Dormancy in the origin, evolution, and persistence of life on Earth

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Abstract

Life has existed on Earth for most of the planet's history, yet major gaps and unresolved questions remain about how it first arose and persisted. Early Earth posed numerous challenges, including harsh, noisy, and fluctuating environments. Today, many organisms cope with such conditions by entering a reversible state of reduced metabolic activity, a phenomenon known as dormancy. This process protects inactive individuals and minimizes the risk of extinction by preserving information that stabilizes life-system dynamics. Here, we develop a framework for understanding dormancy on early Earth, beginning with a primer on dormancy theory and its core criteria. We hypothesize that dormancy-like mechanisms acting on chemical precursors in a prebiotic world may have facilitated the origin of life. Drawing on evidence from phylogenetic reconstructions and the fossil record, we show that dormancy is prevalent across the tree of life and throughout deep time. These observations lead us to consider how dormancy might have shaped nascent living systems by buffering stochastic processes in small populations, protecting against large-scale planetary disturbances, aiding dispersal in patchy landscapes, and facilitating adaptive radiations. Given that dormancy is a fundamental and easily evolved property on Earth, it is also likely a feature of life elsewhere in the universe.

Introduction

Life on Earth today can only originate from existing organisms, but there was a time in the distant past when life arose from non-living substances. During that period, before organisms diversified and transformed the planet, primitive life had to overcome several major obstacles. First, chemical building blocks needed to be supplied at rates that exceeded decay caused by processes such as hydrolysis, photolysis, and thermal decomposition. Hydrothermal vents on early Earth were environments where fluids with contrasting redox potentials met for sustained periods, leading to the generation of reduced substrates that could support life [1–3]. Second, primitive life required compartmentalization between the protocell components and the external environment. The rise of membrane-bound vesicles made of fatty acids or phospholipids afforded protection and selective permeability, facilitating homeostasis and the establishment of proton gradients necessary for more sophisticated forms of metabolism [4]. Third, the origin of life was highly susceptible to chance events and errors in reproduction. The evolution of information-directed storage and replication ensured that the blueprints for

life were transmitted to offspring with sufficient fidelity, meeting the criteria for evolution by natural selection [5].

To persist through time, primitive organisms also had to contend with the forces of entropy. Individuals had to endure harsh, fluctuating, and unpredictable conditions long enough to reproduce and expand into new, uninhabited landscapes, all without the evolutionary refinements that developed over the eons that followed. These fundamental problems could have been overcome in several complementary, non-mutually exclusive ways. For example, individuals could have survived by living in spatially restricted patches of habitat with relatively stable conditions that were suitable for growth and reproduction [6]. Individuals that ventured into less optimal habitats may have survived by living in groups, where protection was provided through cooperation, exchange of metabolites, and the division of labor [7]. Other individuals exposed to more stressful conditions would have faced strong selective pressure, potentially leading to the rapid evolution of specialized traits such as enhanced motility, light sensing, resource storage, or osmolyte balance, thereby increasing population stability [6].

Dormancy is another strategy that likely played a crucial and multifaceted role in the persistence of life on early Earth. The ability of organisms to enter a reversible state of reduced metabolic activity could have contributed to the origins and emergence of life in several ways. Beyond supporting higher abundances and greater biomass within populations, dormancy would have maintained community-wide biodiversity, thereby ensuring sustained ecological functions, energy dissipation, and material recycling [8]. By decreasing rates of mortality in the face of harsh and fluctuating conditions, dormancy would reduce the probability of local and global extinction extinction events [9]. Also, dormancy creates a 'seed bank' of inactive individuals [10](Fig. 1). The resuscitation of inactive propagules from this reservoir may have eliminated the need to repeatedly restart the life-building process under early Earth conditions.

While dormancy has been invoked as playing a role in the origins of life [11–13], its logical foundation and supporting evidence have yet to be rigorously developed. Here, we establish a framework to explore dormancy's role in the origin and emergence of life on Earth. We hypothesize that in a prebiotic world, dormancy-like mechanisms acting upon chemical precursors may have facilitated the origin of life. Drawing on phylogenetic reconstructions and evidence from the fossil record, we trace the roots, history, and potential origins of dormancy. We also examine how dormancy could have influenced population genetic processes, provided protection against planetary-scale disturbances, and ultimately contributed to the dispersion and diversification of life on Earth. Finally, given that dormancy is a general and easy-to-evolve property of living systems, we propose that it is likely a feature of life elsewhere in the universe.

1 A dormancy primer

Although initially developed to understand population dynamics in biology, the principles of dormancy can be applied to other systems, including cancer, network science, and interacting particle systems [10]. In abstract terms, dormancy can operate on any agent – defined as an individual component within a complex system that interacts with other agents and its environment – provided it meets the following criteria: 1) an agent can exist in different states of activity, 2) an agent can transition between these states of activity, and 3) an agent experiences some degree of protection from decay while in a less active state. For simplicity, we consider an agent existing in one of two states of activity: 'on' or 'off' (Fig. 1). Although, in some systems, agents

can occupy states along a gradient or spectrum of activity and protection [14].

