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Unlocking the potential of cyanobacterial biomineralization: Mechanisms, advances and promising applications

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ABSTRACT

Biomineralization results directly from microbial metabolic processes creating the conditions for inorganic minerals to deposit within and around cells. Across diverse habitats, many cyanobacterial species, biofilms or planktonic, promote extracellular calcium carbonate ($CaCO_3$) precipitation or intracellular $CaCO_3$ deposits. Although biomineralization occurs across all domains of life, cyanobacteria display an exceptional capacity for this process. Cyanobacterial mineralization is largely a byproduct of photosynthetisis, supported by carbonic anhydrases (CAs), the carbon-concentrating mechanism (CCM), and the production of extracellular polymeric substances (EPS). Environmental factors including pH, ion concentration, nutrient levels, temperature, salinity, and hydrodynamic conditions influence the occurrence and rate of mineral precipitation and its composition and morphology. Through these mineralizing activities, cyanobacteria modify sediment properties, contribute to global carbon cycling, and generate extensive geological formations. Simultaneously, the formation of mineralized structures, often associated with organic matrices, enhances cyanobacterial survival by providing mechanical protection, improving metabolic efficiency, and increasing ecological competitiveness. In this review, we present an integrated perspective on the biological, metabolic, molecular, and environmental foundations of cyanobacterial biomineralization. Highlighting the mechanisms connecting EPS synthesis, biofilm dynamics and photosynthesis to mineral formation in natural and artificial environments. Compared with other microbial systems, cyanobacterial biomineralization offers a sustainable safe option for promising applications, particularly bioconsolidation for cultural heritage conservation. Their controllable growth, adaptability to diverse substrates and challenging environments, and ability to form cohesive mineral–organic matrices make them especially suitable for novel and impactful applications such as the bioconsolidation of weathered stone heritage and the production of geomaterial under microgravity.

1. Introduction

Biomineralization, is the biologically mediated process by which organisms precipitate minerals. It is a widespread and fundamental natural phenomenon that has shaped Earth's biosphere and geosphere for billions of years (Falkenroth and Dann, 2025). It encompasses diverse mechanisms by which living organisms or cells interact with their environment to produce inorganic structures,

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often embedded within or associated with organic matrices (Gilbert et al., 2022). These processes fulfill critical biological and physiological roles, ecological interactions and have significant geochemical impacts, contributing to sediment formation, elemental cycling, and the long-term regulation of Earth's climate (Cosmidis and Benzerara, 2022; Kamennaya et al., 2018; Wild et al., 2022).

Cyanobacteria, a group of gram-negative photosynthetic bacteria, are important primary producers and are among the most significant microbial taxa contributing to biomineralization, particularly in the formation of carbonates and phosphates (Benzerara et al., 2014). For instance, cyanobacterial carbonate mineral precipitation, ranging from calcite to magnesite, was investigated in a variety of fresh to saline-alkaline lakes on the Cariboo Plateau in central British Columbia, Canada (Ferris et al., 1994). Elevated magnesite saturation occurred in areas where water chemistry is controlled by the weathering of Mg-rich olivine basalt, whereas high calcite saturation was observed where the bedrock consists of mixed lithologies including basic lava flows, limestone, argillite, and chert. Another study in British Columbia evidenced that cyanobacteria could induce the precipitation of magnesium carbonates, specifically dypingite ($Mg_5(CO_3)_4(OH)_2{\cdot}5H_2O$), in an alkaline wetland (Power et al., 2007). Batch reactor experiments performed in the presence of Salda Lake (Turkey) cyanobacteria demonstrated a linear 1:1 molar relationship between Mg-carbonate precipitation and cyanobacterial biomass production, consistent with the theoretical values of mineral formation during photosynthesis (Shirokova et al., 2013). Although Mg-silicate mineral precipitation by cyanobacteria is also possible, Lamérand et al., showed that Mg-carbonate precipitation rates were similar in the presence and absence of silicon, indicating a strong control exerted by cyanobacterial activity (Lamérand et al., 2022a). Cyanobacteria form Mg-rich carbonate minerals only in specific surface environments, whereas Ca-rich carbonates are far more widespread (Shirokova et al., 2013), and therefore the following discussion focuses primarily on calcium carbonate bioprecipitation.

Aquatic and terrestrial cyanobacteria have been reported to precipitate calcium carbonate ($CaCO_3$), considered a byproduct of the photosynthetic metabolism, driven by environmental factors that promote $CaCO_3$ crystal formation and morphology (Jung et al., 2024; Raven and Giordano, 2009). When the microbial metabolism modifies the microenvironment surrounding the cells, factors like alkaline conditions in the nearby aqueous stage, availability of calcium ($Ca^{2\ +}$) cations, and presence of heterogenous crystallization nuclei facilitate the process (Falkenroth and Dann, 2025; Jroundi et al., 2022). Extracellularly, cyanobacteria provide all these conditions as follows. Photosynthetic carbon assimilation of environmental CO_2 (from HCO_3^-) releases hydroxide ions (OH^-) which in turn mediate the alkalization of the media and increase the pH to ~10.5 (Martinho de Brito et al., 2022). This process is potentially aided by active carbonic anhydrase (CA) enzymes present in some cyanobacteria (Tang et al., 2022). CAs catalyse the hydration of water-dissolved CO_2 into HCO_3^-/H^+, re-capturing CO_2 leaving the cell by diffusion and concentrating it near the RuBisCO (Falkenroth and Dann, 2025; Piatka et al., 2022), aided by bicarbonate and CO_2 transporters (Kamennaya et al., 2018). Biofilms are formed at the fluid–mineral interface accompanied by or just with the production of cell-surface components such EPS (specifically acidic exopolysaccharides) (Kamennaya et al., 2018; Martinho de Brito et al., 2023, 2022; Wild et al., 2022) and negatively-charged surface-layer (S-layer) proteins (Schultze-Lam et al., 1992). These components attract Ca^{2+} and provide nucleation sites for $CaCO_3$ mineralization (Falkenroth and Dann, 2025) (Table 1).

Cyanobacterial biomineralization is not solely extracellular and a byproduct of photosynthesis, but intracellular calcium deposits have also been documented in numerous species of cyanobacteria indicating a controlled biomineralization process (Benzerara et al., 2022, 2014; Ragon et al., 2014). These deposits composed of amorphous calcium carbonate (ACC), are a less stable, highly soluble (and therefore transient) form of $CaCO_3$ that appear to be encapsulated in granules (Cam et al., 2018; Mehta et al., 2022). Although calcite accumulation has been suggested to be enhanced by nucleation of ACC (Oppenheimer-Shaanan et al., 2016), whether it is released during cell maturation and/or precipitated externally as $CaCO_3$ crystals is still undetermined (Cam et al., 2018; Kolodkin-Gal et al., 2023).

The importance of biomineralization lies not only in the evolutionary success it confers to organisms but also in its role as a biogeochemical driver. By forming mineralized structures, organisms enhance survival through mechanical protection, improved metabolic efficiency, and ecological competitiveness. Modern day cyanobacteria retain and exhibit remarkable physiological plasticity possibly derived from their evolutionary genetic history (Kamennaya et al., 2018), adapting their metabolism to a wide range of environmental conditions like changes in light, nitrogen availability, temperature, and carbon dioxide levels (Aguilera et al., 2020; Kamennaya et al., 2018). This plasticity allows them to survive in diverse and extreme habitats by modulating metabolic capacities such as photosynthesis, nitrogen assimilation from alternative sources, and carbon fixation through the carbon-concentrating mechanism (CCM) (Kamennaya et al., 2018; Puszynska and O'Shea, 2017); which in turn enhances their survival and ecological competitiveness. Cyanobacteria-dominated microbial mats in aquatic environments, uniquely adapted to their mineral environment, prevail by forming biofilms encased in $CaCO_3$ (stromatolites or microbialites) at the fluid–mineral interface (Jung et al., 2024; Wild et al., 2022). In contrast, cyanobacteria that occupy a different ecological niche in terrestrial environments (i.e., caves), form $CaCO_3$ sheaths (biocrusts) around individual filamentous heterocytous cells (Jung et al., 2024). Unicellular planktonic cyanobacteria can produce large amounts of EPS that can protect a cell from its environment by creating a mechanical and a diffusion barrier and by accumulating protective compounds. In these microenvironments, both biofilm and planktonic cyanobacteria, can bypass the average conditions by regulating locally the chemical potential of targeted species to generate favorable conditions (i.e., pH) and protect themselves. For instance, a highly hydrated EPS creates a diffusion barrier, moving the reactive boundary away from the cell surface, preventing harmful interactions between iron (Fe^{2+}) and oxygen and protecting the cell from oxidative damage and desiccation. Also, the immobilization of toxic heavy metals by the EPS would prevent them from reaching the cell. Finally, accumulation of UV-screen pigments and retention of metal cations and Fe-oxides in the EPS matrix could shield the planktonic cell from desiccation and harmful radiation (Jung et al., 2024; Kamennaya et al., 2018; Wild et al., 2022). The release of planktonic cells accompanying these processes, could help colonize other surfaces to grow as mats/biofilms and persist encrusted until having to move again (Kamennaya et al., 2018).

