

REVIEW

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Early life on land and the first terrestrial ecosystems

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Abstract

Terrestrial ecosystems have been largely regarded as plant-dominated land surfaces, with the earliest records appearing in the early Phanerozoic (<550 Ma). Yet the presence of biological components in pre-Phanerozoic rocks, in habitats as different as soils, peats, ponds, lakes, streams, and dune fields, implies a much earlier type of terrestrial ecosystems. Microbes were abundant by ~3,500 Ma ago and surely adapted to live in subaerial conditions in coastal and inland environments, as they do today. This implies enormous capacities for rapid adaptations to changing conditions, which is supported by a suggestive fossil record. Yet, evidence of “terrestrial” microbes is rare and indirect in comparison with fossils from shallow or deeper marine environments, and its record has been largely overlooked. Consequently, the notion that microbial communities may have formed the earliest land ecosystems has not been widely accepted nor integrated into our general knowledge. Currently, an ample record of shallow marine and lacustrine biota in ~3,500 Ma-old deposits, together with evidence of microbial colonization of coastal environments ~3,450 Ma ago and indirect geochemical evidence that suggests biological activity in >3,400 Ma-old paleosols endorses the idea that life on land perhaps occurred in parallel with aquatic life back in the Paleoproterozoic. The rapid adaptations seen in modern terrestrial microbes, their outstanding tolerance to extreme and fluctuating conditions, their early and rapid diversification, and their old fossil record collectively suggest that they constituted the earliest terrestrial ecosystems, at least since the Neoproterozoic, further succeeding on land and forming a biomass-rich cover with mature soils where plant-dominated ecosystems later evolved. Understanding how life diversified and adapted to non-aquatic conditions from the actualistic and paleontological perspective is critical to understanding the impact of life on the Earth’s systems over thousands of millions of years.

Introduction

Definition of “terrestrial”

Habitable, non-aquatic environments must have existed all throughout the geologic history of Earth unless its surface was entirely under water, which seems unlikely. The definition of a terrestrial environment may not be as trivial as it sounds. “Terrestrial” is defined here as non-aquatic environments. However, even fully aquatic ecosystems, such as lakes and coastal environments, cover a wide spectrum of mixed environments where aquatic and non-aquatic landscapes develop and overlap over time. Habitats above sea level include aquatic (ice-covered and ice-free lakes, ponds and wetlands, peats, rivers and streams, geothermal fields) and non-aquatic environments (especially areas with low rain regimes) that experience drastic changes governed by tectonic activity and climatic

conditions, including the rise and fall of sea level, glaciations, and rain regimes (e.g., Romans and Graham 2013). Microbes can be expected in all these environments and, in the long term, they may have strongly influenced the regional topography, sedimentation rates, sedimentary dynamics, and the reworking of previously emplaced materials. This might be difficult to interpret sometimes from the sedimentary record, especially in environments whose configuration and sedimentary dynamics can change in a relatively short time (days to decades), such as coastal areas (deltas, estuaries, lagoons, evaporitic flats, dunes, etc.; e.g., Hamblin and Christiansen 2007), going from aquatic to non-aquatic environments in a few centimeters or meters of rock strata.

Sedimentary deposits originating in fully aquatic environments (fluvial, lacustrine, shallow marine) can be further exposed to the atmosphere for long periods of time and undergo pedogenetic processes, which transform some of the original features of the deposit into a soil

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(e.g. Paul et al. 2001 and references therein). The rocks thus keep gross characteristics of the primary deposit but are overprinted with the in situ, secondary features derived from completely different environmental conditions. Besides, elucidating timescales at the outcrop scale is not always feasible and is frequently overlooked in less resolved regional studies. Ultimately, this has surely contributed to biases in the interpretation of the evolution of the biosphere. In this regard, the study of pedogenetic (e.g., development of horizons, hardpans or duricrusts, peds, and clay compositional and mechanical—e.g., slickensides—features, etc.) and microbial processes in spring and stream microbialites (e.g., travertines, tufas, sinters) and exposed sedimentary and rock surface habitats (endolithic habitats and cryptogamic covers), is of particular importance for the more comprehensive understanding of past life because these represent terrestrial habitats expected on ancient continental surfaces.

Caution and re-interpretation of the rock record

Through the integrative study of rocks and the understanding of the processes that formed them, including the fossil record and our ability to date materials isotopically, we have built a concept of the evolution of the geosphere and the biosphere (see compendiums by Schopf 1983; Canup and Righter 2000; Eriksson et al. 2004; Schieber et al. 2007; Van Kranendonk et al. 2007a; Kasting 2009; Taylor et al. 2009; Knoll et al. 2012), despite important and ongoing debate on the details. One key element in this picture is the inception of life, which has been interacting with and changing, maintaining, and recirculating most of the materials existing in the atmosphere and the supracrustal section of the Earth for over ~80% of Earth's history. This scenario has been studied and interpreted over the years, aided by the technology available at the moment, not always correctly and also biased sometimes by the general consensus (e.g., Hallbauer 1975; Gray and Boucot 1994; Windley 2007). Also, our appreciation of the timing of geological phenomena (soil formation, seafloor spreading, mountain building, rock erosion, lake succession, etc.) may be difficult to relate to other global changes (e.g. rapid and profuse volcanism and rapid climatic oscillations coexisting with slow seafloor spreading and continental drift) when interpreting the rock record.

Besides the record being incomplete, the speed at which biology operates compared to geology implies that hiatuses of tens of millions of years (negligible in Precambrian timescales), represented by only a few centimeters or meters of rock strata, bear enormous opportunities for biological developments and adaptations that may have not been preserved. This conceptualization of the speed at which biotic and geological events occur

simultaneously requires a careful examination and re-evaluation of Precambrian geological materials (aided by the advancement of scientific knowledge and technology around it) with a readiness to consider challenging ideas (e.g., Retallack 2013), especially when recognizing fossils or when trying to reconcile them with their paleoenvironments (Xiao and Knauth 2013).

