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Trends in
Plant Science

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Opinion

The greening ashore

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More than half a billion years ago a streptophyte algal lineage began terraforming the terrestrial habitat and the Earth's atmosphere. This pioneering step enabled the subsequent evolution of all complex life on land, and the past decade has uncovered that many traits, both morphological and genetic, once thought to be unique to land plants, are conserved across some streptophyte algae. They provided the common ancestor of land plants with a repertoire of genes, of which many were adapted to overcome the new biotic and abiotic challenges. Exploring these molecular adaptations in non-tracheophyte species may help us to better prepare all green life, including our crops, for the challenges precipitated by the climate change of the Anthropocene because the challenges mostly differ by the speed with which they are now being met.

The green origin of life on land

Among all life, the **Archaeplastida** (see Glossary) represent the main carbon sink. Plants (Box 1) make up 80% of Earth's biomass [1]. They are pioneer settlers and transform wastelands into habitable landscapes for other lifeforms, and exhibit a remarkable ability to adapt to the most diverse environmental conditions. Land plants display beautiful symmetric structures, and interact and communicate among each other as well as with various other organismal groups, thus forming complex communities such as forests [2–4]. Over at least 500 million years our planet's flora has spread across all continents and transformed 71% of Earth's surface not covered by water (of which today more than half is used for agriculture and pasture, see Figure I in Box 2) into fertile land [5]. Without their supply of oxygen and biomass, macroscopic body plans would have evolved differently. For about three billion years, life evolved almost exclusively in aquatic habitats. On land, temperature and light changes are more severe and fluctuate consistently more than in water. Without buoyancy, early land plants needed to find a way to deal with gravity and evolve a phenotype suitable for the terrestrial habitat. The algal ancestor of land plants underwent many molecular adaptations that made the conquest of the new environment possible.

Exploring how life evolved on land requires the study of fossils, the geochemical record, and more so the expansion of genomic resources for subsequent comparative and evolutionary developmental studies. As we move forward, the establishment of new model organisms and exploration of individual genetic and physiological adaptations along the evolutionary trajectory of the Archaeplastida are crucial for comprehensive and exhaustive understanding of the basic processes that enabled the transition to land (Figure 1, Key figure).

1 + 1 + 1 = 1: the Archaeplastida

The origin of life and the beginning of its continuous development into progressively more diverse and complex forms, through adaptation to constantly changing conditions and ever new habitats, traces back some four billion years (Figure 2). Under the assumption of a single last universal common ancestor (LUCA) of all extant life, to which all credible evidence points, the split between Archaea and Bacteria dates back about to 3800 million years ago (Mya) [6]. More than 1400 million

Highlights

Two decisive endosymbiotic events, the emergence of eukaryotes followed by the further incorporation of a photosynthesizing cyanobacterium, laid the foundation for the development of plant life.

Increasing cellular complexity, the development of new body plans, new molecular adaptations, and constant colonization of novel habitats probably paved the way for plant evolution from fresh water to salt water and, at least 500 million years ago, to land.

The history of plant life, and particularly the greening ashore, is inseparably linked to the success of all life as we know it today.

Plant life enriched the atmosphere with oxygen and fixed CO_2, thereby paving the way for the success of further life in this previously hostile habitat – and ultimately enabled the emergence of our own species.

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Box 1. What is a plant?

This might sound like a trivial question, but is it really? A photosynthetic organism as an answer does not work because there are Cyanobacteria and photosynthesis does not always lead to oxygen release. The original taxonomic use of the term *plantae* in biology, uniting algae and land plants, is also problematic. The term originally traces back to the latin word *planta* that denotes 'sole' or 'sole of the foot', the connection being the action of tramping down a fresh sapling. In taxonomy, what the term comprises has changed over time. Aristotle and his student Theophrastus once divided the world they observed into two groups – sessile plants anchored into the ground and food-consuming motile animals. In his famous tree of life, Haeckel in 1866 then used the term *plantae* to unite all known phototrophic eukaryotes – basically algae and land plants – juxtaposed to his other eukaryotic supergroups (protists, fungi, and animalia).

