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Life's a beach- the colonization of the terrestrial environment

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Bristol, UK, July 2016

Introduction

One of the most transformative events in the Earth's history was the transition of life from aquatic environments to the land. This not only changed the subsequent evolutionary history of these newly-terrestrial organisms but also reshaped the global environment: the land, the oceans and the atmosphere (Fig. 1). In order to understand this process, scientists cannot look at single aspects in isolation. Accordingly, in 2010 a multidisciplinary symposium took place to act as a forum for scientists from numerous biological and physical disciplines to exchange ideas and to determine the extent of our current knowledge (Coates *et al.* 2011). Six years on, the 38th New Phytologist Symposium 'Colonization of the Terrestrial Environment 2016' (www.newphytologist.org/symposia/38) brought together many of the same scientists plus plenty of newcomers to reflect on how far we have come, and what still remains to be answered.

The first plant colonizers- origins, evolution, timing and impact

Phylogenetic analysis indicates that all extant terrestrial plants (embryophytes) have a common ancestor (Qiu *et al.* 2006), arising from within the 'Green Plant' lineage of algae (Viridiplantae) around 470 million years ago (Mya) (Fig. 2a). This monophyly strongly supports a single land colonization event by 'plants'. The relative contribution of such one-time events during the course of colonization was compared to those that have occurred repeatedly (homoplasies) in a keynote address by William (Ned) Friedman (Harvard University, USA). To survive environmental stresses on land (desiccation, ultraviolet radiation damage, nutrient acquisition, etc.), embryophytes underwent dramatic changes from their algal ancestors. In contrast, the complex morphologies that enabled animals to survive on land evolved in aquatic environments and were subsequently 'pulled up' onto land several times ('Zoologists talk about the importance of the Cambrian explosion [542 Mya] in terms of human evolution, but humans would not have evolved without land plants').

Why has only one algal lineage successfully colonized the terrestrial environment? Did unique traits enable this transition? The common ancestor of land plants was apparently multicellular. The acquisition of multicellularity ultimately led to innovations in transport, reproduction and dispersal that have enabled land plants to dominate terrestrial ecosystems, but this trait has evolved independently at least 25 times in the eukaryotes, including just 250 Mya in the Chlorophyte Volvocine algae (Fig. 2a). Using comparative transcriptome analysis, Brad Olson (Kansas State University, USA) demonstrated that, contrary to expectations, the origins of multicellularity in this group required co-option of only a few critical cell-cycle genes to transform single-celled algae into colonial organisms, with later gene changes underpinning cell specialisation (Hanschen *et al.* 2016). All embryophytes share a lifecycle alternating between multicellular haploid and diploid generations whereas only the haploid generation is multicellular in their extant sister group, the charophytes (Fig. 2a). However, other aquatic algae (including Ulvophytes, and Rhodophytes; Fig. 2a) also possess alternating multicellular generations. It has recently been argued that traits enabling ‘terrestrialisation’ predate the embryophytes, (Harholt *et al.* 2016), so perhaps a unique combination of traits enabled this one-time event.

Another key characteristic of the embryophytes is oxygenic photosynthesis which evolved in cyanobacteria long before land plant colonization. Oxygenic photosynthesis likely triggered a Global Oxygenation Event approximately 2.3 billion years ago (Ga) that introduced oxygen (O₂) to the atmosphere and created today’s ozone layer, which blocks UV radiation. John Raven (University of Dundee, UK) described the most basal extant terrestrial organisms containing chlorophyll A, *Gloeobacter* cyanobacteria, which exhibit traits advantageous for survival on land such as desiccation tolerance. The acquisition of a cyanobacterium as a primary endosymbiont (chloroplast) in the algal lineage that led to land plants (Fig. 2a) appears to be another unique evolutionary event. Oxygenic photosynthesis in ancestral land plants may itself have conferred a degree of UV resistance to these organisms.

The first evidence of land plants found in the fossil record comes from cryptospores, appearing approximately 470 Mya (Fig. 1) (Rubenstein *et al.* 2010). Detailed analysis