At the same time, cyanobacterial mineralizing activities can alter sediment properties, influence global carbon cycling, and create

Table 1
List of reported cyanobacterial strains that perform extracellular biomineralization *in situ* and in experimental settings and/or applications. The biomineralization associated genes/proteins are detailed as follows: CO$_2$ uptake: NDH-1$_4$ complex (*ndhD4, ndhF4, cupB* genes), NDH-1$_3$ complex (*ndhD3, ndhF3, cupA*), *BicA* (Na+ - dependent symporter; *bicA2*); HCO$_3^-$ transport: *cmpABCD* operon (ATP-binding cassette transporter; BCT1), *BicA* (Na$^+$ - dependent symporter; *bicA1* and *bicA2*); *ccmKLMNOP* (CCM gene cluster corresponding to β-Carboxysomal shell proteins), *Sbt* (Na+ - dependent symporter; *sbtA, sbtB*); Regulation: *CmpR* (transcriptional activator of BCT1),*CcmR* (*NdhR*; negative regulator of CO$_2$-responsive genes *ndh-I3, sbt,bic*, and CO$_2$-responsive genes different to *cmpABCD*), CyABrB2 (blocks the expression of NDH-1$_3$ and *SbtA* along with *CcmR*); Oscillin (single calcium-binding protein; helically arranged as surface fibrils constituting the external layer on top of the S-layer of the cells).

EXTRACELLULAR BIOMINERALIZATION

Species	ID	Environment of Origin	Type of growth[a]	Validated CCM	CA genes[b, c]	Biomineralization associated genes/proteins	Calcified environment/ Application	References
Dichothrix sp.		Marine	Biofilm				Microbial mats (Microbialite, Stromatolites).	(Jung et al., 2024; Kamennaya et al., 2012; Planavsky et al., 2009)
Entophysalis major		Marine, sand	Biofilm				Intertidal microbial mats (Stromatolites). Calcite nucleation on cyanobacterial sheaths (Laboratory).	(Jung et al., 2024; Pentecost and Bauld, 1988)
Gloeocapsa sp.	PCC 73106	Sphagnum bog (wetland ecosystem)	Biofilm				Limestone building material. Improved performance of cement mortar. Experimental modeling of CaCO$_3$ precipitation (Laboratory).	(Bundeleva et al., 2014; Cam et al., 2018; Rodriguez-Navarro et al., 2012; Zhu et al., 2017)
	PCC 7428	Thermal	Both					(De Wever et al., 2019)
Geitleria (calcarea, appalachiana, floridana)		Aerophytic	Biofilm				Calcareous, limestone, and terrestrial caves.	(Friedmann, 1979; Jung et al., 2024; Kilgore et al., 2018)
Homoethrix spp. (crustracean, gracilis, borneti, poljanskii)		Freshwater (calcareous stream)	Biofilm				Microbial mats (Microbialites, Stromatolitic cushions). Calcareous streams.	(Kamennaya et al., 2012; Merz, 1992; Pentecost, 1988)
Leptolyngbya sp.	NIES-2104	Freshwater, marine	Biofilm				Evaluation of CaCO3 nucleation (Laboratory). High CO2 fixation (Laboratory).	(Shiraishi et al., 2020)
Lyngbya spp. (aestuarii, incrustatum)		Marine, sand	Biofilm				Microbial mats. Stream crusts in travertine deposits.	(Jung et al., 2024; Kremer et al., 2008; Pentecost, 1995; Pentecost and Bauld, 1988; Power et al., 2007)
Loriella osteophila		Aerophytic	Biofilm				Human bones. Limestone and cave walls.	(Hoffmann, 1990; Jung et al., 2024; Roldán et al., 2004)
Oscillatoria willei	BDU130791	Marine	Both				Ossein effluent treatment.	(Sidhu et al., 2022; Sundaram et al., 2014)
Phormidium valderianum	BDU20041	Marine	Both					(Ojha et al., 2025; Sidhu et al., 2022; Sundaram et al., 2014)
Phormidium ambiguum	NIES-2119	Freshwater	Biofilm				Evaluation of CaCO3 nucleation (Laboratory). High CO2 fixation (Laboratory).	(Shiraishi et al., 2020)
Phormidium spp. (crosbyanum, TK1, hendersonii,		Marine (Lagoon), freshwater	Biofilm			*P. uncinatum* has oscillin (single calcium-binding protein).	Microbial mats (microbialite domes).	(Gautret et al., 2004; Jung et al., 2024; Kamennaya et al., 2012; Komárek et al., 2003; Shiraishi et al., 2020)

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Table 1 (*continued*)

EXTRACELLULAR BIOMINERALIZATION

Species	ID	Environment of Origin	Type of growth[a]	Validated CCM	CA genes[b, c]	Biomineralization associated genes/proteins	Calcified environment/ Application	References
laysanense, incrustatum, uncinatum)								
Pleurocapsa sp.		Marine (soda lake), aerophytic	Biofilm		*ccaA* (β-CA; C)	*Pleurocapsa sp.* PCC 7327 has CO_2 uptake genes (NDH-1_4 and NDH-1_3 complexes), HCO_3^- transport genes (*cmpABCD* operon, *bicA1*) and CCM gene cluster (*cmKLMNO*).	Microbial mats (microbialites, stromatolites).	(Jung et al., 2024; Kamennaya et al., 2012; Kaźmierczak et al., 2011; Kempe et al., 1991; Klanchui et al., 2017)
Plectonema gloeophilum		Freshwater	Biofilm				Microbial mats encrsuted with $CaCO_3$.	(Jung et al., 2024)
Pseudanabaena minuta		Alkaline lake	Biofilm				Microbial mats (Tufa deposits). Calcite nucleation on cyanobacterial sheaths (Laboratory).	(Pentecost and Bauld, 1988)
Rivularia halophila		Hypersaline, alkaline lake	Biofilm				Microbial mats encrusted and surficially whitened with $CaCO_3$. Alpine tufas (CaCO3 rocks). Calcareous streams.	(Shalygin et al., 2018)
Rivularia spp. (haematites, dura, rufescens)		Freshwater, marine, tufas	Biofilm				Microbial mats encrusted and surficially whitened with $CaCO_3$. Alpine tufas ($CaCO_3$ rocks). Calcareous streams.	(Brandes et al., 2015; Kamennaya et al., 2012; Merz, 1992; Pentecost and Talling, 1997; Sanders et al., 2011; Shalygin et al., 2018)
Spirulina spp. (platensis, subsalsa)		Marine, freshwater (alkaline lakes)	Both				Evaluation of $CaCO_3$ nucleation (Laboratory). High CO_2 fixation (Laboratory).	(Arumugam et al., 2022; Ojha et al., 2025; Ramanan et al., 2010; Shiraishi et al., 2020; Sidhu et al., 2022)
Synechococcus elongatus	PCC 7942	Freshwater	Both	Yes	*ccaA* (*icfA*; C), *ecaA* (α-CA; N-C)	*chpX* / *chpY* genes. CO_2 uptake: NDH-1_4 and NDH-1_3 complexes, *bicA2*, regulator *CcmR*. HCO_3^- transport: *cmpABCD* operon, *SbtA*, regulator *CmpR*. CCM gene cluster: *ccmKLMNOP*	Increased strenght cement mortar. Living Building Materials (LBM).	(Heveran et al., 2020; Liang et al., 2013; Ludwig et al., 2000; Maeda et al., 2002; Noreña-Caro and Benton, 2018; Obst et al., 2009; Price et al., 2008; Reinhardt et al., 2023; Srinivas M et al., 2021; Tang et al., 2022)
Synechococcus sp.	PCC 7002	Marine	Both	Yes	*icfA* (C)	CO_2 uptake: NDH-1_4 and NDH-1_3 complexes, *bicA2, regulator CcmR.* HCO_3^- transport: *BicA* (*bicA1, bicA2*), *SbtA*. CCM gene cluster: *ccmKLMNOP*	Increased strenght cement mortar. Living Building Materials (LBM).	(Burnap et al., 2015; Jiang et al., 2013; Ludwig et al., 2000; Ludwig and Bryant, 2012; Noreña-Caro and Benton, 2018; Price et al., 2008)
	PCC 8806	Marine (lagoon)	Both				Concrete restoration	(Kamennaya et al., 2018; Lee et al., 2006, 2004; Liang et al., 2013; Ojha et al., 2025; Zhu et al., 2015)
	PCC 8807	Marine (lagoon)	Both					(Lee et al., 2006, 2004; Liang et al., 2013)

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Table 1 (*continued*)