The problem with the term became evident when, based on sequencing and modern phylogenetic tools, it emerged that algal groups are polyphyletic and are spread across several major eukaryotic groups because of **secondary endosymbiosis**. If we would simply use *plantae* in its most embracing form to unite all eukaryotes carrying an organelle of cyanobacterial origin, it would need to include the fungus *Geosiphon*, the cercozoan *Paulinella chromatophora*, and some might argue even sacoglossan sea slugs such as *Elysia timida*. For these reasons, *plantae* as a taxonomic term has increasingly lost its relevance and more a specific nomenclature was introduced such as Viridiplantae (green plants), which itself was then updated in 2005 to Chloroplastida [79]. It might hence be best to use the term 'plant' only in its vernacular form and for those things that we can indeed plant in gardens, and otherwise follow modern taxonomic nomenclature. Its linguistic ancestry worked for some time in early taxonomy, but only until DNA and protein sequences were recognized to be documents of evolutionary history [80].

years probably elapsed before the **endosymbiotic** merging of an archaeal host and a proteobacterial endosymbiont triggered the emergence of the eukaryotic branch in the tree, or a better 'ring of life' [7] in the early Paleoproterozoic [8]. Before the endosymbiotic origin of eukaryotes, the emergence of oxygenic photosynthesis was the trigger that changed the chemistry of Earth [9] (Figure 2).

Endosymbiosis was the mechanism behind the emergence of eukaryotes, and the same process underlies the monophyletic origin of the Archaeplastida. The integration of a cyanobacterium into a heterotrophic host led to the first **plastid** surrounded by two membranes and the subsequent speciation into the main lineages that are the **Rhodophyta**, **Glaucophyta**, and the **Chloroplastida** or 'green lineage' [10] (Figure 1). A neglected question concerns the initial evolutionary driver behind plastid origin. Perhaps the ability to fix atmospheric nitrogen was important [11], perhaps not [12], but we see no reason to bet on carbon fixation purely because it might appear obvious. Primary plastids of the green and red lineages that are surrounded by two membranes spread further via serial secondary and tertiary endosymbioses, thereby generating ecologically important groups such as the stramenopiles or the parasitic Apicomplexa [13].

Endosymbiotic relationships are found across the diversity of all eukaryotic supergroups [14], but few have had an impact comparable to the origin of mitochondria and plastids – pivotal for the emergence of complex life. The steps of streamlining a once free-living cell into an organelle inside the cytosol of another are plentiful and the transitions fluid [15]. Formerly independent genomes need to interact, nutrient and protein transport must be coordinated, and differently operating division machineries and cell cycles must be synchronized. The origin of the plastid is connected to a **monoplastidic bottleneck** [16] and a plastid-specific checkpoint in the cell cycle of algae [17]. Most algae and some tissues of non-vascular land plants carry only one plastid per cell (monoplastidy) and the occurrence of many (polyplastidy) coincides with complex macroscopic morphology, both in the red and green lineages [16]. The transition coincides with the transfer of some plastid division genes (such as *minD/E*) to the nuclear genome, or their loss and the addition of novel regulatory proteins such as ARC3 or PDV1 [18]. Multicellular body plans and tissue specification evolved several times independently and correlate with an increase in the complexity of transcriptional regulation [19]. How some lineages passed the monoplastidic bottleneck, and how regulatory transcriptional networks evolve and coordinate tissue specification, are among

Glossary

Anydrophyta: the term unites zygnematophyceaen algae and land plants based on their molecular adaptations, potentially obtained through horizontal gene transfer (HGT), that mediate the ability to deal with drought and potentially aided in terrestrialization.
Archaeplastida: a eukaryotic supergroup with plastids of primary monophyletic origin that comprises the Rhodophyta, Glaucophyta, and Chloroplastida.
Bryophyta: sister lineage to the Tracheophyta. Unites hornworts, liverworts, and mosses, all of which are non-vascular land plants.
Chlorophyta: a group of highly diverse algae that are found in both fresh and salt water; can be unicellular or multicellular and are adapted to a wide range of environmental conditions.
Chloroplastida: the largest group among the Archaeplastida, also termed the Viridiplantae, also known as the green lineage.
Embryophyta: all land plants, characterized by the embryo and the alternation of generations, and are divided into the Bryophyta and vascular plants.
Endosymbiosis: the process in which two taxonomically distinct organisms engage in a mutual interaction in which one organism is integrated into (the cytosol of) the other.
Eukaryogenesis: the process of the origin of the eukaryotic cell.
Glaucophyta: a very small group of unicellular freshwater algae, one of the three main archaeplastidal lineages.
KCM grade: unites the Klebsormidiophyceae, Chlorokybophyceae, and Mesostigmatophyceae; uni- and multicellular (non-branching) streptophyte algae.
Monoplastidic bottleneck: an evolutionary phenomenon associated with the synchronization of plastid and cell division during the origin of the plastid. Only a few lineages that also evolved complex multicellularity have escaped the bottleneck and house multiple plastids per cell.
Plastid: a general term that encompasses all subtypes including chloroplasts, rhodoplasts, cyanelles, gerontoplasts, and amyloplasts.
Prasinodermophyta: a recently discovered third phylum of the green lineage formed by a group of marine

