ELSEVIER

Invasion of the continents: cyanobacterial crusts to tree-inhabiting arthropods

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The colonization of continental environments (land and fresh water) has focused historically on a major event during the mid-Paleozoic Era characterized by the relatively sudden emergence of megascopic embryophytes, fungi, arthropods and tetrapods. A significant earlier phase of Precambrian (Archean and Proterozoic Eons) terrestrialization extends to the first 80% of the history of life and records the colonization of subaerial soils or rock surfaces predominantly by cyanobacterial mats and crusts. These two phases are separated by a ~90-million-year early Paleozoic interlude of minimal terrestrial colonization. Trophically modern ecosystems appeared during the Late Silurian–Middle Devonian (425–375 million years ago), consisting of complex symbiotic, parasitic and other trophic associations, including detritivory and limited herbivory. The integration of these two historically disparate fields (Precambrian microorganisms and their biochemical and sedimentological signatures, and the paleoecology of mid-Paleozoic ecosystems) has resulted in a wider perspective on terrestrialization. Here, I present an ecological and evolutionary context for the emergence of terrestrial ecosystems and examine associations among organisms, from the endosymbiotic capture of organelles by eukaryotes to modes of metazoan nutrition on land. Such studies now enable the tracking, in ecological detail, of the invasion of continental environments during the past 3.5 billion years of life.

The colonization of the non-marine environment represents the greatest expansion of species-level diversity in the history of life, with vascular plants and insects alone representing ~71% of all extant species [1]. How is this ecological and taxonomic diversification documented in the historical record? What types of new evidence and approaches have been used to understand this transforming event in the history of life? Here, I address these pressing questions by discussing a broad spectrum of geological, paleobiological and biological data and provide a multidisciplinary overview of the invasion of continents by living organisms.

The greening of land and fresh water involves vast scales at several levels. The relevant portion of the

sedimentary rock record that contains biogenic strata includes most of the geochronological time of Earth, possibly extending back ~3.83 billion years (Ga) [2]. Also the full compass of life will have been involved, as all major lineages have produced at some point at least a few representatives that inhabit past and/or present continental space [3]. Last, the numerous inter-relationships of these organisms to each other and to their environment are crucial to our understanding of the origin of continental ecosystems. Recent developments in the study of continental invasions include new geochemical techniques for examining biogenic organic compounds in Precambrian sedimentary rocks [4], rapidly evolving phylogenetic techniques for investigating the genomes of the most ancient microorganismic lineages that have colonized the continents [5], finer grained examination of the continental trace-fossil record of the earlier Paleozoic [6], and the multidisciplinary and increasingly detailed study of mid-Paleozoic macroorganismic colonization of the continents [7]. This last event has provided the ecological infrastructure for extant land and freshwater ecology.

Four major events leading to continental life
The fossil record and the phylogenetic relationships among organisms show four major events that have led to the emergence of continental life (Here, I define 'continental' as constituting subaerial land and aquatic freshwater environments, and 'terrestrialization' as the process by which the colonization of these habitats is achieved; see Glossary.)

Origin of life
First and foremost is the origin of life itself, originally thought to have occurred in a semiprotected shallow marine pool, bombarded by intense radiation or possibly local energy sources [8], but now considered by some to have occurred in a deeper water hydrothermal vent environment [9], for which there now is some fossil evidence from 3.32 Ga [10]. Older geochemical data from layered, partially oxidized sedimentary rocks, known as banded iron formations, provide indirect geochemical evidence for life minimally at 3.83 Ga [2]. This date probably represents the earliest known evidence for an autotrophically based, prokaryotic and archaean microbiota.

Life on earth has always been overwhelmingly trophically based on prokaryotes [4]. For example, the first 80%

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Glossary

Archaea: a domain of prokaryotic microorganisms, including methanogenic, extremely halophilic and some thermal- and acid-resistant bacteria, that is genetically distinct from all other prokaryotes; not to be confused with the Archean Eon, which is an interval of Precambrian time.

Autotroph: an organism that uses carbon dioxide as its principal or sole source of carbon; includes photoautotrophs (light is the principal energy source) and chemoautotrophs (energy is provided by the oxidation of inorganic compounds).

Arbuscular mycorrhizae: a type of mycorrhizae in which the fungal mycelium only exhibits minute tufted processes (arbuscules), rather than vesicles, which then grow into host-plant cells.

Bacteria: microorganisms with a prokaryotic cellular organization.

Biomarker: a distinctive set of geochemical compounds, typically degradative organic structures, occurring within a narrow stratigraphic interval that indicates the former presence of a particular type of life, such as eukaryotes.

Continental: inclusive of land (subaerial) and freshwater (aquatic) environments; contrasted with 'marine'. This designation lacks the confusion frequently implied in 'terrestrial', which might or might not include freshwater environments.

Coprolite: a fossilized fecal pellet, typically of an arthropod or a vertebrate.

