sustains not only the herbivores but also the predators and humans that feed on them. In this way, bacteria act as powerful biological "food upgraders", linking plants to higher levels of the food web.

Some of the most important bacterial symbiosis in animal terrestrialization



During the terrestrialization process and across environments, animals rely on diverse microbial partners—bacteria, archaea, fungi, and protists—that support digestion, detoxification, defense, and nutrient cycling. These microscopic allies transform complex materials into energy, protect hosts from pathogens, and contribute to ecosystem stability and productivity. This symbiosis are still important today, as in the case of herbivors like cow that without their rumen microbiome cannot get energy to growth from their grass-diet.

Image credit: modification of ChatGPT illustration with icons avilable in BioRender and PowerPoint.

These examples are just a few, but they show how life's move to land was not a solo journey. It was a cooperative venture, in which microscopic partners helped animals eat, grow, stay healthy, and reproduce—making the colonisation of Earth's surface not just possible, but sustainable. As well, it is clear that microbes are not just ancient helpers—they are still vital to life on land: from fueling primary production, sustaining herbivores, and maintaining nutrient cycles, bacteria ensure the productivity, diversity, and stability of life on Earth.

Such a microbial perspective also helps clear up common misconceptions. Terrestrialization wasn't a single heroic event but a slow, branching process that unfolded over millions of years. Many species tried and failed to adapt to land. Some evolved beneficial traits, such as stronger fins or lungs, but eventually died out. Others succeeded and became the ancestors of today's land animals.

From then until today, no animal lives without microbes. Humans, too, host thousands of bacterial species in their guts and on their skin. They help us digest food, make vitamins, and train our immune systems. In a way, every animal—from a worm to a whale—is a walking "team" made of many kinds of life (i.e., metaorganisms).

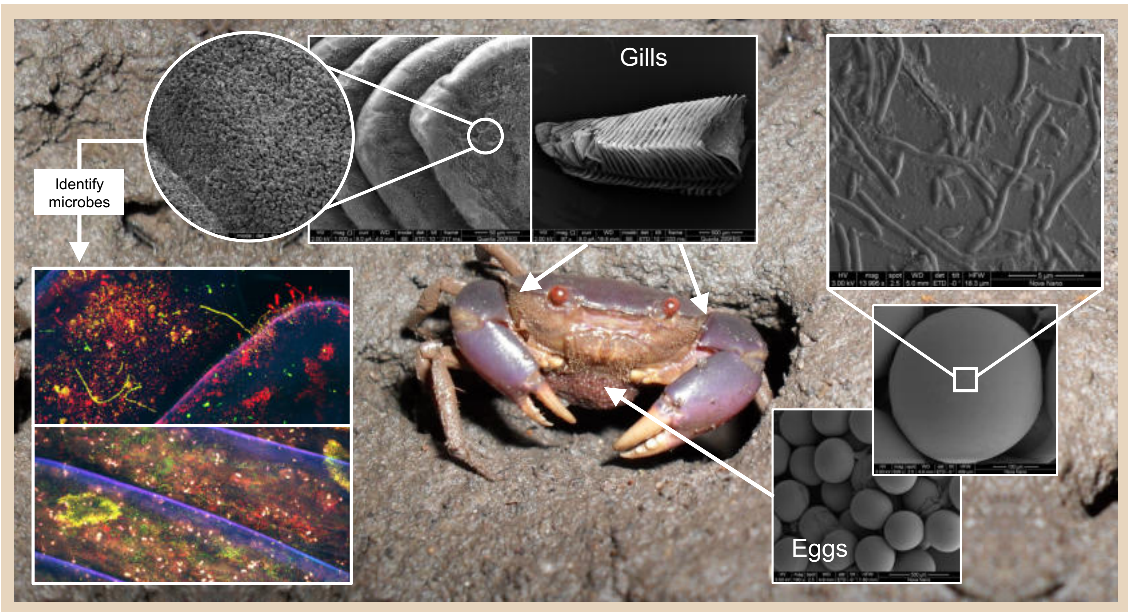
As scientists continue to explore this microbial frontier, they reveal how tiny organisms had a massive impact on one of Earth's most significant evolutionary transitions, reminding us that life on Earth evolved through both cooperation and competition.

