

Biological Soil Crusts as Modern Analogues for the Archean Continental Biosphere: Insights from Carbon and Nitrogen Isotopes

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Abstract

Stable isotope signatures of elements related to life such as carbon and nitrogen can be powerful biomarkers that provide key information on the biological origin of organic remains and their paleoenvironments. Marked advances have been achieved in the last decade in our understanding of the coupled evolution of biological carbon and nitrogen cycling and the chemical evolution of the early Earth thanks, in part, to isotopic signatures preserved in fossilized microbial mats and organic matter of marine origin. However, the geologic record of the early continental biosphere, as well as its evolution and biosignatures, is still poorly constrained. Following a recent report of direct fossil evidence of life on land at 3.22 Ga, we compare here the carbon and nitrogen isotopic signals of this continental Archean biosphere with biosignatures of cyanobacteria biological soil crusts (cyanoBSCs) colonizing modern arid environments. We report the first extended $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data set from modern cyanoBSCs and show that these modern communities harbor specific isotopic biosignatures that compare well with continental Archean organic remains. We therefore suggest that cyanoBSCs are likely relevant analogues for the earliest continental ecosystems. As such, they can provide key information on the timing, extent, and possibly mechanism of colonization of the early Earth's emergent landmasses.

Key Words: Isotope biosignature—Early life—Archean—Carbon isotope— Nitrogen isotope.

1. Introduction

During the Archean, the absence of an ozone layer resulted in higher short-wavelength irradiance than today despite the fact that the sun was 30% dimmer (Kasting et al., 1989). Due to these extreme environmental conditions, Berkner and Marshall (1965) initially hypothesized that the colonization of Earth's emergent landmass would have been impeded until the formation of an ozone shield. However, later findings showed that sulfur vapor and hydrocarbon smog in the primitive ozone-free atmosphere may have strongly attenuated ultraviolet (UV) radiation (Kasting et al., 1989), and that the Archean landmasses could have been provided sufficient refugia to early photosynthesizers even under high UV fluxes (Garcia-Pichel, 1998). From a theoretical perspective, a continental¹ microbial phototrophic biosphere could have therefore existed early, before the Great Oxidation Event (Beraldi-Campesi et al., 2009; Lalonde and Konhauser, 2015), and have colonized emergent land surfaces (Thomazo et al., 2018).

¹Continental referring throughout the text to environments experiencing subaerial exposure and desiccation (e.g., fluvial systems, alluvial fans, dryland, and playas) associated with a strictly terrestrial biosphere and excluding fully aquatic ecosystems (e.g., lakes, ponds, and geothermal springs).

Today, the strictly microbial terrestrial phototrophic biosphere is dominated by biological soils crusts (BSCs). They represent Earth's largest biofilm, covering 12% of the continents (Rodriguez-Caballero et al., 2018), typically in areas where plant growth is restricted. While they are composed of a high diversity of microorganisms, they are primarily built by cyanobacteria performing oxygenic photosynthesis (Garcia-Pichel, 2002).

Robust and direct evidence for ancient fossil BSC is found in the 1.2 Ga mid-Proterozoic Apache Supergroup in the Dripping Springs Formation of Arizona (Beraldi-Campesi et al., 2014). Indirect evidence for the presence of an Archean phototrophic biosphere is based on sedimentological observations of paleosols (3.0–3.2 Ga; Retallack et al., 2016) and geochemical arguments suggesting that microorganisms capable of photosynthesis colonized Archean continents before the Great Oxidation Event (Lalonde and Konhauser, 2015; Havig and Hamilton, 2019). An early time line for land colonization, between 3.05 and 2.78 Ga, is also suggested by ancestral state reconstruction and relaxed molecular clock analyses of cyanobacterial diversification (Blank and Sanchez-Baracaldo, 2010; Uyeda et al., 2016; Garcia-Pichel et al., 2019).

Two recent pieces of work made significant advances in the early Earth continental biosphere conundrum. Homann et al. (2018) showed that siliciclastic sediments of the 3.22 Ga Moodies Group (South Africa) preserved fossil microbial mats inhabiting continental habitats (i.e., fluvial with periods of terrestrial subaerial exposure and desiccation) and that their coupled carbon isotope compositions of organic matter and bulk nitrogen isotope compositions are statistically different from strictly marine examples preserved elsewhere in the Moodies Group (Homann et al., 2015). In addition, Thomazo et al. (2018) carried out a meta-analysis of the biogeochemical cycling of nitrogen by the modern terrestrial phototrophic biosphere and highlighted that this ecosystem would have been capable of importing nitrogen gas from the early atmosphere and exporting ammonium and nitrate to the Archean ocean, presumably through fluvial networks. The present contribution fills the gap between these two recent studies by addressing the N and C isotopic signals of modern cyanobacteria biological soil crusts (cyanoBSCs) to compare their biosignatures with the emerging geochemical continental record of Archean continental life.

