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The planetary scope of biogenesis: the biosphere is the fourth geosphere

The origin of life was a planetary process, in which a departure from non-living states led to a new kind of order for matter and energy on this planet. To capture the role of life as a planetary subsystem we draw on the concept of geospheres from geology. Three traditional geospheres – the atmosphere, hydrosphere, and lithosphere – partition terrestrial matter into three physical states, each associated with a characteristic energetics and chemistry. The emergence of life brought the biosphere into existence as a fourth geosphere. The biosphere is an inherently dynamical state of order, which produces unique channels for energy flow through processes in carbon-based chemistry. The many similarities, and the interdependence, of biochemistry with organometallic chemistry of the lithosphere/hydrosphere interface, suggests a continuity of geochemistry with the earliest biochemistry. We will argue that dynamical phase transitions provide the appropriate conceptual frame to unify chance and necessity in the origin of life, and to express the lawfulness in the organization of the biosphere. The origin of life was a cascade of non-equilibrium phase transitions, and biochemistry at the ecosystem level was the bridge from geochemistry to cellular life and evolution. The universal core of metabolism provides a frame of reference that stabilizes higher levels of biotic organization, and makes possible the complexity and open-ended exploration of evolutionary dynamics.

1.1 A new way of being organized

The emergence of life on Earth brought with it, for the first time on this planet, a new way for matter and energy to be organized. Our goal is to understand this transition, how it happened and what it means. The question how life emerged – what sequence of stages actually occurred historically – can at present be answered only at the level of sketches and suggestions, though for some stages we believe good enough arguments can be made to guide experiments. To arrive at a sketch, however, we cannot escape making many choices of interpretation, of things known about life and its planetary context.

Life emerged in an era not accessible to us through historical reconstruction. Our claims about what happened in this era will depend on the principles we use to generalize, simplify, and extrapolate from knowledge of modern life and a few fossilized signatures that become increasingly fragmentary and difficult to interpret on the approach to the beginning that we wish to understand. More important than any claim we can make about past events will be whether we frame the problem of emergence in terms that capture its most important abstractions.

Life appeared on Earth in a period known as the Hadean, the Earth's oldest eon, a reference to the etymology of Hades as "the unseen" [196]. Other than gross features of planetary composition, it has left no detailed signatures in the present because it is a time from which later eras preserved no memory.[1] The Hadean was, however, a time we think of as governed by laws of geophysics and geochemistry, and therefore open to understanding. (Indeed, the absence of memory makes the Hadean, more than later periods with accreted history, a simpler period to study with general laws.) The earliest stages of life were scaffolded by these geological laws, and in some respects may even have been continuous with them. Thus in geology the complement to historicity is lawfulness. What we cannot infer from preserved memories we seek to deduce by understanding the action of laws.

We argue in this book that the same is true for life. The complement to historicity in its earliest periods was not chaos, but lawfulness, albeit perhaps lawfulness of a statistical nature. Life inherited the laws of geochemistry, and grew out of geochemical precursors because some of those laws required the formation of a new state of order qualitatively unlike any of the lifeless states of matter. Life is still in large part lawful, if looked at in the right way, and some of the laws that govern the living world today are good candidates for laws that were at work during its emergence. However, modern life is also historical, to a much greater degree than modern geology, so one of the challenges to making the correct abstractions about its origin is to recognize and separate the contributions of law and of history.

The origin of life was a process of departure and a process of arrival: a departure from non-living states that we understand with natural laws, and an arrival at a new living mode of organization that is robust, persistent, and in its own respects law-like. To understand why a departure was prompted, and why the arrival has been stable, we must begin by recognizing that life is a planetary process, and that its emergence was a passage between two planetary stages.

1.1.1 Life is a planetary process

The emergence of life was a major transition in our planet's formative history, alongside the accretion of its rocky core, the deposition and eventual persistence of its oceans, and the accumulation of its atmosphere. Several facts about the timing, the planetary impacts, and the organizational nature of living systems establish the context within which any theory of origins must make sense.

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[1] As is fitting, one of the five rivers in Hades from Greek mythology is Lethe, the river of forgetfulness.

Life apparently emerged early Conditions on Earth earlier than about 4 billion years ago appear to have been too hot and desiccated from asteroid infall to permit even the chemical constituents that we now associate with life to exist, much less to permit its processes to take place.[2] Yet evidence, either from explicit microfossils or from reworking of element compositions and isotope ratios that we associate with life, suggests that as early as 3.8 billion years ago, and with much greater confidence by 3.5 billion years ago, cells existed that must have possessed much of the metabolic and structural complexity that is common to all life today [444]. Given the extremely fragmentary nature of the rock record from this ancient time, the existence of the signatures we know suggests that life first became established on Earth in a geological interval that was shorter than 200 million years – possibly much shorter – an interval that was also a period of geological transition on a still young planet.

Living systems have (in some cases radically) altered planetary chemistry Living systems have always altered the chemistry of their local environments (these changes are the most reliable ancient biosignatures), and they have gone on to change global planetary chemistry. The most striking change was the filling of the atmosphere and oceans with oxygen, which changed the profiles of elements in solution in the oceans, altered continental weathering, and increased as much as threefold the diversity of minerals formed on Earth [348]. By capturing trace elements in biomass, effectively creating microenvironments for them vastly different from the surrounding physical environments, organisms also govern the concentration and distribution of metals, phosphate, and sulfur, and influence the great cycles of carbon, nitrogen, and water [236].

Living systems are ordered in many ways at many levels Whether in terms of composition, spatial configuration, or dynamics, living systems are ordered in many different ways at many scales. The chemical composition of biomass is distinguished from non-living matter by at least three major classes of synthetic innovation, in small molecules (metabolites), mesoscale molecules (cofactors), and macromolecules (lipids, polynucleotides, polypeptides, and polysaccharides). These components are organized in physical-chemical assemblies, including phase separations and gels, non-covalently bonded and geometrically interlinked molecular complexes, various compartments, cells, colonies, organisms, and ecosystems of a bewildering array of kinds. The essential heterogeneity of the many different kinds of order, and the diversity of processes that have been harnessed to generate them, is a fundamental and not merely incidental aspect of life's complexity.

Although diverse and heterogeneous, living order is also highly selected At the same time as the diversity and heterogeneity of living order creates a complex challenge of

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[2] Whether asteroid infall underwent a late pulse, known as the "late heavy bombardment," sufficient to melt and desiccate the entire Earth's surface concurrently, or tapered more gradually so that sub-crustal water was only locally and intermittently removed, is a point of uncertainty, and this creates uncertainty of as much as 200–300 million years in estimates of the earliest time the Earth could have sustained organic compounds.

explanation, it is important to recognize that, within each “kind” of order, the observed ordered forms comprise a vanishingly small set within the possible arrangements of similar kind.[3] We may characterize the sparseness of observed kinds of order by saying that each ordered form is “selected” – for stability, for functionality, or by some other criteria – but in first surveying the qualitative character of life, we wish to suspend theoretical assumptions about how the selection is carried out, because (we will argue) this turns out to be a complicated question to frame properly. Whether observed forms of living order are sparse because they are uniquely specified by first principles, or because the unfolding of a historically contingent evolutionary process has only sparsely sampled its possibilities, will be fundamental to our understanding of the role of laws in biology, including life’s origin.

An invariant simple foundation underlies unlimited complexity at higher levels At the core of life lies a network for the synthesis of the small organic molecules from which all biomass is derived. Remarkably, this core network of molecules and pathways is small (containing about 125 basic molecular building blocks) and very highly conserved. If viewed at the ecosystem level – meaning that, for each compound, one asks what pathways must have been traversed in the course of its synthesis, disregarding which species may have performed the reaction or what trophic exchanges may have befallen pathway intermediates along the way – the core network is also essentially universal. Some gateway reactions are strictly conserved. In areas where synthetic pathways do show variation, the network tends to be highly modular, and variations take the form of modest innovations constrained by key molecules that serve as branching points.[4] This universality made possible S. Dagley’s and Donald Nicholson’s assembly of a chart of intermediary metabolism [173] that generalized across organisms. Other universal features of life include its use of several essential cofactors and RNA, and some chemical aspects of bioenergetics and cellular compartmentalization. A more complex and enigmatic, but also nearly universal, feature of life is the genetic code for ribosomal protein synthesis. These higher-level universals are discussed in Chapter 5.

This small and universal foundation of life is a platform for the generation of apparently unlimited variation and complexity in higher-level forms. These range from cell architectures to species identities and capabilities, and ecological community assemblies and their coevolutionary dynamics. The contrast that is so striking is that in its invariant core elements, life is universal down to much more particular components and rules of assembly even than other broad classes of matter such as crystalline solids. Yet in its higher levels of aggregation, it appears to have open-ended scope for variation that has no counterpart in non-living states of matter.

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[3] We return in Chapter 7 to a more systematic discussion of possible versus realized forms of order, and the significance of the fact that realized order has vanishingly small measure relative to possible forms.

[4] We provide a much more detailed discussion of metabolic modularity, conservation, and variations, to explain these claims, in Chapter 4.

Life as a whole has been a durable feature of Earth The presence of living systems has apparently been a constant and continuous feature of the Earth since their first appearance at least 3.8 billion years ago. The persistence or tenacity of life bears a resemblance to features that arise in the geological progression of a maturing planet, and we will see that this resemblance extends to the incremental elaboration of complexity in life's universal core as well. The perplexity in this observation is that other stable, invariant geological features result from physical processes under conditions that, at least in principle, we know how to produce in the laboratory or in computer simulations. The states of matter to which they correspond also tend to be reproducible under broadly similar conditions, so they tend to recur in broadly similar environments. In contrast, we currently have essentially no understanding of what laboratory conditions would reproduce the emergence of life. Current observation of non-Earth systems, including meteorites and other planets or moons, is also consistent with the absence of signatures we would characterize as unequivocally biotic. These observations have been interpreted by Francis Crick [168] and Jacques Monod [561] (among others) as circumstantial evidence that life is improbable or accidental.[5] While we believe this interpretation is unjustified, the observations do imply at the least that the conditions for life to emerge and persist are much more *particular* than we have come to associate with robust and persistent physical states of matter.