EXTRACELLULAR BIOMINERALIZATION

Species	**ID**	**Environment of Origin**	**Type of growth**[a]	**Validated CCM**	**CA genes**[b, c]	**Biomineralization associated genes/proteins**	**Calcified environment/ Application**	**References**
	GL24	Meromictic lake	Both				Microbial reef in lake shore (thrombolitic biotherm on the steep sides of the lake basin and on almost every solid surface (sticks, rocks, etc.) within the photic zone).	(Douglas and Beveridge, 1998; Kamennaya et al., 2012; Schultze-Lam and Beveridge, 1994)
Synechocystis sp.	PCC 6803	Freshwater	Both	Yes	*ccaA* (C), *ecaB* (β-CA; N-C)	Ca^{2+}/H^{+} Exchanger (*Slr1336*). CO_2 uptake: NDH-14 and NDH-13 complexes, *BicA* (*bicA1, bicA2*), regulators *CcmR* and *CyABrB2.* HCO_3^- transport: *cmpABCD* operon (BCT1 transporter), *BicA* (*bicA1, bicA2*), *Sbt* (*sbtA, sbtB*), regulators *CmpR and CyABrB2.* CCM gene cluster: *ccmKLMNOP.*	Increased calcification rate and stronger Ca^{2+} binding ability. Induction of calcite precipitation.	(Han et al., 2013; Jiang et al., 2013; Lieman-Hurwitz et al., 2009; Ludwig et al., 2000; Noreña-Caro and Benton, 2018; Price et al., 2008; Tang et al., 2022)
Synechocystis pevalekii	BDHKU 35101	Marine	Both				Sand consolidation. Enhancement of mechanical and permeability properties of cement mortar.	(Ojha et al., 2025; Sidhu et al., 2022)
Schizothrix sp.		Freshwater (calcareous stream), marine lagoon	Biofilm	Yes				(Gautret et al., 2004; Kamennaya et al., 2012; Merz, 1992)
***Scytonema spp.* (*crustaceum, myochorus,* NIES-2130, *mirabile, julianum*)**		Aerophytic, freshwater, alkaline lakes, soil	Biofilm	Yes			Aerial or subaerial growth (on alkaline substrata, wet rocks, wood, and soil), sometimes encrusted with calcium carbonate. Some species grow in the periphyton in lakes (mainly calcareous) and at sea coasts, terrestrial caves and stone walls. Alpine tufas ($CaCO_3$ rocks). Evaluation of $CaCO_3$ nucleation (Laboratory).	(Défarge et al., 1994; Hoffmann, 1992; Jones and Peng, 2014; Jung et al., 2024; Komárek et al., 2003; Merz, 1992; Pentecost and Bauld, 1988; Roldán et al., 2004; Sanders et al., 2011; Shiraishi et al., 2020; Thiel et al., 1997)
Trichodesmium erythraeum	IMS101 (CCMP1985)	Marine	Planktonic			CO_2 uptake: NDH-14 complex. HCO_3^- transport: *BicA.*	Calcified bloom (Laboratory)	(Kamennaya et al., 2012; Kranz et al., 2010; Price et al., 2008)

[a] The type of growth is classified as biofilm, planktonic or the capability of growing as both.

[b] C: Carboxysomal

[c] N-C: Non-carboxysomal

large-scale geological deposits that persist for millions of years. The reciprocal interactions between microorganisms and the Earth's surface minerals were evident with the terrestrial expansion of early photosynthetic communities in the Precambrian (Wild et al., 2022) and the origin of fossilization and preservation of microorganisms in rocks is their entombment within a mineral matrix (Cosmidis and Benzerara, 2022). Depending on the environmental or experimental conditions, the entombment could likely limit the transport of essential nutrients and energy sources to the bacteria, while also limiting the transport of waste away from the cells and preventing their motility (Cosmidis and Benzerara, 2022; Miot et al., 2015) potentially leading to cell death. Cyanobacteria can also cause erosion and release of nutrients from their substrate, increasing rock weathering rates, contributing to global elemental cycling and to the development of ecosystems (Gholipour-Shahraki et al., 2025; Kamennaya et al., 2018; Wild et al., 2022). For instance, endolithic cyanobacteria such as Chroococcales (*Chroococcidiopsis* and *Gloeocapsa*), *Synechococcus* Nägaeli, Nostocales and Oscillatoriales, have developed the capacity to colonize pore spaces and cracks of translucent rock substrates as a strategy to overcome xeric stress and extreme solar irradiance (Gholipour-Shahraki et al., 2025; Murray et al., 2022; Saiz-Jimenez et al., 1990). They can induce the localized dissolution of calcium carbonate for intracellular uptake (Fiore et al., 2025) mediated by calcium-specific ATPases (Ramírez-Reinat and Garcia-Pichel, 2012). Microbially mediated dissolution of calcium carbonate for inorganic carbon assimilation into methane (CH_4) in alkaline pH has also been reported (Fiore et al., 2025). This process is mediated by hydrogenotrophic methanogenesis (oxidation of hydrogen coupled to the reduction of carbon dioxide or bicarbonate using solid-phase carbonate minerals) (Fiore et al., 2025) and filamentous cyanobacteria can provide the necessary hydrogen for CH_4 production in archaea using this process (Berg et al., 2014). More recently, it has been demonstrated that freshwater, marine, and terrestrial cyanobacteria convert fixed inorganic carbon into CH_4 under light, dark oxic and anoxic conditions although the exact biochemical pathways involved in photosynthetic-derived CH_4 formation are still unknown (Bižić et al., 2020). All these metabolic capabilities could be translated into applications with real impact in the mitigation of greenhouse gases and the consequences of climate change (Myhr et al., 2019). This dual role, linking organismal adaptation with planetary scale processes, illustrates the profound significance of biomineralization as a biological and environmental phenomenon.

Cyanobacterial biomineralization has been previously discussed both in the context of microbially induced carbonate precipitation (MICP) involving other bacterial species and alone as a distinct topic, including the intrinsic metabolic capabilities of phototrophic bacteria such as biofilm (EPS) production and the CCM. More recently, intracellular biomineralization and applications in carbon capture and storage technologies (CCS) mostly focused on building materials, have also been extensively discussed. In this article, we highlight the contribution of cyanobacteria to biomineralization processes and provide a comprehensive view of all the cyanobacterial species with calcium carbonate biomineralization capabilities (including their genomic/molecular repertoire in the frame of their ecology) by addressing: i) biomineralization as a natural process that shapes organisms and structures; ii) environmental factors affecting biomineralization in; iii) mechanisms facilitating biomineralization in cyanobacteria iv) biomineralization occurring within cyanobacterial cells, and, finally, v) promising applications: cyanobacterial biomineralization as a strategy for bioconsolidation and the production of geomaterial under microgravity.

2. Biomineralization as a natural phenomenon shaping organisms and structures

Biomineralization encompasses both biologically induced mineralization (BIM), where metabolic activity alters environmental conditions to trigger mineral precipitation, and biologically controlled mineralization (BCM), where organisms precisely regulate nucleation and crystal growth within specialized cellular or extracellular compartments (Benzerara et al., 2014; Cosmidis and Benzerara, 2022; Mann, 2001). Many eukaryotic biominerals are formed by controlled mineralization with well-studied biological functions, such as structure (e.g. apatite in bones), protection (e.g., aragonite or silica in shells), or food acquisition (e.g., apatite in teeth) (Cosmidis and Benzerara, 2022). Prokaryotic biomineralization is mostly classified as a biologically "induced" or "influenced" process (active or passive accumulation), both can take place separately or simultaneously (Ojha et al., 2025). During biologically induced biomineralization, microorganisms play an active role in mineral precipitation by causing and/or increasing solution supersaturation though there is no organic control on crystal nucleation or growth. BIM is a result of local chemical changes (e.g. redox or pH changes) caused by the metabolic activity of viable cells (Cosmidis and Benzerara, 2022; Kolodkin-Gal et al., 2023). In contrast, alive/metabolically active cells are not necessary during biologically influenced biomineralization (alternatively "organomineralization") (Dupraz et al., 2009; Jung et al., 2024) as shown for *Sporosacina pasteurii*, where non-growing cells precipitate calcite (Mostafa et al., 2025); instead microbial cell walls or extracellular organic structures (EPS) act as nucleation surfaces catalyzing biomineralization in supersaturated solutions (Cosmidis and Benzerara, 2022; Dupraz et al., 2009; Martinho de Brito et al., 2023; Wang et al., 2012).

The biomineralization phenomenon spans all domains of life. The most common biogenic minerals formed by eukaryotes are calcite and aragonite, both $CaCO_3$ polymorphs with different crystal structure (trigonal and orthorhombic, respectively) due to their atomic configuration. They support the three-dimensional organization of mollusks, echinoderms, calcisponges, corals, certain algae, and other organisms (Dhami et al., 2013; Kolodkin-Gal et al., 2023). Marine invertebrates, corals (e.g., *Acropora* spp.) and mollusks (e.g., oysters and abalone), exemplify BCM through their ability to produce aragonite and calcite skeletons or shells (Dhami et al., 2013; Kolodkin-Gal et al., 2023). These structures provide mechanical protection and play foundational ecological roles in reef building and shoreline stabilization (Weiner and Dove, 2003). Many studies focus on the marine coccolithophore *Emiliania huxleyi* as a model organism for unicellular calcification and its role in oceanic carbon capture during climate change and ocean warming (Jung et al., 2024; Smith et al., 2012). Coccolithophore algae are the most productive calcifying organisms on the planet, covering themselves with a calcium carbonate shell called a coccosphere (Monteiro et al., 2016). They are of particular interest to those studying global climate change because, as ocean acidity increases, their coccoliths may become even more important as a carbon sink in the ocean floor after dieback (Jung et al., 2024; Smith et al., 2012). Unicellular algae contribute significantly to deep-sea carbon storage (Raven and Waite, 2004). In terrestrial systems, plants such as grasses, deposit silica as phytoliths (microscopic, rigid structures of silica that form inside and between plant cells), which strengthen leaves against herbivory and influences soil chemistry after decomposition (Saranya et al., 2024). In the animal kingdom, vertebrates produce hydroxyapatite in bones and teeth, enabling structural support, protection, and ion storage (Mondal et al., 2023).

In prokaryotes, biomineralization can take the form of intracellular magnetite crystals inside magnetotactic bacteria, providing geomagnetic navigation (Bazylinski and Frankel, 2003); or calcium, which promotes the formation of structured organic−inorganic matrices reminiscent of the calcium scaffolds generated by eukaryotic organisms in surface-associated bacterial communities called biofilms (Cosmidis and Benzerara, 2022; Kolodkin-Gal et al., 2023). Cyanobacteria are among the most significant microbial biomineralizers given their ancient evolutionary history and their impact on carbonate sedimentation throughout Earth's history. They induce carbonate precipitation by elevating local pH through photosynthesis and their activities have been instrumental in the formation of layered sedimentary structures that constitute some of the oldest macroscopic evidence of life, called stromatolites (Grotzinger and Knoll, 1999; Riding, 2011). Through their ability to mediate $CaCO_3$ precipitation, cyanobacteria not only contributed to shaping ancient landscapes (sediment stabilization and reef formation) but also to regulating atmospheric CO_2 over geological timescales (Kamennaya et al., 2018; Ludwig et al., 2000; Riding, 2006). Although microbial biomineralization of $CaCO_3$ in aquatic environments is well recognized, calcification has been observed also in terrestrial cyanobacteria in various habitats, near potential sources of Ca^{2+}, such as limestone, karst, or even bone material. The principal metabolic mechanisms mediating the cyanobacterial calcification process in aquatic and terrestrial cyanobacteria might be comparable, though it is likely that differences in environmental interactions, metabolism, and excess production of EPS in terrestrial species will show unique features of adaptation (Jung et al., 2024).