Cyanobacteria: prokaryotic, bacterium-like microorganisms containing phycocyanin and other pigments (not chlorophyll *b*), and capable of oxygen-producing photosynthesis.

Embryophyte: a clade of green plants defined primarily by the gametophyte–sporophyte life cycle, multicellular sporophytes, distinctive cuticle, and reproductive organs organized into archegonia and antheridia, among other features; also referred to as 'land plants' by some.

Heterotroph: an organism using organic compounds as its source of carbon; includes holozoic animals, parasites and saprophytes.

Lichen: a large group of organisms that comprise a symbiotic association between a cyanobacterium or alga and a fungus, and are classified by the affinities of the fungal symbiont.

Microbiota: a local group of microscopic organisms used especially in reference to communities of fossil microorganisms that occur within a stromatolite.

Mycoparasitism: a form of symbiosis in which one symbiont is a fungal parasite and receives a typically nutritional advantage to the detriment of its host.

Mycorrhizae: an association of a fungal mycelium with the roots of a higher plant.

Paleosols: a fossilized soil horizon, recognizable by sedimentological, geochemical and biological features.

Precambrian: an informal designation for the time interval before the base of the Cambrian Period of the Paleozoic. It includes, from youngest to oldest, the Proterozoic, Archean and Hadean Eons.

Sauropsid: a clade of early vertebrates characterized by a skull with two temporal openings and representing the ancestors of reptiles and birds.

Stromatolites: a megascopic, accretionary structure of finely layered sedimentary and organic material that is bound by the mat-building activities of mucilage-secreting microorganisms, such as cyanobacteria.

Synapsid: a major clade of tetrapods characterized by a skull with a single temporal opening, and representing the progenitors to the mammals.

Terrestrialization: the process by which a marine group or clade of organisms acquires the adaptations necessary to inhabit the land or fresh water of a continental environment.

Vesicular arbuscular mycorrhizae: a type of mycorrhizae in which the fungus is a glomeromycotan and the roots of the plant host do not show morphological peculiarities; the hyphae bear globular swellings (vesicles) and minute processes (arbuscules), which grow into the host cells.

Box 1. A brief history of continental organisms

Figure Ia details the history and phylogeny of major continental clades of organisms before the Early Carboniferous at 359 Mya. Phylogenetic data are summarized in [3], to which additional data have been added, including the relationships of microorganisms [5,75,76], invertebrates [77], fungi [78,79], embryophytes [7] and vertebrates [70]. Continental clades were determined by the author variously by: (i) a preponderance of species that are currently living on land or freshwater; (ii) those that have origins or basal clade synapomorphies that are tied to a significant non-marine existence; (iii) having a predominantly non-marine fossil record; (iv) occurrence principally on continental hosts if the terrestrialized clade is parasitic; or (v) combinations of the above. Many early microorganismic dates are not supported by Precambrian (Archean+Proterozoic) fossils, although the Cyanobacteria and Archaea are; additionally, dates from molecular clock estimates often are often overestimated based on estimates of calibration points and divergence nodes that lack statistical error as well as methodological biases [50,80,81]. The phylogeny in Figure Ia does not depict extensive lateral transfer of genes among groups and subgroups; such reticulate evolution was significant during the Precambrian [5,75,76,82], and explains the absence consensus among comparisons of trees from different gene systems [82]. Some marine clades are omitted at the level of this phylogenetic analysis. For archaeans and eukaryotes, marine clades are dotted lines, freshwater clades are dashed lines, and land-based clades are thick solid lines. Four terrestrialization phases are detailed in Figure Ia, indicated by the fossil record, phylogenetic relationships and ecological roles in past and present ecosystems. There is a change of scale at the Proterozoic–Paleozoic boundary.

Figure Ib details important environmental events and organismic occurrences that occurred before the Paleozoic, and is pegged to the same scale as Figure Ia. Panels of columns from left to right are: (i) an inferred secular trend for atmospheric oxygen levels [15] (PAL, present atmospheric level of 21%); (ii) sedimentological and biological features of fossil soils that indicate a subaerial microbiotal existence [21,23,27]; (iii) important milestones in the history of continental microbial life from data such as the presence of eukaryotic biomarkers, geochemical signatures and important microfossil occurrences [22,24,25]; (iv), the temporal distribution of some stromatolites, including cyanobacterial crusts on soil or rock surfaces older than 1.2 Ga [10,15,19,20,23,83–85]; and (v) global geochemical, sedimentological and atmospheric indicators [25,86] (BIFs, banded iron formations, indicating oxygenating atmospheric conditions). General abbreviations for Figure Ia: A, the microorganismic domain Archaea, Eo., Eoarchean; Ga, billion years; Ma, million years; Meso., Mesoarchean; Mesoprot., Mesoproterozoic; Neo., Neoarchean; Neoprot., Neoproterozoic; Paleo., Paleoarchean.

