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The Architecture of Life

Chemistry, Information, Selection and the Recurring
Organisation of Living Systems

Origin of life · Cells · Evolution · Ecosystems · Biosphere

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H Heuristics · Architecture of Creation series

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About This Report

This report asks how living systems could have emerged from nonliving chemistry, and whether the same structural principles recur as life builds organisation from molecules to the biosphere. It is the second major application of the framework set out in [The Architecture of Creation](#), the foundational report in the H Heuristics series of that name. That report asked why the same forms recur across unrelated systems and answered with a layered model in which physical constraints define a small space of viable forms, generative processes explore that space, and filters decide what persists. The first application, [The Architecture of Creation in the Universe](#), took the model to cosmology and ended where chemistry becomes biology. This report begins there.

The two reports are designed as a progression. The first explains how physical processes generate cosmic structure: nuclei, stars, galaxies and planets. The second asks how, on at least one planet, chemistry crossed into systems that maintain themselves, store and copy information, harvest energy, reproduce and evolve, and how those systems then built cells, organisms, ecosystems, minds and a biosphere that reshaped its own world. The companion report [The Architecture of Entropy](#) supplies the thermodynamic background that both rely on.

The report is written for readers who want a rigorous but readable account of origin-of-life research, cell biology, evolution, ecology, neuroscience and astrobiology, and for those interested in whether a general theory of biological organisation is possible. It integrates established science with the H Heuristics framework but keeps the two apart. Every major claim is graded for strength of evidence, analogies are labelled as analogies, and the framework's own propositions are flagged as such.

How to read this report

Each section starts on a new page and can be read on its own. Sections 1 and 2 state the thesis and translate the framework into biological terms. Sections 3 to 10 form the core of the report and follow the eight-part structure shown in Figure 1: prebiotic chemistry, the first living systems, the cell, evolution, multicellularity, ecosystems, intelligence and the biosphere as a planetary system. Section 11 tests whether a common architecture runs through all eight. Section 12 asks what the framework implies for life elsewhere. Sections 13 and 14 set out testable propositions and an overall verdict.

	I. The Architecture of Prebiotic Chemistry Carbon, water, energy and the chemistry before life	Section 3
	II. The Emergence of the First Living Systems Replication, catalytic networks and compartments	Section 4
	III. The Architecture of the Cell Membranes, metabolism, information and regulation	Section 5
	IV. Evolution as a Generative Process Variation, heredity, selection, drift and symbiosis	Section 6
	V. The Emergence of Multicellular Complexity Cooperation, specialisation and development	Section 7
	VI. The Architecture of Ecosystems Food webs, nutrient cycles, stability and diversity	Section 8
	VII. Intelligence and Information Processing Sensing, nervous systems, learning and culture	Section 9
	VIII. Life as a Planetary System How life and Earth have shaped each other	Section 10

Figure 1. The structure of the report. The eight core parts move from chemistry to the planet. The origin of life (Parts I and II) is treated separately from the evolution of life once it existed (Parts III to VIII), because different mechanisms and different standards of evidence apply.

Source: H Heuristics. Illustrative.

Blue underlined text is a hyperlink. Links to the primary literature go to a DOI record where a specific result is cited, and to a reference article where a concept is introduced. Every link was checked for resolution before publication, and every DOI was checked against its registered title. A full reference list follows Section 14.

Evidence grades

Claims are graded using the same four-level scale as the rest of the series.

Table 1. Evidence grades used in this report

Grade	Meaning	Biological example
A: Established	Derived mathematically, or confirmed repeatedly by independent observation or experiment.	All known life shares a common ancestor and a nearly universal genetic code
B: Well supported	Strong evidence from several lines of work, with unresolved detail or some dissent.	Mitochondria descend from an engulfed bacterium; RNA preceded DNA and protein
C: Plausible or contested	A credible mechanism and partial evidence; the field is actively debating it.	Life began at alkaline hydrothermal vents, or in volcanic ponds
D: Speculative	A hypothesis offered for testing, labelled as such wherever it appears.	Life elsewhere would converge on carbon, water and a cell-like architecture

The grade describes our knowledge of a claim, not its importance. Many of the most important questions in this report, including how life began and how common it is, are graded C or D.