Box 2. Green life changes the climate and so do we

Following the successful colonization of the terrestrial habitat by a streptophyte alga about 500 Mya, the CO_2 concentration in the atmosphere started to decrease from peaks of around 1500–2000 ppm to below 300. An individual land plant lineage, the water fern *Azolla*, fixed such vast amounts of CO_2 that a hot Earth transitioned into an ice age [81]. Such events lasted many hundreds of thousands of years, providing the fauna and flora with time to evolutionarily adapt. We humans, who evolved for a million years or more at an atmospheric CO_2 concentration of around 280 ppm, are now reversing this process with unprecedented speed. In only 100 years since industrialization we have released an amount of carbon that likely took green life 100 million years to fix and deposit.

At the beginning of the Neolithic period 10 000 years ago, at the transition of nomadic hunter-gatherers to sedentary farmers, 40% of land mass had not experienced any human interference. Then, 3000 years ago, about 1% of available land surface was used for agriculture and animal husbandry, 2000 years later 10%, and by the end of the 19th century it was 25% [82]. Millennia ago, our ancestors began cutting down forests on a larger scale to create agricultural land, then to also build ever more ships, colonize new continents, and establish trade routes. The landscapes of for example the Netherlands, Denmark, Spain, and the UK are a testament to excessive deforestation and they lack large, interconnected forests.

All life depends on an energy gradient, and major expansions in evolution are linked to exploring new sources of energy [83]. The latest 'energy epoch' was the use and burning of wood and later fossil fuels by humans. Ironically, the very source that literally fuelled human history and our global expansion as a species, leading Earth into the Anthropocene, might be the cause for the reversal of this success story. The science is clear [84], and within only a few generations we could witness the rise and fall of modern civilization if we continue with business as usual.