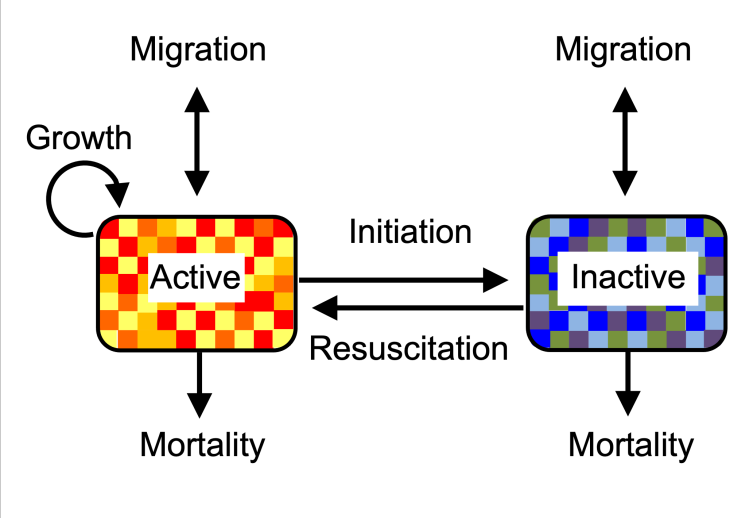

Fig 1. A generalized model of dormancy. Dormancy is a set of processes acting on agents that exist in different states of activity. Active agents transition into inactive agents through the process of dormancy initiation, while inactive agents transition into active states through the process of resuscitation. Transitions can occur stochastically, or in a responsive manner through the interpretation of internal or external cues. Mortality rates are assumed to be higher for active agents than for inactive agents, which can facilitate migration and colonization. This form of protection can also lead to the accumulation of inactive individuals and the creation of a 'seed bank', which serves as a reservoir of information (colors) that can generate complex behaviors through the preservation of diversity and memory. Modified figure from [10].

Dormancy provides benefits to agents in fluctuating environments [15]. At the individual level, dormancy reduces the probability of mortality under adverse conditions and allows an agent to resume activity when favorable conditions return. At the population level, dormancy minimizes variance in abundance over time, reducing the probability of extinction and thereby increasing geometric mean growth, i.e., fitness [16]. The benefits of dormancy depend not only on the mechanisms through which agents transition between states of activity but also on the environmental dynamics in which these agents exist. For example, in a rapidly and unpredictably fluctuating environment, it may be optimal for agents to transition between states in a stochastic manner consistent with bet-hedging [16]. However, in an environment that changes slowly or more predictably, it maybe be optimal for agents to responsively transition between states of activity based on the interpretation of internal or external cues [15] (Fig. 1).

Regardless of the transitioning mechanism, dormancy results in the accumulation of inactive agents, forming what is known as a 'seed bank'. This reservoir preserves information and diversity in the population of agents, which leads to emergent phenomena and complex dynamics [10]. There are a number of important attributes that affect seed bank behavior. The absolute and relative sizes of the seed bank are critical for determining how dormancy influences population dynamics [10]. The turnover rate of the seed bank is also crucial and is influenced by the balance of processes governing transitions into and out of dormancy. Some dormant agents are short-lived, while others may persist in the seed bank for extended periods [9]. Physical and spatial aspects of the seed bank are important considerations. In some systems,

inactive and active agents may be well-mixed. However, in other systems, movement is affected by differences in the size and density of active and inactive agents, resulting in spatially segregated seed banks (Fig. 1) [10]. Taken together, the features and attributes of dormancy can lead to rich and complex dynamics that are important for both living and non-living systems.

2 Dormancy in a prebiotic world

We propose that dormancy theory provides a valuable framework for understanding the dynamics of biomolecules in both modern living systems and the prebiotic conditions of early Earth. Specifically, we hypothesize that chemical dormancy could have been an important yet overlooked factor contributing to the origins of life. We suggest that this framework can be tested within the context of existing theories, such as autocatalytic sets, which aim to understand the stability of chemical reaction networks and the origins of life [17].

2.1 Criteria for chemical dormancy

The first criterion for chemical dormancy is that a molecule must exist in different states of activity. Sometimes, a molecule is considered 'active' or 'inactive' based solely on its concentration [18], since the reaction rate varies with the abundance of reactants in accordance with the rate law. However, this does not satisfy the first criterion of dormancy, which requires individual agents to occupy distinct states of activity. Instead, many biomolecules, including nucleic acids [19], vitamins [20], and proteins [21, 22], exist in different states of activity depending on chemical reactions, environmental conditions, and stochastic processes (Fig. 2)

The second criterion for chemical dormancy is the ability of a molecule to reversibly transition between active and inactive states (Fig. 2). Such transitions can occur stochastically, driven by diffusion and random molecular encounters, which highlight the probabilistic nature of finite molecules within a specific volume. Examples include the formation of disulfide bonds between cysteine residues and other post-translational modifications, which can induce conformational changes that impact ligand binding and various aspects of protein function. [21, 22]. Transitions in chemical activity can also happen in a deterministic manner if initiated by environmental conditions such as pressure, salinity, pH, water potential, or interactions with another protein [23]. For example, the activity of an mRNA strand is temperature-dependent. Portions of the molecule may form secondary structures at low temperatures, blocking translation, while higher temperatures cause these structures to melt, thereby allowing translation to proceed [19]. Taken together, these stochastic and deterministic transitions can affect reaction rates across molecules and contribute to the formation of complex, interacting, and interdependent metabolic cycles.