A note on the figures and calculations

The report contains 43 figures of three kinds. The first kind are original simulations and calculations of standard published models, made for this report: competition between replicators with different growth laws, the emergence of autocatalytic sets in random chemical networks, Eigen's error threshold, a stochastic-corrector model of protocells, a Bayesian analysis of what life's early appearance implies about its probability, regulatory feedback and a synthetic genetic oscillator, a test of the genetic code against one million random alternatives, Wright–Fisher simulations of selection and drift, rugged NK fitness landscapes, predator–prey cycles, May's stability bound for complex communities, Daisyworld and Turing pattern formation. Each caption says what was computed. The second kind are charts of published measurements, credited in their source lines. The third kind are scientific illustrations drawn for this report, of molecules, protocells, cells, neurons, food webs and Earth's layers; these are marked as illustrative and are schematic, not to scale unless stated.

How to cite

Hughes, H. (2026). *The Architecture of Life: Chemistry, Information, Selection and the Recurring Organisation of Living Systems*. H Heuristics Research Report, Architecture of Creation series. The report synthesises published research and presents original calculations and propositions, which are labelled as such.

Executive Summary

The question

Roughly four billion years ago the surface of a young planet held water, rock, gases and a great variety of small carbon compounds, none of them alive. Today the same planet carries about 550 billion tonnes of carbon in living tissue, perhaps ten million or more species of eukaryotes and an uncounted diversity of microbes, ecosystems that span every surface, and at least one species that studies the rest. Living matter has changed the air, the oceans and the rocks. This report asks how chemistry could have become life, how life then built its many levels of organisation, and whether the same principles of construction recur from molecules to the biosphere.

The defining question. How did a form of organised matter that maintains itself, processes information, uses energy, reproduces and evolves emerge from nonliving chemistry, and what recurring architecture connects its molecules, cells, organisms, ecosystems and biosphere?

The thesis

Life is a remarkable form of organised matter, but it is matter obeying the same physics and chemistry as everything else. The thesis of this report is that living organisation is generated by the same combination the series has found elsewhere, with one decisive addition. Chemistry and physics act as **constraints** that define what molecular systems can do. Autocatalysis, replication, mutation, recombination and symbiosis act as **generators** that produce variants. Thermodynamic persistence, natural selection and ecological filtering act as **filters** that decide which variants spread. The decisive addition is **heredity**: once a system can copy the information that specifies it, filters no longer act only on what exists but on what is passed on, and the filter becomes cumulative. That turns the creation structure into an engine that can accumulate design-like complexity without a designer and without a goal.

Principal findings

- 1. The ingredients of life are ordinary and the conditions were available early.** Water, carbon compounds, energy gradients and mineral surfaces were present on Earth by about 4.4 billion years ago. Amino acids, sugars and all five nucleobases form under plausible early-Earth conditions and are found in meteorites and in asteroid samples returned to Earth. Prebiotic chemistry is now a mature experimental field (Grade A for the availability of ingredients; Grade B to C for specific pathways).
- 2. The origin of life is a separate problem from the evolution of life, and it remains unsolved.** No experiment has produced a self-sustaining, evolving chemical system from plausible starting materials, and the setting is contested. The report distinguishes the transition to life, where the evidence is chemical and inferential, from later evolution, where the evidence is direct and abundant (Grade C to D for origin scenarios).
- 3. Three subsystems had to be coupled: metabolism, information and compartments.** Simulations made for this report show why each matters. Autocatalytic networks appear suddenly once molecules catalyse on average only about one reaction each. Replicators with sub-exponential growth coexist instead of competing to extinction. Copying is limited by an error threshold that real genomes respect across five orders of magnitude of genome size. Compartments let cooperative molecular systems

persist against faster-copying parasites (Grade A for the models; Grade B to C for their application to the origin).