Land plant habitats are threatened by drought, heat waves, floods, and fires. Rising CO_2 concentrations and temperatures are affecting germination, growth, reproduction, fitness, and resilience [85]. Life on land relies on and owes its success to the amazing adaptability of plant life. A detailed understanding of the present biodiversity, its evolutionary history, and its ability to adapt and acclimate to new conditions will enable us to thoughtfully address the current challenges and put us on track for a sustainable future.
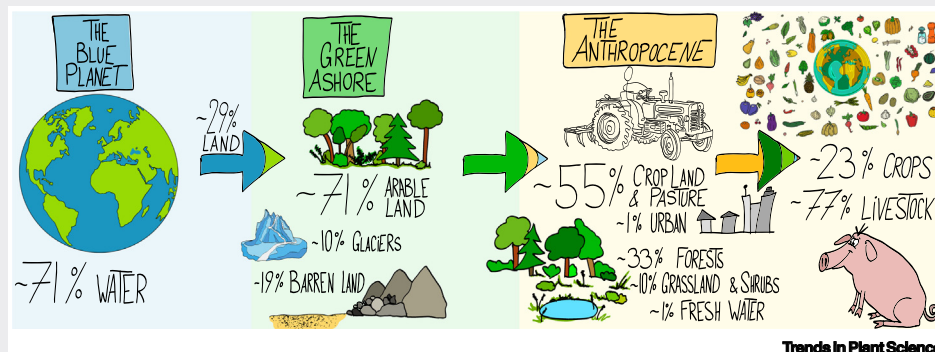
picophytoplankton that are adapted to low-light and low-nutrient conditions.
Rhodophyta: the red algae, one of the three main subgroups of the Archaeplastida. They are characterized by phycobiliproteins and Floridean starch.
Spermatophyta: land plants with seeds; they are subdivided into the gymnosperms and angiosperms.
Streptophyta: 'strepto' derives from Greek 'twisted' and refers to the shape of the sperm cells of those species that have not secondarily reduced it to pollen. Includes streptophyte algae and all land plants.
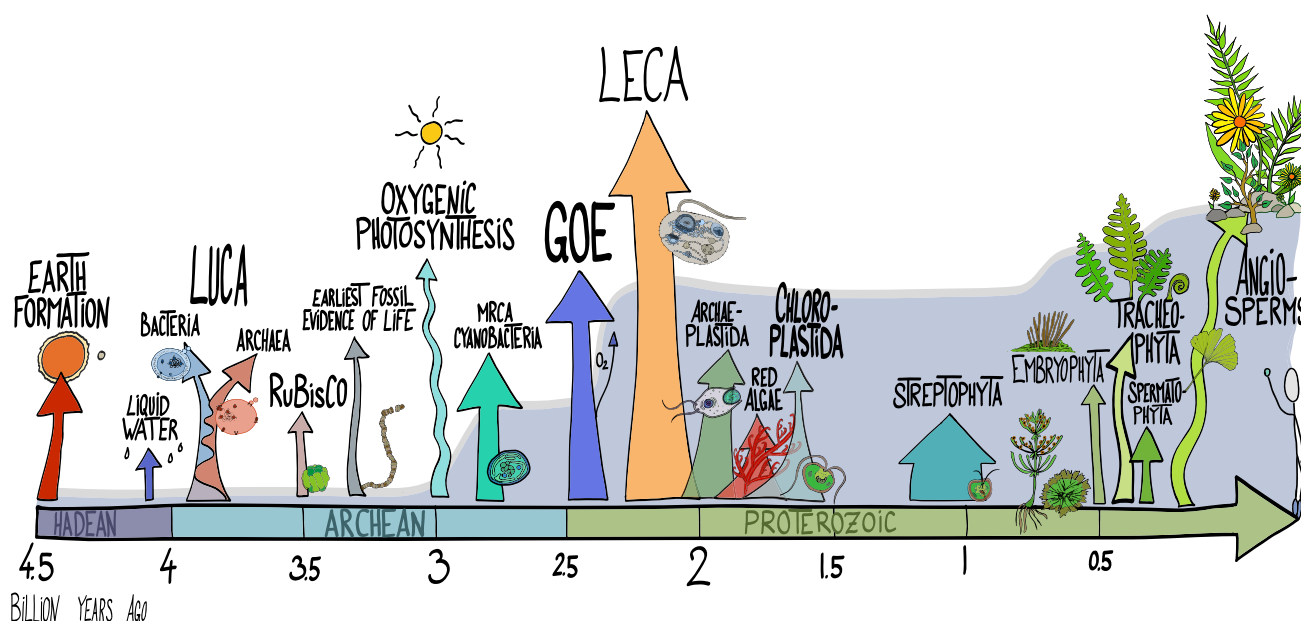**Tracheophyta:** unites the lycophytes, ferns, and seed plants, all of which are vascular land plants.
ZCC grade: a group of algae (Zygnematophyceae, Coleochaetophyceae, and Charophyceae) that are thought to have separated from the KCM algae at ~700 Mya; land plants trace back to a zygnematophyceaen ancestor.

Figure I. Global use of land mass. Approximately 71% of the Earth's surface is covered by water, and 71% of the 29% of the land mass is covered by fertile soil. 19% is 'wasteland', namely deserts, salt deserts, or rocky areas. The steadily receding glaciers and ice surfaces still account for about 10%. Today, more than half of the fertile land is used for agriculture, but of that only 23% for the cultivation of crops and 77% for livestock farming [5]. Owing to the limited space available, this is without doubt not sustainable in the long term.

the core questions associated with exploring terrestrialization (see Outstanding questions). The emergence of plastids and later land plants had a transformative impact on the Earth's atmosphere [20].