In summary, biomineralization is both a biological strategy and a geochemical force. Organisms as diverse as bacteria, diatoms, corals, mollusks, plants, and vertebrates employ mineralization for survival and ecological success. At the same time, these processes collectively shape Earth's surface environments and biogeochemical cycles, making biomineralization a phenomenon of central importance.

3. Environmental conditions influencing biomineralization in cyanobacteria

The ability of cyanobacteria to induce or control mineral precipitation is closely linked to environmental conditions that regulate metabolic activity, ion availability, and physicochemical equilibria (Falkenroth and Dann, 2025; Jroundi et al., 2022; Jung et al., 2024) (Fig. 1). Parameters such as microbial species, Ca^{2+} concentration, temperature, pH, and dissolved carbon levels govern the scale and morphology of the precipitates (Ojha et al., 2025). They can range from nanoscale mineral deposits that enhance soil texture and compressive strength to large stromatolites (Grotzinger and Knoll, 1999; Ojha et al., 2025; Riding, 2011).

Two driving forces of biomineralization are **pH**, which modulates carbonate chemistry and ion speciation, and **dissolved inorganic carbon (DIC)** availability. DIC regulates biomineralization by providing the substrate for both photosynthesis and carbonate formation (Kamennaya et al., 2012; Piatka et al., 2022). Cyanobacterial photosynthesis consumes dissolved inorganic carbon (HCO_3^-, CO_2^-) and releases hydroxide ions, raising local pH and promoting carbonate supersaturation (Arp et al., 2001; Piatka et al., 2022). Conversely, respiratory processes can lower pH and dissolve existing minerals. The balance between these processes depends on light availability and photosynthetic activity, linking biomineralization rates to diurnal cycles and seasonal dynamics (Merz, 1992; Riding, 2006). The ambient pH significantly influences the ratio of CO_2 to HCO_3^-, affecting which form of DIC the cyanobacteria will predominantly use. At pH 8.9 and higher, the activation of the CCM takes place; a switchover of the carbon source from CO_2 to increasingly active uptake of HCO_3^- (Piatka et al., 2022). Consequently, enhanced photosynthetic carbon uptake could lead to higher

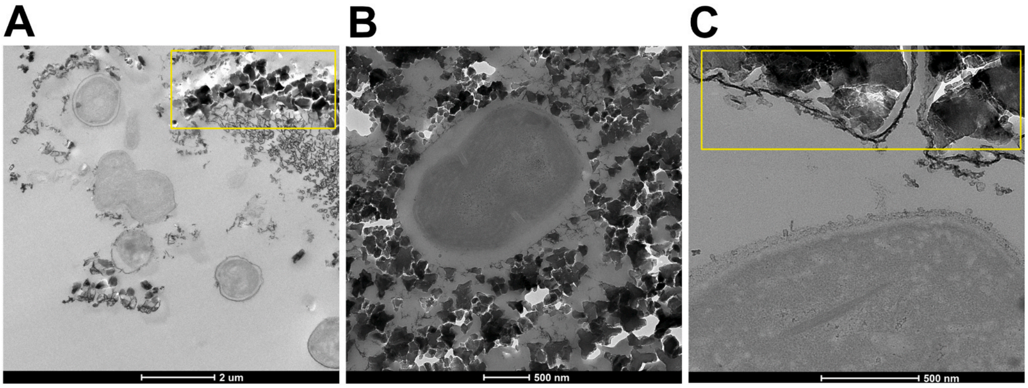

Fig. 1. Precipitation of calcium carbonate by *Synechococcus sp.* PCC 7002 in liquid media. Transmission electron microscopy images taken from biomineralization experiments performed in our laboratory (unpublished data), display normal cellular ultrastructure with the adjacent precipitated minerals (electron dense clusters, also highlighted in yellow). Group of cyanobacterial cells **(A)** and individual cells in higher magnification (500 µm) **(B, C)**.

calcification rates, potentially increasing the biomineralization efficiency (Jiang et al., 2023). At alkaline pH, high bicarbonate and carbonate ion concentrations facilitate precipitation of calcium carbonate and related minerals (Cosmidis and Benzerara, 2022; Monteiro et al., 2016). Although during MICP, the optimal pH in terms of enhancing the strength of rocks and soil ranges from 7.0 to 8.0, the growth of larger crystals with stronger interparticle bonding has been observed at a pH below 8, where the supersaturation concentration of carbonate ions tends to be relatively low (Jiang et al., 2023). Different morphologies of calcium carbonate crystals have been shown to be pH dependent. In *Bacillus sp.*, irregular polygonal plates at pH 7, diamond-shaped structures at pH 7.5, and double-spherical shapes at pH 8.0 have been observed (Li et al., 2013).

Ion availability in the surrounding environment is another key determinant. Elevated concentrations of calcium, magnesium, and other divalent cations enhance carbonate mineral formation (Dittrich and Sibler, 2010; Han et al., 2013). For instance, lowering of solution saturation by active uptake of Ca inducing calcium carbonate dissolution has been shown for some cyanobacterial euendoliths (Cam et al., 2018). The ratio of magnesium (Mg^{2+}) to Ca^{2+} influences whether calcite, aragonite, or dolomite phases dominate (Kenward et al., 2009), and high Ca^{2+} availability favors nucleation and precipitation, while low calcium conditions may suppress carbonate formation even under alkaline conditions (Kamennaya et al., 2012). In cyanobacteria, Ca^{2+} signaling plays a crucial role during stress responses to reactive oxygen species (ROS), changes in pH, temperature, salt, or osmotic stress (Mantovani et al., 2023; Müller et al., 2025; Torrecilla et al., 2004, 2000; Verma et al., 2018). Ca^{2+} is also implicated in the regulation of photosynthesis, specific sugar and fatty acid metabolic pathways, and carbon/nitrogen metabolism by yet unknown mechanisms (Mantovani et al., 2023; Müller et al., 2025; Verma et al., 2018; Walter et al., 2020, 2019). It has been found that Ca^{2+}−transporting ATPases, motility proteins, and two−component systems in bacteria can act in calcium concentration−dependent ways (Lee and Park, 2019). At least in some cyanobacteria, Ca^{2+}/H^{+} transmembrane exchangers regulate the intracellular concentration of Ca^{2+} at low levels by exporting calcium extracellularly, favoring further $CaCO_3$ biomineralization (Cam et al., 2018; Falkenroth and Dann, 2025; Jiang et al., 2013). In cyanobacteria, Ca^{2+} was found to stimulate intracellular pH homeostasis in low external pH, thus preventing acidification of the cytoplasm and protecting physiological processes such as growth, photosynthesis and nitrogen fixation from inhibition (Walter et al., 2019).

The **availability and concentration of nutrients** influence biomineralization potential. Nitrogen and phosphorous are key limiting nutrients that affect cell density and growth (Corredor et al., 2021; Ferreira-Mendes et al., 2022). Nitrogen and phosphorus limitation often enhances calcification because nutrient scarcity increases the reliance on photosynthetic carbon uptake, driving localized alkalinization (Merz, 1992; Merz-Preiß and Riding, 1999). Conversely, nutrient−rich conditions can suppress carbonate precipitation by stimulating heterotrophic activity within microbial consortia, increasing respiration and CO_2 release (Dupraz and Visscher, 2005). Phosphorous can alter the properties of cyanobacterial cell surfaces and affect the synthesis of EPS, which in turn affects their ability to promote the nucleation of calcium carbonate to facilitate biomineralization. Phosphorus limitation has a greater impact on *Synechococcus* cellular and extracellular properties than does nitrogen limitation. Under P−limiting conditions, many cyanobacterial cells store polyphosphate reserves and increase the production of extracellular phosphatases to obtain phosphate from organic substrates (Paulo et al., 2018; Prieto et al., 1997).

Temperature and **salinity** also exert important controls. Higher temperatures generally accelerate metabolic rates and carbonate precipitation kinetics, though extreme heat can limit cyanobacterial growth (Arp et al., 2010). Salinity influences both ion activity and cyanobacterial physiology, with hypersaline environments often yielding distinctive mineral fabrics associated with halotolerant taxa (Merz-Preiß and Riding, 1999). Finally, **hydrodynamic conditions** such as water turbulence, flow, and mixing determine the diffusion boundary layer around cells and mats, thereby controlling the extent of localized pH shifts and ion gradients (Stal, 2002). Stagnant waters may enhance supersaturation near the microbial surface, whereas strong currents could disperse ions and inhibit precipitation.

In summary, cyanobacterial biomineralization emerges from the interplay of biological metabolism with environmental drivers such as pH, ion concentration, nutrient availability, temperature, salinity, and hydrodynamics. These factors not only dictate the occurrence and rate of mineral precipitation but also shape the mineralogical composition and morphology of the resulting deposits. Such sensitivity to environmental conditions makes cyanobacteria valuable recorders of past environments and promising agents for applied biomineralization strategies (Dupraz et al., 2009; Riding, 2011).

