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Cryptogamic ground covers as analogues for early terrestrial biospheres: Initiation and evolution of biologically mediated proto-soils

Ria L. Mitchell[1,2] | Christine Strullu-Derrien[1,3] | Dan Sykes[4,5] | Silvia Pressel[6] | Jeffrey G. Duckett[6] | Paul Kenrick[1]

[1]Earth Sciences Department, The Natural History Museum, London, UK

[2]Sheffield Tomography Centre (STC), Kroto Research Institute, The University of Sheffield, Sheffield, UK

[3]Institut de Systématique, Evolution, Biodiversité (ISYEB), UMR7205, Muséum National d'Histoire naturelle, Sorbonne Université, CNRS, Paris, France

[4]Imaging and Analysis Centre (IAC), The Natural History Museum, London, UK

[5]Henry Moseley X-ray Imaging Facility, School of Materials, The Royce Institute, The University of Manchester, Manchester, UK

[6]Life Sciences Department, The Natural History Museum, London, UK

Correspondence

Ria L. Mitchell, Sheffield Tomography Centre (STC), Kroto Research Institute, The University of Sheffield, North Campus, Broad Lane, Sheffield, S3 7HQ, UK.
Email: r.mitchell@sheffield.ac.uk

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Abstract

Modern cryptogamic ground covers (CGCs), comprising assemblages of bryophytes (hornworts, liverworts, mosses), fungi, bacteria, lichens and algae, are thought to resemble early divergent terrestrial communities. However, limited in situ plant and other fossils in the rock record, and a lack of CGC-like soils reported in the pre-Silurian sedimentological record, have hindered understanding of the structure, composition and interactions within the earliest CGCs. A key question is how the earliest CGC-like organisms drove weathering on primordial terrestrial surfaces (regolith), leading to the early stages of soil development as proto-soils, and subsequently contributing to large-scale biogeochemical shifts in the Earth System. Here, we employed a novel qualitative, quantitative and multi-dimensional imaging approach through X-ray micro-computed tomography, scanning electron, and optical microscopy to investigate whether different combinations of modern CGC organisms from primordial-like settings in Iceland develop organism-specific soil forming features at the macro- and micro-scales. Additionally, we analysed CGCs growing on hard rocky substrates to investigate the initiation of weathering processes non-destructively in 3D. We show that thalloid CGC organisms (liverworts, hornworts) develop thin organic layers at the surface (<1 cm) with limited subsurface structural development, whereas leafy mosses and communities of mixed organisms form profiles that are thicker (up to ~ 7 cm), structurally more complex, and more organic-rich. We term these thin layers and profiles proto-soils. Component analyses from X-ray micro-computed tomography data show that thickness and structure of these proto-soils are determined by the type of colonising organism(s), suggesting that the evolution of more complex soils through the Palaeozoic may have been driven by a shift in body plan of CGC-like organisms from flattened and appressed to upright and leafy. Our results provide a framework for identifying CGC-like proto-soils in the rock record and a new proxy for understanding organism–soil interactions in ancient terrestrial biospheres and their contribution to the early stages of soil formation.

KEYWORDS
palaeobotany, plant evolution, soil development, plant-soil interactions, weathering, X-ray computed tomography

1 | INTRODUCTION

Cryptogamic ground covers (CGCs) are a type of biological soil crust comprising a complex association of early divergent organisms including non-vascular plants (bryophytes; liverworts, hornworts, mosses), fungi (free-living, saprotrophic and mycorrhizal), bacteria (free-living and symbiotic), algae, and lichens (Edwards et al., 2015; Mitchell et al., 2016; Porada et al., 2014). Modern CGCs are present in almost all habitats on Earth, ranging from deserts (Williams et al., 2012) to polar tundra (Belnap & Lange, 2001) being able to tolerate extremes of aridity, temperature and altitude (Belnap & Lange, 2001). They contribute towards hydrological, geomorphological and ecological cycles (Elbert et al., 2012; Menon et al., 2010) by resisting surface run-off and erosion (Gao et al., 2016) and by promoting dust capture (Williams et al., 2012). CGCs form complex interactions and relationships with their substrates where they promote weathering (Mitchell et al., 2016; Mitchell et al., 2019) and contribute to biogeochemical cycling through organic (carbon) burial (Belnap & Lange, 2001; Porada et al., 2014) and nitrogen fixation through cyanobiont symbiosis (Elbert et al., 2012; Porada et al., 2014). Additionally, diverse symbiotic associations exist between plant elements (liverworts, hornworts) and filamentous fungi (Duckett et al., 2006; Pressel et al., 2010; Rimington et al., 2018; Strullu-derrien et al., 2014) and a smaller number of cyanobacteria (Adams & Duggan, 2008), as well as lichen associations (Du et al., 2019), all of which play a key role in nutrient acquisition (Field et al., 2012). Importantly, modern CGCs are considered analogous to the earliest terrestrial ecosystems (Kenrick et al., 2012; Mitchell et al., 2016), although in these the plant component were not bryophytes but rather cryptophytes, a grade of extinct bryophyte-like plants (Edwards et al., 2015) that likely originated in the Mid-Ordovician (Strother et al., 2015; Wellman & Gray, 2000). Moreover, the evolutionary context of other modern CGC components remains uncertain; the earliest fossil Ascomycota fungi (the most ancient fungal component in lichens) (Taylor et al., 1999) and the earliest fossil macrolichens (Honegger et al., 2013) are from the Lower Devonian; however, convincing lichen evidence is rare in the fossil record. The earliest well-understood terrestrial community is the Lower Devonian Rhynie chert (Edwards et al., 2018; Garwood et al., 2020; Strullu-derrien et al., 2019; Trewin, 2007), an exceptionally preserved geothermal wetland. Bryophytes are widely regarded as the closest living relatives to the first land plants; however, major uncertainties remain on the phylogenetic relationships amongst the three bryophyte groups and with respect to the vascular plants. Until recently, the prevailing hypothesis was that of a bryophyte grade with liverworts as the earliest divergent lineage and hornworts as sister to the vascular plants (Chang & Graham, 2011; Gao et al., 2010; Kenrick & Crane, 1997; Qiu et al., 2007). However, latest molecular analyses now strongly support a moss-liverwort clade but with questions remaining on bryophyte monophyly and the position of hornworts as either sister to the moss-liverwort clade, sister to all other embryophytes, or sister to the vascular plants (Harris et al., 2020; Puttick et al., 2018; Sousa et al., 2019, 2020). While improved resolution of these relationships will allow for better understanding of how plants arose on land, it remains that bryophytes represent highly suitable modern analogues to study soil forming processes associated with early plant-based biotas, in particular thalloid liverworts and hornworts, which are also known to form fungal associations with members of the early divergent mycorrhizal fungal clades Glomeromycotina and Mucoromycotina (Desiro et al., 2013; Field et al., 2016; Field, Rimington, et al., 2015; Rimington et al., 2020; Rimington et al., 2018, 2019). It is widely assumed, based on fossil, molecular, and physiological evidence that the evolution of mutually beneficial symbioses between plants and fungi was a key factor in terrestrialisation (Field, Rimington, et al., 2015; Rimington et al., 2018; Selosse & Strullu-Derrien, 2015), which augmented mineral weathering (Mitchell et al., 2016) in early proto-soils, reportedly leading to changes in Earth's atmosphere through consumption of CO_2 (Porada et al., 2014), and perhaps triggering the Ordovician glaciations (Lenton et al., 2012). While these studies indicate that biological terrestrialisation had a profound effect on the Earth system, little is currently known about the micro-to-macroscale physical and chemical processes that drove these large-scale weathering, landscape and climatic shifts through the Palaeozoic.

Estimates of the timing of plant terrestrialisation vary considerably between molecular, phylogenetic and fossil data. Land plants (embryophytes) evolved from the transmigration of freshwater streptophyte algae onto exposed land surfaces in the earliest Palaeozoic (Harholt et al., 2016; Kenrick et al., 2012). Recent molecular genomic analyses place the emergence of land plants in the Cambrian (~500–450 million years ago) (Morris et al., 2018; Puttick et al., 2018), and the body fossil record of bryophyte-like plants suggests the Early Silurian (Tomescu & Rothwell, 2006) or possibly the late Silurian/Early Devonian (Kenrick & Crane, 1997). The bryophyte-like spore record provides the most conclusive evidence of cryptophyte macro/meso fossils, which is generally accepted as the Mid-Ordovician (Wellman et al., 2003). These disparities highlight the need for other proxies for the presence, structure and composition of early terrestrial CGC-like communities, particularly where fossils are absent. Investigating early soil forming processes in modern analogues is not only crucial for understanding the impact of early terrestrial organisms on the Earth system through organic carbon burial, drawdown of atmospheric CO_2 through weathering and global-scale biogeochemical cycling, but may also enable us, for the first time, to recognise CGC-like proto-soils in the sedimentological record. This would add new biomarker proxies for studying early terrestrialisation (Mitchell et al., 2019) and complement a limited sedimentological early record of fossil soils (palaeosols), fossils and geochemical proxies in both the Proterozoic and Phanerozoic (Finke et al., 2019; Horodyski & Knauth, 1994; Mitchell & Sheldon, 2010; Strother et al., 2011; Strother & Wellman, 2020). Indeed, the key may be found within early CGC-like soils.