The third criterion is that inactive molecules must be protected in ways that reduce the rates of decay from processes such as thermal degradation, photolysis, hydrolysis, dehydration, or enzymatic reactions. For example, enzyme persistence is enhanced through interactions with inorganic substrates. Extracellular enzymes released by microorganisms can adhere to and be preserved by minerals in soils during dry periods, allowing them to resume activity upon rewetting [24]. Another example of protection afforded by inactivity is seen in DNA. The formation of chromatin, in which DNA coils around histone proteins, not only enhances the molecule's stability by increasing its resistance to degradation from radiation and denaturing agents but also suppresses gene

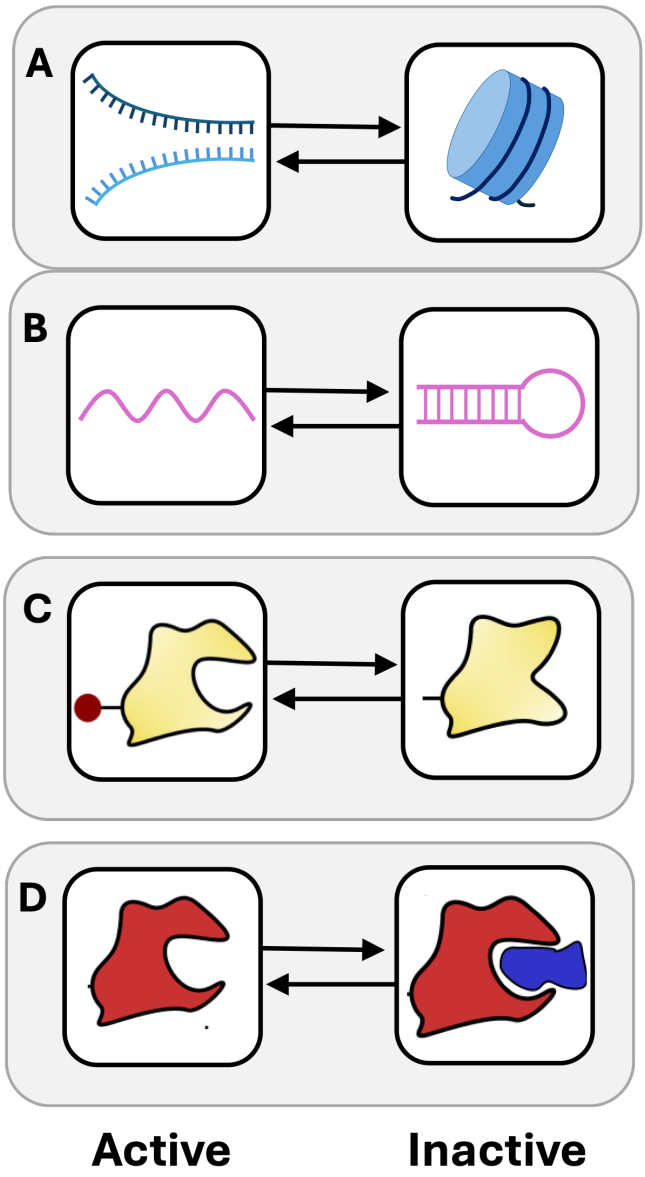

Fig 2. Examples of chemical dormancy. Biomolecules can be viewed as agents that exist in either active (left column) or inactive (right column) states. **A)** In eukaryotic organisms, DNA typically exists in an inactive state, tightly bound to histones forming a nucleosome. DNA becomes active when helicases unwind the molecule, enabling promoter binding and the initiation of replication. **B)** Secondary structures in RNAs arise from the hydrogen bonding between complementary base pairs within the molecule. Hairpin loops and other types of folding can reduce translational efficiency, but also protect the RNA from enzymatic degradation. **C)** Protein activity is altered by phosphorylation events, where the addition of a phosphate group (red circle) to an amino acid changes the size, shape, or charge of a protein with consequences for function. **D)** Enzymes can be deactivated by interactions with proteins or other molecules that bind to or obstruct the active site, preventing the enzyme from catalyzing its reaction.

expression and DNA repair [25] (Fig. 2A). Similar processes have been observed in archaea, where histone-like proteins facilitate DNA binding, thereby raising the DNA's melting temperature and reducing the rate of radiolysis [26].

2.2 A test of chemical dormancy

Since many biologically relevant chemicals meet the criteria for dormancy (Fig. 3), hypotheses can be formulated regarding how dormancy and molecular dynamics may have contributed to the origin of life. Let us consider a prebiotic molecule, A, which exists mostly in an inactive state (A_i), but is capable of replication when in an active state (A_a). Another molecule, B, acts as a catalyst. It binds to A and increases its replication rate. Over time, molecule A will accumulate in environments where molecule B is present. If B also has the ability to engage in dormancy, the synthesis of A will occur when and where B is active (B_a). In this scenario, dormancy modifies chemical interactions, shifting the optimal conditions for replication in ways that affect proliferation and persistence (Fig. 3). We used a simple individual-based model to explore these ideas where molecule A replicates and decays while stochastically transitioning between active (A_a) and inactive (A_i) states in the presence of catalyst B, similar to what is depicted in Fig. 3B. We found that the proportion of active molecules (A_a) increases with catalyst (B) abundance (Fig. 4A). Furthermore, dormancy-mediated protection from decay increases the total abundance of A, making it less susceptible to molecular extinction (Fig. 4B).