Endosymbiosis

The second major event was the incorporation of an aerobically respiring bacterium into a recipient of an early eukaryotic stock to form a eukaryotic cell with a mitochondrion [11,12]. This event provided the means for aerobic respiration and the emergence of a new, efficient cohort of heterotrophic microorganisms coupled with a transformation of the nuclear region and the origin of sexual means for reproduction. Eventually, some members of this more advanced eukaryotic stock captured several bacterial lineages of photosynthesizing cyanobacteria, some singly and others iteratively [13]. These incorporations produced a second biochemical powerhouse, the plastid, which defines photosynthesizing eukaryotes [14]. These lateral transfers of mitochondria and plastids were a prelude for the subsequent invasions of the continents by photosynthesizing, saprobic and heterotrophic eukaryotes. The earliest fossil eukaryotes have been determined by biomarkers that represent

of the history of life was dominated by Precambrian chemosynthetic and photosynthetic prokaryotes (Box 1), of which oxygen-producing cyanobacteria had a leading role. These microbiotas principally consisted of thinly layered cyanobacterial colonies of single cells and filaments, occurring as mats or crusts in a variety of marine and eventually continental habitats, known as stromatolites, and are perhaps the most important organismic group that affected the future course of life. Cyanobacteria were initially responsible for the accumulation of atmospheric oxygen that propelled much of the aerobic metabolism of eukaryotes, which have fossil representatives dated ~1.75 Ga.

Figure I.

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unique chemical signatures and the presence of larger cell sizes than those of prokaryotes [15].

Multicellularity

After the emergence of eukaryotic life, the third major event was the origin of multicellularity during the Late Proterozoic ($\sim$0.8 Ga), and its subsequent diversification (Box 1). In marine habitats, the first major manifestation was the Ediacaran fauna, which typically inhabited sandy, shallow marine substrates and whose body plans are bizarre by current invertebrate standards [16]. This was followed by another independent proliferation of multicellular life immediately before the Proterozoic–Paleozoic boundary at 0.542 Ga and continuing into the Cambrian Period of the earliest Paleozoic. This event is exemplified by the Burgess Fauna of the early Middle Cambrian, replicated in several other recently discovered and earlier Cambrian deposits [17]. For these macroorganisms, multicellularity required cohesion and coordination among cells that allowed for differentiation into specialized functions that became crucial in subaerial environments, including the presence of a protective envelope to ward off thermal and osmotic stress, formation of a self-contained oral and digestive tube for consumption and processing of food, and the delivery of sperm and eggs to specific areas for fertilization that are outside the diluting influence of fluid media.

Colonization of continental environments by macroscopic organisms

Equally profound has been the fourth major event, the expansion of life from the marine realm onto land and into freshwater habitats along the interiors of coastlines. Although this colonization had a significant Precambrian prelude, it was ratcheted up by diminutive macroscopic organisms during the Late Ordovician, and continued with the appearance of woodland-like communities of trees and associated organisms during the Late Devonian. The basic ecosystem structure of major trophic roles and feeding groups qualitatively has not changed dramatically since the Devonian [18].

Subaerial crusts, mats and paleosols during the Archean and Proterozoic Eons

Beginning in the older Archean Era, during deposition of the oldest sedimentary deposits and microbiotas currently known, there is indirect evidence for prokaryotic life on land. Although the evidence for life $\sim$3.83 Ga is controversial [2,10,19], several pre-3.0 Ga occurrences are accepted based on geochemical, biomarker and microfossil data [10,19]. The earlier of the more compelling studies are in rock types that are interpreted as being deeper water marine hydrothermal vents that harbored chemoautotrophic bacterial communities that are analogous to those of today [20]. Other deposits represent stromatolitic mats that occurred within the zone of light penetration but often above the depth of wave action [15]. The earliest Archean and Proterozoic microbiotas assigned to a land-derived deposit (Figure 1) have sedimentary structures that are reminiscent of soil-surface cyanobacterial crusts;

they occur on consolidated sediments, rock surfaces and limestone karsts of several continents [21–24].

Determining the subaerial nature of these deposits and their microbiotas is essential for establishing the presence of life on land. Such evaluations are based not only on sedimentary structures that are recognizable as subaerial paleosols (fossil soils) [23], but also on carbon isotopic data in which values containing the lighter isotope of carbon, ^{12}C, are known to be preferentially fractionated by photosynthesizing organisms [19,25], and thus indicate a biological rather than physical origin [26]. Such carbon isotope analyses, as well as the vertical profile of trace elements, have been done on a variety of Precambrian paleosols, and indicate a continental rather than marine origin [21,24,27]. Based on many of the above studies and in the absence of any evidence indicating colonization of upland environments, Precambrian microbiotas were probably limited to zones inland of the shoreline, which persisted throughout the Proterozoic and possibly into the early Paleozoic [28]. It is possible that cyanobacteria-dominated communities occurred in more extreme continental sites, analogous to extant desert crusts [29], but such upland environments are rarely preserved in the stratigraphic record. However, evidence for the presence of subaerial microbial crusts or algal vegetation is scarce throughout the entire fossil record, especially for the Cambrian–mid-Ordovician.