We investigated modern CGC volcanic substrate soils and CGC-colonised hard substrates (rocks) from Iceland (Figure 1) and applied a combination of novel imaging techniques (e.g. X-ray micro-computed tomography (μCT), optical microscopy (OM), scanning electron microscopy (SEM)) to determine the impact of combinations of CGC organisms on (a) the origination of soils from regolith and weathering residues from hard substrate weathering and (b) on CGC proto-soil structural development. Our overarching goal is to identify variations in processes and structure caused by different CGC organisms (thalloid, moss, mixed, lichens) that can be used as a framework to recognise potential CGC-like proto-soils in the sedimentological/fossil record and to understand better the impact of various CGC organisms on early soil development as well as how this may have evolved through the Palaeozoic.

2 | METHODS

2.1 | Fieldwork and sample collection

CGC soils and rock samples were collected from various sites in Iceland (Figure 1a; Appendix S1). Samples containing an assortment of CGC organisms were collected from volcaniclastic and geothermal field sites (Figure 1b,c); these were chosen to provide a variation in geomorphological setting, grain size and soil composition. Geothermal soils are also the most analogous to the Early Palaeozoic Rhynie chert. CGC soil cores (variable in size, but 25 mm x 80 mm at their largest; Figure 1d) were collected using a cork-borer and housed in plastic vials following fixation with 10% formalin. Soil cores were collected with the principal aim of performing non-destructive 3D X-ray tomographic imaging of CGC structural properties as near to in situ conditions as possible. Duplicate samples were collected for thin sectioning for optical/light and scanning electron microscopy. Rocks were also sampled to establish biological interactions with "hard" substrates. No molecular analyses were employed. A table of sample information is presented in Appendix S1.

2.2 | X-ray micro-computed tomography (μCT)

μCT scans of all soils and rocks were performed at the Imaging and Analysis Centre (IAC) at the Natural History Museum, London, UK. μCT was used to visualise the 2D and 3D structure of soil cores and rocks non-destructively. Cores and rocks were scanned using a Nikon Metrology HMX ST 225 μCT scanner with a tungsten reflection target. Soil scans were performed at an X-ray tube voltage of 170 kV and a tube current of 180 μA, and 3,142 projections were collected over an average scan time of 35 min. Rocks were scanned at 190 kV, 180 μA and 6,284 projections were collected. A 0.1 mm thick copper filter was inserted to remove low energy X-rays and pre-harden the X-ray beam (Appendix S2). All scans were collected at 708 ms exposure. Soil core voxel (3D pixel) sizes range between 19μm and 37μm, and rocks 53μm (Appendix S2). Scans were reconstructed into 3D tomographic datasets as tiff image stacks using CT Pro Software (Nikon Metrology) and were rendered in Drishti v2.5,

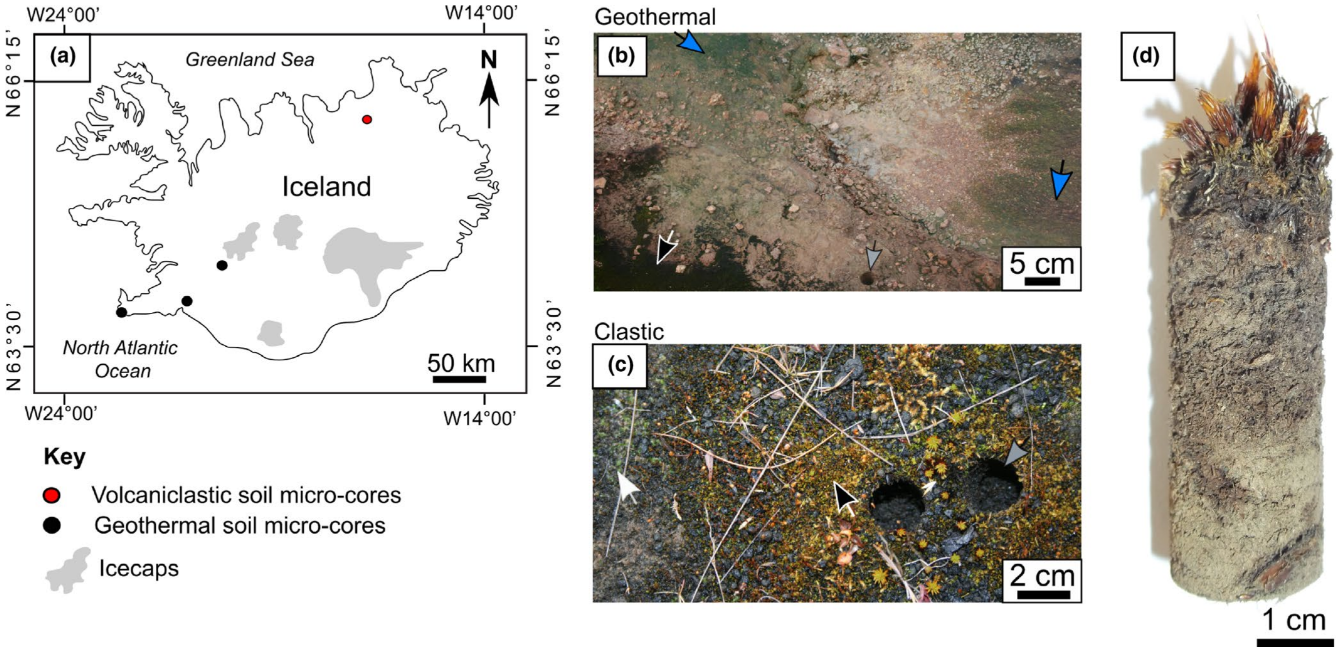

FIGURE 1 (a) Sample location map of Iceland adapted from Mitchell et al., 2016 (b, c) field examples of geothermal and volcaniclastic soil surfaces and (d) example CGC soil core. Arrows = moss (black), sampled hole (grey), microbial crust (blue), liverworts (white)

Volume Graphics (VG) Studio Max v2.1/2.2, and ORS Dragonfly to reveal 3D and 2D (X, Y, Z axes) views (Figure 2). No staining agents (e.g. iodine) were used, and fixation of soil and plant material with 10% formalin aided in prevention of plant desiccation during scanning.

2.2.1 | μCT analysis

Soil component analysis was achieved using Thermo Fisher Scientific Avizo software (version 9.0.0) within the Advanced Imaging of Materials (AIM) Facility at Swansea University (UK). Individual soil components (i.e. inorganic grains and matrix, organics and porosity) were each segmented using the histogram interactive thresholding tool, which segments different materials based on the specific density and greyscale values of each individual soil component (Figure 2a, Appendix S3). Relative quantities (in voxels) were generated of the three soil components using the material statistics function as volume per slice and converted to percentages through the total volume accordingly. This provides slice-by-slice (down-profile; Z axis) volume data (Figure 2b, Appendix S3 and Appendix S4).

2.3 | Scanning Electron Microscopy (SEM) and optical microscopy (OM)

Thin sections were prepared via a standard method of vacuum impregnation and were cut to ~ 30 μm thickness. SEM imaging of CGC soil cores was achieved on a Zeiss Leo 1455 variable pressure SEM housed within the IAC at the Natural History Museum (London, UK). Imaging was completed at variable pressure under backscattered mode, 20 kV, a 550 μm spot size, and a working distance of 14 mm. Chemical data as maps were gathered via scanning electron microscopy emission dispersive spectroscopy (SEM-EDS) using Oxford Instruments Aztec software (Abingdon, UK). Parameters include 20 kV, 6 mm working distance and 800 μs dwell time to generate over three million counts per mapped area. Thin sections were fixed to sample holders with copper tape to prevent charging, were without cover slips, and uncoated. Thin sections of soil cores were studied on a Nikon Eclipse LV100ND compound light microscope housed within the Earth Science Department at the Natural History Museum (London, UK).

3 | RESULTS

3.1 | CGC soil structure

CGC soil structure was investigated using μCT (Figure 3). Comparisons were drawn from an assortment of typical CGC organisms (thalloid liverworts and hornworts, lichens, mosses and mixed organisms; Appendix S1) collected from two contrasting geomorphological settings (geothermal and volcaniclastic). CGC organisms were grouped according to their morphology into four categories: thalloid appressed to soil (thalloid liverworts and hornworts), leafy upright (mosses), lichens, and mixed organisms (mostly mosses and lichens). Grain sizes varied, with coarser (100 μm > fraction) grains in volcaniclastic settings, and a higher proportion of finer grained silts and clays (<100 μm fraction) in geothermal settings (Figure 3).