The fossil record of microbes is largely related to aquatic environments, and while abundant morphological, chemical, and geochemical evidence of diverse, aquatic Archean life has reached wide acceptance and consensus, the existence of life on Precambrian lands is not always taken for granted. The historical perception of plants as the dominant group on the land, together with the first discoveries of macroscopic fossils only in Phanerozoic rocks and the inability to correctly interpret microbial and algal biosignatures, has perhaps infused the generalized understanding of “colonized” terrestrial ecosystems exclusively for plants (e.g., Bambach 1999). In some instances, even when the existence of Precambrian terrestrial ecosystems may be recognized, they are still treated doubtfully or not given adequate attention (Shear 1991; Behrensmeier et al. 1992; DiMichele and Hook 1992; Gray and Shear 1992; Gray and Boucot 1994) even after previous and important discussions on the topic (e.g., Wright 1985; but see also Labandeira 2005).

The possible misinterpretation of terrestrial paleoenvironments and their relatively poor preservation in the sedimentary record does not necessarily mean that terrestrial life did not exist on the early continents. Today there is growing evidence indicative of non-aquatic environments colonized by microbes early in Earth's history, which is consistent with the extent of modern microbial life on analog “barren” lands (deserts, polar plains, alpine rocks, etc.) their outstanding diversity and metabolic capabilities, and by the great diversity and distribution of Precambrian microfossils, which is a reflection of the microbial ubiquity at that time.

The setting for early life

The oldest materials yet found in the Solar System occur in meteorites and are ~4,570 Ma (Mega annum, million years) of age (Bouvier and Wadhwa 2010), which may serve as a starting point for the condensation of the first solids in our Solar System. By contrast, the oldest materials on Earth (zircon crystals) go back ~4,400 Ma (Wilde et al. 2001), leaving a hiatus of ~170 Ma in Earth's geological history. Regardless, it is assumed that the Moon was already formed before 4,400 Ma (Canup and Righter 2000; Yu and Jacobsen 2011) and that the Earth's nucleus, mantle, and lithosphere were already differentiated (Nelson 2004; Boyet and Carlson 2005). At least by ~4,200 Ma, but perhaps 200 Ma earlier, large

water bodies were in place (Mojzsis et al. 2001; Nutman 2006; Cavosie et al. 2007, but see alternative views by Deming 2002), while granitic (continental) and basaltic (oceanic) crusts were constantly growing, resurfacing, and remelting, interacting with water in non-uniform regimes that evolved drastically from the Hadean to the Neoproterozoic (Komiya et al. 1999; Nutman et al. 2002; Myers 2004; Rino et al. 2004; Van Kranendonk 2004 and references therein; Furnes et al. 2007a; Adam et al. 2012), changing from plume-dominated to plate-dominated tectonics toward the late Proterozoic (Van Kranendonk et al. 2007b). It is plausible then, that by the end of the heavy bombardment (Gomes et al. 2005; Hartmann et al. 2000) some ~3,800 Ma ago, the primitive lands and oceans were open niches ready for the pioneering and rapidly evolving microscopic life forms, for which occasional “sterilizing” perturbations may be irrelevant given the resilience and time scales at which biology operates compared to geology.

Although life may have appeared only a few hundred million years after Earth’s accretion (e.g., Lopez-Garcia et al. 2006), sedimentary rocks older than ~3,850 Ma (Nutman et al. 1996; Ishizuka 2008; Nutman et al. 2010; O’Neil et al. 2011; Mloszewska et al. 2012), where biotic events are most likely to be imprinted, are uncommon on Earth. Yet, potential traces of life (e.g. biogenically precipitated carbonates) may even be present in this ancient record (Nutman et al. 2010), suggesting that life itself can be several million years older than the oldest known stromatolites and microfossils. Other putative biosignatures older than 3,500 Ma (carbonaceous spherules associated with apatite globules; see McKeegan et al. 2007; Papineau et al. 2010a, 2010b) are also controversial (see Myers 2001; van Zuilen et al. 2002; Fedo and Whitehouse 2002; Papineau et al. 2011) and may not imply a syngenetic timing of formation with the host rock. Biosignatures of particular interest would be those associated with biogenic banded iron formations (e.g., Dauphas et al. 2004; Trendall and Blockley 2004; Kappler et al. 2005; Konhauser et al. 2005; Koehler et al. 2010; Mloszewska et al. 2012) given their potential antiquity of ~4,300 Ma (O’Neil et al. 2009).

Microfossils, microbialites, and isotopic and molecular biomarkers indicate that prokaryotic life was abundant by 3,500–3,400 Ma ago in shallow and deep marine environments (Lowe 1980; Walter et al. 1980; Awramik et al. 1983; Schopf 1983; Walter 1983; Walsh, 1992; Walsh and Lowe 1985, 1999; Rasmussen 2000; Westall et al. 2001; Furnes et al. 2004; Shen and Buick 2004; Tice and Lowe 2004; Allwood et al. 2006; Banerjee et al. 2006; Westall et al. 2006a, 2006b; Ueno et al. 2006; Schopf et al. 2007 and references therein; Shen et al. 2009; Westall 2010; Wacey et al. 2011), which supports the notion that coastal and estuarine areas could have

been very productive by that time and that photosynthesis was already operating (Awramik 1992; Rosing and Frei 2004; Tice and Lowe 2004; Buick 2008; Hoashi et al. 2009; Kato et al. 2009; Kendall et al. 2010), though perhaps not necessarily oxygenic (Kirschvink and Kopp 2008; Westall et al. 2011; Li et al. 2012).

Many different settings have been proposed as likely or “optimum” for the emergence and prosperity of life, ranging from deep-sea hydrothermal vents and geothermal springs, to land surfaces and mineral-water-air interphases (Baross and Hoffman 1985; Retallack 1986a; Holm 1992; Battistuzzi and Hedges 2009; Aller et al. 2010; Hazen and Sverjensky 2010; Mulikidjanian et al. 2012). However, one preferred environment where many of the oldest signs of life are found is shallow marine continental margins (see references in Schopf and Klein 1992). Whether this is a true fact or a consequence of the incompleteness/selectivity of the record is still to be resolved. However, in these coastal environments microbes were likely to have been periodically exposed and desiccated, as happens in most such environments today, and likely developed adaptations for long-term desiccation regimes (e.g., thick hygroscopic sheaths) and high UV radiation (e.g., living interstitially).