5. The case of crabs: from sea to land and again to sea

Crabs offer one of the clearest examples of how evolution can repeat itself. Over millions of years, different crab lineages have independently moved from the ocean to land more than a dozen times, and some have even reversed course, returning to aquatic life. These multiple terrestrialization and re-colonisation events make crabs an extraordinary natural model for studying how animals adapt—or readapt—to entirely different environments.

Each move between water and land demanded sweeping anatomical and physiological changes. To breathe air, marine crabs evolved vascularized gills, allowing them to retain moisture and extract oxygen from the air. Their exoskeletons became thicker and less permeable, and helped them conserve water to prevent desiccation while burrowing or being active at night. Reproduction also had to change: many land crabs evolved strategies to keep eggs moist.

Microbial symbionts supporting crab adaptation and terrestrialization



Crabs have repeatedly transitioned between marine and terrestrial environments throughout evolution. Their success in these extreme shifts is supported by complex microbial symbioses. Microbes living in crab gills, guts, and eggs help them breathe, digest, detoxify, and protect against pathogens, enabling survival in both aquatic and terrestrial habitats.

Image credits: photographs by Marco Fusi, Ramona Marasco, and Jenny Booth.

But crabs did not accomplish these transitions alone, because also in this case microbes were essential allies in this evolutionary adventure. In their guts, diverse bacterial communities help break down plant fibres, algae, and detritus, providing enzymes to digest cellulose and complex carbohydrates that marine ancestors could not process. Some bacteria fix nitrogen or synthesise vitamins, turning terrestrial diets into rich energy sources. In mangrove and land crabs, gut microbiomes have adapted to process tannins and other plant toxins, allowing these animals to feed on leaf litter and mangrove debris that few others can digest.

On their gills and shells, symbiotic bacteria form protective biofilms that prevent pathogen invasion and help regulate salt and ion balance during shifts from saltwater to freshwater or from freshwater to air. These microbial coatings may also assist in detoxifying waste products, such as ammonia, an essential function when water is unavailable or scarce for diffusion. Some species harbour epibiotic communities on their limbs and carapaces that metabolise organic residues, effectively recycling nutrients on the crab's surface.

Even the crab's burrows and surroundings reflect this partnership. Terrestrial and intertidal crabs host microbial communities that enrich sediments and mediate nitrogen and carbon cycling. By digging and excreting, they promote the growth of bacteria that improve soil fertility, influence mangrove root health, and stabilise coastal ecosystems. In this sense, crabs and their microbes act as ecosystem engineers, jointly transforming land and sea environments.

Finally, when certain crab lineages returned to the ocean, their microbial symbionts shifted again—adapting to marine diets and salinity, showing that these relationships are not fixed but evolutionarily dynamic. The story of crabs moving from sea to land and back again reveals that evolution is not a straight line but a recurring dialogue between animals, their bodies, their microbial partners and their environment. Without these tiny companions guiding digestion, detoxification, and protection, crabs might never have mastered such extreme environmental leaps.

6. How do scientists study and understand the history of terrestrialization?

The story of how life moved from water to land is written not in words, but in rocks, bones, and even DNA. Understanding this grand transition requires scientists to act like detectives, piecing together evidence from many sources. No single clue can tell the whole story. Instead, researchers combine discoveries from palaeontology, anatomy, genetics, ecology, and experimentation to reconstruct how early lifeforms learned to breathe air, walk on solid ground, and survive in completely new environments. Each tool provides a different piece of the puzzle, helping us see how small changes can build into one of the most extraordinary events in Earth's history. For instance, fossil bones show how limbs, hips, and skulls gradually changed over millions of years, becoming stronger and better suited for movement on land. Trace fossils, such as footprints and trackways preserved in ancient mud, reveal how animals walked and also when they first ventured beyond the shoreline. Comparative anatomy allows researchers to study similarities between living fish fins and tetrapod limbs, showing how the same bones were reshaped into arms, elbows, and fingers. Experiments add another insight: by observing living species such as lungfish, mudskippers, and salamanders, scientists can visualise how ancient creatures may have moved, breathed, and balanced in shallow waters. Finally, by studying how brains and senses, such as vision and hearing, evolved, researchers gain a deeper understanding of what life was like during this crucial evolutionary step.

a. What fossils tell us about the evolution from sea to land. One of the most famous fossils is Tiktaalik, which was discovered in Canada. It looked like a mix between a fish and a salamander, with gills and scales, but also a neck and strong fins with bones like arms and legs. Acanthostega is another important fossil, with eight fingers on each limb, showing that early tetrapods experimented with different numbers of digits. Ichthyostega had a stronger spine and ribs, which made it better suited for supporting its body on land. Even older trackways from Poland show that four-legged animals were already walking about 395 million years ago. On the invertebrate side, the fossil record of millipedes and arachnids tells us that arthropods were among the very first true land dwellers.

