MODERN STROMATOLITE-FORMING PROCESSES AS A FRAMEWORK FOR EVALUATING BIOGENICITY

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Stromatolite formation results from the lithification of microbial mats, which is driven by interactions among microbial communities, carbon cycling, and environmental forcing (Dupraz et al. 2009; Fig. 1). The microbial activity of the entire mat community is referred to as the "alkalinity engine," which alters the saturation index (SI) of local solutions with respect to carbonate minerals. Microbial mat communities also synthesize extracellular polymeric substances (EPS) and exude low-molecular-weight organic compounds that collectively form a matrix of extracellular organic matter (EOM). This EOM concentrates cations (e.g., Ca^{2+}, Mg^{2+}) and serves as a nucleation site (Dupraz et al. 2009). Combined, the alkalinity engine and EOM properties form lithified laminae; through iterative growth modulated by environmental variability, this shapes the macroscopic stromatolite structure (Grotzinger and Knoll 1999; Dupraz et al. 2009). Grazing, epiphyte colonization, and diagenesis (e.g., temperature and pressure) may obliterate the most prominent biogenic features of the stromatolite (Zeyen et al. 2026 this issue; Iniesto et al. 2026 this issue). A delicate balance between microbial community dynamics and environmental forcing governs the characteristic stromatolite architecture. The relative dominance of these two factors determines whether net biomass accumulation or mineral precipitation prevails, ultimately controlling lithification and preservation.

Stromatolite biogenicity is constrained by coupled biogeochemical cycles that can be resolved using molecular, geochemical, and microbiological approaches. In addition to the laminated meso-structures, biosignatures in stromatolites include stable isotopes (^{13}C, ^{34}S, ^{56}Fe, ^{98}Mo, ^{112}Cd, ^{138}Ba) (Wacey et al. 2011; Hohl and Viehmann 2021; Thomazo et al. 2026 this issue; Bruggmann et al. 2026 this issue); organic molecules (e.g., lipid biomarkers, (metalo)porphyrins) (Summons et al. 2022); microbial morphologies (e.g., filaments, EPS remnants) (Baumgartner et al. 2024); metal enrichments (e.g., bioessential metals, biogenic metals, rare earth elements) (Bruggmann et al. 2026 this issue); mineral fabrics (e.g., pyrite and other authigenic microstructures) (Baumgartner et al. 2024; Thomazo et al. 2026 this issue); and gas bubbles/gaseous metabolic products (e.g., methane, oxygen, nitrous oxide, and methyl sulfides).

Biogeochemical carbon cycling can provide important insights into stromatolite biogenicity, particularly when evaluated in concert with other biosignatures. In the early Archean, carbon cycling was likely coupled to the cycling of iron, (cryptic) sulfur, and/or arsenic (Wacey et al. 2011; Sforna et al. 2014; Baumgartner et al. 2024), all of which can support phototrophic and respiratory metabolisms. Cycling of selenium and manganese appears to have become more prominent later, during the Neoarchean. Although iron and sulfur are abundant in Archean rocks, these elements participate in both biotic and numerous abiotic processes, complicating their use as standalone biosignatures (Lepot 2020). In contrast, arsenic tends to be more spatially concentrated and closely associated with organic carbon (Lepot 2020). Molecular phylogenetic analyses place the emergence of arsenic-based metabolisms at ~3.4 Ga (Lebrun et al. 2003; Van Lis et al. 2013), a timeline supported by observations of As in fossil stromatolites of that age (Lebrun et al. 2003; Baumgartner et al. 2024), highlighting arsenic cycling as a potential biosignature in Precambrian stromatolites. Consistent with this interpretation, contemporary mats that are permanently anoxic support the oxidation and reduction of arsenic, with trace amounts of arsenic present in carbonate and pyrite precipitates, as well as in EOM (Sforna et al. 2014; Visscher et al. 2020). Arsenic is associated with organics, pyrites ((As-I) replacing S(-I) or, less common, As(III) replacing Fe(II)) and As(V) is preferentially incorporated into EPS and then coprecipitates with carbonates (e.g., $Ca_x(AsO_4)_y(CO_3)_z$). Although further evidence is needed, the presence of this metalloid is thus a promising biosignature.

Morphology (e.g., domal, branching) is another key characteristic of stromatolites (Grotzinger and Knoll 1999; see Hofmann et al. 2026 this issue). Oddly, the use of the most distinctive internal property, the lamination, as a structural biosignature in the fossil record is controversial, especially for Eoarchean specimens (Allwood et al. 2018). Yet, a few stromatolitic microstructures can be confidently interpreted as biosignatures, with micropeloidal textures being particularly compelling. Micropeloids are micritic aggregates with diffuse margins that reflect progressive mineralization of EOM. They range from the Precambrian to the present and record microbial mat lithification processes, providing strong evidence of biogenicity even when cellular preservation is poor. However, it is conceivable that organic films formed abiotically through prebiotic chemistry or wet–dry cycling could mimic biological EOM. Further studies on carbonate mineralization in these abiotic organofilms are needed.