The continental nature of these Precambrian microbial communities should be qualified. For those stromatolites, laminated algal or bacterial structures that bind and trap fine-grained sediment and which occur in the intertidal range, there is periodic exposure to marine waters (a 'splash zone'). Although such environments are extreme in many ways, and are subject to high levels of desiccation, temperature variation and alternating periods of extensive subaerial exposure and shorter periods of submergence, they are not truly continental because stromatolites initially required a marine environment for growth [19]. However, mat-like freshwater versions of such 'microcommunities' probably existed during this time [19]. Other similar Precambrian structures might have occurred outside the reach of tidal influence, such as soil crusts, which represent continental, subaerial ecological associations, analogous to lichens that evolved later on rock, soil and wood. It is noteworthy that 1.43-Ga shallow benthic fossils from Canada, up to 0.5 mm long, exhibit features that are assignable to the sister-group of higher fungi [12]. Unlike the episode of invertebrate herbivory that befell typically marine stromatolites during the latest Proterozoic [4], terrestrialized crusts and mats might have existed throughout most of the Archean and Proterozoic Eons, during which land animals were absent or rare and before the appearance of plant-feeding terrestrial arthropods during the mid Paleozoic [18].

Was there colonization of land during the Cambrian and earlier Ordovician?

One anomaly in the history of terrestrialization is the sparse evidence for the colonization of land during the Cambrian–mid-Ordovician interval. Documentation is absent for Precambrian-style microbial communities
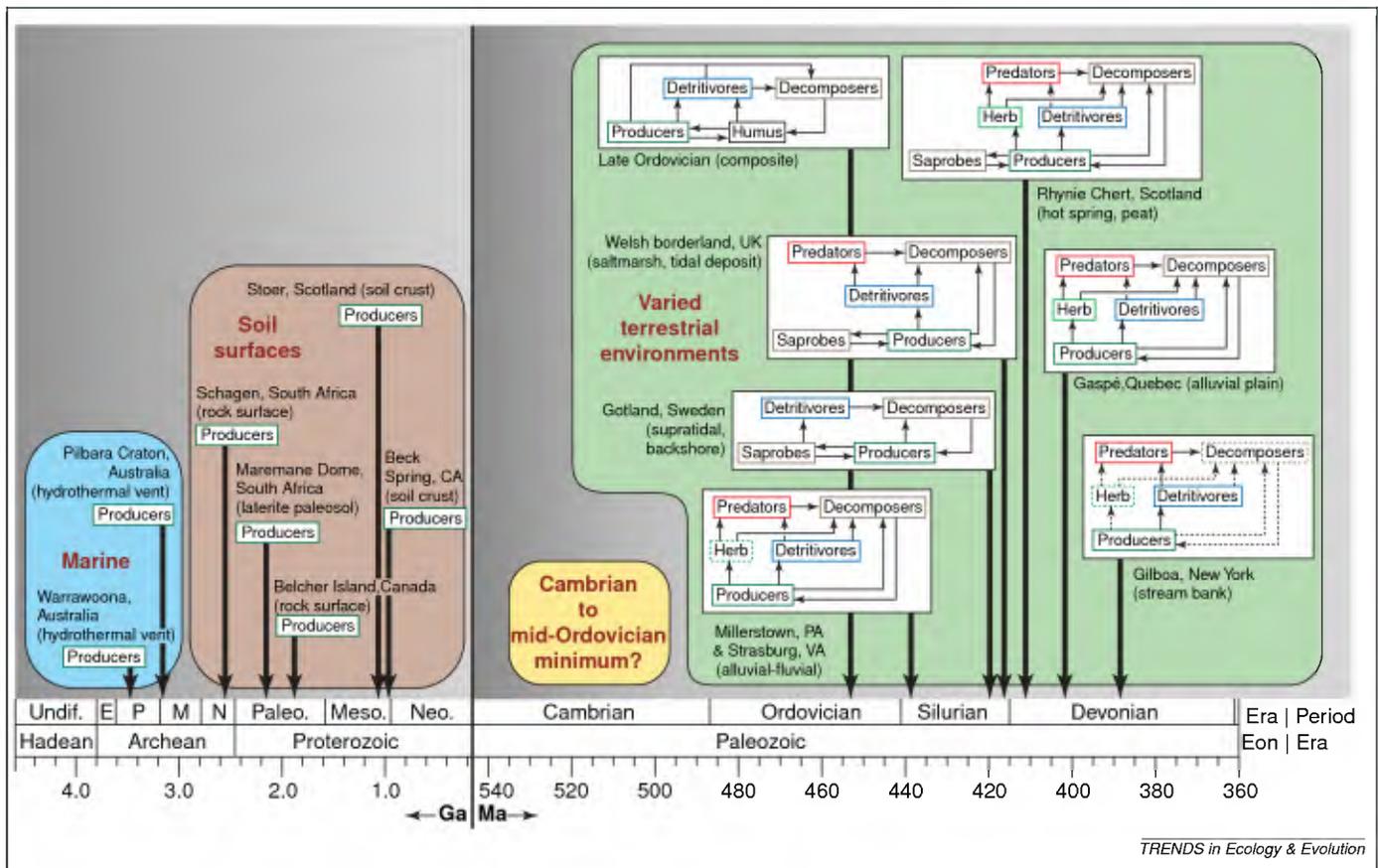
Figure 1. The fossil history of continental food webs before the Early Carboniferous (359 Mya). For the Archean and Proterozoic Eons, several data sources were used to establish the presence of earlier marine stromatolitic and older microbial crusts on paleosols and other subaerial substrates [10,15,20,21,23,24,27,84], and possibly freshwater environments [19]. There is a major change of scale at the Paleozoic–Proterozoic Era boundary. For the Paleozoic Era, little is known of the fossil history from the Cambrian to the mid-Ordovician (see text). All data are from the paleocontinent of Euramerica. The mid-Ordovician evidence is based on spores, phytodebris, and limited macroscopic vegetative tissues, organs and whole organisms for continental biotas, as well as associational evidence [7,18,28,54,59,62,64,66,91]. Abbreviations: E., Eoarchean; Ga, billion years; M., Mesoarchean; Ma, million years; Meso., Mesoproterozoic; N., Neoarchean; Neo., Neoproterozoic; P., Paleoarchean; Paleo., Paleoproterozoic; undiff., undifferentiated.