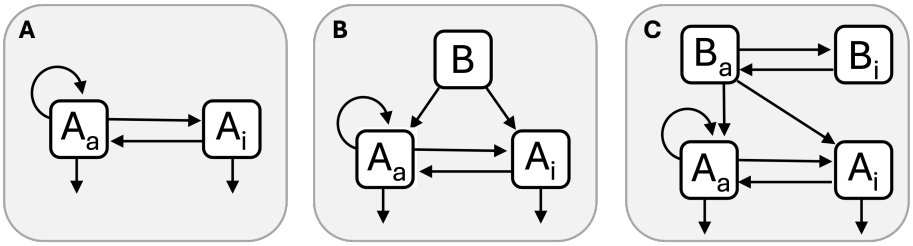

Fig 3. Chemical dormancy with a catalyst. A) Molecule A only replicates when it is in an active state (A_a), but most individuals in the population exist in an inactive state (A_i). **B)** Molecule B is a catalyst that binds to A, triggering its activation and leading to increased replication. **C)** If B can also engage in dormancy, the activity and replication of A will be greater where and when B is active (B_a) as opposed to inactive (B_i). To meet the third criterion of chemical dormancy, we assume that inactive molecules decay more slowly than active molecules.

In our modeled scenario, molecule A has properties that are analogous to DNA. Due to its double-stranded nature, DNA predominantly exists in a dormant state where it is physically protected from decay and experiences lower mutation rates compared to single-stranded nucleic acids. The recruitment of promoters and helicases facilitates the unwinding and activation of DNA, enabling its replication. It is conceivable that its dormancy-like properties contributed in part to DNA becoming the dominant information molecule in organic systems. For example, simulations of polymer formation from monomers suggest the existence of a mutation threshold for self-replicating molecules. At mutation rates above this threshold, the system cannot replicate with sufficient fidelity to sustain efficient self-copying. Below this threshold, mutations are minimized enough to maintain functional integrity while still allowing for genetic variation during replication, which is required for evolution by natural selection [5]. In this way, DNA-based life may have avoided 'error catastrophe', which

could have posed challenges to RNA-based life [27–29]. This analogy highlights how a molecule that is difficult to replicate, such as DNA, may have facilitated the information-driven energy processing of life through its interactions with other molecules by controlling activity through dormancy-like mechanisms.

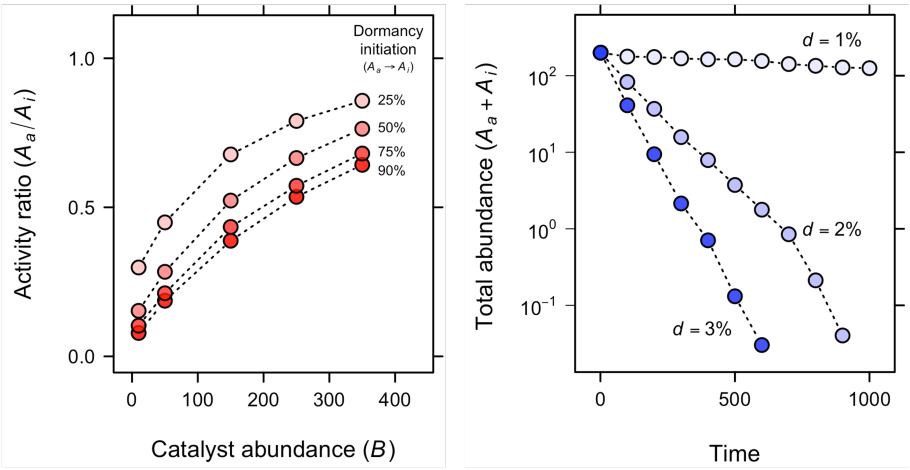

Fig 4. Autocatalytic simulations of chemical dormancy. A The proportion of active molecules (A_i) increases with catalyst (B) abundance in a simple autocatalytic simulation. **B** The total abundance of molecule A exponentially decreases with the rate that inactive molecules decay consistent with the view that protection afforded by dormancy can contribute to the persistence of molecules over time.

3 Tracing the roots of dormancy in living systems

Dormancy is prevalent throughout the tree of life, with well-documented instances among extant lineages of viruses, bacteria, fungi, protists, worms, insects, crustaceans, amphibians, fish, birds, plants, and mammals [10]. Despite its widespread occurrence, the genes and pathways that facilitate dormancy are not conserved across these diverse groups. Similar to traits such as vision, flight, and echolocation, dormancy represents an example of homoplasy, more specifically, convergent evolution [30, 31]. It has independently and repeatedly emerged across various lineages, suggesting that dormancy may be a common solution to one of life's universal challenges, that is, living in a fluctuating, noisy, and unpredictable environment. Here we take a deep-time perspective to explore the distribution of dormancy throughout Earth's history and investigate its potential origins.