4. Mechanisms that facilitate cyanobacterial biomineralization

4.1. Biofilm growth and EPS formation

Cyanobacteria commonly grow as biofilms embedded within extracellular polymeric substances, which are central to their ability to induce and control biomineralization (Martinho de Brito et al., 2023). EPS are complex matrices of polysaccharides, proteins, lipids, and nucleic acids with high abundance of predominantly negatively charged biomolecules. They include amino acids and saccharides (with carboxyl, hydroxyl, and sulfate moieties), as well as divalent cations (Ca^{2+} and Mg^{2+} ions) for charge neutralization and bridging between the organic molecules (Decho and Gutierrez, 2017; Jung et al., 2024; Lee and Park, 2019). Several excellent reviews have explored the complexity of cyanobacterial EPS—including their composition, structure, regulatory drivers, biosynthetic genes, and functional roles—and the reader is referred to these works for further detail (Mota et al., 2021; Pereira et al., 2009; Rossi and Philippis, 2015).

EPS provide structural stability, retain moisture, and mediate interactions with the surrounding environment (Decho and Gutierrez, 2017). The production and composition of EPS can differ depending on the species of microorganisms, their metabolism and stage of growth; and are also affected by their specific environment and abiotic stressors (e.g. nutrient availability, pH, temperature, light, salinity) (Martinho de Brito et al., 2023).

Within the context of mineral formation, EPS act as reactive interfaces where biochemical activities and physicochemical conditions converge to promote nucleation and growth of carbonate minerals (Dittrich and Sibler, 2010; Jroundi et al., 2022) (Fig. 2). One of the key roles of EPS in cyanobacterial biomineralization is their ability to bind Ca^{2+} and Mg^{2+}, not only to concentrate ions near the cell surface but also to reduce their mobility, facilitating the necessary local supersaturation required for precipitation (Dittrich and Sibler, 2010; Jung et al., 2024). The decrease in carbonate saturation through complexation of Ca^{2+} by the EPS in biofilms has been reported in field observations (Arp et al., 1999). Therefore, the EPS function as mineralization (carbonate precipitation) templates by providing nucleation sites initially binding Ca^{2+} and subsequently releasing calcium ions during EPS alteration and degradation (Dupraz and Visscher, 2005; Martinho de Brito et al., 2023), while also actively shaping mineral morphology and crystal orientation (Addadi and Weiner, 1992; Liang et al., 2013). The EPS may also control the morphology and/or abundance of the minerals that are formed through specific functional group composition and structural architecture (Dupraz et al., 2009; Martinho de Brito et al., 2023; Wang et al., 2012). From the perspective of microbial signatures and in terms of polymorphic differences, abundant EPS apparently favors the precipitation of calcite, the more stable polymorph of calcium carbonate (Mehta et al., 2022; Tourney and Ngwenya, 2009). In *Bacillus licheniformis*, the release of dissolved organic carbon (DOC) indicated that the EPS complexes calcium ions, reduces the $CaCO_3$ saturation and favors the precipitation of calcite over that of vaterite (Rodriguez-Navarro et al., 2012; Tourney and Ngwenya, 2009).

EPS also play protective and adaptive roles that indirectly support biomineralization. By forming hydrated gels, EPS buffer cells against desiccation, UV stress, and fluctuations in salinity or temperature (Kamennaya et al., 2018); common conditions in carbonate−precipitating environments such as arid soils and shallow lakes (Rossi et al., 2018). It has been shown that cells excrete the assimilated excess carbon as polysaccharides, with the formation of mucilage-rich cell aggregates (Kamennaya et al., 2018). Additionally, EPS can encapsulate and immobilize precipitated minerals, contributing to the mechanical stability of biofilms and their role in bioconsolidation of substrates such as soil or stone (Decho and Gutierrez, 2017; Jroundi et al., 2010; Kimura and Okuro, 2024; Rossi et al., 2018).

Biofilm formation further enhances biomineralization by creating microenvironments with steep gradients in pH, oxygen, and inorganic carbon species (Dupraz et al., 2009). Photosynthetic activity within biofilms elevates pH and depletes dissolved CO_2, favoring carbonate precipitation, whereas respiration and fermentation in deeper biofilm layers generate localized acidity that can dissolve and recycle carbonates. This dynamic balance between mineral dissolution and precipitation contributes to the development of laminated structures characteristic of microbialites and stromatolites, where complex microbial communities have distinct metabolic capabilities at play (Dupraz et al., 2009; Jung et al., 2024; Lamérand et al., 2022b; Riding, 2006). In natural systems and in blooms, biofilm growth and EPS production in cyanobacteria are frequently associated with biomineralization (Arp et al., 2001; Jung et al., 2024; Martinho de Brito et al., 2023; Thompson et al., 1997). It has been shown for diatoms and *Synechococcus* that nutrient−deficient conditions can enhance the production of EPS during stationary phase, as carbohydrate reservoirs (Bhosle et al., 1995; Ciebiada et al., 2020; Martinho de Brito et al., 2023). For *Synechococcus* the greater amount of negatively charged functional groups of EPS from the late stationary phase resulted in a higher Ca-binding capacity (Martinho de Brito et al., 2023), potentially aided by the presence of sulfated constituents (Maeda et al., 2021). Terrestrial cyanobacteria often produce large amounts of EPS as a strategy to move, exchange metabolites, as well as protection from desiccation and strong radiation; while typically white structures of fine crystals with varying thicknesses and crystal orientations develop around the filamentous cells (Jung et al., 2024). In aquatic environments, cyanobacteria−dominated microbial mats form living biofilms or stromatolites, but cyanobacterial blooms also have the potential for biomineralization. *Synechococcus spp.* blooms can cause whiting events, determined by the presence of $CaCO_3$ minerals in the surface of the water (Martinho de Brito et al., 2023; Thompson, 2000) Although, the precise mechanisms involved in cyanobacterial bloom calcification are still unknown, de Brito et al., hypothesized a model for biomineralization during blooms (Martinho de Brito et al., 2023): depending on the three-dimensional structure of the EPS and surface properties, nucleation may yield

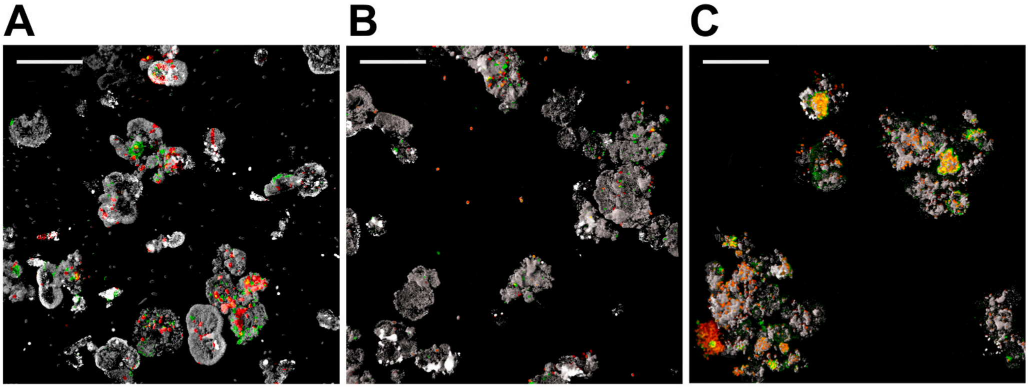

Fig. 2. Confocal fluorescence microscopy of the mineral/biofilm interface in *Synechococcus sp.* PCC 7002. A, B and C. The living cells display red autofluorescence and the biofilm matrix (EPS) display green fluorescence (concavalin A, Alexa fluor 488 staining). $CaCO_3$ aggregates (in grey) precipitated during biomineralization and surrounding the cells constitute the mineral phase. Scale bars correspond to 150 µm. All images were taken from biomineralization experiments performed in our laboratory (unpublished data).

larger $CaCO_3$ crystals in early growth and smaller crystals as the bloom progresses. Small crystals will expand the residence time of the bloom on the surface. The larger $CaCO_3$ crystals, cyanobacteria and EPS aggregates, will sink faster because mineral precipitation in EPS increases the cyanobacteria−specific density. In addition, the normal progression of the cell growth in the bloom will lead to increasing rates of cyanobacterial cell lysis and release of photosynthetically derived organic carbon (Corredor et al., 2025, 2021), a major source of carbon and energy for heterotrophic bacteria (Allgaier et al., 2008). Increased microbial respiration and production of HCO_3^-/CO_2 may decrease the saturation index of $CaCO_3$ but still enhance the whiting phenomenon. Respiration could promote the breakdown of larger $CaCO_3$ crystals into smaller particles, increasing their suspension time at the water surface and contributing to the observed whitening phenomenon. The associated heterotrophs can degrade EPS and liberate bound Ca^{2+} with a similar effect (Diaz et al., 2017; Ionescu et al., 2015).

Despite these insights, the biochemical and genetic regulation of EPS production and its coupling with mineralization remain poorly understood. Variability in EPS composition across strains and environmental conditions suggests that EPS−mediated biomineralization is not a uniform process, but rather context-dependent. Surprisingly, *B. subtilis* and *M. smegmatis*, rely on the extracellular calcite scaffolds in the extracellular matrix for the structural organization of colony biofilms (Oppenheimer-Shaanan et al., 2016). Unraveling the molecular mechanisms linking EPS synthesis, biofilm dynamics, and mineral precipitation is thus critical for advancing both fundamental knowledge and applied strategies, such as engineered bioconsolidation for ecological restoration and construction materials.