Some of the oldest examples of life activity, which come precisely from aquatic, shallow marine (Klein et al. 1987; Schopf and Klein 1992; Van Kranendonk et al. 2008; Westall 2010; Van Kranendonk 2011; Hickman and Van Kranendonk 2012), shallow lacustrine (Awramik and Buchheim 2009; Hickman and Van Kranendonk 2012), and intertidal environments (e.g., Noffke et al. 2006; Noffke 2010; Noffke et al. 2011; Westall et al. 2011), show signs of evaporation (e.g., Noffke et al. 2008; Westall et al. 2011; Hickman and Van Kranendonk 2012), which suggests that early microbial communities in shallow waters had to deal with periodic desiccation and UV radiation >3,400 Ma ago. This further implies adaptations to resist desiccation, salinity fluctuations, and UV radiation that could be successfully used even after prolonged desiccation. Dry conditions can be expected also for lacustrine and fluvial environments. Desiccation allows dispersion by wind, which seems like a reasonable means for land colonization. Through this mode of dispersion, communities would tend to be at or near the surface instead of underground, even when migration to aquifers can occur. Perhaps environments with periodic subaerial exposure (especially estuarine and intertidal) were crucial scenarios for a biological transition from water to land.

Apparently not only prokaryotes were abundant in shallow Precambrian environments; the oldest eukaryotic-like fossils (acritarchs; Buick 2010) found so far (that perhaps needed oxygen for advantageous energetic and metabolic capabilities) are ~3,200 Ma old and were also present in estuarine environments (Javaux et al. 2010). This indicates

that life achieved a relatively rapid global presence and had diversified enough (Kandler 1994; Altermann and Schopf 1995; Ueno et al. 2006; Blank 2009; David and Alm 2011) to occupy a wide variety of ecological niches by the Paleoproterozoic, even in places that may have been severely disturbed by asteroid impacts (see Walsh 1992 and references therein). Even greater biological diversity, ubiquity, abundance, and habitats are seen in the younger Proterozoic record (e.g., Schopf 1992a; Schopf and Klein 1992), for which rocks are better preserved and more abundant than Archean ones.

The fossil record of terrestrial life

The earliest remnants of continental crust may derive from $\geq 3,500$ Ma-old submillimeter zircons (Nutman 2006) and regional rock outcrops (Buick et al. 1995; Iizuka et al. 2006; Stern and Scholl 2010; Adam et al. 2012). Supplementary evidence for exposed lands may consist of thick soils developed on these ancient surfaces (Buick et al. 1995; Hoffman 1995; Ohmoto et al. 2007; Johnson et al. 2009, 2010). The further growth of continents and their sedimentary cover, implying extensive intracratonic terrestrial settings that remained relatively stable (although still affected by erosion, sea level changes, tectonics, and volcanism), is reflected in the ample record of paleosols onward (see study approaches and examples by Jackson 1967; Gay and Grandstaff 1980; Holland 1984; Aspler and Donaldson 1986; Grandstaff et al. 1986; Kimberley and Grandstaff 1986; Reimer 1986; Retallack 1986b; Farrow and Mossman 1988; Zbinden et al. 1988; Palmer et al. 1989; Holland 1992; Gall 1994; Macfarlane et al. 1994; Martini 1994; Retallack and Mindszenty 1994; Driese et al. 1995; Banerjee 1996; Ohmoto 1996; Prasad and Roscoe 1996; Gutzmer and Beukes 1998; Thiry and Simon-Coincon 1999; Rye and Holland 2000; Watanabe et al. 2000; Retallack 2001 and references therein; Yang and Holland 2003; Driese and Gordon-Medaris 2008; Pandit et al. 2008; Bandopadhyay et al. 2010). This record of old paleosols holds indirect proof of the early environmental conditions on Earth and early life on land.

Currently, the oldest and direct evidence of terrestrial life comes from $\sim 2,900$ – $2,700$ Ma-old (see age determination of Witwatersrand deposits in Kositcin and Krapez 2004; Zhao et al. 2006), organic matter-rich paleosols (Watanabe et al. 2000), ephemeral ponds (Rye and Holland 2000) and alluvial sequences, some of them bearing microfossils (Hallbauer and van Warmelo 1974; Mossman et al. 2008). Interestingly, their occurrence in such settings coincides with drastic changes in Earth's crustal configuration and the —perhaps abrupt—emplacement of large continental masses in the late Archean (Condie 2004; Eriksson and Martins-Neto 2004; Van Kranendonk 2004 and references therein; Hazen et al. 2012), a marked step in