3.1 Dormancy among ancient multicellular organisms

Convergent evolutionary processes often point to the ancient origins of a phenotypic traits [32, 33]. Fossil evidence and phylogenetic reconstruction suggest that dormancy has been a long-standing strategy among plants, animals, and microorganisms. For example, the discovery of slime mold sporocarps in 100-million-year-old amber are consistent with the evolutionary stasis of dormancy-related morphological structures [34] (Fig. 5A). Similarly, resting stages produced by crustacean zooplankton (ephippia) have been recovered from 130-million-year-old lake sediments [35] (Fig. 5B). Evidence from the Early Triassic (250 Ma), suggests that a group of stem-mammals (synapsids) engaged in torpor to survive seasonal cycles at high latitudes, as indicated by growth marks on tusks [36]. Burrows used by lungfish for aestivation during prolonged periods

of desiccation have been found in Devonian deposits [37]. Ancestral state reconstruction indicates that morphological and physiological aspects of dormancy had already emerged 370 million years ago among some of the earliest seed plants [38, 39]. It is possible that dormancy may have even played a role in the transition of some primitive phototrophs from water to land based on the recovery of cryptospores 480 Ma [40, 41].

3.2 Dormancy among ancient unicellular organisms

Dormancy existed among some major groups of microorganisms even before the Cambrian explosion. For example, fungus-like spores discovered in karst cavities dating to the Ediacaran period (635 Ma) led to speculation about the role of dormancy in population recovery following Snowball Earth events [42]. More compelling evidence of dormancy from the Proterozoic Eon come from bacteria. Certain lineages of filamentous cyanobacteria (Nostocales and Stigonematales) produce akinetes (from Greek: "motionless"). These specialized resting structures are formed in response to environmental stresses, such as light or phosphorus limitation [43], and involve cell-cell signaling [43–45]. Akinetes are characterized by their reinforced cell walls, composed of a multilayered extracellular envelope. Their larger size accommodates the storage of carbon (glycogen) and nitrogen (cyanophycin), allowing akinetes to tolerate cold temperatures and desiccation for extended periods of time [43]. Remarkably, viable akinetes have been resurrected from ocean sediments over 400 years old [46]. Although microfossils resembling modern filamentous cyanobacteria have been found in 3.5-Ga cherts from Western Australia [47], the integration of phylogenetic, paleontological, and geochemical data suggests that akinetes evolved much later, between 2.10 and 2.45 Ga [48, 49].

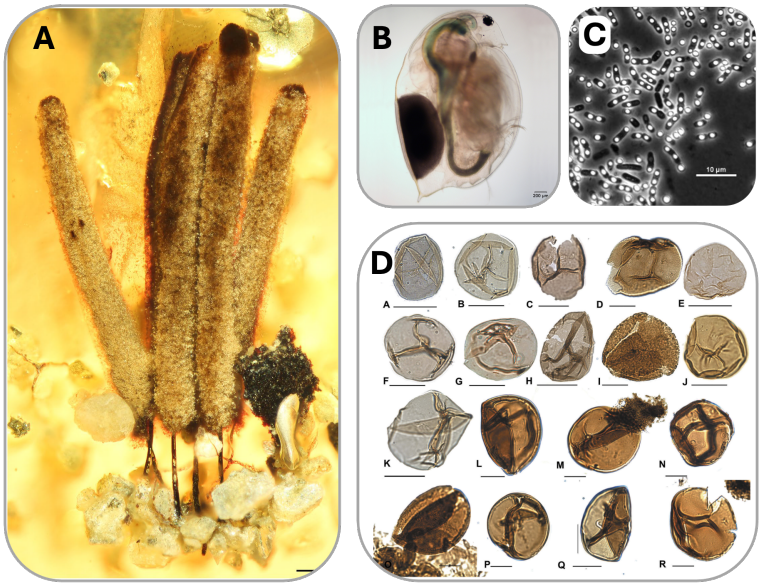

Fig 5. Examples of ancient dormancy. Dormancy is prevalent among extant lineages, but is also common in Earth's fossil record. **A)** Sporocarps of slime molds preserved in 100 million-year-old amber [34], **B)** Resting eggs from aquatic crustaceans (*Daphnia*) have been recovered from 130 Ma sediments [35], **C)** Some bacteria related to *Bacillus* form long-lived endospores that have been resuscitated from ¿1 Ma permafrost [50], and **D)** Cryptospores related to primitive plants have been dated to 450 Ma [51]

Another ancient form of bacterial dormancy is endospore formation (Fig. 5C). It is estimated that modern-day marine subsurface sediments harbor approximately 10^{28} endospores [52]. Considering the total number of bacterial and archaeal cells on Earth is around 10^{29} [53], dormant endospores comprise at least 10% of the global microbial biosphere. Endospore formation is restricted to a few major lineages within Bacillota phylum. These bacteria make endospores in response to energy limitation and other environmental stresses [54]. This well-studied mechanism of dormancy involves a complex development program that requires the regulation of more than 100 genes [55]. The resulting endospore is a water-depleted structure composed of over 70 different proteins [56]. Endospores can withstand extreme environmental conditions, including the vacuum of space [57] and simulated surface conditions on Mars [58]. As a result, endospores are capable of persisting for extended periods, as demonstrated by their revival from million-year-old permafrost samples [50].