4. **The cell is an information-processing, energy-transducing, self-repairing system with a remarkably conserved core.** All known cells use lipid membranes, a proton or sodium gradient across them, ATP, DNA, RNA, ribosomes and a nearly universal genetic code. The code is not arbitrary: in this report's test against one million random alternatives, only about one in 7,600 was better at buffering the effects of point mutations (Grade A).
5. **Evolution is a generative process, not merely a sieve.** Mutation, recombination, horizontal gene transfer, gene duplication and symbiosis generate variation; selection and drift filter it. Whether selection or chance dominates depends on the product of population size and selection strength. Laboratory evolution shows open-ended improvement for more than 75,000 generations (Grade A).
6. **The largest steps in complexity were mergers and new forms of cooperation.** The eukaryotic cell arose from a partnership between an archaeon and a bacterium. Multicellularity evolved at least 25 times. These major transitions created new levels of individuality, each requiring mechanisms to suppress conflict among the parts (Grade A to B).
7. **Ecosystems are organised by energy flow and constrained by stability.** Only about a tenth of energy passes between trophic levels, which keeps food chains short. Random complexity destabilises communities, so real ecosystems must be structured; May's bound, reproduced here by simulation, makes the point quantitatively (Grade A).
8. **Intelligence is one of several nested information-processing systems, not the destination of evolution.** Bacteria sense and anticipate; nervous systems evolved to integrate information quickly; learning and culture add further layers. Complex cognition evolved independently in mammals, birds and cephalopods on different neural architectures (Grade A to B). Evolution shows no built-in trend toward intelligence or complexity; the maximum has increased while most life has remained microbial (Grade B).
9. **Life is a planetary process.** Photosynthesis oxygenated the atmosphere in two great steps, about 2.3 and 0.6 billion years ago, transforming chemistry, climate and the mineral record. Life and Earth have co-evolved through feedbacks that run through the oceans, atmosphere and crust. Whether those feedbacks stabilise climate is contested; this report's Daisyworld simulation shows how they could (Grade A for co-evolution; Grade C for planetary self-regulation).
10. **A coherent architecture of life exists, but it is a family of related mechanisms, not one law.** Energy flow, feedback and emergence recur as shared mechanisms at every scale. Information, boundaries, selection and cooperation are shared mechanisms within organisms but are analogies, sometimes weak ones, at the ecological and planetary scales. The framework predicts the general features of life elsewhere but not its frequency, which one example cannot establish (Section 11).

What follows from it

The practical payoff is a way of reading any living system. Before asking what a biological structure is for, ask which chemical or physical constraint makes it possible, which generator produced its variants, which filter keeps it, where its energy comes from, and what information it inherits. That checklist, set out in Section 14, separates what life had to do from what it happened to do, and keeps purpose-language from substituting for mechanism.

01

CENTRAL THESIS

1. Central Thesis and Scope

1.1 What is being explained

Earth formed about 4.54 billion years ago. Zircon crystals show that it had liquid water and continental-type crust by about [4.4 billion years ago](#). The oldest widely accepted evidence of life, layered microbial mats called stromatolites in the Pilbara of Western Australia, dates to about [3.48 billion years ago](#), and older claims reach back to 3.7 billion years and beyond, though each is disputed. Molecular-clock analyses place the last universal common ancestor of all living things, known as LUCA, at around [4.2 billion years ago](#). If those estimates hold, life appeared within a few hundred million years of the planet becoming habitable.