of these structures (Edwards *et al.* 2014) together with contemporary spore-bearing plant (cryptogam) macrofossils demonstrated that the developmental strategies and bodyplans of extant terrestrial taxa represent only a fraction of the early land plant morphological diversity. The appearance of land plants roughly coincides with a second increase in atmospheric oxygen predicted by the appearance of charcoal (the formation of which requires a minimum of 15% O₂) in the fossil record (Fig 1). Tim Lenton (University of Exeter, UK) presented new data using updated Carbon-Oxygen-Phosphorous-Sulphur-Evolution (COPSE) atmospheric modelling (Bergman *et al.* 2004) that suggests this increase in atmospheric O₂ was dependent on photosynthesis by these first terrestrial plant assemblies (Lenton *et al.*, 2016). Dramatic increases in available genome and particularly transcriptome data over recent years across the green lineage, from initiatives such as OneKP (Wickett *et al.* 2014), have refined and strengthened our understanding of how different plant groups relate to one another- crucial to our interpretation of plant evolution- but the relationships between extant non-vascular plants (bryophytes) are still contentious. The majority of recent phylogenies have placed bryophytes as a paraphyletic grade, with liverworts as the most basal clade (Qiu *et al.* 2006; Fig. 2b), but both Sean Graham (University of British Columbia, Canada) and Cymon Cox (Universidade do Algarve, Portugal) presented new phylogenetic evidence that two of the bryophyte groups, liverworts and mosses, are more closely related to one another than to either hornworts or vascular plants (tracheophytes) (Fig. 2c). The precise relationship between these basal lineages remains unresolved.

Embryophytes did not colonize the land by themselves, as evidenced by fossil assemblies such as the Rhynie Chert (Fig. 1) which preserves diversity around a geothermal spring that included lichen, algae, fungi and arthropods alongside cryptogams. Such highly preserved fossils demonstrate that symbiotic relationships between plants and fungi (ectomycorrhizal associations) were already established by this time. Whilst the first fungal-plant associations were thought to have been with the Glomeromycota, Katie Field (University of Leeds, UK) presented evidence for ancestral symbioses with an older group of fungi, the Mucormycota (Field *et al.* 2015), and the potential for liverworts to form simultaneous associations with both fungal groups. By analysing 1000 fungal genomes, Francis Martin (INRA, France) demonstrated that ectomycorrhizal associations have influenced the evolutionary

history of the fungi themselves, which at present is not taken into account in models of nutrient cycling ('Don't forget the fungi!'). Such interactions improved nutrient scavenging by cryptogams, which were growing in the absence of existing soil. The environmental impact and functioning of these early ecosystems was a theme throughout the Symposium. They increased chemical weathering of the rocks upon which they grew, to form the earliest soils, and may have significantly reduced atmospheric CO₂ concentrations (Fig. 1; Lenton *et al.* 2012; Porada *et al.*, 2016). Paul Kenrick (Natural History Museum, UK), Lyla Taylor (University of Sheffield, UK) and Andy Ridgewell (University of Bristol, UK) each discussed attempts to model the productivity and environmental impact of the first cryptogamic ecosystems ('biocrusts') by comparing to modern equivalents- in the case of the Rhynie Chert, to cryptogamic covers colonizing Icelandic lava flows. Modern cryptogamic ground covers represent ~7% of carbon uptake and up to 50% of biological nitrogen fixation by terrestrial vegetation (Elbert *et al.* 2012). Derek Vance (ETH Zurich, Switzerland) highlighted both the current paucity of tools (such as lithium isotope ratios) with which to investigate historical geochemical changes caused by biotic weathering, and the limited sampling so far conducted from the Ordovician (Fig. 1).

Beyond the bryophytes- the evolution of vascular plants

Our understanding of early land plant evolution has improved dramatically thanks to the detailed investigation of the moss *Physcomitrella patens* and liverworts in the genus *Marchantia*. These were repeatedly highlighted throughout the meeting as tools to understand the evolution of important embryophyte characters, such as rhizoids (Liam Dolan, University of Oxford, UK), stomata (Julie Gray and Bobby Caine, University of Sheffield, UK), spore germination (Eleanor Vesty, University of Birmingham, UK; Vesty *et al.* 2016) and ectomychorrhizal associations (Katie Field, University of Leeds, UK; Aisling Cooke, John Innes Centre, UK). The limitations of these bryophyte models was highlighted, focussing on the debatable function of stomata (which are absent from liverworts) in *P. patens* and the failure of the predominant model liverwort, *Marchantia polymorpha*, to form ectomychorrhizal associations. Importantly, the meeting also focussed beyond the bryophyte world to colonization by vascular plants (tracheophytes). We currently understand vascular plants largely through the lens of the now-dominant flowering plants (angiosperms) but the debate over stomatal evolution highlighted the importance of understanding

development in more basal tracheophyte lineages (lycophytes and ferns; Fig. 2a), with disagreement in the literature (and in the meeting!) over whether their stomata respond to environmental stimuli similarly to angiosperm stomata (e.g. McAdam and Brodribb 2014; Franks and Harper 2016). As yet there are few tools available to study lycophyte and fern development directly, but these limitations are now being overcome, with increasingly powerful transcriptomic analyses and the advent of stable genetic transformation in a fern (Plackett *et al.* 2014).