occurring on land that could represent a continuation from the Late Proterozoic. However, the presence of such communities today might indicate a lack of fossil discovery for the early Paleozoic. Shallow marine stromatolites, however, are present during the Cambrian, as are other microbial associations, some of which form leathery to hardened, laminated crusts in intertidal and supertidal deposits. These lithified mats become fragmented and redeposited by wave action to produce the characteristic flat-pebble conglomerates seen in many Cambrian strata [30]. Nevertheless, there is evidence for primitive, diminutive embryophyte floras that appear as early as Middle Cambrian [31]. (Embryophytes are defined by the key synapomorphy of an alternation of a sporophyte generation that produces spores sexually with a gametophyte generation that produces gametes asexually.)

Evidence has been presented for the existence of rare 'enigmatic' arthropods in questionably non-marine habitats from the early Paleozoic [28]. In two of the more promising sites, from the Early Cambrian of Siberia, Russia [32] and the mid Ordovician of Tennessee, USA [33], it is unclear whether these strata were deposited under freshwater conditions, and it is even less clear whether the entombed arthropods are local or transported from a marine environment [28]. Continental body fossils

have not been identified for the Paleozoic before the mid Ordovician [34]. A few rare occurrences of trackways made by sizable arthropods [35,36] were more amphibious than truly continental and might be analogous subaerial tracks produced by horseshoe-crab mating swarms.

A 90-million-year absence separates the Precambrian microbial phase of terrestrialization from the more-structured ecosystems of plants, fungi, arthropods and eventually vertebrates that occurred during the Late Ordovician–Late Devonian. It is during Late Devonian that the two major megaclades containing continental invertebrates were launched: the lophotrochozoans and the ecdysozoans. These clades each contain several phyla and were major participants in the Cambrian explosion [16], as were a few basal lineages of the Deuterostomia, a third major clade, whose primary diversification occurred later during the mid-Paleozoic (Box 1). The Lophotrochozoa are defined by having primitively a trochophore or derivative larva, whereas the Ecdysozoa is a clade of molting animals unified by having a chitin-bearing skeleton [37,38], which is considered as an exaptation for a continental existence (Box 2). For the lophotrochozoans, major terrestrialized taxa are gastropod and bivalve mollusks, oligochaete annelids, rotifers and, to a lesser extent nemerteans, platyhelminths and acanthocephalans; by

Box 2. Dramatic habitat shifts among early ecdysozoan phyla and the Acanthocephala

Figure I shows a transformation of habitat occupied by three ecdysozoan lineages and the Acanthocephala, conventionally treated as phyla, during the early Paleozoic to the present day. These clades occupied shallow marine habitats during the Cambrian–Middle Ordovician. During the later Paleozoic or possibly Mesozoic, descendant taxa became continental, either as predators in the case of Onychophora and Tardigrada, or as internal parasites in the respiratory or digestive tracts of land tetrapods, exemplified by the Pentastoma and Acanthocephala [87]. These clades not only currently occupy continental habitats, but are also taxonomically depauperate, and probably have always been so, with extant diversities ranging from one- to several

hundred species, depending on the clade. Three have a basal phylogenetic position within the Arthropoda ([87], also see [88]).