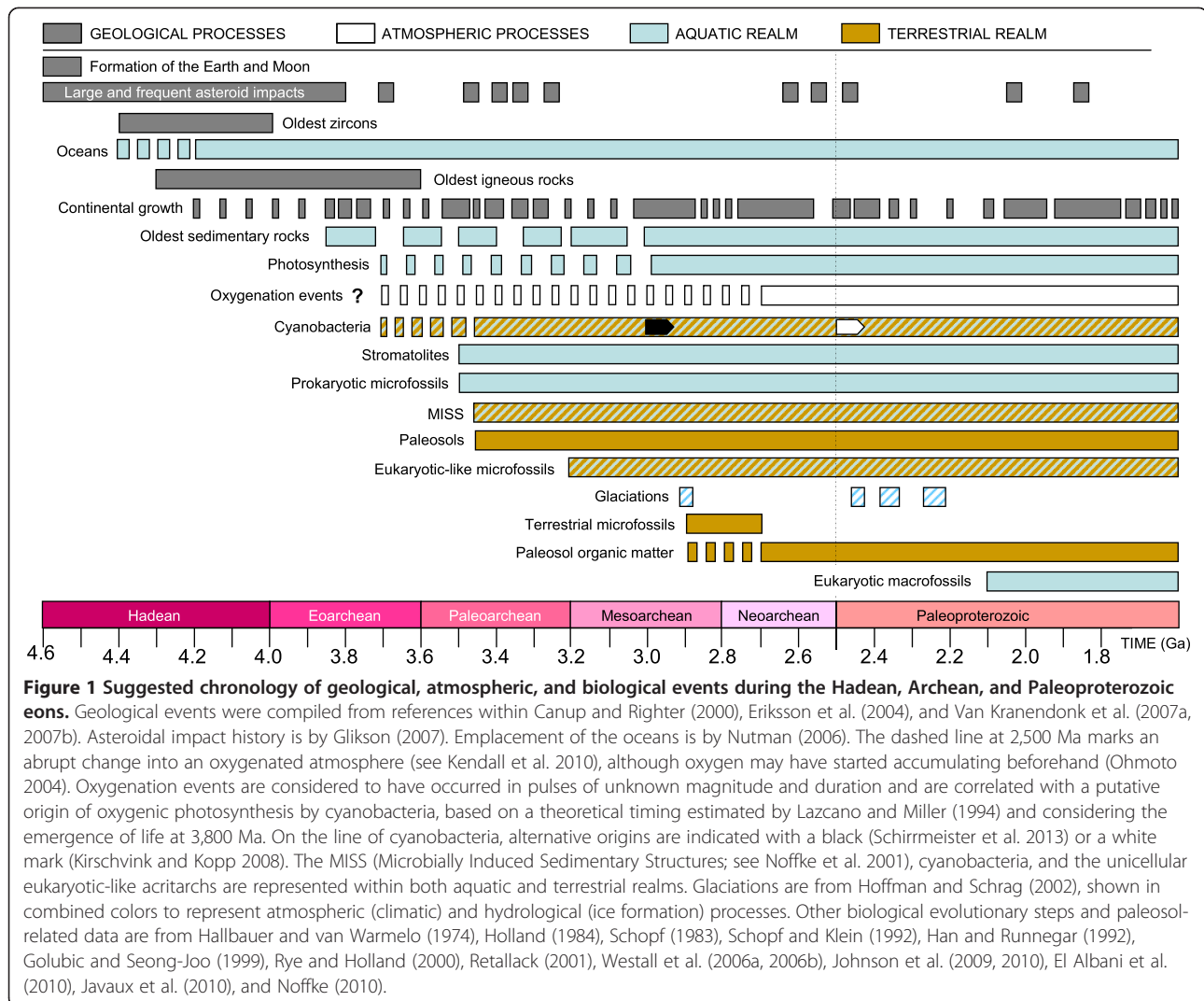
the oxygenation of the atmosphere (Kendall et al. 2010), and also with estimations of land colonization by microbes based on phylogenetic relationships (Battistuzzi et al. 2004). Although microbes could have colonized the land before this time, the Meso- to Neoproterozoic appears to be an important evolutionary time period for terrestrial microbial communities, perhaps linked to supercontinent growth (Santosh 2010) and the emergence of potential new habitats.

Later in time, the amount of organic matter-rich and possibly “biologically weathered” paleosols (Ohmoto 1996; Beukes et al. 2002; Driese and Gordon-Medaris 2008), terrestrial sedimentary structures of presumed biotic origin (Hupe 1952; Lannerbro 1954; Voigt 1972; Eriksson et al. 2000; Prave 2002), and microfossils themselves (Cloud and Germs 1971; McConnell 1974; Horodyski and Knauth 1994; Strother et al. 2011) drastically increased throughout the Proterozoic. Likewise, marine microfossils display increasing biological developments and adaptations (Knoll et al. 2006). Biotic diversity and abundance become even greater from the Neoproterozoic-Phanerozoic transition to the recent (see Zhuravlev and Riding 2001; Xiao and Kaufman 2006; Gaucher et al. 2010). This timeline suggests a rapid and global development of life on Earth, with life forms adapted to live on the land more than 2,000 Ma before the earliest fossil record of land plants (Heckman et al. 2001; Gensel 2008). Important events in this chronology are depicted in Figure 1.

Functioning of primitive terrestrial ecosystems and cyanobacteria

A conceptualization of the functioning of the ancient terrestrial biosphere necessarily requires a general understanding of modern, analog microbial communities to evaluate their living requirements, diversity, physiology, and environmental impact, and to characterize any potential biosignature that could be used to recognize them in the rocks. Modern terrestrial microbial communities are found worldwide and in a great variety of local conditions, in surface (solid rock, regolith) and subsurface (caves, groundwater, deep ground) environments (although the latter could be considered aquatic by some). However, it is unclear which one is more productive in terms of biomass (Pace 1997) and what metabolisms have dominated those systems—and to what extent—over geologic time scales (Sleep and Bird 2007).

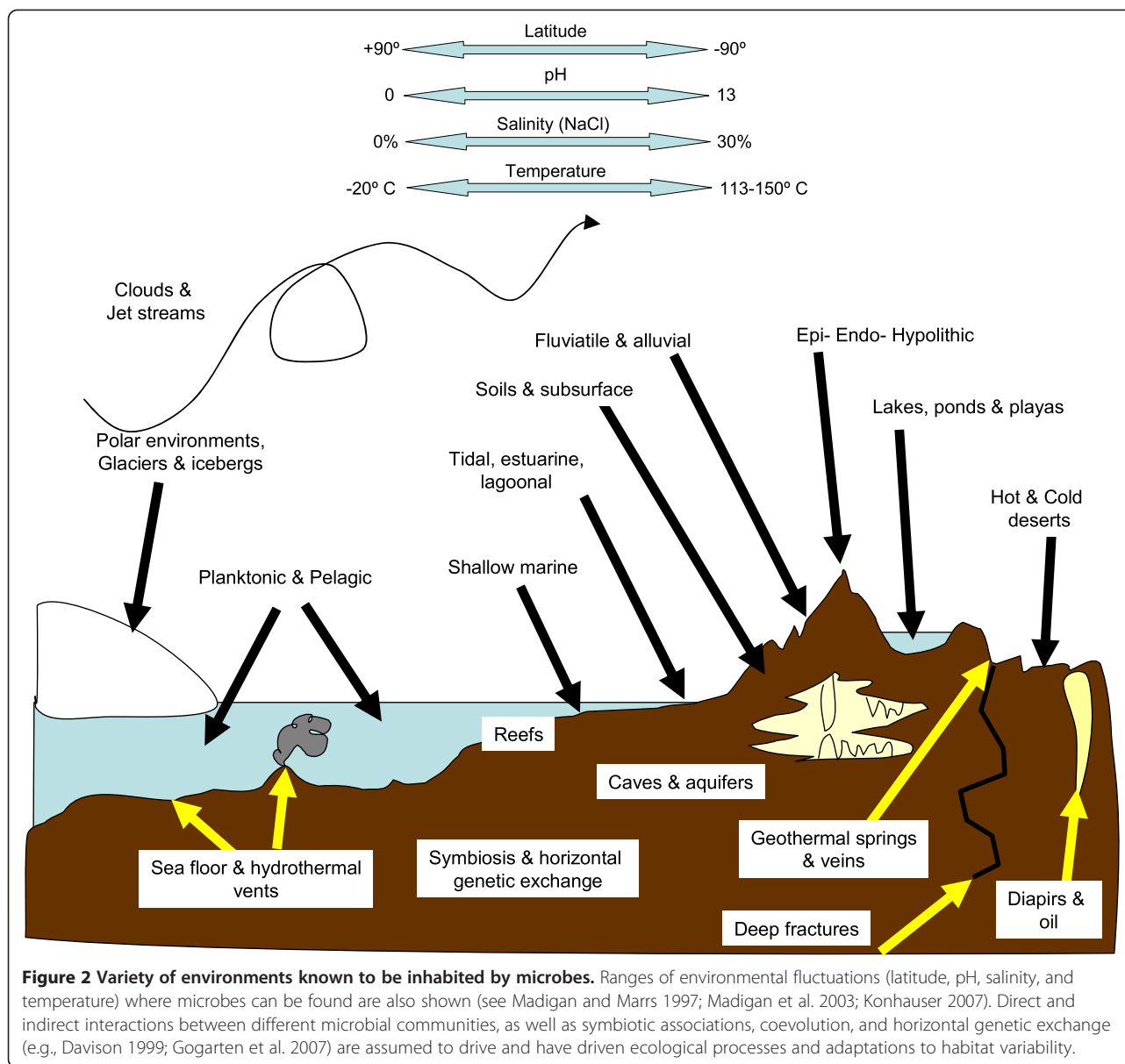
An understanding of the biology and distribution of modern microbes, which are ubiquitous in today's Earth's biosphere (Figure 2), seems essential for an understanding of their ancient counterparts and their impact on early terrestrial ecosystems. Estimates of the genetic diversity and biomass distribution in drastically different environments (e.g., Garcia-Pichel et al. 2003; Lozupone and Knight 2007; Nemergut et al. 2011) depict the ample range of strategies