The persistent presence of living states on Earth, including persistence of the universal core, is more striking because higher-level systems such as cell form and catalytic capability have undergone major episodes of innovation, while still higher levels such as species identities or ecological community structures exist in a state of almost constant flux or turnover. These higher-level systems appear, at any time, to be essential to carrying out core processes, yet they have been much more variable than either the core that depends on them, or the broad characteristics of the living state by which all life shares a family resemblance. Reconciling such signatures of accident and fragility, with other signatures of robustness that we normally associate with inevitability, is one of the longstanding puzzles in understanding the nature of the living state.

1.1.2 Drawing from many streams of science

Natural languages for the origins of order can be drawn from many areas in biology, including functional and comparative studies of metabolism and cell physiology, molecular and cellular architecture, the nature of catalysis, genomic mechanisms of hereditary memory and regulation, the complex and multilevel character of individuality, the ways selection and regulation interact to produce developmental programs broadly construed, the reconstructed evolutionary history of many of these systems and their functions, and a host of regularities in ecological productivity, community assembly, and dynamics in both extant

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[5] Crick's characterization was "a happy accident, indeed nearly a miracle."

and reconstructed ecosystems. We will summarize some of these, and pursue others in greater depth, in Chapters 2 through 5.

In addition to the biological sciences, we have paradigms of architecture and control from engineering, and important theories of stability from physics and (closely related) of optimal error correction from information theory. These provide potentially useful abstractions of functions performed in living systems, and in some cases strong theorems about the limits of possibility. They will be developed in Chapters 7 and 8.

All of these provide windows on the nature of life. They capture patterns in the living world that do not exist without life, and in a piecemeal fashion, they often partially characterize mechanisms by which those patterns are created and maintained. We would like them to define the problem of departure from a non-living planet that must be understood.

1.2 The organizing concept of geospheres

The problem of unifying diverse phenomena is not new with biology. Similar problems have arisen in planetary science, involving as it does a variety of chemistries, physical phases of matter, and classes and timescales of dynamics. Here a traditional coarse-grained partition of planetary systems into "geospheres" has remained useful into the modern era. The 1949 text *Geochemistry* by Kalervo Rankama and Thure G. Sahama [664] partitioned the non-living matter of Earth into three "geospheres": the atmosphere, hydrosphere, and lithosphere.[6] The concern of the authors was to provide an overview of the chemical partitioning and physical states of all matter on the planet.

The "geosphere" designations are very coarse, and to understand their use it is helpful to keep in mind the kinds of distinctions they are *not* meant to make. The geosphere partition, for the most part, does not separate regions with sharply defined boundaries; their components often interpenetrate and interact. The geospheres also do not aim at strict chemical partitions. For example, water, the primary constituent of the hydrosphere and source of its name, is present in the atmosphere, and in the lithosphere both as hydrate of minerals and as a component in trapped fluids.

Despite (and in some ways, because of) its qualitative and approximating nature, the language of geospheres is useful because it groups *multiple classes of distinctions* that are inter-related and that share the same domains of space and often similar states of matter. A coarse partition into regions and aggregate states and dynamics, by pre-empting other classifications according to specific chemical identity or sharp spatial boundaries, emphasizes

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[6] These three coarsely defined geospheres are all subject to much more refined description. In modern usage, the atmosphere subdivides into an ionosphere, mesosphere, stratosphere, and troposphere, and the hydrosphere layers into epipelagic, mesopelagic, bathypelagic, abyssalpelagic, and hadalpelagic zones plus crustal and sub-crustal water. The lithosphere, used by Rankama and Sahama to refer to the totality of rocky and metallic zones on Earth, is now refined into zones that are in some respects almost as different from one another as they are from the hydrosphere. The term "lithosphere" is now used specifically to refer to the crust and rigid layer of the upper mantle, followed in depth by the plastic asthenosphere, the stiff (though still plastic) lower mantle, the liquid iron/nickel metal outer core, and the solid (also Fe/Ni metal) inner core. The refinement, however, only changes in degree but not in spirit the original function of qualitatively partitioning fine-scale structures and dynamics into useful aggregate domains.

that the system-level relations and interactions are the unifying concept for each geosphere, rather than an exclusive list of material components.

1.2.1 The three traditional geospheres

Each of the three traditional geospheres is associated with one or a few primary groups of chemical constituents, a primary phase of matter, and a characteristic class of chemical reactions.

Atmosphere Gas phase, composed of small molecules made principally from non-metals and noble gases, which exist as gases over large ranges of temperature from ~ -40 to $\sim 100\,^\circ\mathrm{C}$. Primary chemistry is photolytically excited gas-phase free-radical chemistry, with some ionization chemistry in the upper layers. High activation energies of excited states produce reactive compounds, which persist only at low density.

Hydrosphere Liquid phase, water solutions. Oxides of nitrogen and sulfur may be present as solutes in relatively high concentrations; the concentration of metals (particularly transition metals) depends sensitively on oxidation/reduction (or *redox*[7]) state through reactions to form insoluble compounds with non-metals. Primary chemistry is oxidation/reduction, acid/base, and hydration/dehydration chemistry. Radical intermediates have high energies and are not produced except very near the surface due to screening of light by liquid-water scattering and absorption, and they quench rapidly when formed. Acid/base and oxidation/reduction reactions may be coupled due to the high solubility of protons in water, in contrast to extremely low solubility of electrons.

Lithosphere Solid phase, dominated (outside the core) by the crystallography of silicate and sulfide minerals, with carbonates, hydroxides, and other metal oxides as lesser constituents. Much of the chemistry of the lithosphere is physical chemistry of phase transitions including melt-fractionation, dissolution, precipitation, and stoichiometric rearrangement in solid solutions. Many phase transitions involve changes in oxidation states of metals, driven by the crystallography of silicates as a function of temperature and pressure. Changes in compatibility of minor elements with temperature and pressure can be a large determinant of pH for included fluids. Although redox changes for transition metals often result from coordination changes in crystallographic contexts, they are of major importance to the chemical activity of the Earth as a whole. Mantle convection can convert heat energy, through long-range transport across temperature and pressure zones, into redox disequilibria that are too energetic to be created by thermal excitations in near-equilibrium conditions.

We return to give a more detailed characterization of some of these properties of the Earth in Chapter 3.

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[7] Oxidation and reduction are introduced in Chapter 2.

1.2.2 The interfaces between geospheres

1.2.2.1 Complexity often arises at interfaces where matter is exchanged

Because the same chemicals can pass between geospheres, the interfaces between them can be concentrating centers for thermodynamic disequilibrium and the emergence of complexity. For example, volcanic outgassing, believed to be the main source of the present atmosphere, can release both methane and carbon dioxide from carbon trapped in the mantle when the Earth cooled. It also supplies hydrogen, ammonia, and hydrogen sulfide. Continental weathering is a process at the interface of the lithosphere and atmosphere also involving water, which alters minerals, replenishes trace elements (particularly Ca^{2+}) in the ocean, and plays a major role in sedimentation of carbonates and regulation of both the CO_2 partial pressure of the atmosphere and the atmospheric greenhouse. The ocean/atmosphere interface, where the cross section for absorption of sunlight energy changes drastically between two matter phases, is a primary generator of surface heat that powers evaporation and drives the global weather system. On the early Earth, it was also a boundary across which N_1 compounds could diffuse, between a region where only nitrogen oxides could survive and one in which only ammonia could survive. In the present Earth with its marine biota, the surface (photic) zone is the major zone of primary productivity. Organisms actively regulate not only light absorption and scattering, but also the viscosity of the air/water interface, controlling rates of evaporation, droplet formation, entrainment of bubbles, and thus gas exchange between the atmosphere and oceans. Finally, the lithosphere/hydrosphere interface is an extraordinarily rich zone of disequilibria in temperature, chemical potentials, geometries, and physical properties of matter, which we consider next.

1.2.2.2 The lithosphere/hydrosphere interface is particularly important to life

Of great interest to us, as we try to situate the materials and processes of life in their planetary context, will be convective currents of sub-crustal water near spreading centers and volcanos. This water is part of the lithosphere/hydrosphere interface, and is one of the most chemically active zones of terrestrial matter. Whereas local regions within the mantle, crust, or oceans generally exist very near chemical equilibrium, the interface between the hot, convected rock and surface water is constantly pushed far from equilibrium by the mismatch between the primordial reducing character of the bulk Earth and an atmosphere driven to be more oxidizing through escape processes. The mismatch at the interface is constantly replenished as a secondary effect of the dissipation of heat from fission of radioactive elements present when the planet formed. Sub-crustal convected water systems are a particularly interesting feature of the Earth, because they depend on its composition and its internal heating, and their chemical activity depends on its internal convection as well.[8] The chemical activity at the rock/water interface is closely connected to the chemical

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[8] Whether tectonics in the current sense of oceanic basin subduction was a feature of the Hadean Earth is currently debated. We return to this question in Chapter 3.

activity *within* living systems, and modern-day hydrothermal vent systems host rich and ancient biota capable of exploiting this overlap.

Chemical systems tend to equilibrate to within the scale of thermal fluctuations ($k_BT \sim 0.026\,\mathrm{eV}$ at room temperature) if they are not continually re-energized. The thermal activation energy of typical covalent bond modifying reactions ($\gtrsim 0.5\,\mathrm{eV}$) is at least 20 times the available thermal excitation energy under conditions where liquid water exists at surface pressures. Therefore covalent bond modifying chemical activity is seen only at extremely low rates in systems that are only activated thermally. The most important physics question for a chemical origin of life within geophysics is where on Earth chemical potentials can be sufficiently insulated from one another to form large differences, but then brought together rapidly enough to drive chemical reactions rather than simply dissipating as heat.

The key to this creation of sharp chemical disequilibria is **mantle convection**. The tendency of hydrogen to escape from planetary atmospheres, leaving complementary oxidants behind, is a ready source of disequilibrium between the interior and surface of the planet. The insulating layer of the crust provides a strong barrier between these systems so that their redox potentials can move far apart. Mantle convection, resulting in volcanism and under some conditions in plate tectonics, is the force that breaks through this insulating barrier to create local disequilibria. The surface phenomenon of water circulation through heated, cracked rock – a process that is particularly efficient and active at spreading centers and faulting systems on tectonically active planets – then leads to mixing zones where disequilibria that accumulate over millions of years are brought into contact on the molecular scale.