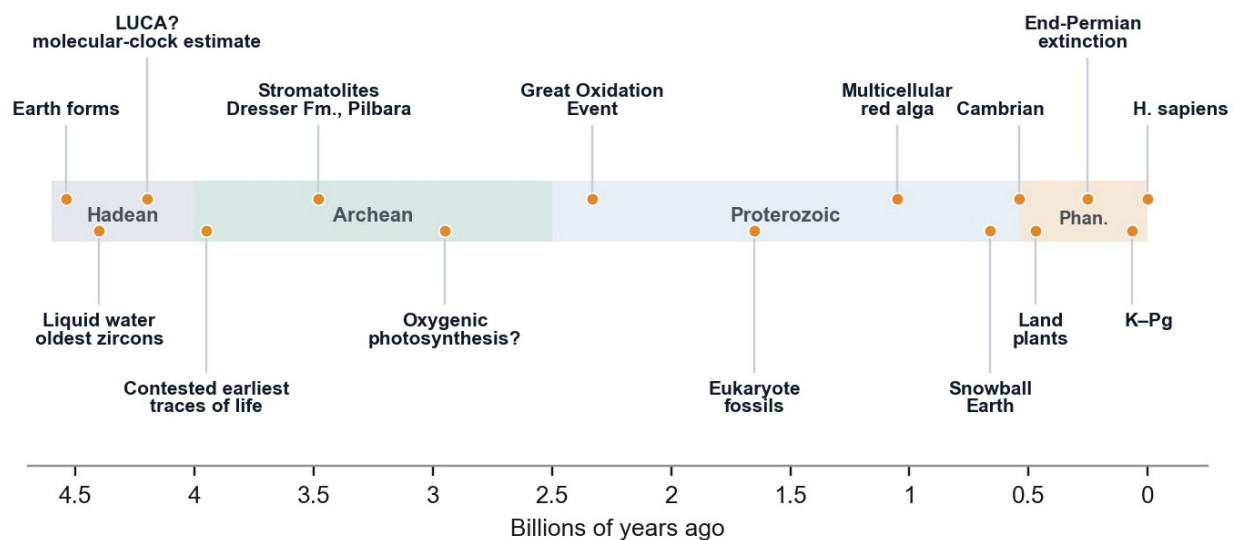


Figure 2. A timeline of life on Earth. Life appears early in the record; complex multicellular life appears late. Most of the history of life is microbial, and the oxygen-rich atmosphere that complex animals depend on was produced by life itself.

Source: H Heuristics, from the studies cited in Sections 1, 6, 7 and 10. Dates are approximate; contested dates are marked with a question mark.

Two features of Figure 2 frame this report. The first is that the transition from chemistry to biology happened once, as far as we know, early and in conditions we can only partly reconstruct. Everything alive today descends from a single ancestral population; the evidence is the shared genetic code, shared core machinery and the consistent branching pattern of gene sequences ([Woese and Fox, 1977](#); [Weiss and colleagues, 2016](#)). The second is that most of the complexity people associate with life came late.

For roughly two billion years all life was single-celled and prokaryotic. Eukaryotic cells, with nuclei and mitochondria, are recorded from about 1.65 billion years ago, multicellular algae from about [1.05 billion years ago](#), and large animals only from the last 575 million years.

1.2 The thesis

Thesis. Life is a remarkable form of organised matter capable of maintaining itself, processing information, using energy, reproducing and evolving. It emerged from nonliving chemistry through processes that are not yet fully understood, but its later organisation was shaped by a small, recurring set of principles: energy flow through networks of reactions, compartmentalisation, feedback, heredity, selection, cooperation and hierarchical assembly. These principles recur from molecules to the biosphere, though the mechanisms that implement them differ from level to level.

The thesis makes three claims of increasing ambition. The first, that life is chemistry obeying ordinary physical law and needing no special vital force, has been the working assumption of biology since the nineteenth century and is supported by every successful explanation in molecular biology (Grade A). The second, that biological organisation at every scale is generated by a limited set of mechanisms, is well supported for heredity, selection and energy flow and partly supported elsewhere (Grade B). The third, that the recurrence of the same principles across scales reveals a coherent architecture of life and not just a set of convenient analogies, is the distinctive claim of the H Heuristics framework. Section 11 grades it principle by principle.

1.3 What counts as life

There is no agreed definition of life, and the report does not need one to proceed. What it needs is a clear list of the properties that any explanation must account for. Several working definitions are in use, summarised in Table 2. They differ in emphasis but converge on a short list: a boundary that separates a system from its surroundings, a metabolism that captures energy and builds components, heritable information, reproduction, and the capacity to evolve by natural selection. Philosophers [Carol Cleland and Christopher Chyba](#) have argued that definitions are premature with only one example of life; [Steven Benner](#) has surveyed the alternatives. The report treats the list as a description of known life, not a boundary that must hold everywhere.