- Tiktaalik (Canada, ~375 Ma): Has fish traits (scales, gills), land-style limb bones, and a neck; hips and hind fins hint at bottom-walking/pushing.

- Acanthostega (~365 Ma): Had digits but was still mostly aquatic—great for paddling among plants.
- Ichthyostega (~365 Ma): Early tetrapod with a sturdier spine and ribcage for some weight-bearing on land.
- Oldest tetrapod trackways (Poland, ~395 Ma): Footprints with digits show walking earlier than we once thought.
- Pioneering arthropods (Silurian–Devonian): Millipedes and relatives are among the first animals truly at home on land.

b. How modern technology helps us understand terrestrialization. Today, advanced technologies are opening new avenues for studying these ancient transformations. 3D imaging and CT scanning allow palaeontologists to look inside fossils without damaging them, reconstructing soft tissues such as muscles and blood vessels that no longer exist. Isotopic analysis can determine whether an animal lived in saltwater, freshwater, or on land by studying the chemical signatures in its bones. Biomechanical modelling and robotics let scientists test how ancient limbs might have worked by digitally or physically "rebuilding" them.
These technologies parallel the use of molecular tools to study DNA—the genetic code found in every living organism—to look deep into the history of life on Earth. By comparing the genes of different animals, researchers can trace when and how essential traits for living on land evolved, such as lungs for breathing air, limbs for walking, and skin that prevents dehydration. These comparisons show how the same genes were modified or reused as species adapted to new environments. Living animals that still bridge the gap between water and land, like frogs, crabs, mudskippers, and lungfish, serve as living windows into the past. For example, studying how a lungfish "walks" along the bottom of a pond helps scientists imagine how ancient fish like Tiktaalik first pushed themselves onto land. In this way, DNA acts like a biological time machine, allowing scientists to reconstruct the steps of terrestrialization that fossils alone cannot fully explain.

c. How microbes and their hosts tell the rest of the story. DNA technology has also opened the possibility of understanding the role of the microbial world in the terrestrialization process. Using advanced tools such as metagenomics and molecular phylogenetics, scientists can now explore the ancient and ongoing partnerships between microbes and their animal or plant hosts. By sequencing and comparing microbial genomes, researchers can build microbial family trees that show how bacteria, fungi, and archaea evolved and spread from the oceans to soils, plants, and animals. These genetic clues confirmed that microbes were not bystanders but active players in shaping Earth's chemistry: they produced oxygen, formed the first soils, and entered into symbiotic alliances that supported the rise of complex ecosystems on land. As well, studying modern host–microbe interactions provides powerful analogues for the past. For example, gut bacteria in animals today help digest plant material, recycle nutrients, and produce vitamins, functions that likely existed in ancient land pioneers as they adapted to new diets. By combining genomics, fossil evidence, and ecological models, scientists can now reconstruct not only how animals conquered land, but also how their microbial partners made that conquest possible.

This field is still developing because microbes rarely leave behind visible fossils, so scientists rely on creative molecular detective work. Sometimes, traces of ancient microbial DNA are preserved in fossils, sediments, or mineral deposits. By analysing these fragments, researchers can determine when key genes first evolved. For example, suppose genes that protect cells from ultraviolet light or prevent desiccation became common in samples from around 400 million years ago. In that case, it proves that microbes were beginning to adapt to life on land. Studying ancient microbes also helps scientists understand how animals later evolved disease resistance, developed new diets, and adapted to environmental stress.

Even though we cannot travel back in time, DNA acts as our time machine. Each genetic code sequence is a record of evolution, allowing scientists to read how tiny microbes helped build the breathable, fertile, and biodiverse planet we live on today.

Archaeology and modern DNA-based tools to study terrestrialization

By combining archaeological discoveries with modern DNA-based technologies, scientists can reconstruct how life transitioned from water to land. Fossil evidence reveals anatomical adaptations, while genetic and molecular analyses trace the evolution of key traits—such as lungs, limbs, and microbial symbioses—that supported survival on land. Together, these tools allow researchers to connect ancient remains with living species, illuminating the evolutionary pathways that shaped Earth's terrestrial ecosystems.