In volcaniclastic settings (Figure 3a–c), CGC soils associated with thalloid plants have an upper, thin, consolidated zone, which is fine-grained compared with the underlying unconsolidated regolith, and appears to fine-upwards (Figure 3a). The plant thallus envelops the soil surface and sometimes develops "pillars," while buried organic material is limited and concentrated at the soil surface (Figure 3a). The upright leafy growth of mosses (e.g. Figure 3b) results in a different interaction with the soil; the surface organic material in volcaniclastic moss CGCs is thicker than in thalloid CGCs due to higher

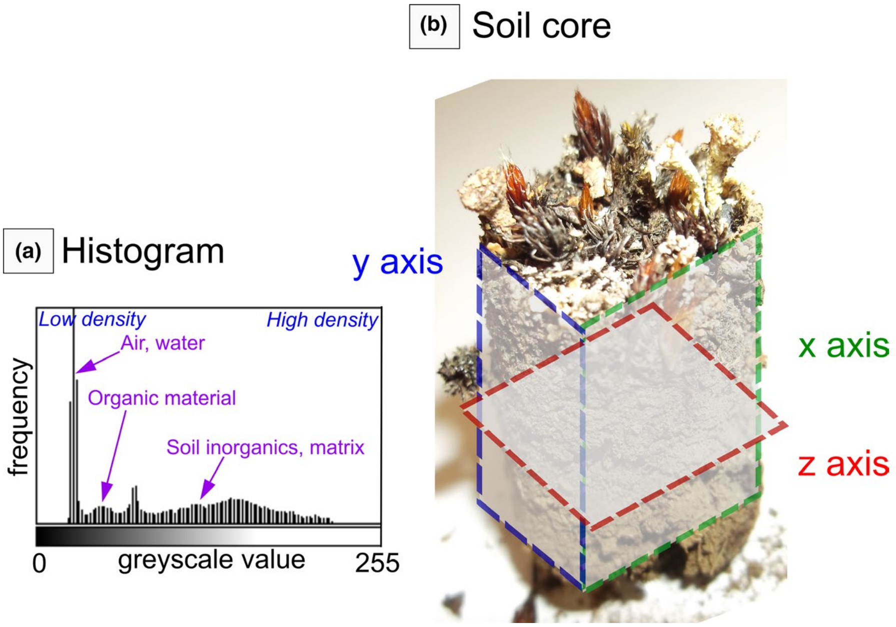

FIGURE 2 (a) Histogram displaying typical greyscale values/densities in Iceland CGC soils, (b) Typical x-, y- and z-axis orientations for each soil core

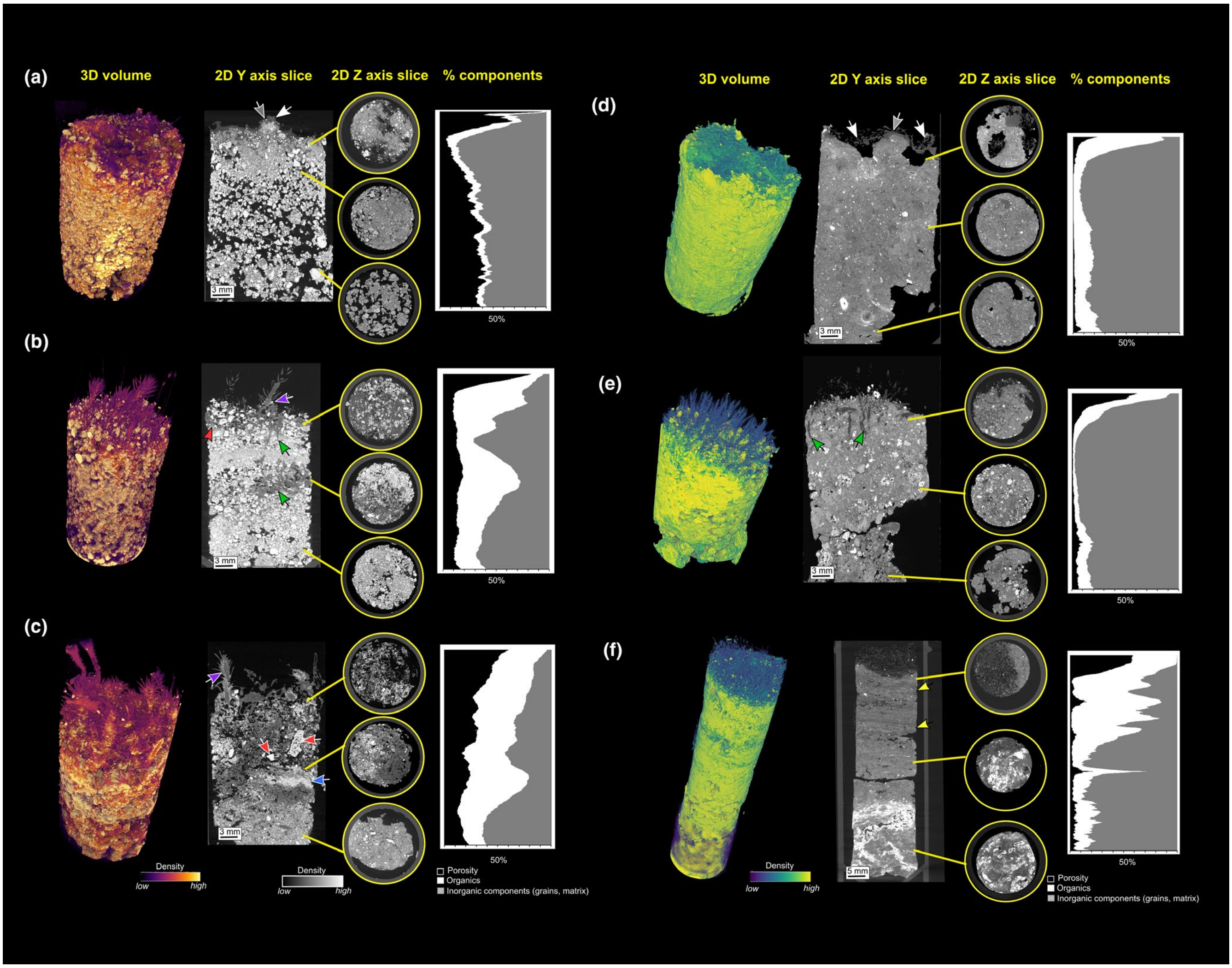

FIGURE 3 3DA and 2D µCT images showing the structural and compositional variations through volcaniclastic (a-c) and geothermal (d-f) CGC soils containing combinations of different CGC plants and organisms. Slices through y- and z-axes are shown displaying variations in structure and composition through soil profiles. Comparison of percentage porosity, organic material and inorganic components derived from µCT analysis also illustrated. (a) = thalloid liverwort (*Blasia pusilla*), (b) = moss (*Polytrichum juniperinum*, *Ceratodon purpureus and Pohlia rottii*), (c) = mixed moss and lichen (*Ceratodon purpureus and Cladonia sp.)* CGCs. (d) = thalloid hornwort (*Phaeoceros carolinianus*), (e) = moss (*Oligotrichum sp.)* and (f) = mixed moss, lichen and bacteria (*Pohlia annotina and Polytrichum commune)* CGC soils. White arrow = thallus, grey arrow = pillar structures, red arrow = organically trapped coarse grains, green arrow = buried moss stems, purple arrow = trapped grains in upright moss structure, blue/yellow arrow = subterranean layered organic material

amounts of buried moss stems below the soil surface and buried organic detritus (Figure 3b). Coarse soil grains, likely aeolian in origin, are trapped within the upright moss "leafy" body, accumulate at the soil surface and become trapped and entwined within the surface organic layer (Figure 3b). The moss example in Figure 3b also appears to have two organic layers, one at the surface and one ~ 15 mm beneath; this might reflect growing periods over two consecutive years and the subsequent burial of a previous surface organic layer. The underlying regolith contains less organic material than the surface (21% to 9%, respectively; Figure 3b). Mixed CGCs develop dense surface coverings, which affect the complexity of the soil structure (Figure 3c). Mixed moss and lichen volcaniclastic CGCs develop ~ 30 mm thick surface organic zones containing entwined grains of varying sizes, and again evidence of grain trapping within the structure of upright "leafy" mosses (Figure 3c). At the base of the CGC, organic material and soil mineral material can develop alternating and undulating layers (Figure 3c). This may also represent a previous organic-rich soil surface that has been buried, potentially representing the layered architecture of lichens.