Earth's history and the transformative impact of photosynthesis

Earth's second eon, the Archean, spans the majority of our planet's early timeline. Isotopic analyses of atmospheric particle signatures in sediments suggest a rather stable and moderate climate, with temperatures ranging between 0°C and 40°C, and O_2 levels below the Pasteur

Key figure

The evolution of the Archaeplastida with a focus on the green lineage (Chloroplastida)

Figure 1. The phylogenetic diagram commences at the bottom right with the origin of eukaryotes (**eukaryogenesis**) through the endosymbiotic integration of a bacterium (today's mitochondrion) into an archaeal host. The Archaeplastida

(Figure legend continued at the bottom of the next page.)

Trends in Plant Science

Figure 2. Timeline of major evolutionary events leading to the conquest of land by a streptophyte alga at least 500 million years ago (Mya) (515.1 Mya to 470.0 Mya; middle Cambrian–Early Ordovician [33]) and the rapid diversification of plant life on land. Key steps towards the extant flora, after the origin of life and the split into Bacteria and Archaea, included the origin of oxygenic photosynthesis in the common ancestor of Cyanobacteria, the acquisition of a cyanobacterial ancestor by a heterotrophic protist, which marks the origin of the Archaeplastida, and the split and origin of streptophyte from chlorophyte algae, one of which carried the necessary adaptations to thrive on land. This ancestor subsequently evolved the land plant diversity we witness today – 3.5 billion years after the emergence of life. Abbreviations, GOE, Great Oxidation Event; LECA, last eukaryotic common ancestor; LUCA, last universal common ancestor; MRCA, most recent common ancestor.

point throughout most of the Archean [21]. The emergence of the first biochemical pathways such as N_2 and CO_2 fixation, methanogenesis, anoxygenic photosynthesis, and later the origin of the oxygen evolving complex, set the stage for the Archean atmosphere to change and transition into the Proterozoic [21]. The emergence of the water-splitting complex in the cyanobacterial ancestor triggered what is known as the Great Oxidation Event (GOE), a period characterized by mass extinction events [22] and significant steps in the diversification of prokaryotic biochemistry [23]. Cyanobacteria kick-started the rise of oxygen, but it was an algal member of the green lineage that colonized land, diversified, and fostered the second major increase in O_2 [20] together with tectonic revolutions [24] (Figure 1).

The terrestrial habitat was a hostile place. The atmosphere was fed by volcanism, the magnetic field was less pronounced than today [25], the ozone (O_3) layer ~40% thinner such that more harmful radiation broke through [26], and the sea surface temperature at about 45°C was rather hot [27]. Land was mostly barren rock, weathered through heavily fluctuating climate conditions

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emerged as a eukaryotic supergroup after the endosymbiotic integration of a cyanobacterium (today's plastid). Archaeplastida comprise red and glaucophyte algae, as well as the green lineage (Chloroplastida). The latter splits into Chlorophyta and Streptophyta, which gradually evolved new features such as the phragmoplast, plasmodesmata, alternating generations, and polyplastidity that support life on land. Finally, the **Anydrophyta** (that can cope without a constant supply of water) achieved a transition to land and gave rise to the Embryophyta in which the bryophytes are sisters to the vascular plants (Tracheophyta). The latter comprise lycophytes, ferns, and seed plants (Spermatophyta). The gymnosperms and the flowering plants (top right) dominate today's macroscopic floral life in the majority of habitats. The elements around the phylogram provide some detail on individual aspects of plant evolution and their impact on the atmosphere. A high-resolution version of this figure can be found in the supplemental information online and at www.madland.science/greening.php.

and covered with a thin microbial proto-soil [28]. Water is a reliable protection against UV radiation and fluctuating temperatures, but the shielding effect and the light spectrum vary with depth and composition. Therefore, it is assumed that the adaptations that eventually enabled terrestrialization began with the algal colonization of new aquatic, subaerial, and (temporary) terrestrial habitats, and the subsequent gradual adaptation of biochemical, molecular, and morphological features [29].