Before the 1970s, it was believed that all life on Earth ultimately owed its existence to energy captured photosynthetically from sunlight. The discovery of hydrothermal vent systems by John Corliss and collaborators [162] using the deep submersible Alvin first revealed a diverse and thriving biota existing out of contact from sunlight, and apparently fed by minerals dissolved in vent fluids and not by detrital carbon. This life was effectively decoupled from the solar energy system except by the existence of liquid water (and, though this is now known not to be limiting, the presence of oxygen produced by photosynthesizers).

Four decades of study of microbial metabolisms and energy sources [481] have gone on to show that an enormous diversity of bacteria and archaea obtain energy from geologically produced electron donors and acceptors in both surficial and subsurface environments,[9] and that this energy is sufficient to maintain self-sufficient life and growth from one-carbon inputs, molecular nitrogen, a few inorganic salts, and trace metals. Hydrothermal systems are profuse sources of these inputs, and support life in anoxic environments that provide better models for the early oceans than oxygenated environments such as surficial hot springs. Vents were quickly proposed [161] as plausible geochemical environments for the origin of life, and since phylogenetic reconstructions increasingly suggest reductive,

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[9] Some vent environments support not only microbial assemblies, but complex ecosystems of worms, mollusks, and crustaceans supported by these microbes.

thermophilic metabolisms occupied all the deepest branches of the tree of life, this proposal seems historically plausible as well as energetically feasible.

Within the abiotic matter on Earth, the chemistry at the lithosphere/hydrosphere interface most closely resembles the chemistry of life both in its general character and even in detail. Biochemistry takes place in condensed phases, meaning either aqueous solution or microenvironments created by enzymes or membranes. Gas-phase chemistry is essentially impossible, and photoionization in the strict sense (such as occurs in space) is not used. Much of the bulk of biochemistry consists of reactions that are facile in water and involve either full bonding-pair exchange (oxidations and reductions), proton exchange, or group transfers. When radicals are used, they are formed at metal centers and either hosted on metal centers (as in ferredoxins) or transferred to a limited inventory of highly evolved cofactors. Several investigators (to whose ideas we return in Chapter 6) have emphasized the similarity of biological metal centers to metal sulfide minerals that would have been present in the surface and near-surface on the Hadean Earth. Even the temperatures at which biochemistry is carried out fall within the range found in hydrothermal systems.

1.2.3 The biosphere is the fourth geosphere

The three geospheres of Section 1.2.1 subsume, though only in general terms, the domains of scientific knowledge that would apply to matter and events on a lifeless planet. The part of Earth as we know it that is not even qualitatively accounted for within the three abiotic geospheres naturally defines a fourth geosphere. This is the **biosphere**, a term coined by Vladimir Vernadsky [832] to refer to the totality of living systems and their interconnections, and approached by us as a component of Earth's matter and dynamics. The phase of matter in the biosphere is defined not only by its physical state but even more fundamentally by its necessarily non-equilibrium condition. Its chemical constitution draws from a sector of covalently bonded organometallic compounds, which are not produced by abiotic processes.[10] Its chemical process comprises the reactions that these compounds mediate and by means of which they are also produced and maintained. Its characteristic activating energy scales are the barrier- and reaction-free energies typical in reactions that make and break covalent bonds among C, H, O, N, and S atoms and phosphate groups, and dative bonds of O, N, and S to metals. Its characteristic temperature covers the range for liquid water in near-surface terrestrial (including submarine and sub-crustal) environments, $\sim 0-120\,^{\circ}\mathrm{C}$.

In attempting to characterize what the biosphere "is," it is important to us to recognize commonalities with the abiotic geospheres, along with all the levels of organization described within biology, but at the same time to recognize that the biosphere is more than any one of these alone. At the outermost level of abstraction, we emphasize that the order

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[10] Speaking more carefully: some of the compounds are not produced at all, and others, which are produced at small rates in abiotic processes, are not produced with the selectivity, yields, or functions that they take in the biosphere, by many orders of magnitude of difference.

of the biosphere is fundamentally an order of processes, that the "internal" organization of the biosphere consists of flows anchored to the exchange at boundaries with the other geospheres, and that the biosphere as a whole, rather than any organism or ecosystem within it, is the level of aggregation in which to recognize the nature of the living state.

The biosphere is a set of patterns maintained by processes, and patterns *of* processes, and not merely a collection of "living things". Living matter, on one hand, is a subset of terrestrial matter organized into all the levels and patterns mentioned in Section 1.1.1, and maintained in this order by living processes. More fundamentally, it is the processes themselves that are maintained within a state of coordination and pattern. If we adopt the view that both the relations and the ordered state of processes are fundamental to the nature of life, it becomes clear how inadequate it would be to characterize the biosphere as merely a collection of "living things." For this reason, while our emphasis on systems and relations is not fundamentally different from Vernadsky's encompassing view of the biosphere, we approach it as a planetary subsystem to more strongly shift our emphasis away from entities and toward a focus on relations and processes. We will return in Chapter 8 to argue that even the appellation "living things" assumes a category error: life is not a property inherent in things so much as things are instantiations of organizational states that arise within a larger context of life.

In Section 1.2.2 we noted that the organometallic chemistry at the lithosphere/hydrosphere interface resembles in character the chemistry of life, and also that the energy sources at the lithosphere/hydrosphere interface sustain an ancient and autonomous biota today. In both respects, the biosphere's order is anchored in boundary exchanges with abiotic geospheres. However, an important distinction is that the reactions characteristic of *interface* chemistry in the abiotic realm become the *constitutive* chemistry of the biosphere. This is another sense in which the ordering of processes pervades the nature of life in a way that it does not pervade the nature of non-living states. It has the consequence that the organization of living matter is anchored in the conditions for matter and energy exchange with its non-living context, at a finer level of detail than is true for physical phases of matter.

From these and a host of other related observations, we will arrive by the end of this book at the assertion that *the biosphere as a whole is the correct level of aggregation from which to define the nature of the living state.* It is a system of processes, anchored historically and causally in physical laws and geochemical circumstances at many places. Accounting for the robustness of life means accounting for the long-term persistence and stability of this integrated system, across all its levels.[11] It is necessary to understand why multiple kinds of order are possible, and the roles played by different levels of organization in creating a domain of stability for the living state and ensuring that the biosphere remains within

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[11] Sometimes, as in the case of autotrophic bacterial or archaeal species, multiple levels coalesce into a single locus: the cell is both an organism and a biosynthetically complete ecosystem unto itself; the cell coordinates metabolism, compartmentalization, energetics, and molecular replication within the same aligning framework of individuals and generations. Both from history and from comparative and functional analysis of biodiversity, however, we have grounds to distinguish these kinds of organization, and to recognize that each may exist in more general contexts and systems of coordination than only those they possess in autotrophic cells. Therefore we believe it is correct to refer to the joint preservation of all of these kinds of organization, with their distinctions acknowledged, as the essential phenomenon underlying biological robustness.

that domain of viability. The aliveness of things is not defined as a property of structure or function inherent in the things themselves, but rather by their participation within the web of processes by which the systemic integrity of the biosphere is maintained.

1.3 Summary of main arguments of the book

In the next seven chapters we attempt to bring together empirical generalizations and functional knowledge about properties of life and its planetary context, with general mathematical principles about the nature of stability and robustness, to frame the problem of biological emergence and persistence, and to sketch major stages that we think can be proposed with some specificity. Our approach to interpreting regularities of life, and to adopting theoretical frames more generally, will be gradual and will proceed along several threads in parallel.

We will begin by characterizing the biosphere at a very aggregate phenomenological level. What makes life, in its planetary role, and viewed at a system level, unlike the union of the other three geospheres? We recognize the role that evolution plays as a mechanism for imparting and maintaining living order, but we also recognize that evolution as a distinct process depends on the prior organization of living matter into modes of individuality, which is a complex problem. We argue that evolution belongs within a wider class of order-forming processes, some of which have less complicated preconditions and play different roles in the maintenance of living order.

We believe that the problem of maintaining the biosphere within an asymptotically stable operating range, when faced in the full enormity of error, displacement, or degradation that can enter every atom, bond, structure, and process of life, presents the largest conceptual challenge to a theory of the origin of the biosphere and the nature of the living state. The paradigm most likely to address this problem correctly comes from the mathematics of cooperative effects responsible for thermal phases and phase transitions, which is also the mathematics of asymptotically optimal error correction. We argue that cooperative effects, acting to produce dynamical phase transitions, provide error buffering that is essential to maintaining the hierarchical complex systems that constitute the biosphere. Some kinds of dynamical phase transition arise in population processes and thus characterize the aggregate dynamics of evolution, but the concept applies much more widely within the domain of processes that we argue contribute to biological order.

Ordered phases form in response to their boundary conditions, and the boundary conditions for life are the chemical disequilibria created by planetary geochemical activity and (secondarily, we claim) by the flux of visible light from the Sun. The aggregate function of the many ordered phases of life is to conduct energy from sources to sinks through cycles of chemical reactions. The technical question whether the free energy in the non-equilibrium boundary conditions is sufficient to *drive* a biosphere into existence as an energy channel defines an appropriate criterion of necessity for the origin of life.

Phase transitions act through self-reinforcement to introduce robust order into nature by coordinating random small-scale events. Because part of the order in thermal phases is law-like and non-arbitrary, the points at which phase transitions can arise to buffer errors provide a skeleton of lawfulness that anchors the open-ended variation and complexity of evolution of particular species or ecosystems. Because some of the continuity of lawfulness reflects explicit properties within chemistry, we argue that in some chemical properties the biosphere is continuous back to the earliest metabolic departure from geochemistry. In this way we attempt to go beyond mere empirical generalization and provide a sketch of a way to *use* principles – if not an adequate demonstration at the required level of chemical detail – to connect the problem of the origin of life to the understanding of the organization, variation, and persistence of the biosphere as we know it today.

1.3.1 An approach to theory that starts in the phenomenology of the biosphere

To explain what we mean by the gross phenomenology of the biosphere, we imagine confronting the Earth as it might be experienced by an alien visitor who came here expecting to find a world of rocks, oceans, and atmosphere, but no life, and who instead found the planet we know. How are the most basic functions and structures of the planet different because it harbors life than they would otherwise be? How is life responsible for these differences, and what are the essential characteristics of living structure that span its internal heterogeneity and are common across historical eras? Essential properties of life, beginning with the most general and becoming progressively more specific, include the following.