Although there is some debate as to whether Cambrian lobopodan taxa such as *Aysheaia* are truly onychophorans, they do represent members of a more inclusive lobopodan clade [39]. The non-arthropodan Acanthocephala also are thought to have originated during the Cambrian as marine acoelmate organisms [39], and made the shift to continental parasitism. Myriapodan arthropods might be a fifth clade representing such a transition [89], if the identification of a purported Middle Cambrian marine uniramous arthropod [90] turns out to be a myriapod.
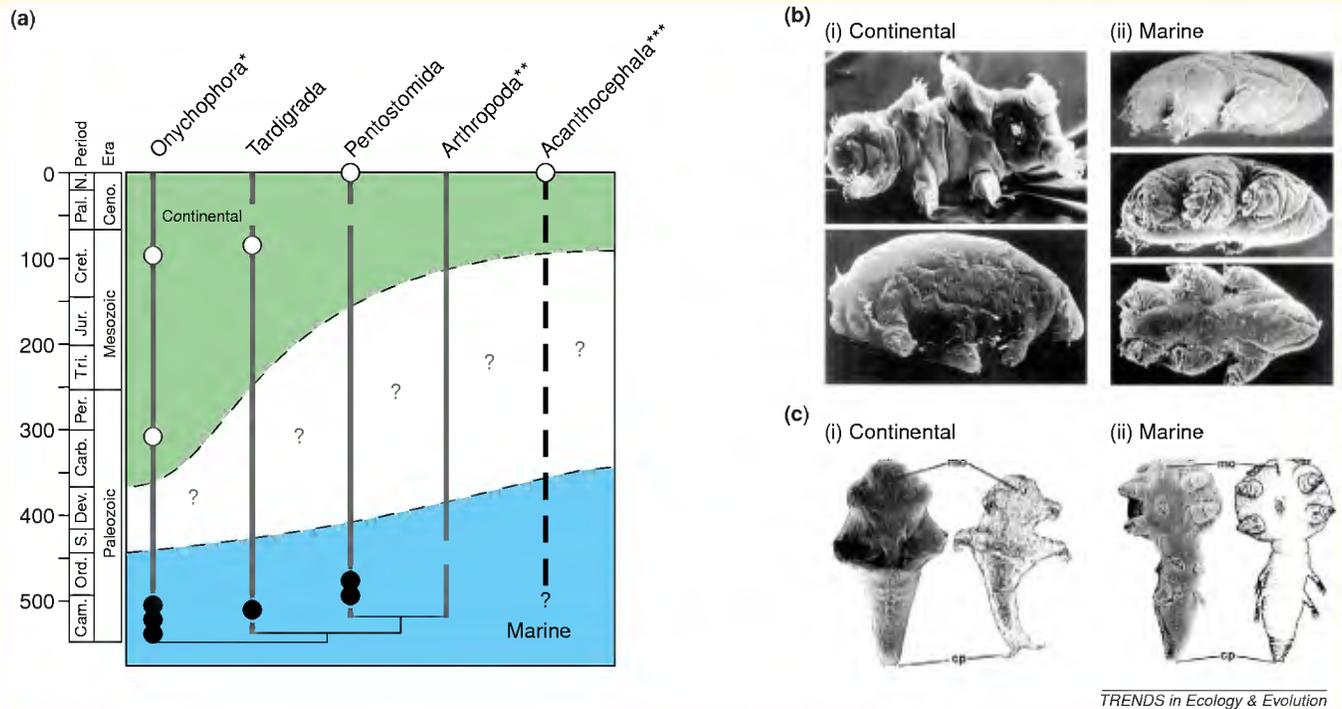

Figure I. Marine–continental shifts in major invertebrate clades from the early Paleozoic to the present day. Solid dots represent marine and open dots continental occurrences. (a) Phylogeny of basal arthropodized clades and their subsequent distribution in the fossil record (*, includes lobopods, assignable to a more inclusive clade; **, numerous occurrences throughout the Paleozoic; ***, no fossil record available). (b) SEM micrographs of extant (i) and Middle Cambrian (ii) adult tardigrades. (c) SEM micrographs of extant (i) and Upper Cambrian (ii) larval pentastomids; numbers refer to segment appendages. Abbreviations: cp, caudal papillae; mo, mouth. (b,c) reproduced, with permission, from [87].

contrast, ecdysozoans are the dominant continental clade of animals, and include prominently the hyperdiverse arthropods and nematodes, and the less diverse onychophorans, tardigrades, pentastomes, nematomorphs and gastrotrichs [39].