Geothermal soils on the other hand are generally finer grained, poorly sorted, and are more compact because of low porosity (Figure 3d–f). Thalloid plants in geothermal settings have little effect on the structure of the CGC soil (Figure 3d). The thalli envelop the soil surface with limited buried organic material, though surface pillar structures are again observed (Figure 3d). Geothermal moss CGCs display a thin organic surface covering, where below-ground axes deepen the surface organic layer (Figure 3e). Geothermal mixed CGCs have surface organic material and beneath this, layers which are combinations of buried plant material and laminations caused by bacterial filaments (Figure 3f). At the base of the CGC is an area rich in organics (subterranean microbes including bacteria) (Figure 3fi).

Mixed-organism geothermal soils can be subdivided into structurally distinct layers (Figure 4) from correlated complementary imaging techniques (μCT, OM, SEM) at various scales (Figure 4a,b). The surface organic zone (Figure 4c,d) is a mixed zone of buried moss stems and mixed grain sizes where organic laminations have developed and entwine soil grains (Figure 4c,d). The layered zone beneath the surface organic zone (Figure 4e,f) is composed of thin, undulating layers of filamentous organic material within a poorly sorted clay to medium sand-grade matrix (Figure 4e,f). The organic material here is a mix of buried plant detritus and filamentous (probably bacterial) clumps forming elongate layers (Figure 4a,b,e,f). In the ~ 30 mm thick clastic zone beneath (Figure 4g,h), there are coarse silica sinter clasts amongst a fine-grained clay matrix. There are also remnants of buried organic material (Figure 4h), but much less compared with the zones above. Clasts are poorly sorted and so do not form obvious layers or lenses. The lower organic zone (Figure 4i–k) contains some fine-grained silica sinter but is mostly clay. There are numerous patches of high-density (bright) areas in this zone identified in the μCT scans (Figure 4a); chemical comparisons from SEM-EDS indicate this is because of numerous and patchy accumulations of framboidal iron pyrite (Figure 4i,k,l), which often accommodate organic cellular spaces. Also common are bundles of bacterial filaments inhabiting deeper parts of the CGC soil (Figure 4j), some of which again have iron replacement within their structure (Figure 4k). There are also probable purple sulphur bacteria deep in the soil, which give this layer its distinctive colour (Figure 4b).

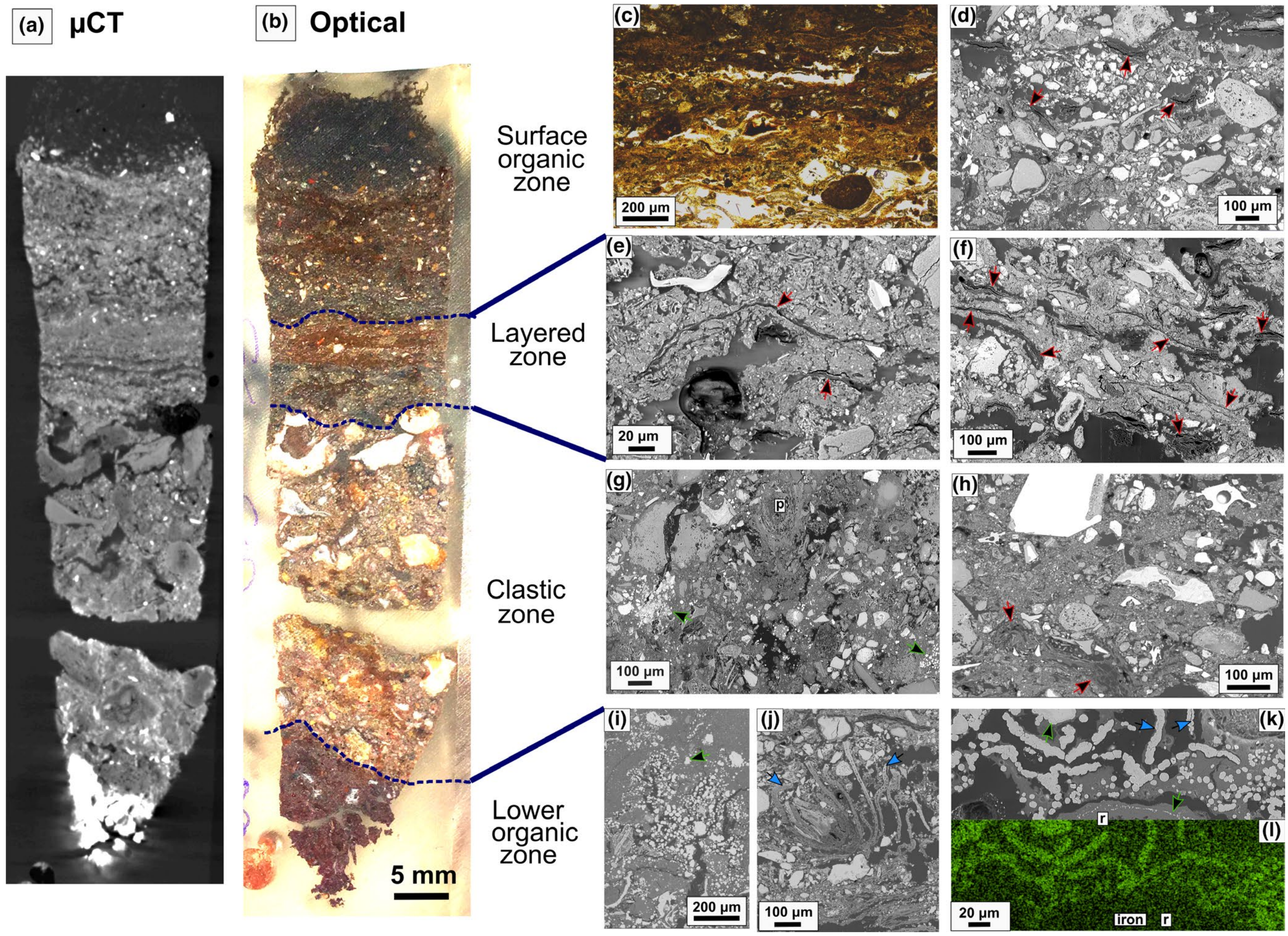

FIGURE 4 Typical geothermal mixed CGC soil, colonised at the surface by moss (*Pohlia annotina* and *Polytrichum commune*). (a) Y-axis μCT slice through whole CGC soil before being cut. (b) Resin block cut through CGC soil core during thin section preparation. Slice in (a) has been correlated with this view. (c) Optical microscope image from thin section of surface organics. (d–k) SEM images from thin sections of specific parts of micro-soil profile. (c, d) Thick, layered organic material in surface organic zone; organics are perpendicular to way-up of soil. (e, f) Undulating organic laminations draping over clastic material in the subsurface layered zone. (g, h) Fewer organic material in the clastic zone, and coarser grain sizes. (i) Pyrite nodules in the lower organic zone. (j) Bundles of organic-rich filamentous (probably) bacteria. (k, l) Replacement of organic material by iron pyrite framboidal nodules; note also iron nodules in subsurface of basalt clast. Red arrow = organic material, green arrow = Fe-rich nodules, blue arrow = bacterial filaments, r = rock (basalt) clast

Component analysis of porosity, grains and organics indicates variation both between substrate type and colonising organism type (Figure 5, Appendix S3 and Appendix S4). There is limited variation between thalloid organisms growing on fine-grained geothermal substrates, whereas thalloid organisms colonising volcaniclastic environments have a large variation in porosity (2 to 80%) and a maximum organic component of 12%. Mosses colonising fine-grained substrates have a consistent organic component but large variations in porosity and inorganic components, and in volcaniclastic settings a larger variation in all components. Mixed CGCs have the largest amount of organic material and high porosity (Figure 5). There is generally an increasing organic component from thalloids > moss > mixed (Figure 5).

3.2 | CGCs on hard substrates

As well as soft substrates cryptogamic organisms commonly colonise "hard" substrates, notably rocks (the example here being a basalt boulder) and attach to smaller hard substrates (grains) at substrate and soil surfaces (Figure 6). Filamentous organics and lichen thalli drape over hard surfaces (Figure 6a,b), which sometimes results in the formation of rock micro-caverns, often containing accumulations of organic material (Figure 6b,c) as endolithic communities. Micro-caverns could be naturally occurring pre-colonisation vesicular rock features that have become enlarged by biological weathering, or originate from penetration by the colonising organisms. Crustose and thallose lichens are closely appressed to hard substrate surfaces, sometimes penetrating to ~ 1 mm depth (Figure 6b). Colonisation at soil and sediment surfaces can also lead to organic attachment on large grains (Figure 6), where in this instance liverwort thalli envelop the soil surface and hold coarse soil grains in place, roughening the grain surfaces and penetrating the grain (Figure 6d). Mosses are common on hard substrates and form micro-caverns (Figure 6f–h) through weathering, resulting in organic infill (Figure 6f–h).