Endospores are conservatively estimated to have evolved at least 3.0 billion years ago. This estimate is supported by two key pieces of evidence. First, comparative phylogenomics of ribosomal and sporulation proteins suggest that the last common ancestor within the Bacillota phylum was a spore-former [59]. Second, time-calibrated phylogenetic reconstructions place the divergence of Bacillota at approximately 2.9 to 3.1 billion years ago [60, 61]. However, observations based on cell wall architecture have led to speculations that endosporulation could be much older. Most bacteria within the Bacillota are monoderms, meaning they have a single membrane as the outermost cellular structure. During sporulation, the mother cell engulfs the developing spore in a phagocytosis-like process, which continues until the spore matures and the mother cell is ultimately lysed. The 'failed endospore origin' hypothesis proposes that an incomplete final stage of endospore development led to the evolution of the first diderm bacteria, which are characterized by having two membranes [12, 62]. An extension of this logic is that the last bacterial common ancestor (LBCA) was a spore-former [12], a claim that is consistent with network-based metabolic models [63]. While sporulation may have helped cells persist during harsh conditions that were characteristic of the early Earth, criticisms have been raised about the singularity of diderm origin [64]. Subsequent studies analyzing a wide range of bacterial genomes have revealed that monoderms are not monophyletic [62, 65], thereby weakening the claim that the LBCA was a spore-forming microorganism.

3.3 Easier forms of dormancy

Dormancy seems to have evolved early and often during Earth's history. However, the examples mentioned above, even those in unicellular bacteria, represent relatively complex forms of dormancy that involve the regulation of numerous genes and pathways. If dormancy played a role in the origins of life, early progenitor cells likely relied on much simpler mechanisms. There are ways in which microbial metabolism can be temporarily suspended without the need to produce cysts, resting stages, or other specialized morphological structures. One way this can be achieved is with toxin-antitoxin (TA) systems. TA systems are diverse and can affect different processes, including plasmid retention and programmed cell death [66], but see [67]. TA systems can regulate cellular metabolism using only a pair of genes, making them a simpler but effective form of dormancy [68]. On a single operon, one gene encodes a protein that is the toxin, while the other gene encodes an RNA or protein that binds to and inactivates the toxin [69]. When a cell is physiologically stressed, antitoxins become degraded by induced proteases, which increase the concentration of unbound toxins in the cytosol. These free toxins can then inhibit process such as DNA replication, mRNA stability, translation, cell wall biosynthesis, and ATP synthesis, ultimately reducing microbial

growth [68, 70]. While the exact timing of the evolution of these systems remains uncertain, it is hypothesized that TA modules, or primitive versions of them, may have emerged shortly after the first cells evolved [71].

3.4 Potential origins of dormancy

The random processes occurring inside cells, which create variability in metabolic activity, may have contributed to the emergence of a primitive, dormancy-like phenotype. Gene expression varies among individual cells owing to stochastic encounters between transcription factors and promoter sequences, a process that is critical for initiating transcription by RNA polymerase [72]. Similarly, protein translation occurs in bursts driven by the stochastic binding of ribosomes to mRNA [73], while signal transduction can be noisy due to the inherent randomness of ligand-receptor binding [74]. Cellular activity can also be influenced by the random binding of methyl groups to genomic regions, which can silence genes essential for metabolic functioning [75]. The stochasticity of these processes introduces a form of internal noise that generates heterogeneity within a population. Even when isogenic cells are maintained under nearly identical conditions, metabolic activity often exhibits a long-tail distribution [76], where a small proportion of cells remain highly active, while the majority exist in a reduced metabolic state.

Variation in metabolic activity among individuals is an inherent and unavoidable feature of life. The discrete and probabilistic nature of molecular interactions, which includes collisions, binding events, and diffusion, is fundamental for the functioning of cells today, but also for life processes on early Earth. This leads us to hypothesize about the origins of dormancy. We propose that variation in metabolic activity among individuals in a population of progenitor cells would be easily — and perhaps inevitably — generated by numerous random multiplicative processes. In a fluctuating environment, some of these primitive organisms would likely survive longer due to their conserved energy and tolerance to stress during periods unfavorable for growth and reproduction. These individuals could then resume activity when conditions improved, not only contributing to the persistence of life but also becoming subject to natural selection. Over time, this process would lead to refinement, ultimately giving rise to more complex form of dormancy that are finely tuned to predictable environmental changes as Earth's conditions became increasingly stable and conducive to life.

4 Consequences of dormancy on early Earth

Dormancy is a life-history strategy that has shaped the complexity and biodiversity of modern-day life on Earth. Given its ancient origins (Fig. 5), dormancy likely played an important role in the past, too, potentially contributing to the emergence and persistence of life on early Earth. Although conditions 4 Ga ago were vastly different from those of today, the fundamental rules of life remain the same. Primitive organisms still would have needed to acquire energy, resist entropy, and adhere to the laws of ecology. From this perspective, we consider how dormancy might have affected the early trajectory of life.