Continental ecological ensembles of the mid Paleozoic

Trilete spores and cryptospores that include spore tetrads are known from fluvial deposits of the Middle Cambrian of Australia, indicating the probable presence of bryophytic-grade embryophytes [31]. The first significant evidence of embryophytes occupying land is from the Middle Ordovician [7,34,40] in the form of palynomorphs. These encompass varied and small cuticular fragments that have been termed 'phytodebris', which also include fungal and arthropod remains [41]. This limited material of plants, fungi and arthropods consists of small cuticular and other tissue fragments, frequently anatomically preserved, that result from chemical digestion of rock

material and the trapping of microfossil fragments by sieves [28,41].

Molecularly based phylogenetic analyses and studies of the cell-wall microstructure of embryophytes and related algal clades indicate that charophytes, a green algal clade, are the closest extant relatives of embryophytes [40,42,43] (Box 1). Depending on the study, any of three major bryophyte lineages (liverworts, hornworts or mosses) might be the sister group to vascular plants [40,44–47], consistent with the view that bryophytes are a grade rather than a clade [47]. After bryophyte establishment, one to a few extinct groups of protracheophytes diverged [7], one of which gave rise to a monophyletic vascular-plant clade defined by robust synapomorphies [45]. Although the embryophyte clade probably originated during the Middle Ordovician [40,48], it is later, during the Devonian, that fossil evidence indicates the presence of liverworts and mosses [7], even though the earliest occurrence of vascular plants is Mid–Late Silurian [7,49].

This incomplete but important record is consistent with molecular estimates for the timing of major cladogenetic events of relevant extant clades [50,51], although such dates should be nuanced regarding precision (Box 1). Subsequently, during the Late Silurian, the vascular plant clade split into three lineages, namely the rhyniophytes (whose appearance is delayed until the Early Devonian), lycopods, and a Euphyllophytina clade, defined by a suite of vegetative characters involving shoot geometry, branching type and vascular structure, among others [7].

The Euphyllophytina, which includes the Devonian *Psilophyton*, underwent cladogenesis during the Middle–Late Devonian to yield the fern-plus-sphenopsid and seed-plant clades [7,52]. During this formative interval, the typical stature of plants varied from prostrate to erect herbaceous plants ranging from a few cm to 2-m tall during the Early Devonian, to woodland-inhabiting trees up to 25-m tall and anchored by robust rooting systems emerging from a shoot up to 1 m in diameter by the end of the period. At this time, most major plant tissue types had originated [53], and anatomical innovations such as leaves, seeds and wood were established in several clades of vascular plants [54–56].

Perhaps the most relevant, earliest continental biotas are two Early Silurian (Llandovery) sites from the eastern Appalachian Mountains: the Tuscarora Formation near Millerstown, Pennsylvania [28], and the Massanutten Sandstone near Strasburg, Virginia [57]. These are combined in Figure 1 because of similar ages, environments, and locations as well as shared taxa. Present in this alluvial–fluvial environment are plant autotrophs, decomposers and predators, which represent one of the first diverse continental communities, although the complete ensemble of the components of this ecosystem is not present in either of the two strata or sites [28,57]; thus, this environment is a composite assemblage. Fossil plants from this deposit represent a grade of organization that is transitional between the relatively unspecialized tissues of some algae and the specialized water- and nutrient-conducting cell types and associated supportive tissues of vascular plants [28], features which also occur in some early land-plant clades discussed above. Animal remains closely resemble continental arthropods [28], and include fragmentary appendages of chitin, tracheae-bearing tubes and ornamented sclerites. Glomeromycotan spores are also found, which have been assigned to a fungal clade. These spores were essential for the establishment of plants in early continental habitats through symbioses such as mycorrhizae, which are important for absorption of soil nutrients by roots [58]. This Early Silurian biota might have occupied a soil surface that was rich in algal or plant mats that harbored fungi and microarthropods. Some of these biotal elements are also found in younger Late Silurian deposits of Gotland, Sweden (Figure 1), which represent an analogous ecosystem that lacks herbivores. Additionally, thalloid plant-like structures, possibly lichens or laminate algae, have been described for several deposits of the Early Silurian–Early Devonian from several sites [41], which indicate anatomically complex internal organization among continental organisms.

In contrast to the Silurian, there was a significant increase in the diversity, biomass and size of continental plant, fungal and animal life during the earliest Devonian, at least in regions surrounding the coasts of Euramerica. This change in ecosystem structure not only included more microorganisms, macroscopic plants, fungi and arthropods, but importantly, a wealth of interactions among these groups. Features such as the lignification of tracheophyte plants [58] and associated detritivory, the entering of mycorrhizal and lichenized associations between ascomycetous fungi and plants [59], and the beginnings of arthropod herbivory [18] provide a prelude to ecosystem expansion during the later Devonian.