The Chloroplastida: stepwise adaptations to conquer land

Both paleobotanical records and phylogenomic studies plot a monophyletic origin for the terrestrial flora from within the Chloroplastida [8,30,31]. This green archaeplastidal lineage is divided into three phyla, the recently identified **Prasinodermophyta** [32], the **Chlorophyta**, and the **Streptophyta**. It is estimated that they comprise about half a million species and diverged up to a billion years ago [8,33]. The Chlorophyta comprise a group of very diverse algae, including unicellular, colony-forming, multicellular, filamentous/siphonacous, and thallose-like species. They can occur in marine and freshwater environments, or even on land. There is a considerable gap between chloro- and streptophyte biology that is worth exploring, and it is likely no coincidence that land plants and streptophyte algae evolved from a common ancestor.

Streptophyta form a monophyletic clade comprising all land plants (**Embryophyta**; Figure 1) as well as six currently recognized main lineages of streptophyte algae that are divided into two groups of three: the **KCM grade** (Klebsomidiophyceae, Chlorokybophyceae, and Mesostigmatophyceae) that exhibit adaptations to (sub-)aerial habitats and a non-motile vegetative phase, and the **ZCC grade** (Zygnematophyceae, Coleochaetophyceae, and Charophyceae) that have more elaborate phytohormone and retrograde signaling (a signal encoded in the nucleus, localized to an organelle, then signaling back to the nucleus), and an increasingly complex body plan [34]. The KCM grade to some extent displays multicellularity in terms of unbranched filaments, whereas the ZCC group evolved branching and multi-dimensional growth. This paraphyletic group thrives in both fresh and saltwater, but can also be found in wet soil or covering rocks [35].

First adaptations in the most recent common ancestor (MRCA) of the Streptophyta are related to responses to abiotic and biotic stresses, with the establishment of photorespiration, the canonical phytochrome for red-light sensing (p-PHY) [36], highly developed chloroplast grana, and the subsequent establishment of a phenylpropanoid biosynthesis pathway leading to several phytohormones – paving the way to handle exposure to strong UV-B light, drought, and extreme temperature fluctuations [37]. In the green lineage an elaborate high-light stress response is further supported by changes in plastid protein import that enabled a phenylalanine-independent import pathway [38] and the continuous elaboration of retrograde signaling to coordinate the expression of both nuclear and plastome genes [10]. We lack experimental evidence, however, that such modifications allow a higher frequency of protein import (e.g., upon high-light stress) that could have been selected for during terrestrialization. Major retrograde signaling pathways based on the GUN family (GENOMES UNCOUPLED) have experienced an expansion along the trajectory from algae to land plants [39], but the exact biochemical role of GUN1, in particular, has remained enigmatic for decades and a potential role in early evolution has not been thoroughly investigated. Within the plastid stroma, green algae form starch molecules as polysaccharide reserves that enable the organism to pause its activity, thus aiding colonization of a habitat in which continuous growth could be lethal [40].

In the Phragmoplastophyta, comprising the ZCC grade and all land plants, the eponymous phragmoplast is crucial for the development of the new cell wall through fragmented plates

extruded by vesicular flow, a microtubule array, and the rosette-like cellulose complexes that are considered to be the basis of the rigid cell wall in land plants – and potentially provided the evolutionary solution for orchestrating apical growth and asymmetric cell division [41]. Cellulose synthase, a key enzyme in the biosynthesis of the cell wall, enabled the cells of the Phragmoplastophyta to withstand internal turgor pressure, thus improving water-holding capacity and control over substrate exchange [42]. To ensure cell–cell interaction with respect to communication and transport, the plasmodesmata – microscopic channels traversing the cell wall – also evolved within the Phragmoplastophyta [41]. The establishment of apical cells that repeatedly divide enabled cellular tip growth and paved the way to further evolve mechanisms for branching and 3D growth – prerequisites for the development of the erect body plan and the evolution of vasculature [43]. The transition from 2D to 3D growth and body plan occurred in fungi, brown algae, and in the evolutionary trajectory leading to land plants and animals. There is a lot to learn from cross-comparisons of an allegedly small change in division but with a significant impact on morphological evolution.