4 | DISCUSSION

Our results show that there are structural differences between proto-soils that develop under different types of cryptogamic ground cover (CGC) in modern settings. Thalloid liverworts and hornworts form thin, organic-poor proto-soils; upright "leafy" mosses and mixed communities develop thicker, organic-rich proto-soils (Figures 3-5); and lichens form thin laminations of alternating mineralogical and organic material. Further, the proportions of buried organic material increase from thalloids > moss > mixed. The structure of CGC soils does not appear to be affected by geomorphological setting (at least in our examples contrasting volcaniclastic and fine-grained geothermal wetland settings) but rather is largely dependent on the morphological characteristics and growth form of the colonising organism(s) (i.e. appressed versus upright, "leafy"). These findings have important implications for understanding the evolution of soils during the Early Palaeozoic, and potentially before. They indicate that these early proto-soils consisting of thin layers of biologically colonised sediment developed from regolith (and sedimentary detritus derived from hard substrate biological weathering) that were not mature enough in composition, weathering and development to be considered "true" soils, that is soil with well-developed weathering and organic-rich horizons (Figure 7). Our results provide a set of indicators for the recognition of CGC-like fossil proto-soils, which can complement and enhance molecular, phylogenetic and

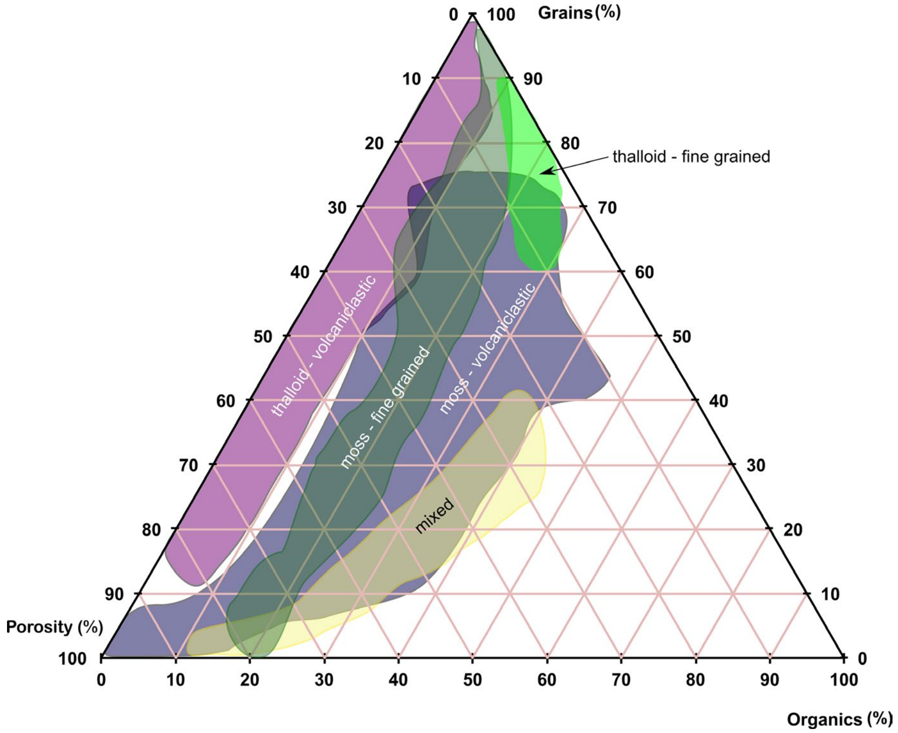

FIGURE 5 Ternary diagram indicating proportion of organics, porosity and grains in 14 CGC soil types (volcaniclastic and geothermal) colonised by different organisms (thalloids, moss and mixed). Labelled fields of different soil types are shown (individual plots found in Appendix S4)

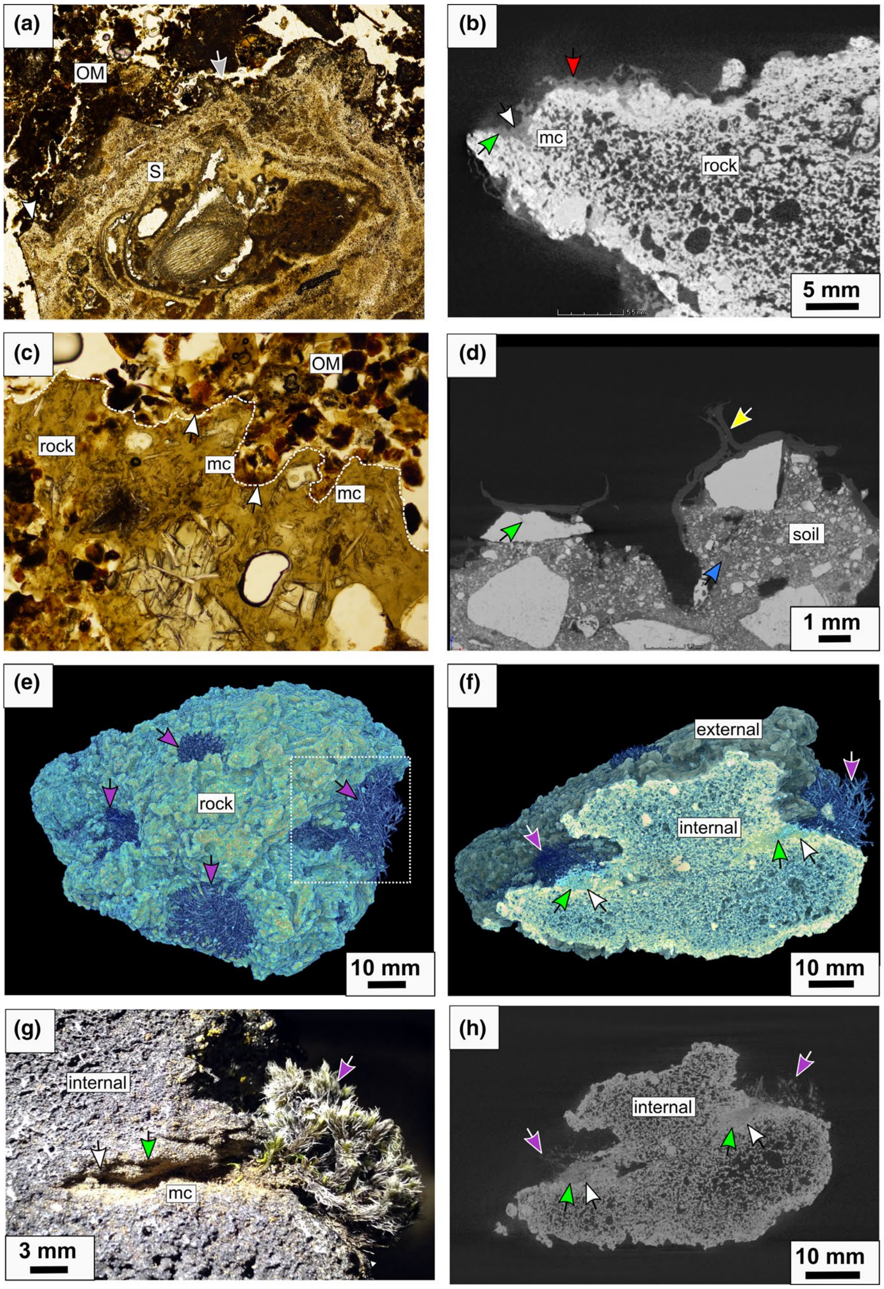

FIGURE 6 Cryptogamic organisms colonising hard surfaces collected via numerous imaging methods. (a, c): Thin section optical microscope images; (b, d–f, h): µCT images; (g): photograph of hand specimen. (a) Draping of organic material over the surface of silica sinter within a geothermal CGC soil. (b) Lichens colonising the surface of a basalt boulder; organic penetration into the rock is highlighted. (c) Organic material accumulation within micro-caverns of a basalt boulder. (d) µCT y-axis view of a CGC soil surface where basaltic soil grains are colonised by liverwort thalli (*Blasia pusilla*) creating stabilised pillar structures. Thallus curling and organic penetration of the grain also seen. (e) External µCT view of a basalt boulder colonised by moss. (f) Slice through the rock in (e), where clear penetration by organic material (moss) is visible. (g) Extent of moss penetration shown in (e) and (f) once the rock had been cut. (h) Greyscale image of µCT slice in (f); rock penetration by moss observed by different greyscale values. White arrow = Organic accumulation in micro-caverns. Grey arrow = draping organic material. Red arrow = lichen thalli on rock surface. Green arrow = Organic penetration. Yellow arrow = Thallus curling. Blue arrow = Pillar structures. Purple arrow = surficial moss colonisation. OM = Organic material. MC = Micro-cavern. S = silica sinter

fossil perspectives on the origin and early evolution of terrestrial ecosystems.