Living systems are chemical The only life we know is a chemical system. This means at least three fundamental things. First, living states are delimited at the microscale by the quantum mechanics of atomic and molecular orbitals. Their dynamics is governed by the orbital-scale dynamics of reactions and a few extended-electron states in organic molecules, and by the physical chemistry of molecular assemblies. It is not necessary to probe scales below the quantum mechanics of electronic states to capture all essential foundations of living structure. Second, the living world inherits the complexity of chemical systems as its microscopic foundation. It may build further complexity by selecting among chemicals in a variety of ways, but it does not need to create the complexity of the chemical state space itself. Third, the combination of a quantum mechanically defined discrete state space, together with discrete reactions divided by energy barriers, enables chemical systems to maintain large differences of free energy within small distances – on the order of atomic radii. Life differs from the phenomena of weather and climate in taking its most basic structures from molecules rather than from soft structures such as diffusive boundary layers.[12]

Life is dynamical Life is an ordered assembly of processes. Living systems operate out of thermodynamic (principally chemical) equilibrium. Energy flowing through them is partly captured to construct states that would be improbable in equilibrium systems. In turn

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[12] Although it may use the latter opportunistically, they are not a foundation for the overwhelming majority of its structure, and perhaps for any essential structure.

these disequilibrium states carry living processes that otherwise would not occur, including those that conduct energy flows between non-equilibrium boundary conditions that furnish sources and sinks. It is conventional (and correct) to say that the order in living states cannot (in most cases) be understood except in the context of the processes that build and maintain them, but it is desirable to go beyond this to emphasize the symmetrically interdependent character of states and processes in the biosphere. The most important meaning of life's being "dynamical" is that it maintains order inherently in a system of processes, as we noted in Section 1.2.3. Non-equilibrium processes may depend on more or less complex and extended histories, ranging from near-instantaneously determined outcomes to outcomes that are highly historically contingent.[13]

No one level or form of biotic order serves as a source for all the others The diverse forms and levels of organization we find in the biosphere do not all seem to be accounted for by dynamics at any privileged level *within* living systems alone. No one kind of living order serves as a foundation from which all the order in life grows, and no distinctively biotic process appears as the source of maintenance at all levels. As we show in Chapter 5, where we review some of the hierarchical complexity in cells, bioenergetics, and molecular control, life consists of subsystems, which are partly integrated and partly autonomous, and are brought together in cooperative assemblies to form living wholes. We characterize life as a "confederacy" of different sources of order, many of which we argue have independent origins within different domains of chemical or physical processes, or planetary conditions. The robustness of the full suite of living regularities results from a parallel appeal at many levels to boundary conditions and constraints of physical laws. The function that distinctively biotic dynamics performs uniquely is to *interconnect* these members of the confederacy into webs of mutual support and interdependence. A view of life as an integration of multiple disparate sources of order may explain how the emergence of life on Earth could have been at the same time an outcome of quite ordinary events, yet one that depends in detail on its planetary context.

Ecosystems are more invariant than organisms We noted in Section 1.1.1 that the small core of metabolism is essentially universal[14] if we define it by asking which pathways must have been traversed in the course of synthesis of essential molecules, anywhere within an ecosystem, without regard to whether an essential pathway was carried out within a single cell or distributed across cells by means of trophic exchange of pathway intermediates. As we will show in Chapter 2 in more detail, the relation of core metabolism to bioenergetics is also simple at the ecosystem level, with the major distinction falling between ecosystems that, in aggregate, rely on geochemically provided donors of energetic electrons for biosynthesis, versus those that produce their own electron donors using energy from sunlight.

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[13] In adopting the term "historical contingency" we follow the usage established by Stephen Jay Gould [312].

[14] We provide a more precise characterization in Chapter 4, which takes account of variations in core pathways by showing how they may reflect redundancy, and factors out the ecological complexity that some organisms may synthesize complex metabolites that other organisms then degrade to produce their simpler precursors.

Moreover, in ecosystems that generate electron donors from sunlight, the biosynthetic networks into which those electrons are fed are essentially the same as those in ecosystems driven directly by geochemical free energy sources.

Any comparable simplicity or universality is emphatically *not* a property of most species considered separately, which consume organic carbon within complex ecological contexts, to provide either energy or biosynthetic intermediates.[15] Thus ecosystems, which in aggregate must be biosynthetically and energetically self-sufficient, assemble a limited inventory of core processes in ways that are much more invariant than the phenotypes of organisms, and are partitioned according to whether they use geochemical or light energy to generate the electron donors required to synthesize organic carbon.

Universal metabolism is an ecosystem property If the simplicity and universality of core metabolism and bioenergetics are expressed in ecosystems whereas they are not generally expressed at the level of organisms, metabolism is in some respects more a property of ecosystems as units of organization than a property of organisms. The added complexity and diversity found among species largely arises in response to the problem of becoming a complementary specialist within a community. Specialization requires the evolution of mechanisms to acquire, transport, and break down organic compounds to deliver to an organism those metabolites that it does not synthesize. Arriving at a stable community dynamic requires balancing trophic fluxes, as well as internal pathway fluxes, through a combination of physiological regulation within member species and adjustments in species' relative population numbers. An ecological community in steady state should minimize waste if it is not to be easily displaced by more efficient alternative community structures. The resulting complex network of constraints, involving gene gain or loss, regulation, and population dynamics, ostensibly supports an enormous variety of possible but mutually exclusive solutions [677].

Thus, while organisms provide the platforms within which metabolic reactions take place, ecosystems carry the patterns of metabolic invariance and record episodes of innovation that move the boundaries of aggregate metabolic constraints, for instance enabling new geochemical environments to be colonized. The organism, as a carrier of a pattern, is an enabler in the short term, but in the long term gene transfer permits metabolic capabilities to assemble in combinations different from those in which they originated,[16] making the organism as a unit of aggregation less important. At all timescales, however, organisms remain important in aggregate, as the carriers of complex networks of constraint for the problem of complementary specialization. These constraint networks may determine regulatory or adaptive flexibility, and the tempo and mode of innovation, which are aspects of community assembly more than of the fundamental chemical constraints on metabolism.

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[15] The distinct ways of life available to carbon consumers are so diverse that current attempts to sample them using computational models of metabolism cannot even provide reliable estimates of their number (Andreas Wagner, personal communication). For efforts to sample the structure of this diversity, see [677].

[16] We provide numerous examples even within the restricted domain of carbon fixation in Chapter 4.

1.3.2 Placing evolution in context

Without doubt, since Charles Darwin's 1859 publication of *On the Origin of Species by means of Natural Selection* [177], evolution in one or another variant on Darwin's framing has become biology's unifying explanatory system [311, 493, 534]. It plays the role in biology that mechanistic notions of causality play in the physical sciences. To the extent that it differs from physical causation – accepting history dependence and relatedness as explicit alternatives to prediction from first principles, as a criterion of scientific explanation – evolution is viewed by many as defining what makes life different from non-life.

As a consequence of the central place evolution is given in biological thinking, many approaches to the origin of life include evolution as a defining characteristic of the system they seek to explain.[17] In many cases, the path of origin proposed is explicitly motivated by a goal of arriving as directly as possible at a chemical system that can be described in Darwinian terms.[18] Thus evolution becomes not only the criterion by which an origin of life is defined, but also the mechanism by which it is assumed to occur.

From our phenomenological approach to life as a planetary subsystem, a central emphasis on evolution poses a problem. Evolutionary processes, as a class, are widely applicable mechanisms that produce a tendency toward order, but their scope is limited and they rely on relatively complex preconditions to be realized. Evolution is neither an exclusive nor an all-encompassing framework for the formation of dynamical order, but only one domain within a larger class of processes that must be considered. Here we will summarize the central concepts that define evolutionary processes as a coherent category, note their limitations, and explain the role we believe they play within a larger framework that is needed to understand the full variety of order that the phenomenology of life includes. We return to a more detailed treatment in Chapter 8.

1.3.2.1 Darwinian evolution as a Kuhnian paradigm

> In the beginner's mind there are many possibilities,
> in the expert's mind there are few.
>
> – Shunryu Suzuki, *Zen Mind, Beginner's Mind* [788]

The acceptance of Darwinian evolution as an explanation for order and function in living systems was, perhaps more than many scientific revolutions, a paradigm shift in Thomas Kuhn's sense of the term [459], with both good and bad consequences.[19] To the good,

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[17] An example is a widely circulated definition reached by a NASA panel: "Life is a self-sustaining chemical system capable of Darwinian evolution" [403].

[18] This is one of the expressed motivations to look for directly self-replicating RNA catalysts as a foundation for the departure from non-life to life [122, 488]. Non-RNA-based approaches likewise invoke evolution, as in the compositional inheritance models of Daniel Segré and Doron Lancet [721, 722, 723].

[19] Kuhn discussed Darwin's formulation of natural selection as the paradigm that had struggled to gain acceptance against entrenched ideas of goal-directedness, which had framed all theories of change in living systems, including Lamarck's version of evolution [467]. The limitations of Darwinian evolution as a paradigm in its own right were yet to be become clearly visible. Some gaps in Darwin's knowledge, when filled, only simplify and reinforce his formulation. For instance, Darwin did not write

evolution by natural selection is a correct framework within which to explain an enormous range of adaptive functions and ordered population states. For the first century after Darwin's *On the Origin of Species*, these included only populations of organisms, but within the past 50 years the explanation has been extended to include many kinds of sub-organismal populations – cell populations governing tissue formation in embryogenesis [567] or antigen specificity in immunogenesis [148], cell processes and synapses in brain development [126], etc. – so that evolution is also recognized as part of the mechanism by which developmental programs are implemented. From the work of William Hamilton and successors [273, 332, 333, 334], the scope of evolution has also been extended outward to describe competition and selection among a potentially unlimited variety of kinds of groups, within the same algorithm that applies to organisms. Evolution by natural selection is thus a very flexible and general algorithm for producing order in populations at many levels.

A detrimental effect of raising evolution to the status of a paradigm is that it creates a default explanation for biological order, which is becoming increasingly exclusive. It is difficult to find serious biological writing that does not suppose – does not feel *obliged* to suppose – that when a mechanism for producing order, function, or stability has been most fundamentally understood, that understanding will reduce to an explanation in terms of evolution. What is true in biology more generally is true for the origin of life in particular.