Key elements to adapt to a changing aquatic habitat and (temporary) drought most likely evolved in the MRCA of the Zygnematophyceae and land plants, as inferred from phylogenomics and the shared transfer of some plastid genes to the nucleus [34,44]. In particular, transcription factors (TFs) of the GRAS family may be acquired by horizontal gene transfer from the realm of bacteria [45], are crucial in the stress response, and are linked a protection against desiccation and the formation of fungal symbioses in the Zygnematophyceae [46]. So far exclusive to land plants are DELLA proteins of the GRAS family that serve as master growth repressors. These emerged in the MRCA of the Embryophyta, followed by two duplication events first in the ancestor of the **Trachaeophyta** and second in Eudicots [47]. The hormone abscisic acid (ABA) acts as a key regulator of the stress response and of development in land plants [48]. Although ABA is found in a large number of algae, no ABA-dependent responses are known [49]; only a few studies have addressed the role of ABA in algae and this deserves more attention. Adaptations such as ABA signaling in land plants are often guided through gene and genome duplications [50], accompanied by a gain in transcriptional complexity and subsequent neo- and subfunctionalization [51]. MIKC^C-type MADS-box TFs for instance are present in high numbers not only in all embryophytes but also in streptophyte algae characterized by a more complex body plan [52]. AP2/WRINKLED TFs are also of interest because they are directly involved in regulating lipid exchange between arbuscular mycorrhizal fungi and *Marchantia*, a member of the **Bryophyta**, thus supporting their potential involvement in terrestrialization [53].

Fungal symbioses and terrestrialization

Long before streptophytes made it ashore, microscopic life in the form of prokaryotes, protists, and some fungi had already established themselves on land [30]. Accordingly, early land plants were exposed to a diverse variety of microorganisms that could be both detrimental and beneficial [4]. The tremendous changes, especially the significant decrease in CO_2 throughout the Palaeozoic, accompanied the colonization of land and drove the rapid diversification of land plants [54,55], most likely shaped by the beneficial mutualistic interaction between land plants and soil-dwelling fungi, known as the mycorrhizal landing hypothesis [56]. Because roots evolved many millions of years after the transition to land [57], it is assumed that early interactions with symbiotic fungi were pivotal. They promote inorganic nutrient uptake and improve biotic and abiotic stress tolerance, while providing carbohydrate and lipids to the fungal partner [58,59]. Mycorrhizal symbioses are a trait of >90% of land plants [30].

The earliest land plants might not have interacted with arbuscular mycorrhizal fungi (AMF) of the Glomeromycota that *form intracellular mycorrhizal symbioses in the majority of seed plants today*

[30], and perhaps instead interacted with (or in a flexible combination with) the Mucoromycotina that engage with some bryophyte groups today [60]. The phytohormone strigolactone is known to induce mycorrhizal signaling and probably evolved during the adaptation from water to the terrestrial habitat [43], although the initial function remains obscure [61]. The same is true regarding the exact timing of the first symbiotic relationships, but evidence is accumulating that a filamentous or perhaps even pseudoparenchymatous streptophyte algae established the first beneficial symbiosis with surrounding substrate microbiota [60]. This is supported by analyses of the mycorrhizal colonization, composition, and function of lineages such as lycophytes, hornworts, and liverworts [4].

How the Earth finally became green

Land plants most likely evolved from a freshwater streptophyte adapted to (sub-)aerial conditions [29]. Although extant bryophytes have the same evolutionary distance to the MRCA of all land plants as a mammoth tree, their less complex body plan, lignin-free cell walls, and water-dependent dispersion of flagellated sperm, to name but a few, resemble a hypothetical MRCA of land plants rather well. Bryophytes, however, appear to have undergone evolutionary reduction [62,63], and the phenotypic consequences are only now being explored [64]. One should also not neglect tectonic forces, the breaking up of Pangea, the formation of mountains, and degassing that added to a constantly changing climate [65] during terrestrialization. The transition from water to land was only one aspect, and the evolution of green life that escaped from the banks of lakes, grew erect above the soil line, and generated massive biomass across all continents was another.

Advances in phenylpropanoid metabolism in land plants contributed novel flavonoids that acted as a molecular sun protection [37], sporopollenin to form an outer cell wall for seeds and pollen [66], and lignin that reinforces secondary cell walls to enhance long-distance water transport and erect growth, enabling vasculature and lignification [67]. The waxy, hydrophobic cuticle protects against dehydration and environmental stresses [68], while stomata help to maintain internal water reserves and enable gas exchange [69]. For the development of leaves, which evolved multiple times independently among land plants [70], YABBY proteins are of fundamental importance as TFs, and these were already present in the MRCA of land plants [51].