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7. Why does this matter to you?

Studying terrestrialization helps scientists understand how life adapts to new environments, survives extreme changes, and evolves over time. It also explains how life might emerge or adapt on other planets. At the same time, understanding how microbes helped terrestrialization is important because it reveals the hidden foundation of Earth's ecosystems. Long before plants and animals could survive on land, microbes like cyanobacteria, fungi, algae, and lichens were already transforming the environment, making the land stable and livable. Without microbes, land would have remained a harsh, barren surface. Cyanobacteria helped create breathable air, while fungi connected with plant roots help them absorb water and nutrients, thus boosting their establishment. These relationships allowed plants to grow and spread, creating food and shelter for future land animals.

Even today, microbes are essential. Amphibians rely on skin bacteria to fight deadly fungi. Herbivores like cows and termites depend on gut microbes to digest tough plants. These examples show that microbes are not just ancient helpers, but they are still vital to life on land. This makes microbial research one of the last frontiers in understanding how life conquered land, helping explain why and how tiny organisms significantly impacted Earth's evolutionary history.

8. Can you make a difference? And how?

When we think about life's move from water to land, we often picture ancient fish with strong fins or early amphibians taking their first steps onto shore. But the real pioneers were microbes, the invisible engineers that prepared the land long before any animal appeared. They created the first soils, released oxygen, and built partnerships with plants and animals that made life on land possible. Without them, terrestrial ecosystems as we know them could never have developed.

Recognising their role and studying these tiny organisms today helps scientists fill in the missing chapters of evolution, i.e., the parts that fossils cannot tell us. By exploring how microbes shaped the Earth's chemistry and continue to support ecosystems, researchers can better understand how life adapts to new challenges, from extreme drought to pollution and climate change. This knowledge also guides modern conservation, because protecting microbial diversity means protecting the hidden foundation of life itself, from the soil under our feet to the roots of plants and the health of animals.

And this is where you can make a difference. Whether learning about microbes, supporting environmental protection, or participating in citizen science projects, everyone can help uncover the secrets of our planet's tiniest yet most powerful inhabitants. Understanding microbes is not just about the past; it's about securing the future of life on Earth.

Classroom activity

Teaching the story of terrestrialization can be exciting and memorable through creative classroom activities. One engaging experiment involves making "fossil trackways" using sand or flour. Students drag toy fish across the surface, then walk toy salamanders with legs, comparing the marks left behind. This hands-on activity helps students understand how scientists use trace fossils to study ancient movement and the shift from swimming to walking. Another activity uses cut-out diagrams of fish fins and tetrapod limbs. Students match bones like the humerus, radius, and ulna to learn how evolution reshaped these structures for new functions—an example of homologous anatomy.

To explore the microbial side of terrestrialization, students can read about how skin bacteria protect amphibians from deadly fungi and brainstorm conservation strategies, such as "probiotic baths" or habitat restoration. This highlights how microbes continue to shape land life today. A "walking like a lungfish" activity, where students crawl using elbows and knees, helps them feel how awkward movement was before proper legs evolved. A classroom timeline showing key stages—from microbial mats to amphibians—lets students visualise the slow, step-by-step nature of the transition.

For deeper engagement, a soil crust experiment with moss spores or cyanobacteria (if safe) shows how microbes stabilise soil, just as they did millions of years ago. Finally, a "Myth vs. Fact" debate challenges students to rethink common misconceptions, like the idea of a single heroic fish leaping onto land. These activities combine movement, observation, and imagination, helping students grasp not just the facts of terrestrialization but also the scientific methods used to study it—and the vital role of microbes in making land life possible.

Relevance for Sustainable Development Goals and Grand Challenges

Studying how microbes contributed to terrestrialization is highly relevant to the Sustainable Development Goals (SDGs) and broader Grand Challenges in science and society. Microbes were the first life forms to make land habitable, forming soils, producing oxygen, and partnering with plants and animals in ways that still shape ecosystems today. Understanding these ancient microbial roles offers insights that directly support goals like SDG 13 (Climate Action), SDG 15 (Life on Land), and SDG 3 (Good Health and Well-being).