4.2. Carbon concentrating mechanisms and carbonic anhydrases

Carbonic anhydrases are zinc metalloenzymes that catalyze the reversible hydration of carbon dioxide to bicarbonate and protons. In cyanobacteria, CAs play a central role in the function of the carbon concentrating mechanism, which enhances the efficiency of photosynthesis under conditions of low inorganic carbon availability. Because ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) has low affinity for CO_2 and is susceptible to oxygenase activity, the presence of CAs allows cyanobacteria to accumulate and convert inorganic carbon into forms that can be efficiently utilized for carbon fixation in the Calvin–Benson–Bassham cycle (Badger and Price, 2003; Falkenroth and Dann, 2025; Jung et al., 2024).

Cyanobacteria encode multiple classes of CAs, α–, β– and γ–type enzymes. These enzymes occur in distinct cellular compartments, reflecting their specialized functions within the CCM. For example, periplasmic CAs catalyze the rapid interconversion of dissolved CO_2 and bicarbonate in the external environment, facilitating inorganic carbon uptake. Cytoplasmic and carboxysomal CAs, in turn, convert accumulated bicarbonate into CO_2 in proximity to RuBisCO, ensuring high local concentrations of substrate for carbon fixation (Piatka et al., 2022; Pulsford et al., 2024).

A particularly important form is the carboxysomal CA, which resides inside the microcompartment housing the RuBisCO. In this setting, CAs release CO_2 from imported bicarbonate, thereby creating a microenvironment enriched in CO_2 and reducing RuBisCO's oxygenase activity (Piatka et al., 2022; So and Espie, 2005). Conversion of CO_2 to bicarbonate outside the carboxysome plays an important role in the function of the CCM, providing the driving force for CO_2 diffusion inside the cells and minimizing CO_2 leakage from them (Badger et al., 2006; Sun et al., 2019). The spatial separation of inorganic carbon uptake and conversion highlights the precise coordination of CA activity with CCM function (Smith and Ferry, 2000). Beyond their role in photosynthesis, CAs have also been implicated in calcifying organisms like sponges and cyanobacterial biomineralization (Cam et al., 2018; Jackson et al., 2007). By catalyzing CO_2 hydration, CAs influence carbonate chemistry at the cell surface, shifting the balance between dissolved inorganic carbon species and promoting $CaCO_3$ precipitation under favorable conditions (Cam et al., 2018; Falkenroth and Dann, 2025; Hazarika and Yadav, 2023; Thompson and Ferris, 1990). This relationship positions CAs as potential molecular drivers of biomineralization, since their activity enhances local supersaturation and provides the inorganic carbon necessary for mineral nucleation (Falkenroth and Dann, 2025). In concert with the EPS, CA–mediated hydration can facilitate the formation of carbonate crusts that stabilize soils, strengthen stone, and contribute to long-term geobiological processes (Cam et al., 2018).

A direct relationship between cyanobacterial calcification and photosynthesis facilitated by the CCMs was observed in mats of filamentous cyanobacteria, *Schizothrix sp.* and *Scytonema sp.,* when the decrease of $CaCO_3$ was quantified after the inhibition of CA and photosystem II inhibitors (ethoxyzolamide (EZ): membrane−permeable carbonic anhydrase inhibitor and 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU)) (Jiang et al., 2013; Merz, 1992). A causal relation of photosynthetic carbon assimilation and carbonate precipitation in cyanobacteria has been shown for freshwater environments, by isotopic studies in whiting events caused by *Synechococcus* (Thompson et al., 1997) and experimental studies on cyanobacterial carbonate precipitation (Merz, 1992). Previous studies show substantial calculated rise in calcite supersaturation upon DIC removal (Arp et al., 2001). The regulation of CA expression is responsive to environmental inorganic carbon concentrations. Under low–CO_2 conditions, cyanobacteria upregulate CA activity as part of their CCM induction, while in high–CO_2 environments, CA expression may be reduced to conserve resources (Badger et al., 2006). This plasticity contributes to the ecological success of cyanobacteria across diverse habitats but also implies that CA–dependent mineralization may vary with environmental context.

Despite advances in understanding CA diversity and function, several questions remain unresolved. The relative contributions of different CA classes to mineralization, the evolutionary origins of carboxysomal CAs, and the mechanistic pathways by which CAs interact with EPS during biomineralization remain underexplored.

5. Intracellular biomineralization in cyanobacteria

Biomineralization in cyanobacteria occurs through both intracellular and extracellular pathways, facilitated by complex

Table 2

List of reported cyanobacterial strains that perform intracellular biomineralization *in situ* and in experimental settings and/or applications. The biomineralization associated genes are detailed as follows: UPF0016: Ca/cation exchanger putative gene; *ccyA* and calcyanin: new gene and protein family possibly associated with cyanobacterial iACC; CO_2 uptake: NDH-1_4 complex (ndhD4, ndhF4, cupB genes), NDH-1_3 complex (ndhD3, ndhF3, cupA), BicA (Na+ - dependent symporter; bicA2); HCO_3^- transport: *cmpABCD* operon (ATP-binding cassette transporter; BCT1), BicA (Na^+ - dependent symporter; *bicA2*); *ccmKLMNOP*: CCM gene cluster corresponding to β-Carboxysomal shell proteins.

INTRACELLULAR BIOMINERALIZATION (Amorphous $CaCO_3$; ACC)

Species	ID	Environment of Origin	Type of growth[a]	Validated CCM	CA genes	Biomineralization associated genes/Proteins	Calcified environment/ Application	References
Chroococcidiopsis thermalis	PCC 7203	Soil	Biofilm			Ca^{2+}/H^+ exchanger and UPF0016 *ccyA* and calcyanin	*In silico*, experimental (Laboratory)	(Benzerara et al., 2022, 2014; De Wever et al., 2019)
Chroococcidiopsis sp.	PCC 7432	Freshwater	Biofilm				Experimental (Laboratory)	(De Wever et al., 2019)
	PCC 7433	Dried pool	Biofilm					
	PCC 7434	Pool	Biofilm					
	PCC 7439	Sand beach	Biofilm					
	PCC 9819	Non reported	Biofilm					
Cyanothece sp.	PCC 7425	Soil	Biofilm			Ca^{2+}/H^+ exchanger and UPF0016 *ccyA* and calcyanin	*In silico,* experimental (Laboratory)	(Benzerara et al., 2022, 2014; Cam et al., 2018; De Wever et al., 2019)
	PCC 8303	Thermal	Biofilm				Experimental (Laboratory)	(De Wever et al., 2019)
	PCC 8955	Swimming pool	Biofilm					
	PCC 9308	Freshwater	Biofilm					
Gloeomargarita lithophora	D10/ C7	Alkaline Lake	Biofilm			Ca^{2+}/H^+ exchanger and UPF0016 *ccyA* and calcyanin	Modern microbialites. *In silico*, experimental (Laboratory).	(Benzerara et al., 2022, 2014; Blondeau et al., 2018; Cam et al., 2018; Couradeau et al., 2012; De Wever et al., 2019)
Synechococcus calcipolaris	G9	Alkaline Lake	Both			*ccyA* and calcyanin	Modern microbialites. *In silico*, experimental (Laboratory).	(Benzerara et al., 2022, 2014)
Synechococcus lividus	PCC 6715	Thermal	Both			Ca^{2+}/H^+ exchanger and UPF0016	Experimental (Laboratory)	(De Wever et al., 2019)
	PCC 6716	Thermal	Both			Ca^{2+}/H^+ exchanger and UPF0016	Experimental (Laboratory)	(Benzerara et al., 2014; De Wever et al., 2019)
	PCC 6717	Thermal	Both			Ca^{2+}/H^+ exchanger and UPF0016	Experimental (Laboratory)	
Synechococcus sp.	PCC 6312	Freshwater	Both			Ca^{2+}/H^+ exchanger and UPF0016 *ccyA* and calcyanin	*In silico,* experimental (Laboratory)	(Benzerara et al., 2022, 2014; De Wever et al., 2019)
	PCC 6603	Freshwater	Both				Experimental (Laboratory)	(De Wever et al., 2019)
ThermoSynechococcus elongatus	BP-1	Thermal, freshwater	Both	Yes	γ-CA (*ccmM*) functional	*ccyA* and calcyanin CO_2 uptake: NDH-1_4 and NDH-1_3 complexes, *BicA* HCO_3^- transport: *cmpABCD* operon, *BicA* CCM gene cluster: *ccmKLMNOP*	*In silico,* experimental (Laboratory)	(Benzerara et al., 2022, 2014; Cam et al., 2018; Noreña-Caro and Benton, 2018; Price et al., 2008; Tang et al., 2022)

[a] The type of growth is classified as biofilm, planktonic or the capability of growing as both.

biochemical and environmental interactions and playing a critical role in their physiology, ecology, and contributions to biogeochemical cycles.

Intracellular biomineralization takes place within the cellular compartments of cyanobacteria, where specific metabolic activities promote mineral formation (Blondeau et al., 2018; Cosmidis and Benzerara, 2022). Key enzymatic processes, notably those involving carbonic anhydrases, catalyze the interconversion of CO_2 to bicarbonate and carbonate ions, enabling the localized nucleation of minerals like calcium carbonate within cytoplasmic vesicles or other organelles (Piatka et al., 2022; Pulsford et al., 2024). Mechanisms regulating ion transport to ensure mineralization occurs without impairing cellular functions, might be at play. In some cyanobacteria, Ca^{2+}/H^{+} membrane transporters regulate the intracellular concentration of Ca^{2+} at low levels by exporting calcium extracellularly, favoring further $CaCO_3$ biomineralization (Cam et al., 2018; Jiang et al., 2013). Therefore, for many years, $CaCO_3$ biomineralization by cyanobacteria has been considered as exclusively extracellular and dependent on the chemical conditions prevailing in the extracellular environments of cyanobacterial cells (Cam et al., 2018).