Another fascinating characteristic of land plants is their haplodiplontic life cycle in which mitotically dividing and multicellular haploid gametophytes and diploid sporophytes alternate (alternation of generations) [71], whereas in streptophyte algae only the haploid phase is multicellular and divides through mitosis [72]. Among various multicellular eukaryotic lineages, embryo-like structures evolved in animals, brown algae, and also in land plants (that possess a diploid sporophyte embryo, giving the Embryophyta their name) [72]. To initiate zygotic gene expression and meiosis, the molecular toolkit of homeodomain TFs of the KNOTTED1-LIKE HOMEOBOX (KNOX) family are essential and a beneficial duplication event in the MRCA of land plants gave rise to the class 1 and class 2 KNOX genes [73]. Early in land plant evolution, the gametophyte is thought to have remained dominant – similarly to the situation in extant bryophytes – whereas in Tracheophyta the haploid phase is reduced and the sporophyte became dominant throughout the life cycle [74].

The Tracheophyta, the land plant sister group to the bryophytes, comprise lycophytes, ferns, and the **Spermatophyta** (seed plants). They are characterized by canonical lignified vascular tissue and the gradual evolution of key traits for water and nutrient transport (xylem/phloem) as well as roots, stems, and leaves – all selected for as a response to the conquest of the new habitat and its competitive challenges. Some changes only result in small but crucial adaptations at the molecular level, but others transformed the entire body plan [41]. Ferns and lycophytes, as extant

descendants of the first land plants that evolved vascular tissue, offer insights into the prerequisites for angiosperm evolution as well as their role in times of climate change and biodiversity loss (Box 2) because angiosperms constitute >90% of all known land plant species [63]. The discussed adaptations enabled the success of vascular land plants and formed the basis for their subsequent diversification and explosive radiation [21] with a tenfold increase in plant species numbers [63] and the decline of atmospheric CO_2 [75], ultimately leading to the greening ashore.

Concluding remarks and future perspectives

The evolution of plants unfolded over hundreds of millions of years, thereby significantly contributing to atmospheric conditions and establishing the foundations for the enormous diversity of micro- and macroscopic life on land as we know it today. To fully understand how plants conquered land, knowledge and methods from a wide range of disciplines such as geology, paleobotany, biophysics, biochemistry, cell biology, and genetics will need to be merged with modern sequencing, bioinformatic, and phylogenomic tools. In the focus are streptophyte algae such as *Chara*, *Klebsormidium*, *Penium*, and *Spirogloea*, bryophytes such as the hornwort *Anthoceros*, the liverwort *Marchantia*, and the moss *Physcomitrium*, and among the vascular but non-seed land plants the lycophyte *Selaginella* and the ferns *Azolla* and *Ceratopteris*, to mention a few. The fast and constant increase in the number of sequenced genomes (including those of the species listed), and the progressive establishment of tools for non-seed plant model organisms which now need to be put to good use [76], has already installed a new field of evo-devo research over the past few years that has provided an impressive list of new insights [4,37,38,70,77].

Understanding the molecular adaptations to land that occurred during terrestrialization can help with identifying or optimizing the mechanisms that are also important for crop resilience. This is vital given the negative impact of increasing atmospheric CO_2 on harvest yields and food quality [78]. The Streptophyta adapted to a life on land and changed the climate in doing so. Anthropogenic rapid climate change exposes crops and other life on land to strong adaptive pressures, not unlike to the adaptation that was necessary when algae and later on land plants first conquered land. Deeper understanding of how plants adapt to a changing environment might allow us to help terrestrial life and ecosystems to cope with these changes.

Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

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Outstanding questions

What was the true nature of the heterotrophic host and the cyanobacterium that engaged in primary endosymbiosis?

Which features enabling the conquest of land evolved in charophyte freshwater algae?

How did organismic interaction of plants with fungi and bacteria evolve in detail?

What are the molecular evolutionary drivers of tolerance to abiotic and biotic stresses?

(Why) was the origin of land plants a monophyletic event?

What is the succession and nature of molecular adaptations in early land plant evolution?

What are evolutionary principles of complexity establishment, such as multicellularity, embryogenesis/ alternation of generations, and polyplastidy?

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