4.1 | Methods, framework and characteristics for recognising CGC proto-soils and interactions in the rock record

We have extended the approach developed in Mitchell et al., 2016 by using X-ray micro-computed tomography (µCT) to investigate the subsurface interactions, diagnostic structural properties and the effect of living organisms on soil development. µCT is a well-established method in "higher" plant–soil science for investigating root architecture (Mairhofer et al., 2015), soil hydraulic properties (Tracy et al., 2015) and porosity (Kravchenko & Guber, 2017). In contrast, it has seldom been applied to analyse CGCs; previous work has focussed on the hydrology of dryland biological soil crusts (Menon et al., 2010) and other studies have applied 2D imaging techniques (OM, SEM) to analyse biological soil crust (CGC) soil structure (Williams et al., 2012). µCT provides a unique perspective for establishing the organism–substrate interactions that govern the structure and thickness of modern CGC soils and hard substrate interactions that potentially illustrate the beginnings of soil development (Figure 7). Furthermore, because it is non-destructive, careful collection of soil can preserve near to in situ field conditions to understand variations in soil structure in multiple axes and orientations. When combined with other imaging and analytical techniques (e.g. SEM, OM) through a correlative approach, µCT allows a more

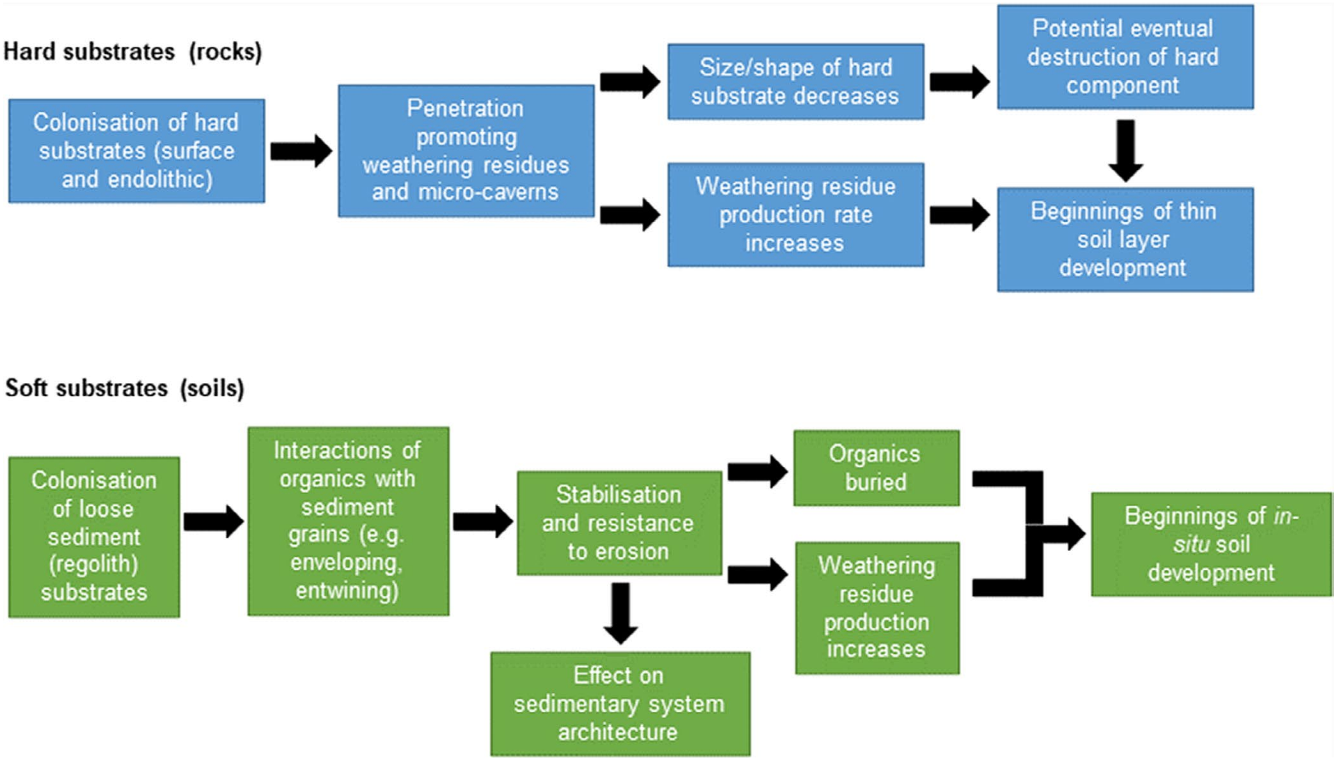

FIGURE 7 Flow charts depicting the effect of biological colonisation on hard and soft substrates, leading to the beginnings of proto-soil development

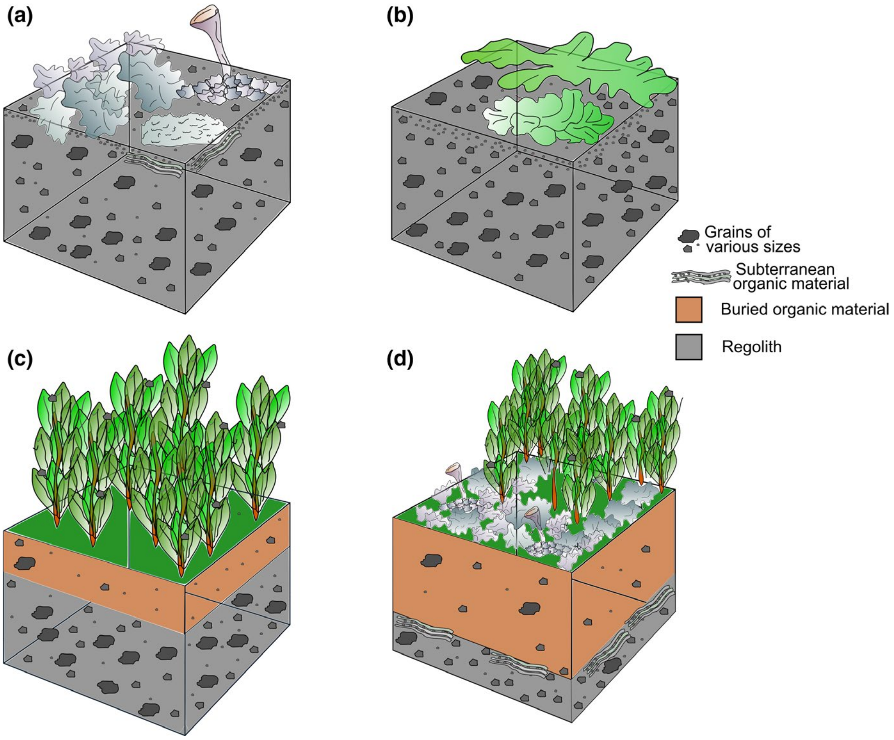

FIGURE 8 Illustrations summarising the key features in modern lichen (a), thalloid plant (b), moss (c), and mixed (d) CGC proto-soils based on μCT, SEM and OM characterisation, which can assist with understanding the developmental stages of CGC-like proto-soils in the geologic past. Not to scale

complete and holistic interpretation across dimensions by combining a range of data types. Our multi-dimensional and multi-modal observations on modern samples provide a new approach to recognising CGC soil types and weathering in the rock record.

Our three categories of plant growth form (thalloid, upright and leafy, mixed) influenced soil structure and thickness (Figure 8). Subterranean microorganisms (e.g. soil dwelling free-living bacteria) probably also have an effect on soil developmental properties and structure through complex interactions (i.e. entwining and sticking) and aggregation of soil grains (Belnap, 2003); these were however undetectable in μCT due to resolution limitations but was discernible to a limited extent in thin section, OM and SEM imaging. The thickness and amount of organic material at the surface and buried within the

“profile” are key characteristics for distinguishing soils formed under thalloid plants and lichens from those that formed under plants with upright and leafy growth forms (Figures 3, 6, 8). Lichens colonising soft sediment develop thin laminations and dome-like undulations that incorporate sediment into their structure (Figures 3, 9); such features have previously been termed “lichen stromatolites” (Klappa, 1979) because of the accretionary similarity to evolutionary ancient microbial stromatolites. Like crustose and foliose lichens, thalloid plants encrust the soil or rock surface with a thin undulating layer of tissue. Because the tissues of liverworts are more cohesive than those of lichens, they are less likely to incorporate sedimentary materials into their structure and to form accretionary structures, highlighting a key interactional difference between the two. Thalloid plants are characterised by thin organic laminations with an accumulation of fine-grained material directly beneath the thallus (Figures 3, 8), likely held in place by rhizoids, and often exhibit diagnostic surface features such as thallus curling and pillar structures. In general, organic content is greater under upright and leafy plants, but soils have the highest organic content when both growth forms are present as mixed CGC soils. Where soils accrete or develop over extended intervals under upright and leafy plants, our results indicate that organic content varies through the profile, likely on a seasonal basis. During active periods of plant growth, organics accumulate more rapidly with respect to aeolian sedimentary input, resulting in a richer organic band in the profile (Figure 3). This information could be useful for understanding the micro-scale developmental history of early leafy and upright soils. In summary, soils that form under CGCs composed of lichens and small thalloid or upright leafy plants exhibit suites of structural characteristics (Figure 8) that could form a basis for their recognition in the rock record.