4.1 Dormancy buffering of small populations

Perhaps one of the most significant differences between the early biosphere and today's biosphere is the overall quantity of life. Population sizes were likely much smaller after life first arose, making them more prone to chance events, which has important

implications for demographic and evolutionary processes. In small populations, genetic drift tends to outweigh selection, preventing beneficial mutations from increasing in frequency and allowing mildly deleterious mutations to persist [77, 78]. Consequently, maladaptive alleles can accumulate, decreasing fitness and potentially driving populations to extinction through a phenomenon known as Muller's ratchet [79]. In addition to lowering the input of mutations associated with genome replication, dormancy also reduces the influence of genetic drift by increasing the effective population size [80], which may have contributed to the maintenance of genetic diversity on early Earth.

4.2 Dormancy-mediated dispersal

Today, it is estimated that there are upwards of 10^{12} species on the planet, a result of the ongoing balance between speciation and extinction over the past 4 Ga [81]. In contrast, the early biosphere contained far fewer species and many more vacant niches. A major challenge for primitive organisms would have been successfully dispersing to these niches. If life first emerged in the oceans, it may have had access to abundant resources and been able to more easily disperse while remaining in a metabolically active state [82, 83]. Alternatively, if life first emerged in inland volcanic hot springs [84, 85], the early Earth could be envisioned as a mosaic of sparsely distributed habitable patches. In this scenario, dormancy could increase survival during transit and facilitate colonization [86] (Fig. 1). Upon reaching an unoccupied site with minimal competition, resuscitation and growth could lead to local establishment and subsequent range expansion. Moreover, by broadening the parameter space for evolutionary branching and promoting genetic divergence between subpopulations, dormancy may have played a key role in facilitating adaptive radiations [87].

4.3 Dormancy protection against disturbance

Life first emerged on Earth during a tumultuous time. Throughout the Hadean Eon (4.6 - 4.0 Ga), meteorites repeatedly bombarded the planet, melting the Earth's crust and potentially driving nascent life to extinction [88, 89]. During most of the Eoarchean era (4.1 and 3.8), large impactors — some exceeding 50 kilometers in diameter — may have struck Earth approximately once every million years [90]. Although these collisions were likely too infrequent to directly select for dormancy in early microbial populations, dormancy may have contributed to post-impact survival and facilitated reseeding events from ejecta [91]. In the unlikely event of surface sterilization during the period of heavy bombardment, life may have survived within igneous rocks [90], forming a subsurface refugium of dormant microorganisms [92, 93].

4.4 Dormancy defense against viruses

One feature of the early biosphere that is thought to be consistent with today's biosphere is that life had to contend with the risk of mortality caused by virus infections. Many viruses are thought to have already been present at the time of the last universal common ancestor (LUCA) [94]. Reconstructions suggest that LUCA, which lived around 4.2 Ga, was an anaerobic acetogen that likely possessed a viral immune system, as inferred from the conservation of more than a dozen CRISPR–Cas effector proteins [95]. Some Cas nucleases induce dormancy in bacterial hosts, thereby clearing viral infections and providing herd immunity to uninfected cells [96]. Other forms of dormancy, such as endosporulation and persister cell formation, can inhibit phage infections [67, 97]. There are even reports suggesting that mere physical contact with virus particles can trigger

cellular inactivity [98, 99]. Collectively, these observations suggest that dormancy may represent a long-standing defense mechanism against the pressures of cellular infection.

5 Astrobiology and dormancy

A major goal of astrobiology is to determine whether life exists elsewhere in the universe. Mars has long been of significant interest, not only because of its proximity to Earth but also due to observations of recurring slope lineae, which may result from seasonal flows of liquid brine [100, 101]. Similarly, some icy moons of Saturn and Jupiter, like Enceladus and Europa, are known to contain liquid water beneath their frozen surfaces. However, life on these planetary bodies would face challenges from multiple stressors, including, but not limited to, high pressure, oscillating temperatures, and limited access to nutrients and energy. It is plausible that extraterrestrial life might possess dormancy-like capacities to survive the noise, variability, and extreme conditions driven by climatic and planetary processes within our solar system. In fact, dormancy has been hypothesized to be an adaptation for potential life on Mars, given the radical changes that have occurred throughout its geologic history [102]. In the search for life within our solar system, astrobiologists have identified a range of biosignatures that may indicate past or present life. These biosignatures include information related to atmospheric gases, isotopic fractionation of key elements, fossilized remains, complex biomolecules such as lipids, nucleic acids, and proteins, as well as microbially induced sedimentary structures [103]. Additionally, dormancy-like phenotypes should be considered as potential biosignatures. If extraterrestrial life exhibits any similarities to life on Earth, it is possible dormancy could be inferred through nucleic acid ratios (RNA : DNA), resuscitation assays, or the detection of cysts, resting cells, and spores [8, 102].