A broad diversity of cyanobacterial species from different environments have been found to form intracellular calcium carbonate as amorphous calcium carbonate (ACC) (Benzerara et al., 2014; Blondeau et al., 2018; Bruley et al., 2025; Chenebault et al., 2020; Couradeau et al., 2012; De Wever et al., 2019; Han et al., 2013; Kolodkin-Gal et al., 2023; Moreira et al., 2017; Ragon et al., 2014) (Table 2). Recently, 13 additional cyanobacterial strains forming intracellular amorphous calcium carbonates (iACC) have been identified by comparative genomics (and confirmed by microscopy) using a new gene (*ccyA*) and protein family (calcyanin) that appears be diagnostic of intracellular calcification in cyanobacteria (Benzerara et al., 2022). The assumption that intracellular ACC biomineralization is related with photosynthesis and may therefore follow a day/night cycle, is consistent with the diel expression of the *cyA* gene, with maximum transcript abundances during the night. In addition, several genes directly co-localized upstream and downstream of *ccyA* involved in carbon concentrating mechanisms and calcium transport show a similar expression pattern to the *ccyA* gene (Bruley et al., 2025).

Bacterial mineralization of $CaCO_3$ involves the formation of ACC precursor phases rather than as a crystalline material (Kolodkin-Gal et al., 2023; Rodriguez-Navarro et al., 2012). Biogenic ACC was first documented in eukaryotic organisms such as mollusks, sea urchins, sponges, ascidians, and crustaceans, where ACC acts as a precursor phase for the formation of calcite and aragonite minerals in skeletal architectures (Mehta et al., 2022). Compared to the crystalline polymorphs of $CaCO_3$ (calcite, vaterite and aragonite), ACC is more soluble and therefore unstable, but the ACC found in prokaryotes remains relatively stable intracellularly with no obvious spontaneous transformation to crystalline phases (Cam et al., 2018; Mehta et al., 2022). The mechanisms behind this phenomenon are currently unknown but intracellular mineral deposits can serve multiple functions, including ion detoxification, regulation of buoyancy, and structural support (Couradeau et al., 2012), the regulation of intracellular pH, and a form of storage for inorganic carbon (Mehta et al., 2022); also favoring a benthic mode of life with the increase in cell density (Couradeau et al., 2012). Alternatively, $CaCO_3$ granules could be implicated in the regulation of the Ca^{2+} concentrations (Cam et al., 2018). ACC storage could be implicated in intracellular calcium signaling, change global and local cytoplasmic calcium concentrations, and play a significant role in the overall relationship between the calcium and the cells (Kolodkin-Gal et al., 2023). It has been shown that at low Ca^{2+} concentrations, the free Ca^{2+} is highly regulated in the cytoplasm of living bacterial cells, including cyanobacteria, with a potential role in physiology and cell division (Barrán-Berdón et al., 2011). Intracellular calcium carbonate storage in biofilm-forming bacteria, both photosynthetic and heterotrophic species, indicates that biofilm cells can maintain a source of intracellular calcium that can be used for biofilm structure or/and signaling function (Kolodkin-Gal et al., 2023).

Intracellular and extracellular biomineralization are integral to cyanobacterial ecological roles and evolutionary history, as they represent sophisticated biological strategies to regulate mineral deposition, shaping both ancient and modern mineralized structures (Kamennaya et al., 2018; Lamérand et al., 2022b). Intracellular calcium storage is expected to affect extracellular matrix calcification directly or indirectly. Lysed cells could release ACC to interact with the organic extracellular matrix, or ACC can be actively secreted to promote/enhance matrix mineralization (Kolodkin-Gal et al., 2023). Manipulating these natural processes could enable sustainable strategies that can implement both types of biomineralization, offering promising potential for innovative biotechnological applications.

6. Interplay of cyanobacteria with other microorganisms

While this work has focused on cyanobacterial species, it should be emphasized that, in natural settings, cyanobacteria occur within complex communities that may further promote bioprecipitation. In microbial mats together with cyanobacteria, other microorganisms such as anoxygenic phototrophs, aerobic heterotrophic bacteria, fermenters, anaerobic heterotrophs, predominantly sulphate reducing bacteria (SRB), and sulfide oxidizing bacteria (SOB) are present (Dupraz and Visscher, 2005). The precipitation of $CaCO_3$ is promoted by an increase in alkalinity associated with sulfate reduction and the release of Ca^{2+} from EPS upon degradation by heterotrophic bacteria (Dupraz et al., 2009). Thus, other organisms carrying out oxygenic photosynthesis (photosynthetic eukaryotes) or other metabolisms (e.g., anoxygenic photosynthesis, sulfate reduction), may also participate in carbonate formation processes (Saghaï et al., 2015). Importantly, in mats the interplay between electron donor supply and their consumption by SRB is essential for driving mineral precipitation (Gallagher et al., 2012). Bundeleva et al., also showed a typical stratified microbial mat including cyanobacteria, anoxygenic phototrophic bacteria and SRB, all leading to carbonate precipitation, in particular $CaCO_3$ (Bundeleva et al., 2016). Analysis of sediments from the southeastern playa–wetland at Atlin, British Columbia(Canada), where a range of biofilms and microbial mats inhabited by filamentous cyanobacteria are present, indicated that cyanobacteria, SRB, and diatoms contributed to creating geochemical conditions conducive to carbonate mineral precipitation (Power et al., 2009).

Another interesting environment, olivine, plays a central role in the sequestration of atmospheric CO_2 via the formation of secondary carbonate minerals during both chemical and biological weathering of mafic rocks. In addition, Lamérand et al., investigated the interaction between olivine and a bacterial consortium composed of the cyanobacterium *Synechococcus* sp. and the aerobic heterotroph *Pseudomonas reactans* (Lamérand et al., 2020). The impact of this consortium on olivine dissolution rates was quantified, and the precipitation of secondary mineral phases was characterized while monitoring relevant biological and physicochemical parameters. From the study it was concluded that the impact of the bacterial consortium exceeds that of individual species and may represent an important and underexplored biotically controlled mechanism for CO_2 sequestration in natural waters (Lamérand et al., 2020).

7. Promising applications: cyanobacterial biomineralization as a bioconsolidation strategy and a pathway to produce geomaterials in space

Cyanobacteria have attracted considerable attention in recent years for their potential use in bioconsolidation, the process of strengthening and stabilizing lithic substrates through microbially induced mineral precipitation. Compared to other microbes, cyanobacteria can derive its own energy from sunlight, as well as absorb and store CO_2 through biological processes. Their metabolic versatility and ability to precipitate calcium carbonate make them promising candidates for eco-friendly applications in soil stabilization, stone heritage conservation, and construction materials (Jiang et al., 2023; Kolodkin-Gal et al., 2023; Myhr et al., 2019; Reinhardt et al., 2023). Their ability to precipitate calcium carbonate through photosynthesis, CA activity, and EPS production provides a sustainable alternative to chemical consolidants. Compared to chemical consolidants, biogenic treatments are valued for their sustainability, low toxicity, and capacity to self-repair under favorable conditions (Ortega-Morales et al., 2021).

The basis of cyanobacterial bioconsolidation lies in their photosynthetic metabolism, which consumes dissolved inorganic carbon and increases pH in the microenvironment (Martinez et al., 2016). This alkalinization, coupled with the release of EPS that bind cations, creates favorable conditions for calcium carbonate precipitation (Dittrich and Sibler, 2010; Falkenroth and Dann, 2025; Piatka et al., 2022; Reinhardt et al., 2023; Wild et al., 2022). EPS plays a critical role in this process. EPS appears to be involved in the aggregation of smaller crystals, resulting in the formation of larger crystals (Dupraz et al., 2009; Perito et al., 2018; Rodriguez-Navarro et al., 2012), that could increase the consolidation effect. Beyond facilitating mineral nucleation, the polymeric matrix enhances adhesion between microbial cells and substrates, ensuring intimate contact between mineral precipitates and the surface to be consolidated (Jroundi et al., 2017; Spairani-Berrio et al., 2023). The resulting mineral layers can coat and cement loose particles, effectively consolidating porous matrices (Jiang et al., 2023; Rodriguez-Navarro et al., 2003; Zamarreño et al., 2009). Laboratory and field studies have demonstrated that cyanobacteria can precipitate carbonate on building stones, stabilize sandy soils, and generate protective biocoatings on deteriorating monuments (Dhami et al., 2013; Kimura and Okuro, 2024; Sanjurjo-Sánchez et al., 2024). It has been shown that *Synechococcus* sp. GL24 produces a layer of calcified EPS that detached from the cell after the synthesis of a nascent S-layer (Kamennaya et al., 2012), potentially enhancing the bioconsolidation performance (Jroundi et al., 2017). Compared to EPS-deficient strains, EPS-rich strains such as *Nostoc* and *Synechococcus* could form stronger crusts that not only provide mechanical stabilization but also regenerate mineral phases under favorable conditions, offering self-repair capacity and highlighting the synergistic role of biological polymers and carbonate precipitation (Decho and Gutierrez, 2017; Jung et al., 2024; Merz-Preiß and Riding, 1999; Paulo et al., 2020). Carbonate crusts produced by cyanobacteria in arid regions improve mechanical strength, reduce erosion and enhance cohesion while stabilizing desert soils and controlling dust emissions (Burbank et al., 2011). In addition, the use of cyanobacterial biomineralization has evolved to the engineering of living building materials (LBMs) composed of sand, gelatin, inorganic nutrients, and cyanobacteria, and can absorb and store CO_2 through biological processes that promote $CaCO_3$ precipitation (Jiang et al., 2023; Reinhardt et al., 2023). LBMs strengthen the mechanical properties of the gelatin scaffold between the sand particles through $CaCO_3$ precipitation (Heveran et al., 2020; Qiu et al., 2021). Recently, the process of 3D bioprinting for the fabrication of LBMs mineralizing cyanobacteria *Synechococcus* sp. was reported (Reinhardt et al., 2023), demonstrating an increase in compressive strength compared to cell-free reference samples without cyanobacteria.