In conclusion, a deeper understanding of the processes and byproducts in modern microbialites is crucial for identifying potential traces of life in rocks. Additional work is required to assess how diagenesis and metamorphism may alter these features.

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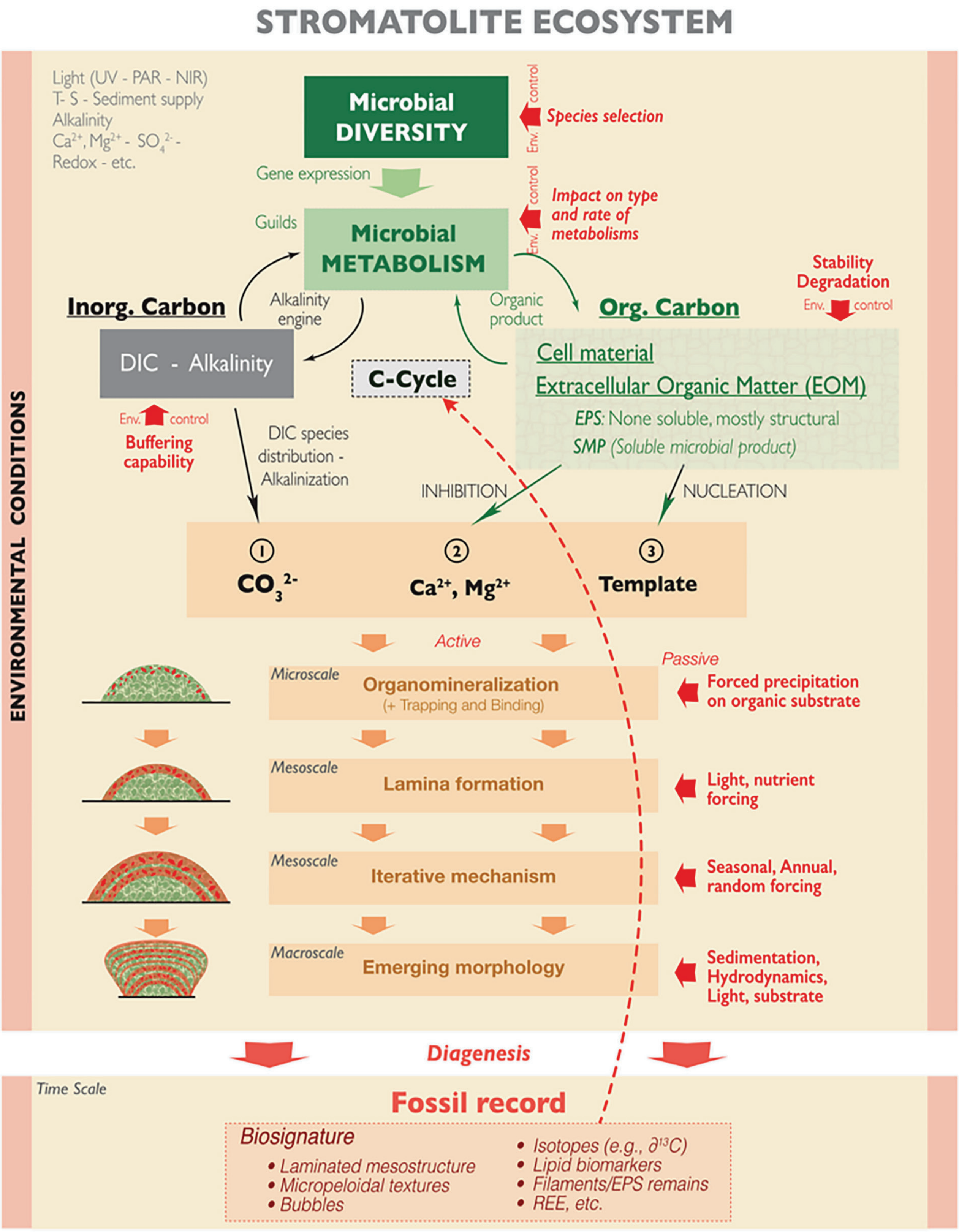

FIGURE 1 From stromatolite formation to preservation in the fossil record. Schematic view linking (i) the biological and environmental factors controlling stromatolite formation, (ii) the different processes involved in stromatolite formation, and (iii) resulting traces of life possibly preserved in the fossil record.