2. Materials and Methods

A total of 67 cyanoBSC samples were collected from different desert areas (Supplementary Table S1). They were analyzed for their organic carbon and bulk nitrogen isotope compositions at the Biogéosciences laboratory, Université de Bourgogne, Dijon, France (Supplementary Data). Their maturity level (successional stage) was inferred based on visual observations according to the sequence provided by Garcia-Pichel (2002). Only cyanobacteria-dominated BSCs were selected for geochemical analyses since moss and lichen biocrusts are not relevant to the early Earth microbial environment. Although cyanobacteria are always largely dominating the biomass of early (light) to middle successional stage (dark) BSCs (Chilton et al., 2018), we ran a nonparametric Mann–Whitney U test to determine if lichen-bearing middle-stage BSCs ($n = 15$) (Supplementary Table S1) bear different C and N isotope distributions. No significant statistical difference was observed in N isotope compositions between early- to middle-stage cyanoBSCs and middle-stage lichen-bearing BSCs (Supplementary Fig. S1). However, for C isotope compositions, measured values are statistically different ($p < 0.01$) between these two categories. Lichen-bearing BSCs were therefore excluded from our analyses. Early- and middle-stage cyanoBSCs are statistically identical in their C and N isotope compositions ($p = 0.37$ and 0.39 , Supplementary Fig. S2).

3. Results

The isotopic signatures of cyanoBSCs show mean values of -22.8 ± 2.3 per mil and 3.4 ± 3.5 per mil for the $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}_{\text{bulk}}$, respectively. With the exception of one study where extreme $\delta^{15}\text{N}_{\text{bulk}}$ values were reported in BSCs from Zambia and Botswana (Aranibar et al., 2003), the $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}_{\text{bulk}}$ data available in the literature are consistent with our measurements (Supplementary Fig. S3). The

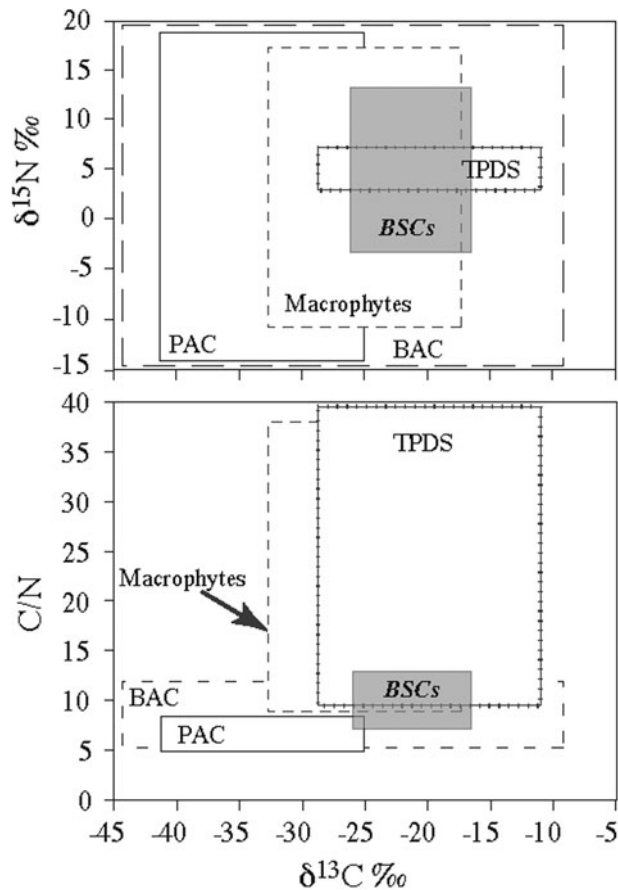


Fig. 1. Typical ranges of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C/N ratio for the main sources of organic matter in continental hydrogeological systems (modified after Finlay and Kendall, 2007), compared with ranges for cyanobSCs. BAC, benthic algae and cyanobacteria; cyanobSCs, cyanobacteria biological soil crusts; PAC, planktonic algae and cyanobacteria; TPDS, terrestrial plant detritus and soils.