Outside of our solar system, interest in life detection has been motivated by the deployment of advanced telescopes that have led led to the discovery of previously unknown exoplanets [104]. To date, nearly 10,000 confirmed and candidate exoplanets have been identified [105], with a small fraction residing in habitable zones based on criteria such as size, composition, orbit, stellar luminosity, proximity to the host star, and the potential for water to exist as a liquid [106]. A major challenge in studying the habitability of exoplanets is their vast distances from Earth, making direct study intractable. Consequently, the search for life on exoplanets often focuses on detecting atmospheric redox disequilibrium through spectrometry [103]. However, distinguishing a lifeless planet from one with a predominantly dormant biosphere could be difficult using atmospheric signatures alone. In such cases, life might still be detectable if it has altered the planet's surface, particularly through adding to the complexity and diversity of the mineral assemblage of a planet [107]. It is estimated that 34% of the minerals on Earth's surface are only formed by biology [108]. Thus, a planet with a dormant yet persistent biosphere could potentially be identified via reflectance spectrometry of surface minerals.

6 Looking forward

Understanding the origins of life is a profound problem that requires insights from biology, geology, chemistry, astronomy, and physics. Despite significant advancements in theory and technology across these disciplines, reconstructing Earth's early history remains challenging, largely due to the loss of material and information over vast expanses of time. Despite this, origins-of-life researchers have developed rigorous approaches to ensure strong inferences can still be made. For example, we demonstrate

how the fossil record and phylogenetic reconstructions can be used to describe the distribution and timing of dormancy-related processes in Earth's past (Fig. 5).

6.1 Opportunities for metagenomic insights

Metagenomics is a field that has revolutionized our ability to assemble and analyze the genomes of bacteria, archaea, eukaryotes, and viruses from virtually all habitats on the planet, including the deep subsurface and other extreme environments that may resemble conditions where life first evolved. These efforts have led to the discovery of numerous deep-branching lineages, shedding light on long-standing debates regarding the evolutionary relationships between the major domains of life [109]. Moreover, metagenomic approaches have facilitated the development of genome-scale models that can generate hypotheses concerning the metabolism and traits of LUCA [95].

In the context of dormancy, metagenomics has helped identify candidate bacterial phyla, like the Dormibacteraeota. As the name suggests, these microbes possess genes that are likely associated with dormancy, including those involved in the synthesis and degradation of glycogen, a storage molecule that may support maintenance energy costs, thus extending the duration of cellular viability in an inactive state [110]. Surprisingly, Dormibacteraeota also harbor a significant number of endosporulation genes [110], although not enough to meet the minimal requirement for producing a functional endospore [111]. These observations raise intriguing questions about the origins and distribution of ancient forms of dormancy, which we anticipate will be elucidated in the coming years.

6.2 Opportunities for modeling insights

Modeling approaches are essential for formalizing and testing hypotheses about the origins, emergence, and evolution of life on early Earth. For example, autocatalytic sets have been developed and widely used to explore chemical reaction networks. Through the emergence of self-sustaining loops, these models offer a mechanistic explanation for the supply of essential building blocks necessary for the evolution of life [17] (Figs. 3, 4). In a similar way, kinetic models have been used to assess key processes, such as chain formation and self-replication, essential for the rise of an RNA world [112].

Incorporating dormancy into origins-of-life modeling has the potential to enhance our understanding of early Earth evolution. For example, panspermia is the hypothesis that life exists throughout the universe and can be transported among celestial bodies. Analytical modeling has explored how debris generated from meteorite collisions could exceed planetary escape velocities and potentially spread life throughout the Milky Way [42]. However, organisms contained in ejecta (i.e., dust, rocks, ice) would experience harsh conditions, including extreme temperatures and elevated exposure to UV and ionizing radiation. For this reason, survival parameters that reflect protection from dormancy are included in models used to make quantitative predictions about panspermia [42].

Dormancy has also been incorporated into models of protocell evolution. The primitive cells contain autocatalytic sets where chemical dynamics are coupled to growth–division dynamics allowing individuals to spontaneously transition between active and inactive states [113]. In a population of protocells with heritable variation, active cell types evolve to become dominant, while inactive types are stably maintained at a lower frequency [113]. In a different way, dormancy has has been integrated into 'Game of Life' models, where individuals of a population transition between metabolic

states according to simple rules that are governed by the density of neighboring individuals [9]. Together, these types of modeling approaches have the potential to shed light on what is minimally required for the emergence of complex behaviors associated with dormancy, which is relevant to origins-of-life research.

6.3 Conclusions

Many living and non-living systems exhibit dormancy-like properties, enabling agents to transition between states of activity either stochastically or in response to environmental conditions. The protection afforded by dormancy allows inactive agents to persist during unfavorable times and resume activity when conditions improve. These features of dormancy create a 'seed bank' that buffers population dynamics and preserves information, which can lead to the emergence of memory, complexity, and feedback. Widespread among diverse lineages today, dormancy was prevalent among various forms of life in the distant past, possibly present at the time of LUCA. Dormancy could have shielded life from extinctions, facilitated dispersal, and enhanced diversification during the development of the early biosphere. By acting on biomolecules in a prebiotic world, dormancy-like properties may have even played a role in the origin of life. The criteria for dormancy are relatively simple and appear easy to evolve, suggesting that dormancy is a general, if not universal, solution to one of life's most fundamental challenges: persisting in noisy and unpredictable environments.

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