For example, microbial partnerships with plants—such as mycorrhizal fungi—enhance soil fertility and carbon storage, which are crucial for sustainable agriculture and climate resilience. Studying how these relationships have evolved helps us design more effective strategies for ecosystem restoration, carbon sequestration, and biodiversity conservation. Similarly, microbes that protect amphibians from disease or help herbivores digest plants are key to maintaining healthy wildlife populations and food webs.

From a Grand Challenges perspective, microbial terrestrialization research addresses fundamental questions about the origins of complex life, the evolution of symbiosis, and how life adapts to new environments. It also informs applied fields such as biotechnology, soil science, and microbiome health, offering tools to address pressing issues such as land degradation, food security, and emerging diseases.

Pupil participation

1. Class discussion on the role of microbes in terrestrialization

Activity I. Objective: To help pupils understand how microbes prepared the Earth for life on land and continue to support all living things today.
Suggested activities: Begin with a short recap of the story of terrestrialization, showing how life moved from oceans to land. Then ask:

- What would the world look like without microbes?
- How did microbes make it possible for plants and animals to survive on land?
- Can we see examples of microbial life helping nature today (for example, in soil, roots, or animals)?

Show images or animations of microbial mats, cyanobacteria, and early land plants to spark discussion.
Discussion: Divide the class into small groups; each group lists three ways microbes helped terrestrialization (e.g., oxygen production, soil formation, plant partnerships). Bring everyone together to share answers and create a "Microbes made it possible!" wall chart that summarises their ideas.
Learning outcomes: Pupils recognise that microbes were essential to the colonisation of land. They understand that microorganisms remain vital to ecosystems, agriculture, and health.

Activity II. Objective: To help pupils understand how food chains and food webs work and how microbes support all living things, even those at the top of the chain.
Suggested activities: Choose your favourite animal! Each student picks an animal they like (for example: lion, penguin, cow, bee, frog, crab). Then draw your food chain or web by placing your chosen animal in the middle of the page; above it, draw what might eat it (predators) and below it, draw what it eats (plants, smaller animals, or detritus).
Discussion: Think about what happens before and after your animal — what decomposes waste or dead organisms? Discuss as a class where microbes fit in your web: label where these microbes act and how they keep the ecosystem healthy.
Learning outcomes: Understand that microbes are the foundation of every food chain and keep ecosystems functioning. Recognise that energy and nutrients flow through interconnected living systems, not isolated organisms.

2. Pupil awareness

Objective: To inspire pupils to connect what they learn with their daily lives and to appreciate

the ongoing importance of microbes in the environment.
Suggested activities:

- Observation task - ask pupils to look around their environment (soil, plants, insects) and imagine the hidden microbial world beneath
- Creative reflection - pupils draw or write a short piece titled "A *day in the life of a micro*be" describing how a tiny organism helps the world
- Awareness campaign - as a class, design posters or short presentations on "*Why microbes matter*" to share with the school community. Encourage pupils to think about how human actions (pollution, waste, antibiotic use) can harm or benefit microbial life, and how this affects their interactions with animals and plants.

Learning outcomes: Pupils become aware that microbes are everywhere and play a central role in life on Earth. They develop a sense of responsibility for protecting ecosystems — from the smallest bacteria to the largest animals.

The evidence base, further reading, and teaching aids

Videos

Terrestrialisation https://www.youtube.com/watch?v=g6NtQ3XNLW0
Tree of Life https://www.youtube.com/watch?v=ii4510LeRXo
Plants https://www.youtube.com/watch?v=ONVpFtiD-fo
Fungi https://www.youtube.com/watch?v=5FqFg-rjzPo

Books

Chipman, Ariel D., 'Terrestrialization', Organismic Animal Biology: An Evolutionary Approach (Oxford, 2024; online edn, Oxford Academic, 30 Apr. 2024), https://doi.org/10.1093/oso/9780192893581.003.0022, accessed 30 Oct. 2025.

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Fusi, M., Ngugi, D. K., Marasco, R., Booth, J. M., Cardinale, M., Sacchi, L., and Daffonchio, D. (2023). Gill-associated bacteria are homogeneously selected in amphibious mangrove crabs to sustain host intertidal adaptation. *Microbiome* 11(1):189.

Puginier, Camille, Jean Keller, and Pierre-Marc Delaux (2022). Plant–microbe interactions that have impacted plant terrestrializations. *Plant Physiology* 190(1):72-84.