Imputing notions of cause or sufficient explanation is often one of the trickiest and most provisional efforts in science. The same empirical regularities, viewed through experience in different domains, can trigger very different default explanations, and each of these is a window on the phenomenon. For the origin of life, which is at the same time a phenomenon in geophysics and chemistry, and also the beginning of biology, it is perhaps easier to shift among paradigms than it is from the vantage point of any one discipline in isolation. We will argue, however, that what the origin of life pushes us to recognize, about sources of order and stability, should ultimately restructure our understanding of the living world including the role of evolution.

1.3.2.2 *Three forms of evolutionary default interpretation to avoid*

Three assumptions about the role of evolution either presume results that should be derived, or pre-emptively frame the problem of understanding the living state in terms that may not recognize all relevant mechanisms. We wish to avoid these assumptions.

about bacteria or other microbes, though they had been discovered by van Leeuwenhoek almost two centuries earlier, and were the subject of Louis Pasteur's experiments on sterilization, for which Pasteur won the Montyon prize [287] in the same year *On the Origin of Species* was published. Other omissions would require almost a century to gain sufficient coherence to enable a critical analysis of the Darwinian framework. Although Darwin was a consummate naturalist, aware at every turn of the complex dynamics of species interactions, the term *Ecology* would not be introduced to denote a scientific field until 1866 by Ernst Haeckel [326]. Regularities in macroecology [99, 521], the molecular biology of development and heredity [179, 295], and the diversity and complexity of lifecycles in many taxa of eukaryotic algae and small metazoans [354], which exemplify the complexity in formulating concepts of individuality, would not come to be understood even in outline until late in the twentieth century.

1. **Supposing that Darwinian selection has sufficient power and scope as an error-correction mechanism to explain all of living order** The potential error is one of false generalization: finding that selection is sufficient to trap errors in a subset of dimensions of variation, but then failing to quantify all dimensions of variation that produce error, and supposing that they are somehow trapped as well without requiring different mechanisms. Within the scope of population models, where the levels and units of selection are given as inputs, some criteria already exist showing the limits of selection's ability to maintain order even in the short term.[20] When the requirements are extended to indefinitely long-term maintenance of complex patterns, and the sources of error are recognized to include the full range of disruptions in both states and events reaching down to the chemical substrate, we anticipate that the problem of persistence will become more like the problem of forming long-range order in condensed matter physics [307, 885]. Here the difficulty of forming stable order has been found to be severe, despite the fact that the systems studied are much simpler than those studied in biology. We return in Section 1.3.2.5 to argue that the Darwinian framework for selection requires support from other error-correcting mechanisms that operate in simpler contexts, to arrive at a mechanism sufficient to explain the emergence, overall organization, and long-term persistence of life from non-living precursors.
2. **Supposing the distinctive character of life must be traceable to uniquely "biotic" order-forming processes** We wish to avoid supposing that because the living state is distinctive, that distinctiveness must have been produced by a process that is likewise distinct from processes at work in the non-living world. In particular, we will argue that Darwinian evolutionary dynamics arises as an emergent process *within the living context*, but that the reverse is not true: the distinctiveness of the living state cannot be accounted for solely in terms of the role evolution plays within it.
3. **Supposing the essential order-forming processes for life are of any single kind** Finally, while Darwinian evolutionary processes contribute to the dynamics of all living systems today, we believe it is an error of false conceptual reduction to suppose that competition and selection within Darwinian populations will thereby be the source of explanation for all relevant forms of order. The universality of metabolism offers a concrete case in point to illustrate that evolutionary mechanisms may be part of a system's dynamics but may not offer the level of description needed to understand its order. To be sure, selection has acted on genes, on chromosomes, on cells, and likely at many other levels, throughout the history of life. At the same time, the modes of evolution have changed significantly through major transitions in genome, cell, and organism organization [106, 180, 227, 790]. Simply knowing that competition and selection have occurred leads to no specific predictions for why metabolism is an ecosystem property, why the universal form we see exists, and why its conservation has apparently been unaffected by major changes in the evolving systems that carry it. More generally, the *co-evolutionary* dynamics among heterogeneous populations in ecosystems may show

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[20] The best known are Muller's ratchet [581] and the Eigen error threshold [213, 214].

long-term constraints and convergences, which are not themselves traits evolved under competition and selection. Again, invoking the selection of the member species does little to elucidate the jointly formed pattern, though the pattern may be clearly expressed in other terms. We will list examples from macroecology in Chapter 8.

1.3.2.3 An alternative breakdown of biodynamics into three layers

We think a more useful approach to the emergence of evolution is to recognize the full transformation as an accretion of three distinct layers of function having different levels of complexity.

1. **The ability to preserve a dynamical pattern essentially indefinitely** The universal feature of life to be explained is its capacity to preserve a distinctive, dynamical, chemical pattern in a planetary context, apparently indefinitely, and under the full range of planetary perturbations from microscopic fluctuations to astrophysical disturbances. Some details of the dynamical pattern, such as species identities and ecological community structures, change through time apparently without end, others change within limited ranges, and still others, such as chemical motifs in core metabolism, may not change at all. The existence and degree of change is *secondary* to the existence of a stable dynamical state of chemical order.
2. **The emergence of forms of organization that bring the Darwinian abstractions of replication, competition, and selection into existence** The second problem in the emergence of living dynamics to be explained is the emergence of organizational forms that can live and reproduce autonomously, and can therefore undergo competition and Darwinian selection. Note that the emergence of a Darwinian process does not by itself imply that the process supports unlimited variation. For example, within core metabolism, enzymes for specific reactions confer the capability of autonomous carbon fixation under wide but still finite limits of pH or oxygen fugacity (we will review these in Chapter 4). More generally, systematic adaptations in protein composition may shift optimal growth over finite ranges of temperature or salinity. For these features, Darwinian adaptation is a source of robustness and environmental flexibility, which does not require (and has not received) a wide range of innovation.
3. **The capacity to support sufficiently complex states that essentially "open-ended" variation becomes possible** Within the systems that undergo Darwinian evolution, we must then understand how it becomes possible to maintain such complex states that at some levels the evolving entities become capable of essentially open-ended variation. The most obvious horizon for the generation of a state space too large to be sampled was the production of oligomers of RNA, amino acids, and later DNA. The chemical underpinnings for such a transition, and especially the integration of RNA and peptide systems into the process of ribosomal translation, pose problems of enormous difficulty. For them to have arisen in an environment already possessing considerable chemical and energetic order is already difficult to understand; for them to have been a precondition for the creation of lower-level order seems to us impossible.

While all three of these capabilities are hallmarks of life, they are conceptually independent. Only the last two are evolutionary, and only in the last does adaptation become exploratory as opposed to merely responsive.

1.3.2.4 The universe of order-forming, Markovian stochastic processes

We wish to understand the special place of evolution within a context provided by the wider class of processes that share a concept of emergent order relevant to the structures of both matter and life. They have in common that they are all *stochastic*: the events of interest, at a microscopic scale, can all be treated as random. The emergence of order is defined by a law-like reduction in the range of this microscale randomness, but the fundamentally random nature at the small scale remains, and it is what makes the formation of order difficult. The processes, as a class, are also *Markovian* [232]: the present state of the world, described in sufficiently fine detail, contains all effects from the past that affect the trajectory of the future. This set includes the full range of phase transitions in equilibrium and non-equilibrium bulk processes [307, 506], it includes models of reliable error correction in information theory [732], and it includes Darwinian evolution. As we will explain in Chapter 7, a shared mathematics[21] associated with robustness lies behind all of these phenomena. We expect that, as a fuller understanding of development, physiology, ecological dynamics, and population processes is formed, many more classes of robust dynamics from these fields will be added as new distinct examples to the list above.

1.3.2.5 The framework of Darwinian evolution is predicated on the emergence of individuality

As Stephen Jay Gould argues in *The Structure of Evolutionary Theory* [312], the essential framework of evolution laid down by Darwin contains all of its major distinguishing assumptions, though details changed in the ensuing 100 years leading to the modern synthesis of Fisher, Wright, and Haldane [652], and even in some emphases made by Gould himself. A widely used concise statement of the key abstractions that define an evolutionary dynamic was given by Richard Lewontin in 1970 [482]. Paraphrased, they are the following.

Evolution is necessarily a *population process*. Members of the population must be sufficiently similar to be regarded as parallel copies of some common template, and to compete for the same niche. The population must persist via reproduction of its members, the members must be capable of some degree of variation, and variations (along with the common template) must be passed down more or less faithfully under reproduction.[22] The change

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[21] This mathematics grows out of the combinatorial properties of large numbers, and it goes under the heading *large-deviations theory* [224, 811].

[22] Here we have deliberately used common-language terms, such as "members" of a population, and "reproduction," for many of the same reasons that we used descriptions in terms of gross phenomenology in Section 1.3.1. Technical terms of art, as a price of being more formal and explicit, often involve many theoretical premises, which we do not wish to take for granted and in some cases wish to modify.

A very common term of art that we will usually avoid is "replicator" [181]. This term presumes the existence of entities that are literally copied during reproduction, whereas most aspects of reproduction involve some degree of assembly as well in the composition of the population over time results from random sampling in the events of reproduction and death, and from non-random selection by the environment of who reproduces (and how prolifically) and who dies. It is by means of the non-randomness in selection that information about the environment comes to be reflected in the composition of the population, a condition that is referred to as the population's becoming adapted to its environment.

The most important assumption that sets evolutionary processes apart, within the larger class of Markov processes, is what evolution assumes it means to be a "member" of a "population." The operative concept is one we will call **individuality**. We will characterize it informally, but ultimately it is a statistical concept extracted from properties of interdependence and autonomy among components within the physiology or reproduction of a living system.

We refer to the two concepts that set individual-based dynamics apart from continuum dynamics as "granularity" and "shared fate" of characters. Individuals in a population process are collections of parts, which are interdependent within an individual, and independent between individuals. The interdependence and independence may be matters of degree and need not be absolute, but in practice living systems often produce large, qualitative changes of dependence between intra-individual components, the individual and its environment, and between individuals. The step-like character of the degree of interdependence at the boundary of an individual identity gives the dynamics in individual-based systems a character we call **granularity** to contrast it with the behavior of continuous systems, much as the rigid interdependence of constraints in granular flows lead to dynamics very different from those in fluid flows [19, 46, 47, 489].