that terrestrial organisms, particularly primary producers, have developed for living on the land. Oxygenic photoautotrophy seems to be a particularly important capability of terrestrial organisms, simply because their energy source (light), reductant power (water), and carbon source (CO_2) are readily available in these environments. In comparison, other primary producers (e.g., chemolithotrophs) are restricted to aqueous environments because they require soluble sources of reductants (e.g., H_2 , Fe^{2+} , H_2S , HS^-) and exergonic reactions to maintain their metabolism (White 2000). Besides being restricted to aquatic environments, chemolithotrophs are also less energy-efficient than oxygenic photoautotrophs (DesMarais 2000; Madigan et al. 2003; Konhauser 2007), and less likely dominant in subaerial environments.

Cyanobacteria have been the only organisms that developed special pigments and enzymatic capabilities for using water as a source of electrons. This process

has allowed them to live outside the water in any suitable environment, even where water might be a limiting factor, such as deserts (e.g., Potts and Friedmann 1981). Oxygenic photosynthesis also contributed to the oxidation of the atmosphere (both by sequestering CO_2 and by producing O_2), a global and ongoing process with profound geochemical, atmospheric, hydrological, and biological implications (e.g., Rosing et al. 2006; Och and Shields-Zhou 2012; Pufahl and Hiatt 2012). Cyanobacteria and other prokaryotes, can also fix gaseous nitrogen, which seems of great advantage for an independence from dissolved N species, such as NH_4 and NO_3 (Glass et al. 2009). The appearance of cyanobacterial akinetes (for N_2 fixation) in the Paleoproterozoic (Tomitani et al. 2006) attests to this early adaptation. For organisms on the land, a limiting nutrient, such as P, can be supplied by dust deposition (Kennedy et al. 1998; Reynolds et al. 2001; McTainsh and Strong 2007), which may be an alternative process for replenishment of nutrient loss by runoff and



leaching in such environments (e.g. Beraldi-Campesi et al. 2009); S can also be acquired from minerals, aerosols, and as gaseous sources, likely present in the early atmosphere (Holland 1984). Thus, the nutritional requirements for oxygenic, photoautotrophic, primary producers seem not to have been a limiting factor for the colonization of the land. This idea has also been discussed in light of physiological and genetic characteristics of terrestrial microbes (Battistuzzi et al. 2004; Battistuzzi and Hedges 2009). Yet, an earlier chemotrophic way of life also needs to be considered (Shen and Buick 2004; Sleep and Bird 2007).

Particularly for the early terrestrial biota, a minimum set of adaptations to live subaerially must have included protection against radiation and desiccation effects. Adaptations such as thick polymeric sheaths with

hygroscopic capacity against desiccation, efficient DNA repair mechanisms to restore metabolic activities as soon as water is available, and the production of UV-shielding pigments are certainly successful strategies displayed by terrestrial cyanobacteria (Shephard 1987; Garcia-Pichel 1998; Yasui and McCready 1998; Potts 1999; Sinha and Hader 2002; Singh et al. 2010). Refined degrees of adaptation of terrestrial organisms include sunscreens that once placed within the extracellular sheaths, passively protect against UV radiation, even when the cell is dormant or dehydrated (Garcia-Pichel and Castenholz 1991; Gao and Garcia-Pichel 2011). Some of these strategies for living on the land likely evolved early and are partially displayed by microfossils (e.g., thick sheaths), which are sometimes associated

with evaporitic sediments, in keeping with subaerial exposure (Schopf 1968; Hofmann 1976; Golubic and Campbell 1979; Awramik et al. 1983).

Modern cyanobacteria-driven communities can be found in any terrestrial environment (~30% of modern Earth's surface area). They include endolithic communities (Friedmann 1980; Sun and Friedmann 1999; Büdel et al. 2004) and cryptogamic covers (CGC) on rocks and soils (Belnap and Lange 2001; Elbert et al. 2012). The latter have been shown to be very complex and dynamic and contain many distinct functional groups of prokaryotes and eukaryotes, ranging from primary producers to decomposers of specific materials, and grazers (Fritsch 1922; Fletcher and Martin 1948; Campbell 1979; Bamforth 1984, 2004; Garcia-Pichel et al. 2001; Nagy et al. 2005; Tirkey and Adhikary 2005; Chanal et al. 2006; Reddy and Garcia-Pichel 2006; Bates and Garcia-Pichel 2009; Neher et al. 2009; Meadow and Zabinski 2012; Bates et al. 2013). This diversity is variable based on local environmental conditions, but all CGC—albeit with few exceptions (e.g., Hoppert et al. 2004)—have in common the presence of cyanobacteria. This speaks for the evolutionary success that cyanobacteria have had over other microbes throughout time.