C/N atomic ratio shows a mean value of 9.9 ± 1.3 , slightly 1.3 above Redfield. Figure 1 compares observed ranges of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and C/N ratio in our analyses of the main sources of organic matter in continental hydrogeological systems (Finlay and Kendall, 2007), including terrestrial plant detritus and soils (TPDS), macrophytes, benthic algae and cyanobacteria (BAC), and planktonic algae and cyanobacteria (PAC). The isotopic and elementary signatures of cyanobSCs define a restricted chemical space, partly overlapping the TPDS, BAC, and macrophyte data. Based on these isotopic signals, the BSCs and PAC reservoirs are distinguishable (Fig. 1).

Figure 2 compares the $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}_{\text{bulk}}$ signals of the cyanobSCs measured in this study with the Paleoproterozoic continental and marine organic remains preserved in the 3.22 Ga old Moodies Group, and with the Paleoproterozoic marine organic matter reservoir (after Thomazo et al., 2009). The $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}_{\text{bulk}}$ signatures of the cyanobSCs and marine Moodies Group are statistically different ($p = 0.03$ and 0.07 , respectively). However, the isotopic signatures of modern cyanobSCs are statistically indistinguishable from the continental Moodies Group ($p = 0.25$ and 0.22 for the $\delta^{13}\text{C}_{\text{org}}$ and $\delta^{15}\text{N}_{\text{bulk}}$, respectively). Moreover, the Moodies Group continental $\delta^{13}\text{C}_{\text{org}}$ values bear this characteristic signature at a regional scale and in different time units (Fig. 2). Paleoproterozoic marine isotopic signatures are consistent with reported data for marine mats from the Moodies Group, and significantly different than the cyanobSCs and the continental mats of the Moodies Group.

4. Discussion

The isotopic biosignatures of cyanoBSCs are different than the PAC reservoir and exhibit a restricted range when compared with the BAC (Fig. 1). In addition to depositional setting information, these new observations can contribute to interdisciplinary sets of data to help make an integrated biosignature assessment in the geological record. In this way, Fig. 2 thus suggests that cyanoBSCs represent modern analogues of communities that colonized Archean continents. This assumption is consistent with studies suggesting that continental colonization by microbial communities may have triggered oxidative weathering on continental surfaces before the Great Oxidation Event (Lalonde and Konhauser, 2015; Havig and Hamilton, 2019). Early life on land would have also enhanced the delivery of nutrients to the oceans such as fixed nitrogen (Thomazo et al., 2018) and would have increased the productivity of Paleoproterozoic shelves and coastal margin environments (Lyons et al., 2014). Cyano- bacterial land-based modern ecosystems may therefore hold keys in understanding how Earth's early terrestrial biogeo- chemical cycles were established and how they were linked to biogeochemical cycling in the marine environment.