Practical applications underscore the value of cyanobacteria in bioconsolidation. In cultural heritage conservation, cyanobacterial consortia could be used to reinforce carbonate stone surfaces, forming thin, breathable mineral layers that protect monuments against weathering without altering the stone’s appearance. Currently used consolidants based on lime water and silicic acid show low efficiency (Zárraga et al., 2010). Nanoconsolidants such as nanolime and nanosilica show good performances (Becerra et al., 2020; Jang and Matero, 2018; Pozo-Antonio et al., 2019; Tortora et al., 2020), but they are costly (Ortega-Morales et al., 2021). Synthetic polymers, such as silane, epoxy, acrylic, and polysiloxane plug the pores when they polymerize, thus causing water retention and internal degradation, while external coatings can peel off (Ortega-Morales et al., 2021). Furthermore, traditional organic and inorganic consolidants, show poor performance and structural drawbacks that may require solvents (Doehne and Price, 2011). Some of them have proven harmful due to the accelerated deterioration of the treated stone (Doehne and Price, 2011; Rodriguez-Navarro et al., 2003). Furthermore, the conservation community does not yet recognize sustainability in the production of the current consolidants, as they are often energy-consuming and harmful for the environment (Baglioni et al., 2021). Alternative bioconsolidation strategies have been proposed: i) the application of a single bacterial strain (either exogenous or collected from the stone substrate to be treated), ii) activation of the indigenous carbonatogenic bacteria present in the stone via the application of a sterile nutritional solution, and iii) application of cell-free bacterial products (Castro-Alonso et al., 2019; Jimenez-Lopez et al., 2007; Jroundi et al., 2012, 2010; Perito et al., 2018; Rodriguez-Navarro et al., 2003). Currently, the most advanced and effective bioconsolidation technology available is the self-inoculation method (Jroundi et al., 2017) consisting of an indigenous carbonatogenic bacterial community isolated from the decayed stone, cultured, and activated in the laboratory with the patented M-3P solution, and then re-applied onto the same stone. It relies on the use of nutrient media and when the breakdown of amino acids to ammonia generates alkaline conditions, the microorganisms produce carbonate crystals. Since the self-inoculation method is based on the structure and activity of the indigenous carbonatogenic bacterial communities, the results might not be reproducible among stone heritage surfaces, being dependent on the *in-situ* biofilm community. Bacteria can induce precipitation of $CaCO_3$ extracellularly through ammonification, denitrification, sulfate reduction, anaerobic sulfide oxidation and degradation of urea by urea-decomposing bacteria that increases pH and alkalinity of the environment, leading to $CaCO_3$ precipitation (Hsu et al., 2018; Ojha et al., 2025). However, undesirable side-effects of these treatments include ammonia production by ureolityc bacteria posing health risks for the conservators and risks for the environment (Dhami et al., 2013; Dranseike et al., 2025; Zhu and Dittrich, 2016).

Compared to the traditional ureolytic bacteria such as *Sporosarcina pasteurii* (Hsu et al., 2018; Leeprasert et al., 2022), cyanobacteria are more sustainable. Ureolytic systems achieve rapid carbonate precipitation but require urea supplementation, posing environmental risks due to the release of large amounts of ammonium, (DeJong et al., 2010). Cyanobacteria, in contrast, are photoautotrophic and self-sustaining, creating living layers with self-repair potential, as well as the capacity to improve the properties of materials (Rossi et al., 2018; Sidhu et al., 2022). Cyanobacteria continue to be of great ecological importance; they are responsible for 40% of the CO_2 capture and sequestration from the atmosphere annually and species such as *Prochlorococcus* and *Synechococcus*, carry out over 25% of the global photosynthesis (Partensky et al., 1999; Reinhardt et al., 2023; Whitman et al., 1998). While cyanobacterial biomineralization has great potential for cost-efficient CO_2 sequestration and several cyanobacterial species that are inherently productive calcifiers have been identified (Han et al., 2013; Heveran et al., 2020; Lee et al., 2004; Liang et al., 2013; Reinhardt et al., 2023), practical applications of this process in bioconsolidation are still in their infancy. Cyanobacteria mineralize more slowly and are dependent on light and moisture availability (Reinhardt et al., 2023). Nonetheless, new approaches to advance the field have been suggested: i) extracellular biomineralization as a target for light-driven and cell-surface catalysed $CaCO_3$ precipitation in planktonic cyanobacteria and ii) genetic engineering to increase the biomineralization capacities (Falkenroth and Dann, 2025) based on the case of *Synechocystis* sp. PCC 6803 knockout of *cax1* (Ca^{2+}/H^+ antiporter) (Jiang et al., 2013). This approach resulted in increased $CaCO_3$ precipitation due to the enhanced transporter activity of BCT1 (Ca^{2+}-dependent HCO_3^- transporter) and the increase in CMM.

Architectural and sculptural stones have been seen to undergo deterioration due to several physical, chemical, and biological weathering (Dhami et al., 2013). The increasing environmental pollution endangers the survival of carbonate heritage stones. Although cyanobacterial biomineralization as a consolidation strategy is not established yet, the conservation of these monuments is urgent, and it requires the use of green, sustainable, efficient, and durable strategies.

Space is another environment in which biomineralization under microgravity is a further promising application with great potential. Although technological advances may enable humans to reach other planets in the coming decades, the high cost of launches makes it impractical to establish permanent crewed outposts reliant on consumables supplied from Earth (Khoshtinat et al., 2025). Biological components are essential because certain resources and products including the generation of food, fuel, and oxygen, as well as geomaterials, can be produced efficiently only through biological systems. In particular the role of cyanobacteria has been highlighted (Verseux et al., 2016). Cyanobacteria are very resistant, after exposure to space and Martian conditions, e.g. UV radiation with wavelengths above 200 nm, *Chroococcidiopsis* was able to survive (Billi et al., 2011; Cockell et al., 2011). Cyanobacterial carbonate precipitation and possible ancient life on Mars in artificial Martian ground was explored by Tarasashvili et al. (Tarasashvili et al., 2023). Khoshtinat and colleagues also investigated the potential of biomineralization as a low-energy, sustainable alternative to conventional construction methods—such as Portland cement and thermal sintering approaches proposed for lunar applications—-which are typically energy-intensive and limited by material specificity (Khoshtinat et al., 2025). Finally, cyanobacteria could be used in symbiosis with other microorganisms to generate biomineral in space. A synthetic lichen system, consisting of diazotrophic cyanobacteria and filamentous fungi, was engineered to generate substantial amounts of $CaCO_3$ and biopolymers, thereby binding Martian regolith into consolidated building materials (Rokaya et al., 2024). The self-growing building blocks obtained could be assembled into a range of structures, including floors, walls, partitions, and furniture. This result is in line with a NASA project dealing with Biomineralization-Enabled Self-Growing Building Blocks for Habitat Outfitting on Mars (Jin, 2023).

8. Concluding remarks

Carbonate precipitation represents likely the key process shaping global carbon cycling. Cyanobacterial biomineralization emerges as a tightly coupled biological–geochemical process which significance spans deep in time, contributing for instance to stromatolite formation and long-term carbon cycling. From an applied perspective, cyanobacterial systems stand out as uniquely promising platforms for sustainable technologies offering notable advantages in sustainability and potential for self-repair. Their reliance on light-driven metabolism, low resource demand, and capacity to generate cohesive mineral–organic matrices position them as compelling alternatives to conventional, carbon-intensive materials. In particular, their use in promising applications as bioconsolidation for cultural heritage conservation and in the production of geomaterials under extreme conditions, including microgravity, highlights their versatility and technological adaptability.

Central to this process is the interplay between EPS and carbonic anhydrases, which together facilitate carbonate nucleation and link cellular-scale metabolism to macroscale material stabilization. In addition, intracellular biomineralization offers several distinct advantages over extracellular mineral formation by providing a high degree of biological control over nucleation, growth, and final mineral properties. Within the cellular environment, mineral precipitation can be tightly regulated through compartmentalization, enzymatic activity, and ion transport systems, allowing organisms to dictate crystal size, morphology, and composition with remarkable precision.

Future research integrating microbiology, molecular biology, geochemistry, and engineering will be essential to optimize these systems. Advancing this field will not only deepen our understanding of microbial influences on Earth's carbon cycle but also enable the development of resilient, low-impact materials and further innovative applications.

CRediT authorship contribution statement

Luisa Corredor: Writing – review & editing, Writing – original draft, Validation, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Francesca Cappitelli:** Writing – review & editing, Validation, Supervision, Data curation, Conceptualization. **Federica Villa:** Writing – review & editing, Validation, Conceptualization.

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Data availability

No data was used for the research described in the article.

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Glossary

$CaCO_3$: calcium carbonate
Cas: carbonic anhydrases
CCM: carbon-concentrating mechanism
EPS: extracellular polymeric substances
MICP: microbially induced carbonate precipitation
(BIM): biologically induced mineralization
(BCM): biologically controlled mineralization
CCS: carbon capture and storage technologies
DIC: dissolved inorganic carbon
iACC: intracellular amorphous calcium carbonates.