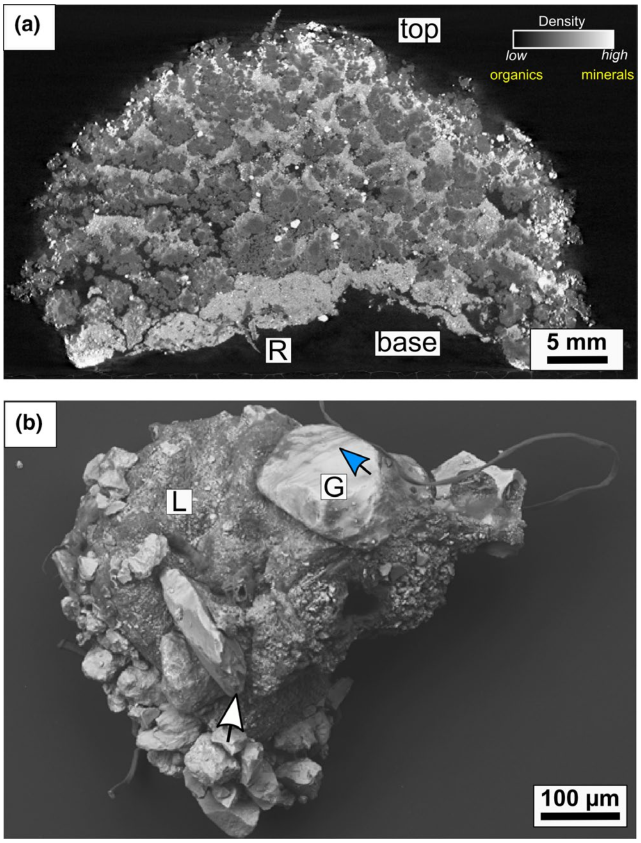

FIGURE 9 Interactions between fruticose lichens and their substrate. (a) μCT slice through the lichen *Stereocaulon* sp. indicating complex (almost stromatolitic) incorporation of mineralogical substrate into the lichen structure. (b) SEM image of a small piece of the same lichen enveloping mineralogical material into its structure. Blue arrow = bacterial filaments holding grain in place, white arrow = denticulated weathering on grain, L = lichen, G = grain, R = lichen rhizome

4.2 | CGC-like evolution and biological drivers of soil development

Results presented here suggest the morphology of the colonising organism(s) in modern CGCs strongly influences soil structure and the proportion of different soil constituents (organics, inorganics, porosity), with increasing thickness and buried organic material from lichen > thalloid plant > upright leafy plant > mixed. This sequence could provide an indication of how primordial proto-soils diversified with the evolution of different CGC-like organisms in the geologic past. However, there is some uncertainty about when various CGC-like communities first appeared, and whether primary succession reflects the order of evolutionary origins (Figure 10).

The most appropriate modern analogue for the earliest primordial land plant systems is thought to be thalloid liverworts where the earliest plants were likely morphologically similar bearing a thallus, rhizoids, and mycorrhizal-like associations with fungi (Edwards & Kenrick, 2015; Strullu-Derrien et al., 2014). The estimated origin from molecular clock analyses of early thalloid plants is ~ 500Ma (Morris et al., 2018; Puttick et al., 2018), whereas the fossil evidence from bryophyte-like cryptospores suggests ~ 470 Ma (mid-Ordovician; Strother et al., 2015; Wellman & Strother, 2015). Direct fossil evidence of probable terrestrial organisms from the Early Silurian (~440 Ma) also indicates thalloid and mat-forming morphologies (Tomescu & Rothwell, 2006). The earliest evidence of the upright leafy growth form of mosses appears very much later during the Carboniferous (~340 Ma, Hübers & Kerp 2012), indicating that the upright, leafy type of CGC-like proto-soils came later. The earliest stem group vascular plants were small, probably less than 10 cm in height, with leafless upright growth and rhizoid-based rooting systems (Edwards et al., 2014). Some uncertainty therefore surrounds the ancestral growth form of land plants. They were most likely leafless with a rhizoid-based rooting system, but whether they were upright or thalloid remains unclear.

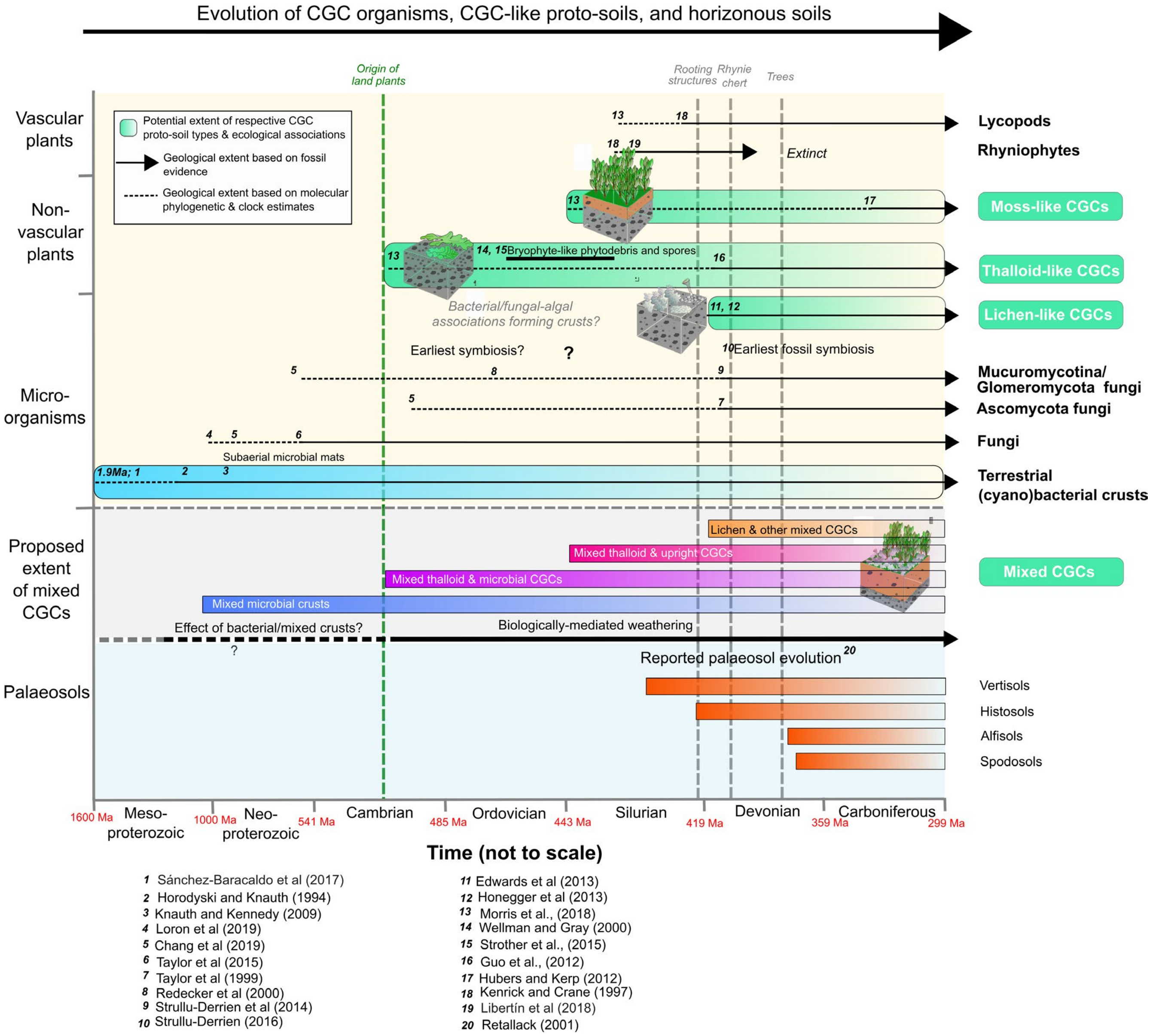

FIGURE 10 The potential extent of CGC-like soils through the geologic past

The evolution of other elements of CGCs is poorly defined. The earliest fossil Ascomycota (Pezizomycotina, the most ancient fungal component in lichens) is from the early Devonian (407 Ma) (Taylor et al., 1999). However, dispersed, Pezizomycotina-like spores appear in the fossil record some 150 million years later in the Mesozoic, suggesting that *P. devonicus* represents an extinct clade of early-diverging Ascomycota (Berbee et al., 2020). There is recent suggestion that fungi were present in the Neoproterozoic (Loron et al., 2019); however, this has been disputed (Berbee et al., 2020). Molecular dating places the first divergences in Mucoromycota (the symbiotic fungi) at 578 Ma (Berbee et al., 2017), and the initial diversification of the Pezizomycotina (Ascomycota) is reported from the Ordovician, around 485 Ma (Beimforde et al., 2014) using the early Devonian Ascomycota for dating the phylogeny. Fossil macrolichens with internal stratification have been described from the Lower Devonian (ca 415 Ma) (Edwards et al., 2013; Honegger et al., 2013); however, evidence of lichens in the early fossil record is scant and controversial, with recent research suggesting that lichens did not emerge prior to the evolution of the vascular plants (Nelsen et al., 2019). Thus, the evolutionary context of fungi and lichens is also unclear.