Although fossil analogs of CGC have been discovered in ancient sediments (Simpson et al. 2010; Beraldi-Campesi et al. 2011; Retallack 2009, 2011; Sheldon 2012), it is unknown what their microbial composition might have been. However, morphological similarities between modern and fossil counterparts are remarkable (Schieber et al. 2007; Noffke 2010). Morphological resemblance between fossils and recent analogs suggests that cyanobacteria are indeed a very old group of bacteria (see Golubic and Seong-Joo 1999) and that at least some morphological traits have been maintained over time (Golubic and Hofmann 1976; Golubic and Campbell 1979; Schopf 1992b). Moreover, as cyanobacteria are such an old group and are so well adapted to colonizing unstable sediments (Booth 1941; Campbell et al. 1989; Mazar et al. 1996; Belnap and Gillette 1998; Malam Issa et al. 2001; Hu et al. 2002; Garcia-Pichel and Wojciechowski 2009), even where available water is scarce and there is considerable UV radiation (Fleming and Castenholz 2007; Giordanino et al. 2011), it is likely that they were also primordial components on land surfaces (Campbell 1979) and influenced the formation of sedimentary biostructures and textures represented in fossil examples (e.g., Prave 2002; Schieber et al. 2007; Noffke, 2011). The antiquity of cyanobacteria has been also estimated by molecular clock analyses of genomic distances to be ~3,000 Ma (Battistuzzi and Hedges 2009; Schirrmeister et al. 2013), which more-or-less coincides with the age of the oldest terrestrial microfossils (Mossman et al. 2008). This timing, however, may vary depending on the calibration points used for

constructing phylogenies and the extent of horizontal gene transfer. Lastly, the capacity of chlorophyll *a* to absorb higher photonic energies to split water in comparison to other photosynthetic bacteriochlorophylls (Xiong et al. 2000) may be the result of selective pressures to use the shorter wavelengths that reached the Precambrian surface where cyanobacteria had to dwell, a capacity not seen in purple or green phototrophic bacteria that use less energetic wavelengths in submerged/shielded habitats. Thus, from a multi-angular perspective cyanobacteria seem the perfect candidates for the colonization of the earliest lands.

As mentioned above, most CGC have in common the presence of filamentous cyanobacteria. One property of these morphotypes is that they can glide through interstitial spaces using hollow hygroscopic sheaths of mucilage as trails, to shield themselves against radiation, to find their optimum light regime, or to track water (Garcia-Pichel and Pringault 2001). The nature of the filamentous members of these communities also provides more surface area and tension for fastening and binding disaggregated particles (Garcia-Pichel and Wojciechowski 2009). Polysaccharides secreted extracellularly provide additional cementing force to the entire organo-mineral framework, resulting in the formation of a (crust/mat) stable microenvironment. The intrinsic characteristic of filamentous microbes to form cohesive layers at sedimentary surfaces is also known to substantially decrease wind and water erosion in modern arid and semiarid areas of the world (Belnap and Gillette 1998; Belnap and Lange 2001). Although some erosive forces may surpass the tear resistance of CGC in high-energy systems (e.g., Corcoran and Mueller 2004), this property of microbes has been invoked to explain the stability of thick, Precambrian siliclastic sedimentary sequences (Dott 2003) and the soft deformation properties of microbial mat-like structures (see references in Schieber et al. 2007). This is an important property of microbes for the functioning of siliclastic ecosystems, and together with the presence of mature and organic-rich soils and microfossils in old Proterozoic strata (see references above), suggests that abundant “cryptogamic” covers were present on Precambrian lands, similar to those covering polar and arid areas of the world today. The addition of new members to these communities over time (most importantly algae and fungi, but also grazers) is expected and may be used to explain increasing weathering rates of the continents (Kennedy et al. 2006) and abrupt changes in the global balance of the C cycle in the Neoproterozoic (Knauth and Kennedy 2009).

Other microbial components

Judging from the rapid achievement of diversity and distribution of early microbial biota and from microbial successions seen in modern “barren” lands (e.g., Sigler

et al. 2002; Schmidt et al. 2008; Fierer et al. 2010), it is expected that heterotrophic organisms were also part of land communities, as they seem to be an inevitable component in this type of consortia. Under this perspective, primitive microbial ecosystems cannot be understood as composed only of autotrophic primary producers, but also a myriad of other microbes finding their niche within such pre-existent microenvironments. For example, actinobacteria in modern CGC not only degrade large quantities of organic exudates from cyanobacteria, a process which influences the C cycle, but they also seem to be structural components of these sedimentary biostructures (e.g., Reddy and Garcia-Pichel 2006). The same applies to other bacteria (e.g., Bacteroidetes and Proteobacteria) that secrete large quantities of mucopolysaccharides, which aid in gluing soil particles together and may also have a critical role in the hydraulic conductivity of the surface substrate (Rossi et al. 2012). One of the most important eukaryotic component of modern CGC are fungi, which must have played a key role in the colonization and weathering of bare rocks in the past (with symbiont cyanobacteria or algae), as well as in the successive development of vascular plants on the land (Smith and Read 2008) and in a radical change toward more “modern” terrestrial ecosystems (Blackwell 2000; Heckman et al. 2001; Taylor et al. 2009. See also Gadd 2006).