The granularity of individual states also leads to reproduction that is discrete in time, and the second characteristic essential to individuality is that the components within an individual tend to be lost or to be reproduced jointly, and thus to have **shared fates.**[23] Shared fate distinguishes individuals from randomly formed coalescences of components, making components that are reproduced together predictable by each other. It is the intergenerational counterpart to the intra-generational functional interdependence characterized by granularity.

Any order-forming process that qualifies as evolution is predicated on the existence of a corresponding form of individuality in terms of which competition and selection are defined. The emergence of forms of individuality is a process that we expect to be dynamically or algorithmically complex. Dynamical coordination of components is a problem of maintaining long-range order, and our experience with long-range order in equilibrium systems has suggested that this is possible only in limited circumstances. We also observe

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as copying. Insistence on a materialist reification of a replicating entity has led to often unproductive debates on the validity of "genic" versus multilevel selection [181, 880], which we mention in Chapter 8. These obscure the more important point that incomplete or probabilistic transmission of patterns is the central process of interest, to which the construction of formal models must adapt.

[23] We will use common-language terms as category terms, introducing technical terms where we can make them operational. Fate may be shared only probabilistically, at many levels in a hierarchical system. Therefore many nested notions of individuality may be appropriate to characterize a complex living system, such as gene, chromosome, or organism.

that only some of the robust patterns in the living world appear to have an individual-based organization. A case in point, as we noted above, is that although metabolism seems to require a cellular milieu to exist under the competitive conditions of a world with evolved organisms, the integration of biochemistry into a self-sufficient system does not usually depend on maintenance of genes for a complete biochemistry within a single genome. In most cases, it is maintained through feedback in the more fluid architecture of ecosystems.

The problem of stabilizing a form of individuality depends on a complicated process of selecting more robust individuals within a population, and creating environments in which the selective forces on components that make up individuals limit the forms of variation they can generate. Some of the process of stabilization may be mediated by transmitting selection criteria up or down within a hierarchy of nested levels of Darwinian dynamics [106]. However it is accomplished, the essential requirement is for sufficient system-level feedback to compensate for destabilization at all levels. This feedback may be carried by either individual-based or more continuous degrees of freedom. Stabilization becomes an easier problem for systems that are inherently capable of less open-ended variation, so we expect that these play an essential role as *reference states* for more variable forms. We emphasize the importance of distinctive but unchanging forms of biological order, such as metabolism at the ecosystem level, because we believe this order reflects the template that stabilizes the entire hierarchy of forms of individuality and their associated levels of Darwinian dynamics.

Understanding closure of error correction in hierarchical dynamical systems promises to be a complex and technically difficult problem even when the questions are properly framed. To understand why that problem has been solvable by living systems, we look for structure within the order-forming process that simplifies problems of error correction and stabilization. Although randomness, stochasticity, and error occur in all microscopic events in living and non-living matter, they are more contained and easier to correct in some domains than in others. This difference of containment in the universe of random events is what we refer to as structure within the order-forming process. Our argument will be that affordances for less costly and more reliable error correction determine to a considerable extent the organization of life today, and there is good reason both empirically and theoretically to believe they also dictated some stages in its emergence.

1.3.3 Chance and necessity understood within the larger framework of phase transitions

If life is a planetary phenomenon, then the emergence of life was a conversion of the state of the Earth. The question what “kind” of conversion this was includes the questions whether it was an unlikely or likely event sequence, whether the persistence of life indicates that its continuing existence is in some way favored over its spontaneous disintegration, and whether the life we know is somehow uniquely required by natural laws (at a coarse level if not in all details) or whether a starkly different alternative could have emerged and persisted in its place.

1.3.3.1 System rearrangement: collective and cooperative effects create global order from locally random events

> aye, chance, free will, and necessity – nowise incompatible – all interweavingly working together. The straight warp of necessity, not to be swerved from its ultimate course – its every alternating vibration, indeed, only tending to that; free will still free to ply her shuttle between given threads; and chance, though restrained in its play within the right lines of necessity and sidewise in its motions directed by free will, though thus prescribed to by both, chance by turns rules either, and has the last featuring blow at events.
>
> – Herman Melville, *Moby-Dick*, Chapter 47, The mat-maker [553]

Questions of chance and necessity, of predictability versus historical contingency, will not be answered by any simple appeal to empirical generalizations in extant life, or by merely listing facts about chemical synthesis from laboratory systems. They must be framed within a larger context of principles, to enable us to judge which facts are relevant and why, and to enable us to abstract from empirical generalizations to causes.

The framework that we propose should capture the roles of chance and necessity is one that originates in the theory of **phase transitions.** In the thermodynamics of ordered phases and the transitions between them, all events are random and unpredictable at the microscale in space and in time. Some chance events can propagate that randomness up to large-scale historical contingency, but for many others the only lasting consequence is a joint participation in a kind of "system rearrangement." The boundary conditions on a macroscopic system can act to filter collections of microscopic events, favoring configurations that respect certain forms of long-range order throughout the system. While the small-scale events are unpredictable, the favored states of order can be predictable and can depend in specific ways on the boundary conditions.

The abstract question, which an understanding of the detailed chemical mechanisms of life must teach us to pose in the correct way, is whether a plausible emergence of life could have occurred as a consequence of a unique and rare event sequence, or whether it must have resulted from a system-level re-arrangement, away from a less favored to a more favored organizational state of the Earth's matter and energy flows. The theory of phase transitions encompasses both the robust order within stable phases, and the amplifying effect of instability, at the cusp of a transition, on those few random events that are most likely to seed the transition. Even when a system changes phase – when a long-range internal rearrangement occurs – the change occurs along limited channels, and its likelihood or its uncertainty are governed by boundary conditions much as the ordered phases are.

The theory built up to explain long-range order in random systems also explains an empirical observation: that order forms under restricted circumstances. Attempting to apply the same filters to the rearrangement of terrestrial matter into a biosphere should distinguish plausible from implausible paths of emergence.

The mechanism that underlies the formation of ordered phases is mutually reinforcing interaction among many small-scale, individually stochastic degrees of freedom known as **collective or cooperative effects** [307, 308, 506]. Ordered phases form where the redundancy of cooperative effects creates a sufficiently strong tendency toward order to overcome a tendency toward disorder that is essentially combinatorial: the condition of being disordered is less restrictive and therefore can be met in more ways. Whereas disorder is generic, sufficiently coherent interactions to produce order are rare, and for this reason the plausible mechanisms to produce any form of order that we observe as robust and stable are limited.

Much of what is understood about phase transitions has accumulated over more than a century of experience with equilibrium systems, including the fundamental particles and forces and thermal states of matter. However, as the essentially mathematical nature of order created through cooperative effects has come to be better understood and communicated across scientific domains, it has become clear that phase transition is a mathematical concept, applicable in the domain of processes or information systems, as much as in the domain of classical theories of matter.[24]

1.3.3.2 The emergence of life was a cascade of phase transitions

Our thesis in this book is that the emergence of life should be understood as a cascade of dynamical phase transitions, as matter in an energetically stressed young planet was rearranged into conduits for energy flow. The function of these conduits, which comprise the ordered states and events of living matter, in a planetary context is to mitigate the accumulation of chemical potential stresses.

Before the period from roughly 1955 to 1975, phase transitions were seen as the objects of a domain-specific theory: a description of a restricted class of phenomena like many other descriptions in physics. The change that occurred over this period, through a coalescence of ideas in several domains, was that the theory of ordered phases came to be understood as an overarching framework for understanding robustness and stability. Phase transitions are not merely isolated events; they form hierarchies where they bring into existence the modes of order that we recognize as elementary entities and interactions. For the same reasons as phase transitions produce the stable states of matter, they also describe the limits of reliability in information systems, and form the basis of a very large part of our modern understanding of error correction and reliable inference.

Cascades of phase transitions organize states and dynamics in natural systems into layers or levels that, though inter-related, have internally consistent and somewhat independent characterizations. Even when we know that an ordered phase exists as one level within a cascade of stages of emergent order, we can characterize the level of interest without a complete knowledge of the hierarchy in which it is embedded, a phenomenon known as **universality**. The implication of a phase transition paradigm for life – that its stages of

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[24] Manfred Eigen develops this perspective on overcoming the threshold for reliable replication in information systems, in [211, 212].

emergence and its internal modules are subject to some degree of universality – will allow us in Chapter 6 to sketch a sequence of stages of emergence. More importantly, it is the feature that has enabled the biosphere's own dynamics to assemble hierarchical complexity without drifting into intractable problems of error propagation. The biosphere is *reducibly* complex. In the phase transition framework, the source of biological reducibility is ultimately the same as the source that makes reductionism successful in the rest of natural science.

1.3.3.3 A theory of ceilings and floors

The picture of a cascade of transitions as the path to complex order has precedent in equilibrium systems, because it is the basis for our current hierarchical theory of matter. A cascade of nested "freezing" transitions at successively lower temperatures (reviewed in Chapter 7) creates the inventory of elementary particles and then the states of cold condensed matter.

We will argue for a similar cascade of transitions that produced living matter from non-living precursors on a prebiotic Earth. The difference between the phase transition cascade of matter, and the cascade to life, is that order in matter results from the constraints of limited energy, whereas the cascade to life results from the constraints of the need to support energy flows through chemical pathways. The difference between temperature and stress as sources of order is fundamental to much of what makes living matter different from the merely "physical" phases in non-living matter. Temperature as a boundary condition makes **energy** the constraining factor leading to equilibrium order. Stress as a boundary condition makes **transport currents** the constraining factor leading to biological order.[25] Transport currents are inherently dynamical properties; hence, the order of life can only be understood in dynamical terms.