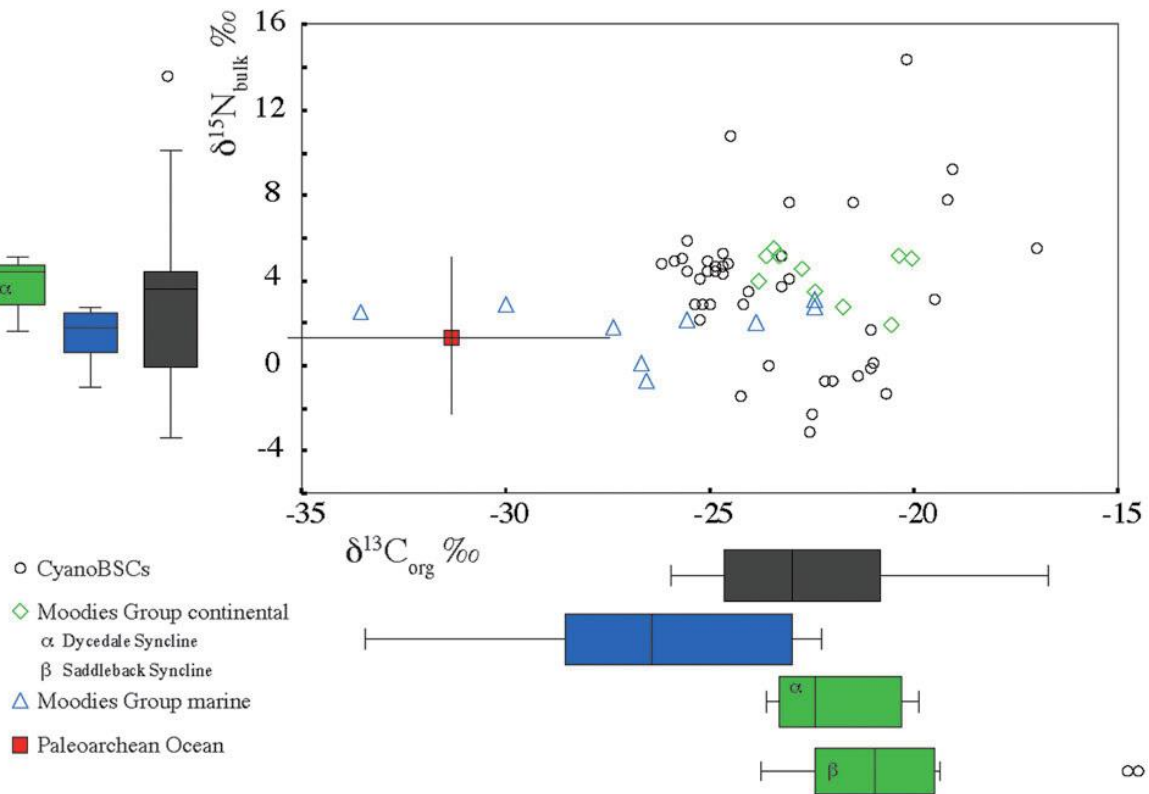


FIG. 2. Comparison of the $\delta^{13}C_{org}$ and $\delta^{15}N_{bulk}$ signals of modern analog cyanoBSCs with the Paleoproterozoic continental and marine organic remains of the Moodies Group (data from unit B of the Dycedale Syncline; Homann et al., 2018 and MdQ1 unit of the Saddleback Syncline; Gamper et al., 2012) and with the Paleoproterozoic organic matter oceanic reservoir (after Thomazo et al., 2009).

Modern examples of cyanoBSCs from desert sandy soils are thus likely close analogues for microbial communities that thrived in environments available for the development of an early phototrophic biosphere on Archean continents and rocky planetary surfaces (with reduced clays and carbonates), given the aggressive weathering regime postulated for the early Earth that was largely dominated by siliciclastic inputs (Bose et al., 2012). The Moodies Group hosts the oldest known occurrence of quartz-rich sandstones, locally interbedded with conglomerates, which were deposited in alluvial, fluvial, possibly aeolian, deltaic, tidal, and subtidal paleoenvironments (Homann et al., 2015). However, given their low preservation potential in the rock record and the multibillion-year geological history of these

terrestrial ecosystems, their detection primarily relies on geochemical proxies. As such, indirect evidence based on element mobility patterns in several Archean paleosols has been suggested to speak to the presence of an ancient terrestrial biosphere where organic ligands chelated metals during weathering (Rye and Holland, 2000). We suggest that coupled carbon and nitrogen isotopic signatures of Archean organic remains, associated with their sedimentological contexts, can provide a direct way to robustly back-track deep-time phototrophic life on land in deep time.

5. Conclusions

Using combined C and N isotope biosignatures, we showed here that biological soil crusts represent, among modern microbial ecosystems, a credible analogue for one of the oldest archives of continental life on Earth. Moreover, these communities, more widespread at the global scale than hot spring and hydrothermal systems, are thus of prime importance for untangling mechanisms and consequences of the early Earth land colonization. They also likely contain key information for understanding the evolution of global biogeochemical cycles toward their modern states.

References

Aranibar, J.N., Anderson, I.C., Ringrose, S., and Macko, S.A. (2003) Importance of nitrogen fixation in soil crusts of southern African arid ecosystems: acetylene reduction and stable isotope studies. *J Arid Environ* 54:345–358.

Beraldi-Campesi, H., Hartnett, H., Anbar, A., Gordon, G., and Garcia-Pichel, F. (2009) Effects of biological soil crusts on soil elemental concentrations; implications for biogeochemistry and as traceable biosignatures of ancient life on land.

Geobiology 7:348–359.

Beraldi-Campesi, H., Farmer J., and Garcia-Pichel, F. (2014)

Modern terrestrial sedimentary biostructures and their fossil analogs in Mesoproterozoic subaerial deposits. *PALAIOS* 29: 45–54.

Berkner, L.V. and Marshall, L.C. (1965) History of major atmospheric components. *Proc Natl Acad Sci U S A* 53:1215–1225.

Blank, C.E. and Sanchez-Baracaldo, P. (2010). Timing of morphological and ecological innovations in the cyanobacteria—a key to understanding the rise in atmospheric oxygen. *Geobiology* 8:1–23.