Although the timing of the origin of these organisms is unknown, terrestrial microbes can certainly drive important chemical transformations in soils (Keller and Wood 1993; Schwartzman and Volk 1989; Chenu and Stotzky 2002; Ehrlich 2002; Chorover et al. 2007) and endolithic habitats (Konhauser et al. 1994; Sun and Friedmann 1999; Büdel et al. 2004; Omelon et al. 2006) that may have operated in the past. These include affecting the reactivity of mineral surfaces with secreted metabolites (Geesey and Jang 1990; Welch et al. 1999), changing the pH and redox potential of the microenvironment (Bennett et al. 2001), or secreting metal ligands and other organic complexes that react with solutes and minerals (Keller and Wood 1993; Schwartzman and Volk 1989; Barker et al. 1998; Welch et al. 1999; Bennett et al. 2001). These mechanisms seem to play a fundamental role in biogeochemistry (weathering, clay formation, nutrient bioavailability, metal concentration and bioavailability, mineral formation or transformation, etc.), and their effects may also be used to trace microbial geochemical biosignatures in the rock record (Beraldi-Campesi et al. 2009). Additionally, the process of soil formation and maturation is usually understood as aided by biology (Keller and Wood 1993; Schwartzman and Volk 1989; Brady and Weil 2008) and differentiated from abiotic regolith development, and involves a critical step prior to plant and animal colonization of the land. All these

characteristics displayed by modern CGC could be expected from ancient analog communities, although with variations in the occurrence and magnitude dictated by their limiting factors.

Dust

The mechanism of dust formation, transport, and deposition reflects one important aspect of the functioning of terrestrial ecosystems because dust can only be formed on the land and because microbes (along with water adhesion and neo-cementation of particles with salts and clays) can stabilize fine dust particles through trapping and binding (e.g., Dong et al. 1987; Liu et al. 1994; Williams et al. 1995; Belnap and Gillette 1998; Hu et al. 2002). Thus, dust production can potentially be regulated by microbes (and other encrusting processes) depending on their degree of development. The more developed, the less dust production.

Dust is an important carrier of nutrients, and its retention on the ground might influence the budget and delivery of those nutrients locally or to other distant ecosystems, such as happens in modern marine environments via deposition of huge loads of dust (Jickells et al. 2005). The capacity of microbes to trap and bind particles has been demonstrated for numerous underwater and subaerial environments (Gunatilaka 1975; Zhang 1992; Takeuchi et al. 2001; Altermann 2008; Gradzinski et al. 2010; Williams et al. 2012). If microbes were responsible for much of the global dust capture, retention, and lixiviation on the early continents, recycling effects may have had profound implications for the evolution of global ecosystems through geologic time, as well as for important climatic processes, such as those rooted in atmospheric albedo variations (Harrison et al. 2001; Jickells et al. 2005; Lau et al. 2006).

Finally, dust is also a carrier of microbes and viruses (Abed et al. 2011; Al-Bader et al. 2012), which implies a means for biological dispersion that must have been operating continuously and over long distances in the past, amplifying the potential biogeography of biological entities over vast areas of the oceans and continents. Although the rate of survival and the success of foreign airborne mixed communities on aquatic environments, barren or already colonized surfaces is not known, it is plausible that such a mechanism was vital for the colonization of the early continents and the increase in ecological complexity and genetic exchange (e.g., Gogarten et al. 2007).

Underground realm

The underground realm (geothermal veins, aquifers, soil subsurface, all types of caves) should also be considered potential continental habitats for early terrestrial life, as life is abundant there today (e.g., Ghiorse and Wilson

1988; Barton and Northup 2007; Engel 2010). The Precambrian record of caves (e.g., karstic environments) or underground aquifers (detected through nodules and concretions in the rocks) is far less known than the typical shallow marine or lacustrine environments (see examples of karstic and underground environments in Nicholas and Bildgen 1979; Schau and Henderson 1983; Glover and Kah 2006; Skotnicki and Knauth 2007; Rasmussen et al. 2009). Nevertheless, these environments must have existed throughout Earth's history, and thus, terrestrial biotas could have adapted to live in those conditions back in the Precambrian (Rasmussen et al. 2009).

In contrast to the most typical subaerial, light-driven primary producer communities, underground microbes require a chemosynthetic metabolism for primary productivity, perhaps relying on the oxidation of sulfur and iron compounds to support growth and continuity, as these are the main energy sources in such environments (Sarbu et al. 1996; Chen et al. 2009; Porter et al. 2009). Because these metabolic pathways are less energetic than photosynthesis, life underground is expected to have been slow-growing, less dynamic in terms of diversity and interactions, and more geographically contained than, for example, subaerial phototrophs. Nevertheless, early underground dwellers may have impacted the sub-surface realm (cave formation, buried oil and dissolved organic matter consumption, methane production, etc.) and contributed to the neof ormation and dissolution of minerals over the long term, as well as to the generation of gaseous byproducts (e.g., H_2S , CH_4 , CO_2) that could be important for geochemical processes on the surface and ultimately for distant communities and global biogeochemical recycling. Moreover, this type of environments could have been better protected from drastic and global crisis than subaerial ones, and thus have functioned as living reservoirs that could later exploit surface environments.

A note on biosignatures

Imprints of life in rocks can be formed in various ways and can be recognized as long as the rocks are preserved and accessible. Although this "fossil" record decreases in outcrop abundance the older the rocks are (basically due to burial, erosion, subduction, and metamorphism), biosignatures can be found in sedimentary rocks (Schopf 1983; Schopf and Klein 1992; Schieber et al. 2007; Noffke 2010), but also in igneous (Banerjee et al. 2006; Furnes et al. 2004, 2007b; Fliegel et al. 2010) and metamorphic (Franz et al. 1991; Hanel et al. 1999; Squire et al. 2006; Bernard et al. 2007; Schiffbauer et al. 2007, 2012; Schiffbauer and Xiao 2009; Zang 2007) rocks of all ages.

Preservation will always be favored in underwater settings, especially if biological materials are buried quickly,

the sediment is fine grained, and the conditions are overall reducing (anoxic). All of these factors promote rapid mineralization and replacement of biological materials (Farmer 1999; Zonneveld et al. 2010; Allison and Bottjer 2011; Lalonde et al. 2012) which can preserve the morphology and organic remains, although this does not mean that preservation always happens (Zonneveld et al. 2010 and references therein). Unless protected, organic matter tends to degrade basically by photo-chemical degradation (if exposed to light), chemical bond breaking, biological recycling, mechanical maceration and dissolution. If body fossils are preserved, the lack of diagnostic morphologies for most bacteria and the possible existence of abiotic, microbe-like morphologies (e.g., Garcia-Ruiz et al. 2002, Garcia-Ruiz et al. 2003) make their determination a challenge. Yet, their presence in a suitable geological context and association with sedimentary biostructures may be used as criteria for biogenicity. Molecular biomarkers in hydrocarbons that can be correlated with extant organisms (e.g., Summons et al. 1999) also require careful confirmation of syngenicity for a correct interpretation (Rasmussen et al. 2008; Brocks 2011).