Vermeij, Geerat J., and Victoria M. Watson-Zink (2022). Terrestrialization in gastropods: lineages, ecological constraints and comparisons with other animals. *Biological Journal of the Linnean Society* 136(3):393-404.

Glossary

Adaptations: Physical or behavioural changes that help an organism survive better in its environment.

Algae/Microalgae: Simple aquatic organisms, often green, that make their own food using sunlight; they include tiny plankton and larger seaweeds.

Arthropods: Animals with jointed legs and hard outer skeletons, such as insects, spiders, and crabs.

Bacteria: Single-celled microorganisms that live almost everywhere on Earth; some cause disease, but many are helpful to humans, animals, and the environment.

Biodiversity: The variety of all living things on Earth, from tiny bacteria to giant trees and animals.

Biological crust (or soil crust): A living skin of microbes, algae, lichens, and mosses that covers soil in deserts and helps hold it together.

Cyanobacteria: Ancient bacteria that can do photosynthesis, releasing oxygen and helping create Earth's atmosphere billions of years ago.

DNA (Deoxyribonucleic Acid): The molecule that carries the genetic code containing the instructions for life in all organisms.

Ecosystem functionality/stability: How well and how consistently an ecosystem performs its natural roles, even when facing change or disturbance.

Ecosystem functioning: The way living organisms and their environment work together, cycling nutrients and energy.

Evolution/Evolutionary shift: The gradual change of species over time as they adapt and new forms of life appear.

Food webs: Networks that show how energy and nutrients pass from one organism to another through eating relationships.

Fungi: Organisms such as moulds, yeasts, and mushrooms that absorb nutrients from their surroundings and often live in partnership with plants.

Genetic code: The set of instructions in DNA that tells cells how to build proteins and control life processes.

Great Oxidation Event (GOE): The time about 2.4 billion years ago when cyanobacteria began producing oxygen, transforming Earth's atmosphere and enabling complex life.

Lichens: Partnerships between fungi and algae (or cyanobacteria) that can live on rocks, bark, or soil and help form early ecosystems.

Metagenomics: The study of all the DNA in a sample (like soil or water) to learn which microbes live there and what they do.

Metaorganism (or holobiont): The idea that every animal or plant and all its associated microbes together form a single biological unit.

Microbe-host partnerships: Relationships in which microbes live with plants or animals, often providing protection or nutrients.

Microbe-mediated adaptation: A change or ability in a plant or animal that happens thanks to the help of its microbial partners.

Microbial mat: A thin, colourful layer of microbes (often cyanobacteria and algae) growing together on rocks or sediments in moist places.

Microbial symbiont (or symbiome): A microbe that lives closely with another organism, forming a partnership that benefits one or both.

Microorganisms (or microbes): Tiny living things such as bacteria, fungi, or algae that are too small to see without a microscope.

Molecular tools: Laboratory methods that let scientists study genes, proteins, or other molecules to understand how life works.

Molluscs: Soft-bodied animals, often with shells, such as snails, clams, and octopuses.

Morphological: Related to the shape, structure, or appearance of an organism.

Mutualistic relationship: A partnership between two organisms in which both benefit.

Mycorrhiza: from Greek: “mykes” = fungus, “rhiza” = root, refers to a special group of fungi that helps plants absorb water and minerals (especially phosphorus) from the soil. This relationship improves plant growth and soil health and is found in most land plants.

Photosynthesis: The process by which plants, algae, and some bacteria use sunlight, water, and carbon dioxide to make food (sugars) and oxygen.

Phylogenetics: The study of evolutionary relationships among species, often shown as a branching “family tree” based on DNA.

Physiological: Related to how the body or cells of a living organism function.

Plant-growth-promoting microbes: Beneficial bacteria or fungi that help plants grow by improving nutrient uptake or protecting against disease.

Spiracles: Small openings on the body of insects or millipedes that allow them to breathe air.

Synthesise: To make or build something; in biology, the process by which living organisms make complex molecules needed for growth, repair, and energy, such as proteins, vitamins, or natural chemicals, from simpler substances.

Terrestrialization: The long process through which life that once lived only in water gradually adapted to survive and thrive on land.

Tetrapods: Four-limbed vertebrates (amphibians, reptiles, birds, and mammals) that descended from ancient fishes.