A principle of fundamental importance, learned through experience with equilibrium phase transitions but applicable to phase transitions more generally, is that each transition is a kind of qualitative boundary that separates the descriptions required "above" and "below" it. In energetic hierarchies, a melted phase lies above any transition, and a frozen phase lies below it. In a cascade of transitions, every ordered phase has two boundaries: one above, which brought properties of that phase into existence through a freezing transition, and one below, which will go on to freeze out some of the current system properties and create an even more ordered (more intricately frozen) phase. The two boundaries make a kind of "ceiling" and "floor" for the scientific description of the ordered phase that falls between them. Most details of the fine structure that lies above the ceiling do not need to be understood to describe the dynamics in the phase below the ceiling, because the dynamics in the fine-scale details have been frozen out and are inaccessible. Likewise, any accidental properties of frozen order that may arise in the phase below the floor do not need to be predicted to know what constraints the dynamics above the floor place on all possible

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[25] For a worked example in an extremely simple system, see [763].

ways of freezing.[26] A valid scientific description of any ordered state produced by phase transition, between its ceiling and its floor, can be largely self-contained.[27]

1.3.3.4 Emergence makes reductionism possible

One sometimes sees emergence put forward as an alternative to, or even a refutation to the validity of, reductionist science, but this is a misunderstanding of reductionism and ultimately a mis-appropriation of the term. Properly understood, reductionism consists of two observations. First, properties of components place limits on the kinds of assemblies that can be made from them. Second, although the possible assemblies of a collection of building blocks are typically much more numerous and diverse than the building blocks themselves, if the goal is to characterize the building blocks, the number of well-chosen experiments that must be performed is comparable to the diversity of the building blocks alone, not of the much more numerous assemblies that could be made from them. This remains true even if the building blocks are not directly accessible, and their properties must be inferred indirectly from experiments carried out on assemblies of them.

Ceilings and floors cut off a potential infinite regress in the reductionist program of inferring properties of building blocks. This cutting off has been essential to the formulation of a consistent theory of matter [861]. One only needs to look through one ceiling at a time, to characterize the relations of parts to wholes; one does not need to jump immediately to a theory of everything. In other words, emergence is the phenomenon that makes reductionist science possible in practice. We will be careful in extending lessons learned from equilibrium into the dynamical domain of life, where feedbacks across levels can become complicated. However, the reasons these relations are true in equilibrium are ultimately mathematical. While care may be required to understand where they are realized in the constraints on living systems, we believe the same ideas will inevitably apply.

1.3.3.5 The "collapse" into the order of life

One of the most longstanding questions physical scientists have posed about the biosphere is: Why doesn't it all collapse to disorder?[28] More formally: Why don't the arrangements of living matter degrade to distributions that more closely resemble those of equilibrium systems? In equilibrium systems we have come to associate disorder with collapse, because in closed systems (and even in many open systems), maximum entropy reflects both the greatest disorder and the largest likelihood.[29] Collapse occurs when a system wanders away from an orderly, and therefore improbable, initial condition, into more disordered conditions from which it never returns.

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[26] Expressed in very informal terms, if bricks can be used to build houses, there are many things about the assembly of any particular house that do not need to be anticipated to understand the capabilities and limitations that the bricks place on all possible houses that could be built from them.

[27] An immediately familiar example is chemistry, which is a self-contained theory of dynamics that takes orbitals as its building blocks. Only a few parameters from the underlying quantum mechanics that derives those orbitals are required in order to entail all of their molecular consequences.

[28] See Section 7.6.1.1 for some historical examples of this question.

[29] For open systems in equilibrium, it is understood that the appropriate measure of entropy includes terms from both the system and its environment, so generally these are various *free energy* functions [441].

However, life is not merely (and not even principally) a collection of things, and the equilibrium entropy captures only part of the regularity we seek to explain in the biosphere. We will argue that life emerged early and has persisted robustly because the origin of life was actually a transition away from a less stable planetary condition devoid of life, and into a more stable condition that includes a biosphere. In entropic terms, this transition was still a "collapse" from an improbable to a more probable phase, but the stable phase in this case was the dynamically ordered living state.

Even at equilibrium, the idea of a collapse into order is not new or radical in open systems that can undergo phase transitions: it happens every time rapidly cooled water vapor nucleates its preferred state of frost, or whenever a supersaturated cloud condenses into a downpour. The frost and the liquid raindrop are both, in entropic terms, more ordered than the phases from which they formed, though the energy loss that makes them more ordered accounts for an even larger amount of entropy as heat in the environment. Systems that undergo non-equilibrium phase transitions can collapse into order in ways even more intuitively like the emergence of life: this happens whenever a fracture suddenly forms and propagates in a stressed elastic solid, or a lightning strike forms across a gap in the atmosphere between a charged cloud and the ground.

The last half of Chapter 7 and the synthesis in Chapter 8 explain how our picture of a "collapse of the Earth into life" is a natural conclusion from the principle of maximum entropy – the same principle that accounts for the tendency toward disorder in closed equilibrium systems – applied in an appropriate dynamical context. The main conceptual shifts are these.

To apply the concepts of cooperative effects and phase transition to a dynamical system like the living state, our ways of thinking about entropy must change from habits that have become long ingrained from experience with equilibrium systems. In equilibrium systems, entropy counts degeneracies of **states**. Information, or a reduction in entropy that often defines a relevant concept of order, measures the reduction in the number of states of *being* required to satisfy whatever constraints the environment imposes. Life, as we have emphasized, is a jointly ordered system of both **processes and states**. The information relevant to life must also measure the reduction in the number of ways of *doing something* required to satisfy the non-equilibrium constraints the environment imposes. Some processes play out over an extended interval of time, in the course of which they pass through series of states. In such cases, the relevant information must measure the reduction in the range of *histories* that perform a function, where each history is an integrated series of states and transformations. For each of these generalizations, worked examples of the principle of maximum entropy are understood,[30] though so far the examples are much simpler than realistic contexts for the emergence of life.

The required shift in our point of view does not entail a change in the meaning of entropy or its relation to information. It requires, rather, that we recognize different spaces of possibility as the domains within which different forms of order emerge. The same entropy

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[30] For pedagogical expositions and a few simple worked examples, see [301, 649, 767, 768, 902].

concept then leads to different entropy functions for different classes of distributions. For applications to life, most of these differ from the equilibrium entropy.

Entropies of processes may be maximized along histories that do not necessarily pass through states that would be most probable in equilibrium. For some functions, no states near equilibrium may perform them robustly or at all, so they can be carried out only far from equilibrium. The entropic question then becomes: in the world of processes, why is a function possible at all that can only be carried on non-equilibrium states? Which functions does life uniquely perform that cannot be performed by simpler systems, and why, in a random world, are there more ways to perform those processes than to remain near equilibrium?

1.3.4 The emergence of the fourth geosphere and the opening of organic chemistry on Earth

Our contention is that, despite the remarkable complexity of living order, the aggregate function of the biosphere is a simple one: *it opens a channel for energy flow through a domain of organic chemistry that would otherwise be inaccessible to planetary processes.* It is analogous to a lightning strike through the graph of chemical possibilities, producing a channel that is stable at the system level but heterogeneous and far from equilibrium when viewed locally.

A planet with only three geospheres can still be a conduit for energy flow. The two primary long-term sources of free energy – disequilibrium between the bulk Earth and atmosphere, liberated by the release of radioactively generated heat, and direct coupling to the high-energy photon flux from stellar burning – are widely present in the universe. Three-geosphere systems can also host chemical interconversion that is limited in either form or extent. The volume of redox transformation in the Earth's mantle is large, though the forms that occur at large scale are limited. A greater complexity of organosynthesis is possible, even in planetesimals such as the parent bodies of carbonaceous meteorites, as attested in the organic contents of the Murchison meteorite [156, 704], but their concentration is more limited and it remains an open question whether a principle can be recognized in these systems that is chemically selective.

The emergence of a fourth geosphere introduces new channels for high-volume, steady energy flux through covalent bond chemistry, which may operate in parallel to, or may subsume, chemical interconversions within the other geospheres. The main network of these pathways on Earth today is **metabolism**. Chapter 4 is devoted to the metabolite inventory, network topology, functions, and historical diversification within this network, and summarizes our reasons for interpreting extant metabolism as a continuous outgrowth from prebiotic geochemistry. The causal link of metabolism to geochemistry in the first life was, we argue, the geoenergetics of electron flow from low-potential donors to high-potential acceptors.[31] The first life gave high-energy geochemically produced electrons paths for

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[31] Due to the convention that the electron has a "negative" electric charge, and voltage is measured so that charge times voltage equals potential energy, a low-potential electron donor is a high-energy donor, while a high-potential acceptor is a low-energy acceptor.

relaxation through covalent bond organic and organometallic chemistry where no other geosphere did. Energetically, life facilitated the descent of electrons. Today geochemical redox energy remains essential to some ecosystems, but in terms of known primary productivity, the more complex but higher yielding harvest of light energy supersedes geochemical redox relaxation.

The opening and maintenance of protometabolic and eventually metabolic channels for energy flow is the aggregate property on which all living processes depend, and which in turn they all impact, whether constructively or parasitically. We believe, and will attempt to show in this monograph, that the establishment of these channels and of the energy flows through them is in a certain technical sense the *central* function of the system rearrangement that was the emergence of life.

Central properties of this kind are known in the theory of phase transitions as the **order parameters** of ordered phases: they are the statistically and causally primary aspects of novel order created in a phase transition. This means that all other forms of order can be explained in reference to them and to the pre-existing framework in which the new phase forms. On Earth the pre-existing framework came from the laws of physics and chemistry and the planetary composition and energy sources, and the new phase is living matter. All other order in the biosphere ultimately appeals to this energy flow through organic chemistry as a source of stability, whether directly or indirectly.

Those aspects of an order parameter that are determined fully by the boundary conditions are the *necessary* properties of the ordered phase. If it is correct to regard the aggregate energy flows through organic chemistry as the order parameter that defined the emergence of life, the relation between these flows and the free energy sources present on the early or contemporary Earth also defines the sense in which energy stresses can be said to have *caused* the emergence of life, and a biosphere can be said to be a necessary part of an energetically active planet like the Earth.