Because of these uncertainties, the approach outlined here could be developed to provide new insights into the early evolution of terrestrial ecosystems, alongside others that have been outlined before (e.g. Mitchell et al., 2016; Mitchell et al., 2019) . A suitable fossiliferous unit to search for CGC-like soils is the exceptionally preserved 407 Ma Rhynie chert. The Rhynie chert formed in a hot spring geothermal wetland, not dissimilar to those outlined here from Iceland, and is considered the earliest multi-organism CGC-like ecosystem (Edwards et al., 2018; Kenrick et al., 2012). Despite the morphological differences between the Rhynie plants and those in modern CGCs (i.e. mostly upright and leafless versus.

thalloid or leafy; Kenrick et al., 2012), the size of the plants, their below-ground rhizoid-like rooting systems (Kenrick & Strullu-Derrien, 2014) and fungal endosymbiotic associations (Rimington et al., 2015; Strullu-Derrien et al., 2014) suggest that soil forming and weathering processes would have been more similar to communities of encrusting or thalloid organisms than to moss dominated systems.

4.3 | Evolution of "CGC-like" proto-soil types

Biology has an irrefutable impact on weathering and soil development in modern environments; it is postulated that it did so also in the geologic past (Porada et al., 2014), fundamentally influencing biogeochemical cycles and the sedimentary environment (Gibling & Davies, 2012; Lenton et al., 2012, 2018). We propose that there may have been a stepwise evolution of different CGC-like proto-soil types concurrent with the evolution of different biological elements in the earliest terrestrial biotas. These proto-soils likely exhibited specific morphological, structural and sedimentological features as different organisms evolved and colonised land surfaces through the Palaeozoic (Figures 3, 7, 10), "filling the gap" between the microbial proto-soils of the Proterozoic and vascular plant "rooted" horizonous soils of the later Phanerozoic (Strullu-Derrien et al., 2018).

Palaeosols (fossil soils) are described for most of the rock record (Retallack, 2001); however, understanding the drivers of soil development and weathering in units pre-dating the earliest land plants, when evidence of extensive terrestrial biospheres is limited (Wellman & Strother, 2015), is problematic. Archaean (e.g. Nedachi et al., 2005) and Proterozoic palaeosols (e.g. Mitchell & Sheldon, 2009) differ from modern soils in being generally poorly developed and lack distinctive weathering horizons, and it is unclear how much of their development is due directly to biological influences when fossil/biogeochemical evidence of sediment-dwelling communities is lacking. Before the evolution of extensive CGC-like biospheres, surface weathering and palaeosol development in some part could have been driven by subsurface and endolithic microbial content, but would likely also have been strongly influenced by abiotic processes. Elevated atmospheric CO_2 levels in the Precambrian (up to 1000x present atmospheric levels in the Archean; Kasting, 1993) may have promoted mineral weathering through aggressive hydrolysis chemical reactions (Mitchell & Sheldon, 2016), promoting soil-like surface weathering, mineral etching of regolith, and eventual destruction of minerals. Indeed, abiotic mineral weathering under simulated Precambrian atmospheric conditions of 10% CO_2 has been achieved in the laboratory (Fabre et al., 2011); however without a biosphere for stabilisation, it is likely that exposed sedimentary surfaces were quickly eroded before "deep" weathering profiles could develop. Biologically mediated weathering likely originated with cyanobacterial mats and microbialites moving into the terrestrial realm in the Mesoproterozoic (Horodyski & Knauth, 1994; Mitchell & Sheldon, 2016). Thin cyanobacterial crusts may have stabilised regolith surfaces while weathering was promoted by below-ground respiration and accumulation of $CO_{2,}$ and percolation of high CO_2 rainwater, leading to mineral attack and hydrolysis reactions, with biological exudates from mats promoting weathering further (Gadd, 2010), forming the first biologically mediated proto-soils. It is possible that established cyanobacterial crusts formed symbiotic relationships with fungi giving rise to lichen-like associations during the Neoproterozoic and Cambrian (Figure 10) forming lichen-like structures in sediments and on hard substrates, although a recent phylogenetic study casts doubt on this hypothesis (Nelsen et al., 2019).

We propose that the proto-soils associated with the earliest plants would probably have resembled those forming under thalloid liverworts today, as in our examples from Iceland (Figures 3, 9). Generally, they would have been thin, a few centimetres in depth, with an organic-rich surface layer overlying a relatively organic-poor regolith comprising a mixture of clasts and finer grained matrix. Based on a combined molecular clock and fossil evidence, we would anticipate proto-soils of this type forming by the Mid-Ordovician (Wellman & Gray, 2000), possibly earlier during the Cambrian (Morris et al., 2018; Puttick et al., 2018). The evolution of rhizoid-like rooting/anchoring systems, and the ability to form symbiotic associations with fungi in the earliest land plants (Strullu-Derrien et al., 2015) likely had a considerable impact on proto-soil initiation, development and weathering (Field et al., 2012) through intricate plant–soil interactions (Mitchell et al., 2019), which also promoted soil clay development (Mitchell et al., 2016) and the stabilisation of sedimentary surfaces (Davies & Gibling, 2010; McMahon & Davies, 2018). It is however unlikely that the primordial symbiotic networks associated with early land plants could penetrate proto-soils on a decimetre-to-metre scale as proposed by other studies (Retallack, 2015) (Figure 3). Deeply penetrating rhizomes and true rooting systems began to appear during the Devonian, leading to much larger plants and trees, the development of forest ecosystems, and palaeosols with deep horizonation by the Middle to Upper Devonian (Berry & Marshall, 2015).

It is likely that an assortment of CGC-like proto-soil types were present by 407 Ma when the Rhynie chert geothermal wetland was in existence (Figure 10). Although caliche and vertisol-type palaeosols have been identified in fluvial units surrounding the geothermal chert beds (Trewin & Rice, 1992), soil profiles are reported as poorly developed, probably due to rapid deposition and erosion from frequent flooding events (Trewin & Rice, 1992). No palaeosols are found associated with in situ surface plant growth in this fossiliferous unit. Our findings on the structure of modern geothermal CGC soils (Figures 3-4) provides a fresh perspective on the potential structure of the Rhynie proto-soils upon which plants may have been growing on solid (regolith) ground; these were likely less than 10 cm thick, contained layered organics and subsurface bacterial communities (Figure 4). Future studies that aim to identify CGC-like proto-soils in sedimentary units associated with the Rhynie chert beds, and other units of known age and terrestrial origin (e.g. the Old Red Sandstone). We propose a need to adjust the search to focus on structures of much smaller scale than what is typically associated with palaeosols in the rock record.

5 | CONCLUSIONS

By studying modern cryptogamic ground covers (CGCs) as analogues of the earliest terrestrial biospheres, it is possible to understand the influence that ancient organisms may have had on the initiation of soils and their structural development. It is likely that (a) analogous CGC-like organisms in the geologic past formed thin (mms to 10s of cm) proto-soils rather than thick horizonous profiles, (b) the earliest thalloid organisms contributed to limited organic carbon burial which increased with more evolved, upright and leafy forms later in the Palaeozoic and (c) by understanding the evolution of different plants and organisms (i.e. lichens), it might be possible to predict when specific CGC-like proto-soil types have evolved. We hope that the soil forming features outlined here, that is alternating stromatolite-like mineralogical and organic layers in lichens, thin organic layers in thalloid-bearing plants, the thickness of surface and buried organic material, may prove useful in identifying CGC-like proto-soils in the fossil/sedimentological record. Identification of CGC-like proto-soils in time periods where the establishment of different terrestrial organisms is unclear (i.e. pre-Ordovician—Neoproterozoic) would allow us to unravel how primordial biospheres affected biologically mediated soil development and biogeochemistry through time. Further work should aim to apply this method to more fossil/sedimentological units in evolutionary critical time periods of terrestrialisation.

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ORCID

Ria L. Mitchell https://orcid.org/0000-0002-6328-3998

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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