Bose, P.K., Eriksson, P.G., Sarkar, S., Wright, D.T., Samanta, P., Mukhopadhyay, S., Mandal, S., Banerjee, S., and Altermann, W. (2012) Sedimentation patterns during the Precambrian: a unique record? *Mar Petrol Geol* 33:34–68.

Chilton, A.M., Neilan, B.A., and Eldridge, D.J. (2018) Biocrust morphology is linked to marked differences in microbial community composition. *Plant Soil* 429:65–75.

Finlay, J.C. and Kendall, C. (2007) Stable isotope tracing of organic matter sources and food web interactions in watersheds. In *Stable Isotopes in Ecology and Environmental Science*, edited by K. Lajtha and R. Michener, Blackwell, pp 283–333.

Gamper, A., Heubeck, C., Demske, D., and Hoehse, M. (2012) Composition and microfacies of Archean microbial mats (Moodies Group, ca. 3.22 Ga, South Africa). *Microbial Mats in Siliciclastic Depositional Systems Through Time*. *SEPM Special Publication*, 101, pp 65–74.

- Garcia-Pichel, F. (1998) Solar ultraviolet and the evolutionary history of cyanobacteria. *Orig Life Evol Biosph* 28: 321–347.
- Garcia-Pichel, F. (2002) Desert environments: biological soil crusts. In *Encyclopedia of Environmental Microbiology*, edited by G. Bitton, John Wiley, New York, pp 1019–1023.
- Garcia-Pichel, F., Lombard, T., Soule, T., Wu, S., Dunaj, S., and Wojciechowski, M.F. (2019) Timing the evolutionary advent of cyanobacteria and the later Great Oxidation Event using gene phylogenies of a sunscreen. *mBio* 10: e00561-19.
- Havig, J.R. and Hamilton, T.L. (2019) Hypolith photosynthesis in hydrothermal areas and implications for cryptic oxygen oases on Archean continental surfaces. *Front Earth Sci* 7:15.
- Homann, M., Heubeck, C., Airo, A., and Tice, M.M. (2015) Morphological adaptations of 3.22 Ga-old tufted microbial mats to Archean coastal habitats (Moodies Group, Barberton Greenstone Belt, South Africa). *Precambrian Res* 266: 47–64.
- Homann, M., Sansjofre, P., Van Zuilen, M., Heubeck, C., Gong, J., Killingsworth, B., Foster, I.S., Airo, A., Van Kranendonk, M.J., Ader, M., and Lalonde, S.V. (2018) Microbial life and biogeochemical cycling on land 3,220 million years ago. *Nat Geosci* 11:665.
- Kasting, J.F., Zahnle, K.J., Pinto, J.P., and Young, A.T. (1989) Sulfur, ultraviolet radiation and the early evolution of life. *Orig Life Evol Biosph* 19:95–108.
- Lalonde, S.V. and Konhauser, K.O. (2015) Benthic perspective on Earth's oldest evidence for oxygenic photosynthesis. *Proc Natl Acad Sci U S A* 112:995–1000.
- Lyons, T.W., Reinhard, C.T., and Planavsky, N.J. (2014) The rise of oxygen in Earth's early ocean and atmosphere. *Nature* 506:307.
- Retallack, G.J., Krinsley, D.H., Fischer, R., Razink, J.J., and Langworthy, K.A. (2016) Archean coastal-plain paleosols and life on land. *Gondwana Res* 40:1–20.
- Rodriguez-Caballero, E., Belnap, J., Büdel, B., Crutzen, P.J., Andreae, M.O., Pöschl, U., and Weber, B. (2018) Dryland photoautotrophic soil surface communities endangered by global change. *Nat Geosci* 11:185–189.
- Rye, R., and Holland, H.D. (2000) Life associated with a 2.76 Ga ephemeral pond?: evidence from Mount Roe #2 paleosol. *Geology* 28:483–486.
- Thomazo, C., Pinti, D.L., Busigny, V., Ader, M., Hashizume, K., and Philippot, P. (2009) Biological activity and the Earth's surface evolution: insights from carbon, sulfur, nitrogen and iron stable isotopes in the rock record. *C R Palevol* 8:665–678.
- Thomazo, C., Couradeau, E., and Garcia-Pichel, F. (2018) Possible nitrogen fertilization of the early Earth Ocean by microbial continental ecosystems. *Nat Commun* 9:2530.
- Uyeda, J.C., Harmon, L.J., and Blank, C.E. (2016) A comprehensive study of cyanobacterial morphological and ecological evolutionary dynamics through deep geologic time. *PLoS One* 11:9.