1.3.4.1 Not one phase transition, but many

The phase transition paradigm for emergence is a general claim that error buffering through cooperative effects is needed to permit the formation of hierarchical complex systems, especially those employing relations of control between levels in the hierarchy. While the formation of a chemical channel for energy flow may be the most fundamental dynamical-phase property in the biosphere and its ultimate reason for existence, the origin of life should *not* be understood as a single phase transition that created a single form of order. Requirements for buffering by ordered phases are found repeatedly in level after level of living order. This is why we have emphasized from the start the heterogeneous and multilevel character of the regularities of life that a theory of origin must explain. Our premise that major transitions in the origin and early evolution of life must correspond to emergences of new incrementally stable ordered phases will allow us to propose a sequence of steps in the origin of life that we believe has some theoretical justification, despite the fact that many links between these transitions are missing. A more detailed sketch of the hierarchy of transitions that we think provided a scaffold for the emergence of the biosphere is presented in Chapter 6. Here, to give a flavor of the kinds of differences that can be important, we compare three transitions in the sequence.

The self-maintenance of metabolism The difference between the complex but limited organosynthesis attested in meteorites, and the more concentrated synthesis of a few compounds that we believe must have preceded any accretion of higher-order structure in life, is one of *yield* and *selectivity*. In cellular life, yield and selectivity result from positive feedbacks that concentrate reaction flux in synthetic networks. Mechanisms of positive feedback include enhancement of specific reaction rates (often by large factors) by molecular catalysts selected under evolution, and also self-amplification from pathway loops that feed metabolites back as precursors to their own synthesis, a process collectively termed *network autocatalysis*.

The universal core metabolic network is remarkable for the presence of autocatalytic feedback in extremely short pathways that also constitute the center and the most invariant domain in the network [769]. The reactions in these short, central loops also exhibit other simplicities, redundancies, and analogies to reactions at mineral/water interfaces. These and other observations, reviewed in Chapter 4, lead us to argue (as many others before us have argued) that metabolism is continuous with geochemistry, and its first departure toward being an independent system was a transition in these autocatalytic core pathways through a threshold of enhanced selectivity and ultimately self-maintenance. Many of the steps in our proposed phase transition to self-maintenance remain undemonstrated – these are areas of ongoing work and incremental progress – and it is a matter of disagreement within the origins community whether such a phenomenon is plausible in geochemistry [614, 733]. However, the argument that the error-buffering character of ordered phases was required for the emergence of life is most important at this first transition, where we assert metabolism was selected for kinetic and topological properties, which continue to make it the anchor for the stability of higher-level structures in life.

The rise of an oligomer world If a phase transition to autocatalytic self-maintenance was the first selector of metabolic pathways, these probably have a minimal component of accident. The small-molecule world has little capacity for long-term memory: whatever is most facile and robust becomes most likely, moment-by-moment independently, and everywhere the boundary conditions provide similar energy supplies. The simplicity of extant metabolism suggests that the orderly core of a protometabolism would have been comparably simple. The main reactions and the primary fluctuations about them would have been fully sampled by the chemicals and reactions that led to the earliest cells.

At some stage, life began to make use of oligomers of large size, and from then onward the combinatorial possibilities for useful functions and structures became much too numerous to be sampled exhaustively by genomes, cells, or whatever were the relevant replicating units. The transition between a (putatively) unique metabolism and an undersampled world of oligomers marks a qualitative change in the problem of maintaining life on Earth. In the former case, self-reinforcement maintains a system around a unique solution. In the latter, selection (probably, we argue, scaffolded by the presence and uniqueness of the underlying metabolism) maintains a system despite the fact that its instantaneous states are not unique.

Emergences of individualities A different kind of character change occurred between chemistry in bulk phases (in volumes or on surfaces), and chemical reactions performed in cells or catalyzed by enzymes encoded in replicating macromolecules. In the bulk phase, selection takes place by means of reaction and diffusion kinetics. In the dynamics of either compartments or genomes, selection makes use of the duplication of many parallel platforms, performing nearly identical copies of the same function, which can be replicated or eliminated independently [184]. Compartments and genomes mark two forms of emergence of individuality, perhaps one of the most important characteristics of the dynamical living phase that has no counterpart in equilibrium phases. The existence of parallel units sensibly regarded as individual is the precondition for Darwinian evolution. Understanding why and how individuality emerges, how many forms it can take and how these interact or are related, will be key to understanding the relation between the more “thermodynamic” and more “Darwinian” aspects of the dynamics that contribute to the stability of life.

1.4 The origin of life and the organization of the biosphere

In Chapter 8, bringing together the empirical facts from Chapters 2 through 5 with the discussion of cooperative effects from Chapter 7, we argue that the origin and subsequent evolution of life have relied throughout on the stable forms of order created by phase transitions as the “building blocks” of emergence and adaptive design. The starting observation is that life is not a naked channel for energy flow through geochemistry, but a complex architecture of structures and functions maintained indirectly to support an energy-flow channel. To capture the problem in erecting and maintaining such an architecture, and to explain why it may be solvable but only in limited circumstances, we must understand not only isolated or abstract phase transitions, but the essential role played by cooperative effects in modular systems that make use of many kinds of ordered phases.

The problem of maintaining long-term stability in hierarchical complex systems may be understood with concepts from classical optimal control theory [604]. We argue that the pervasive role played by ordered phases is **error buffering**: in systems subject to errors in very many dimensions, cooperative effects can provide regression toward sufficiently low-dimensional spaces of variation that the residual errors can be managed within the limits of complexity of controllers and control signals. This buffering is only available, however, where cooperative effects are strong enough to cross thresholds to form ordered states. The capacity to self-buffer many dimensions of internal error is a form of *autonomy*, and we argue that this connection to error buffering and order through cooperative effects is the appropriate interpretation of the quasi-independent character of many modules we exhibit in the earlier chapters.

The deterministic character of phase transition provides a framework of lawful action and a notion of cause that can connect living processes across time and across scales: from the modern era where evolutionary variation provides much of our interpretive frame for comparative analysis, back to pre-cellular geochemistry, and from the aggregate dynamics that stabilizes complex communities of complex organisms, down to their aggregate effect of organosynthesis and energy flow. The unified picture of the emergence, organization, and persistence of life, and of the embedding of life in chemistry, consists of four main premises.

Origin, ongoing organization, and persistence are not separate We argue, from the existence of regularities in chemistry and ecosystem structure that are more universal than the individuals and species that carry evolutionary memory, that processes of biosynthesis and repair are at least partly a reflection of time-invariant *laws of organization*. The biosphere is self-renewing in a literal sense: biosynthesis directs matter into certain modes of organization now for the same reasons biogenesis first directed matter out of non-living states and into these modes of organization which were then novel. To the extent that biological evolution is constrained by time-invariant laws, the origin, organization, and persistence of the biosphere cannot be understood as separate problems. Each provides a view of the underlying constraints, though they act in very different contexts, ranging from pre-cellular geochemistry to genomically dictated physiology and complex population dynamics. We look for the action of laws in absences of evolutionary innovation, in long-range feedbacks that may give slight fitness advantages to organisms participating in favored networks and lead to long-term evolutionary and ecological convergences, and in regularities that are not governed by any one level of selection yet persist as features of coevolution.

Common laws make present and past mutually informative A framework of common laws is the only starting point from which we can reconstruct the origin of life with any specificity or confidence. It is only to the extent that current living processes and pre-cellular geochemistry reflect the same constraints, that we are justified in expecting continuity between prebiotic and biotic patterns, or in extrapolating existing patterns in evolution to an age before a record of evolutionary history was preserved in surviving diversity.

At the same time, a serious consideration of the difficulty of maintaining a complex, multilevel state of dynamical order suggests that it is implausible that order could be maintained without reference to supports that come from outside the biosphere itself, which would play the role of invariant laws with respect to the coevolutionary dynamics of member species.

Evolution builds using the order parameters of phase transitions Evolution is ultimately a commitment to the problem of *induction*. Among variations inherited from the past, a population is filtered according to advantages under present circumstances, and the filtering is more beneficial than chance only if the future reprises the present at least to some degree. It is difficult to select among unreliable components or components that respond to their environments with complex, multivariate dependencies; the future may be likely to resemble the past in coarse features, but is unlikely to repeat it in full detail.

We expect the successful outcomes of evolution to be concentrated among components and functions that best support induction: those that vary sufficiently to distinguish among environmental conditions but that are stable enough internally to permit selection in a few dimensions of variation. These are the kinds of systems, we argue, produced as ordered phases through cooperative effects. The building blocks of evolutionary "design" should be to a large extent the order parameters made available through phase transitions. The limitations in the availability of robust order then dictate limits on evolutionary innovation and maintenance.

An invariant core is the reference enabling evolutionary variation The problem of stabilizing a hierarchical complex system is mathematically equivalent to many problems of preserving messages sent through noisy transmission lines. Our theory of optimal information transmission, like our theory of physical stability, is a theory based on cooperative effects and phase transition.[32] The problem of maintaining an evolutionary system capable of open-ended variation is equivalent to the problem of maintaining an information system capable of preserving an unlimited variety of messages (though no one among the endlessly variable messages needs to be preserved forever). The problem of preserving information in messages leads to a problem of regress of stability. The transmission system protects the messages, but what preserves the integrity of the transmission system? If the system itself is a message, in what medium is it preserved, and how is that medium protected. *Quis custodiet ipsos custodes?*[33]

Considering the problem of regress in a system with even finite but large capacity for variation, we conclude that the system must ultimately have a reference outside itself from which to preserve its ordered state, and that reference must be invariant. For the biosphere, the natural candidate for this reference, from many considerations, is the universal core of small-molecule metabolism as it exists at the ecosystem level. The circumstantial evidence that it is a reference is its apparent universality and its existence as a property spanning all levels from cells to the biosphere as a whole, and all life as far back as we can see with evolutionary reconstruction. Causational arguments that the small-molecule core is a likely source of stability include its digital character, which facilitates error correction, the many reaction and network properties that support self-amplification in a compact system, making it robust, and its function as a biosynthetic gateway through which all matter passes in the course of biosynthesis.

Our claim that integrity and throughput in the universal metabolic network are the continuous and ongoing source of stability for the biosphere anchors the living state directly

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[32] This equivalence is developed in Chapter 7. Although mathematically it is straightforward, we have not seen it emphasized as widely as we would have expected, given its interest and importance.

[33] Who will guard the guardians themselves?

in the laws of chemistry and in the composition and energetic circumstances of this planet. Because life depends in parallel on so many properties of its substrate that are uniquely provided by chemistry, we argue that the living state is fundamentally chemical before it is anything else, and that life will be the premier subject for the study of cooperative effects acting in the structured domain of chemistry.