The tracheophytes do not represent a static group, but have undergone continual evolutionary changes since their divergence from the bryophytes. Understanding how these changes occurred will be a major challenge in future plant evo-devo. A key transition was the rise to dominance of the diploid sporophyte generation of the embryophyte lifecycle, which required the establishment of a persistent shoot meristem. Jill Harrison (University of Bristol, UK) presented genetic studies of the *P. patens* sporophyte that suggest conserved regulators of the angiosperm shoot meristem could be involved with this transition. Similarly, tracheophytes evolved rooting systems with persistent meristems, replacing rhizoids as the primary means of anchorage and nutrient uptake (Raven and Edwards 2001). Sandy Hetherington (University of Oxford, UK) highlighted the continuing importance of fossils to elucidating tracheophyte evolution, demonstrating that the most ancient active root meristem found to date has a novel structure compared to extant lineages (Hetherington *et al.* 2016). Thus we cannot assume that angiosperm developmental processes, about which we know a great deal, reflect those in earlier tracheophytes.

At the ecological level, succeeding tracheophyte lineages have displaced pre-existing groups as the dominant flora, driving evolutionary and ecological change- as Kevin Boyce (Stanford University, USA) reminded us, ‘There were no annual plants before the angiosperms’. The fossil record is littered with now-extinct plant groups, and reconstructing and understanding these paleoecological assemblages remains a major challenge. Isabel Montanez (UC Davis, USA) presented work reconstructing plant physiology from fossil morphologies during the late Carboniferous (325–300 Mya), at which time tree-form lycophytes (lycopsid forests) disappear from the fossil record (Fig. 1A). These estimates suggest lycopsid demise could relate to reduced water use efficiency (WUE) as atmospheric CO₂ reduced. Similarly, Karl Fetter (University of

Vermont, USA) demonstrated the use of stable carbon isotope ratios to estimate photosynthesis from fossil angiosperms in order to reconstruct paleozoic light environments (Graham *et al.* 2014). The rise of the angiosperms approximately 160 Mya (Fig. 1) represents another phase-change in terrestrial colonization. What made them so successful? Mark Puttick (University of Bristol, UK) presented evidence that angiosperm diversification correlates with an increased rate of change in genome size (but not with genome size directly). Kevin Boyce demonstrated that venation in angiosperms is optimised for both maximum photosynthetic capacity and WUE, a relationship not found in either extant or fossil conifers (gymnosperms) or ferns, which may have contributed to the angiosperms' success (Zwieniecki and Boyce 2014). As a corollary, it was proposed that the low vein densities and accompanying photosynthesis estimates in Carboniferous fossils show that these plants were not in competition for light, which until now has been a widely-assumed driver for increased plant size: tree forms represent another homoplasy in land plant evolution.

Perspectives and future challenges

In the last six years we have gained details of when and how ancestral embryophytes colonized the land, but our understanding of this process is still far from complete. We do not know why only one lineage of algae successfully colonized the land or the full environmental impacts of that early colonization, nor do we comprehend the drivers and impacts of the serial rise to dominance of successive tracheophyte lineages beyond the bryophyte world. The emergence of new tools, including model organisms and a wealth of genome and transcriptome data, have dramatically improved the scope of the questions that we can address, but these too have their limitations. New model organisms are needed in lineages where our understanding lags behind the angiosperms and bryophytes, as well as increased study across a broader range of species to better understand plant diversity (Coates 2016). Beyond extant organisms, further exploration and integration of the fossil- and geochemical records will be essential for resolving the details of developmental, ecological and environmental changes that occurred during the colonization of the terrestrial environment.

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FIGURES

Figure 1. Timeline of the colonization of the terrestrial environment, showing the first appearance in the fossil record of surviving land plant lineages against geological time; Mya, Million Years Ago. The times of important ecological systems and events discussed at the Symposium are marked. Predictions of historical atmospheric composition across the same timescale are reproduced from baseline COPSE models (Bergman *et al.* 2004). Oxygen (O₂), black line; carbon dioxide (CO₂), grey line.

Figure 2. Changes in thinking on land plant phylogenetic relationships. **(a)** The relationship of land plants (embryophytes) to other algal lineages, based on Leliaert *et al.* (2012). All lineages shown share a common primary endosymbiotic event leading to oxygenic photosynthesis. **(b)** Current consensus on relationships between extant embryophyte lineages, based on Qiu *et al.* (2006). Bryophytes (mosses, liverworts and hornworts) form a paraphyletic grade with liverworts basal-most. **(c)** Alternative phylogeny (unrooted) proposed during the meeting, in which liverworts and mosses are more closely related to one another than to other embryophytes. Hornworts remain sister group to the tracheophytes. Relationships within the tracheophytes remain unaltered.