The Rhynie Chert deposit in Scotland is the best example of an Early Devonian continental ecosystem. Rhynie Chert contains well preserved land and some freshwater plants, fungi, arthropods and other organisms in silicified rock, including whole organisms [60]. The fossils resulted from entombment in a hot spring deposit that was surrounded by erect vegetation in a lowland basin [60]. Several major clades of terrestrialized plants occur in the Rhynie Chert, including cyanobacteria, green algae, lichens, vascular plants assigned to the extinct rhyniophytes, zosterophyllophytes, and the earliest lycophytes. Because of their role in promoting the early colonization of land by plants, predicted 30 years ago [58], subsequent discoveries have documented that fungi were also part of the early invasion of continental habitats [49,61] and became involved in symbioses and parasitisms [59]. These associations are represented by several types of distinctive cellular abnormality from Rhynie Chert organisms and include cyanobacterial–fungal lichens, glomeromycotan endosymbioses represented by both vesicular-arbuscular mycorrhizae and arbuscular mycorrhizae on vascular plant axes, epibiotic mycoparasitism of chytrid thalli on charophyte and vascular plant axes, and endobiotic mycoparasitism of coenocytic fungal thalli on vascular plant axes [59].

Several continental arthropod groups are represented by body fossils from the Rhynie Chert, including freshwater lipostracan and euthycarcinoid crustaceans, and land-based taxa consisting of spider-like trigonotarbids, mites, collembolan hexapods and a possible insect [60,62,63]. Equally important for food-web reconstruction are damaged stems of vascular plants that are attributable to herbivorous interactions with arthropods, some of which also can be interpreted as examples of detritivory [18,64]. Additionally, commonly occurring coprolites are known that contain monospecific or heterogeneous assemblages of spores, the latter with admixture of vegetative tissues, indicating consumption of spores and possible targeting of particular host-plant sporangia [65]. This represents a continuation of a feeding guild that was established during the Late Silurian [66]. Borings are also known from the massive, pole-like stipes of the fungus *Prototaxites* from somewhat younger sites in eastern Canada [67,68]. Although most plant–arthropod associations were undoubtedly detritivorous, the Rhynie Chert represents the beginnings of the consumption of live stem tissues and sporangial protoplasts that suggests opportunism [62,65]; this was followed during the Carboniferous by

the consumption of roots, leaves, wood and seeds, which indicates a delayed herbivore response long after the Devonian origination of these organs and tissues. By the latest Devonian, arthropods were feeding on the cortical tissues of arborescent fungi [68], and during the Early Carboniferous were consuming spores, seeds and foliage from tree crowns [18].

The timing of the initial tetrapod radiation on land was primarily during the Early Carboniferous [69]. Stem-group tetrapods such as fin-limbed *Eusthenopteron* and ichthyostegalian tetrapods occurred during the last stage of the Devonian [70], but both were more amphibious than truly land based, based on the body and trace-fossil evidence [71]. Although these taxa were quite large, their dentition suggests that land arthropods and small aquatic vertebrates were probable food sources. By the end of the Early Carboniferous, amniotes had originated, giving rise to sauropsid and synapsid clades, many of which were considerably smaller than their Late Devonian and earlier Early Carboniferous forbearers, and probably occupied the feeding niche of micropredators.

Conclusions

Terrestrialization is best regarded as a prolonged process with a multitude of unique outcomes rather than the frequently presented view of a temporally circumscribed event that occurred during the mid-Paleozoic. The origin of continental life extends to the cyanobacterial-dominated microbial communities of the Proterozoic and even Archean, and experienced a lull during the early Paleozoic, but for which there now is evidence of a limited, bryophyte-grade flora. A subsequent reinvasion is documented during the later Paleozoic by an assemblage of mostly macroscopic and eukaryotic organisms consisting of morphologically simple embryophyte and fungal ancestral lineages, but several additional lineages of animals that had more complex body plans. This process of terrestrialization has recently been illustrated by the repeated invasion of available land by crustacean arthropods. This includes talitrid amphipods that invaded continents during the Late Cretaceous [72] and a lineage of grapsid crabs that colonized Jamaica ~4 million years ago [73].

Much remains to be resolved, particularly the taxonomic assignments of fossil organisms as well as their phylogenetic relationships based on extinct and extant taxa. More important, our knowledge is woefully incomplete of how these players interacted with each other. Only during the past ten years has there been a renewed interest in exploring the ecology of past continental communities at all levels of biological organization, from Precambrian microbiotal crusts to the macrobiotal food webs of the Early Devonian. Retrieval of associational evidence will be essential for a more complete understanding of these ancient ecosystems. In particular, more focus is needed on using existing and future geochemical techniques for determining the metabolic roles of Precambrian microorganisms [26,74], examination of histologically well preserved fossils for depicting the interface between host and parasitic organisms [59], greater precision in interpreting the late Precambrian–mid Paleozoic trace-fossil record of continental life [6], and assembling comprehensive data for recording the trajectory of animal-mediated plant damage from the Early Devonian to the Carboniferous.

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