If limiting factors are at play, microbial communities may not develop sufficient biomass to leave behind a biosignature (either chemical, geochemical, mineralogical, or morphological). Water, for example, which is the most basic requirement for survival and reproduction, tends to be a limiting factor on the land compared to a permanent water body. If microbial growth is thus limited, the amount of cells and biomass that can be preserved decreases. Thus, organisms with access to unlimited water resources would be able to grow larger communities and have more possibilities for fossilization, in contrast to terrestrial microbes that depend on dew or rain for their survival and maintenance. For example, the thickness and cohesiveness of a marine-intertidal microbial mat (see Bauld 1981; Bauld et al. 1992) are greater than in a mature biological soil crust (Belnap and Lange 2001), thus the latter will be less prone to fossilization than the marine one. Nevertheless, under favorable climates and landscapes, these too could be preserved (e.g., Prave 2002). Studies on biosignatures left behind by terrestrial microbial communities are needed for comparison against the yet-to-explore rock record.

Conclusions

As the Earth was evolving, gradual degassing and accumulation of liquid water at its surface differentiated aquatic and non-aquatic environments. Because terrestrial environments have always existed, it is possible that life evolved on the land (including in lakes, rivers, streams, and flooding areas) as early as aquatic life itself (see Retallack 1986a and references therein). In any case,

living on the land must have required particular adaptations, such as the capability to acquire nutrients and energy sources outside the aquatic realm, the development of molecular repairing mechanisms, and protection against radiation and desiccation. These adaptations were certainly developed by cyanobacteria, a group with a very old biologic lineage and one of the most conspicuous and successful primary producers on Earth (e.g., Whitton and Potts 2000; Herrero and Flores 2008).

Direct and indirect evidence pointing to inhabited terrestrial environments by the Paleoproterozoic (Johnson et al. 2009, 2010) and the following eras (Stüeken et al. 2012), along with substantive evidence of terrestrialization from the Neoproterozoic onward (Hallbauer and van Warmelo 1974; McConnell 1974; Horodyski and Knauth 1994; Gutzmer and Beukes 1998; Rye and Holland 2000; Watanabe et al. 2000; Prave 2002; Rasmussen et al. 2009), strongly implies that functional terrestrial ecosystems originated well back in the Precambrian. The implications for such colonization have not been completely understood, but the effects of microbial life on land processes that affect the atmosphere, the lithosphere, and the hydrosphere, are widely diverse and act at all scales. Two main consequences derived from the activities of land biota are the continuous oxygenation of the atmosphere (with consequences for the stratification of the oceans, the formation and maintenance of the ozone layer, and the precipitation of oxides, among others) and the weathering of the continents (Holland 1984; Catling et al. 2001; Stüeken et al. 2012), which indirectly and directly affect marine ecosystems. In contrast to marine biota, which indirectly affect terrestrial ecosystems through atmospheric processes (including gas composition and climate), the establishment of life on the land has an enormous significance for the evolution of the planet through time because gaseous byproducts, such as oxygen produced on the land would be released directly into the atmosphere and not dissolved in the oceans first. Once in the atmosphere oxygen would react with reduced species before starting to accumulate and produce a geochemical signature in marine sediments. Thus, land-based life could have been pivotal for the early oxygenation of the atmosphere, which later affected the oceans as well. A more direct influence of land-based communities over aquatic ones would be the production of dust, clays and leachates on the continents (Kennedy and Wagner 2011 and references therein), which would then be carried by rivers and wind into the oceans, and thus increasing the heterogeneity of materials and solutes delivered into oceanic ecosystems and having either beneficial or detrimental consequences for marine life. Yet, an overall retention of sediments on the land via microbial stabilization would be expected for detritic sediments in

places with well-developed cryptogamic covers. Finally, it is expected that the time span from the inception of microbial land-based life to the evolution of the first plant ecosystems took long enough (2,000–2,500 Ma) for coastal and inland settings to be transformed into organic- and nutrient-rich substrates that could later be exploited by more evolved communities and organisms toward the Neoproterozoic-Phanerozoic transition.

In general, the logical transition from cyanobacteria (and other bacteria and archaea), to algae (and protists and fungi), to non-vascular plants, to vascular plants, may still be valid, but the timing of those evolutionary steps needs to be updated with the latest pertinent information available. The notion that the land was virtually sterile in the Precambrian (e.g., Bambach 1999; Blackwell 2000; Corcoran and Mueller 2004; Nesbitt and Young 2004; Gensel 2008) underestimates the impact that microbes could have had on the biosphere. More importantly, the idea the land was first colonized by plants and that they formed the earliest terrestrial ecosystems should be abandoned completely. That is not to say that the advent of plants in the Phanerozoic did not have strikingly enhanced effects on continental weathering, soil formation, and oxygenation of the atmosphere (Labandeira 2005; Taylor et al. 2009), but neglecting the existence of microbial, Paleoproterozoic-to-recent terrestrial ecosystems would impede a realistic understanding of the evolution of the biosphere and its influence on the geo-atmo-hydrosphere over time.

Competing interests

The author declares that there are no competing interests.

Acknowledgments

I am grateful to Kathleen E. Pigg, Anthony R. Prave, Gregory J. Retallack, Nora Noffke, Fernando Ortega Gutiérrez, Dominic Papineau, Marcela Martínez Millán, and Kelaine Ravidin for their important comments and improvements to this paper. I also thank the editors of Springer and Bettina Weber and Jayne Belnap for organizing and editing this special volume. I also thank the people from SIOV (Seminario Interdisciplinario del Origen de la Vida) at UNAM for fruitful discussions on critical aspects of this topic.

Received: 18 October 2012 Accepted: 30 January 2013

Published: 23 February 2013

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doi:10.1186/2192-1709-2-1

Cite this article as: Beraldi-Campesi: **Early life on land and the first terrestrial ecosystems.** *Ecological Processes* 2013 **2**:1.

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