Table 2. Working definitions of life and what they emphasise

Definition	Core idea	What it emphasises	Main difficulty
NASA working definition (after Joyce)	A self-sustaining chemical system capable of Darwinian evolution	Heredity and selection	Excludes sterile organisms; hard to apply to a single sample
Autopoiesis (Maturana and Varela)	A network that produces the components that produce the network, inside a boundary it makes	Self-maintenance and closure	Says little about evolution
Chemoton (Gánti)	Coupled metabolic cycle, template copying and self-assembling membrane	Integration of three subsystems	Abstract; leaves open which came first
Thermodynamic (after Schrödinger)	A system that maintains low internal entropy by exporting entropy to its surroundings	Energy flow and order	Also true of flames, hurricanes and stars
Informational (Walker and Davies)	Information that controls its own physical substrate	Information and causation	Hard to measure

Source: H Heuristics, from the works linked. The report uses the common elements of all five as a checklist rather than adopting one.

1.4 The origin of life is not the evolution of life

The report draws a sharp line between two questions that are often run together. The first is the origin of life: how a system with the properties above arose from chemistry that had none of them. The second is the evolution of life: how such systems, once they existed, diversified into the living world. The distinction matters because the mechanisms and evidence differ.

- **Once heredity exists, natural selection explains adaptation.** The theory of evolution by natural selection, combined with genetics, is among the best-tested theories in science. It does not depend on how life began; it would work the same way whether the first cells formed in a pond, at a hydrothermal vent or somewhere else (Grade A).
- **Before heredity, selection in the Darwinian sense cannot operate.** Chemical systems can still be filtered, because some molecules and networks persist longer than others, but without faithful copying there is no accumulation of improvements across generations. The origin problem is therefore partly a problem of how the filter itself came into being (Grade B).
- **The evidence is of different kinds.** Evolution is documented in fossils, in the genomes of every living species and in experiments run for decades. The origin of life left no fossils; it must be reconstructed from chemistry, from the properties shared by all living things and from geological context. Origin scenarios are therefore graded C or D throughout this report, however plausible.

1.5 What the thesis does and does not claim

- **It does not claim that life was inevitable.** The framework explains how life could arise and how it builds complexity once present; it does not show that the origin of life is likely. Section 4.8 shows that the early appearance of life on Earth is weak evidence about its probability.
- **It does not claim that evolution progresses toward complexity or intelligence.** Evolution has no goal. The maximum complexity of life has increased over time, but the typical organism is still a microbe, many lineages have simplified, and intelligence evolved late and in few lineages. The report uses words such as 'emergence' and 'transition' descriptively and avoids teleological language; where such language is convenient, it is shorthand for the action of selection.

- **It does not claim that every level follows identical rules.** The same principle can be implemented by entirely different mechanisms at different scales, and some phenomena are unique to one level. Distinguishing shared mechanisms from analogies is the central task of Section 11.
- **It does not settle questions of ultimate meaning.** As elsewhere in this series, 'creation' is used in a structural sense: the process by which organised structures come into being. The report states what the evidence shows and where it stops.

1.6 Method and place in the series

The report integrates peer-reviewed literature from origin-of-life chemistry, cell and molecular biology, evolutionary biology, systems biology, ecology, neuroscience, Earth-system science and astrobiology, and it uses thermodynamics and information theory as common languages. Where a principle can be expressed mathematically, the report does so and, where possible, computes it. Each original calculation is a standard model taken from the literature and reproduced so that readers can see what the model implies, not a new result in its own right.

Within the series, this report follows [The Architecture of Creation in the Universe](#), which traced the chain from the hot Big Bang to the chemistry of planets. That report concluded that the architecture explains why life's ingredients and settings are common but not whether life itself is. This report takes up the story at that point.

02

THE FRAMEWORK

2. The Framework: Creation Structures in Living Systems

2.1 Constraints, generators and filters

The foundational report defined a creation structure as the combination of constraints, generators and filters that produces a recurring form. Applied to living systems, the three components take the forms summarised in Figure 3.

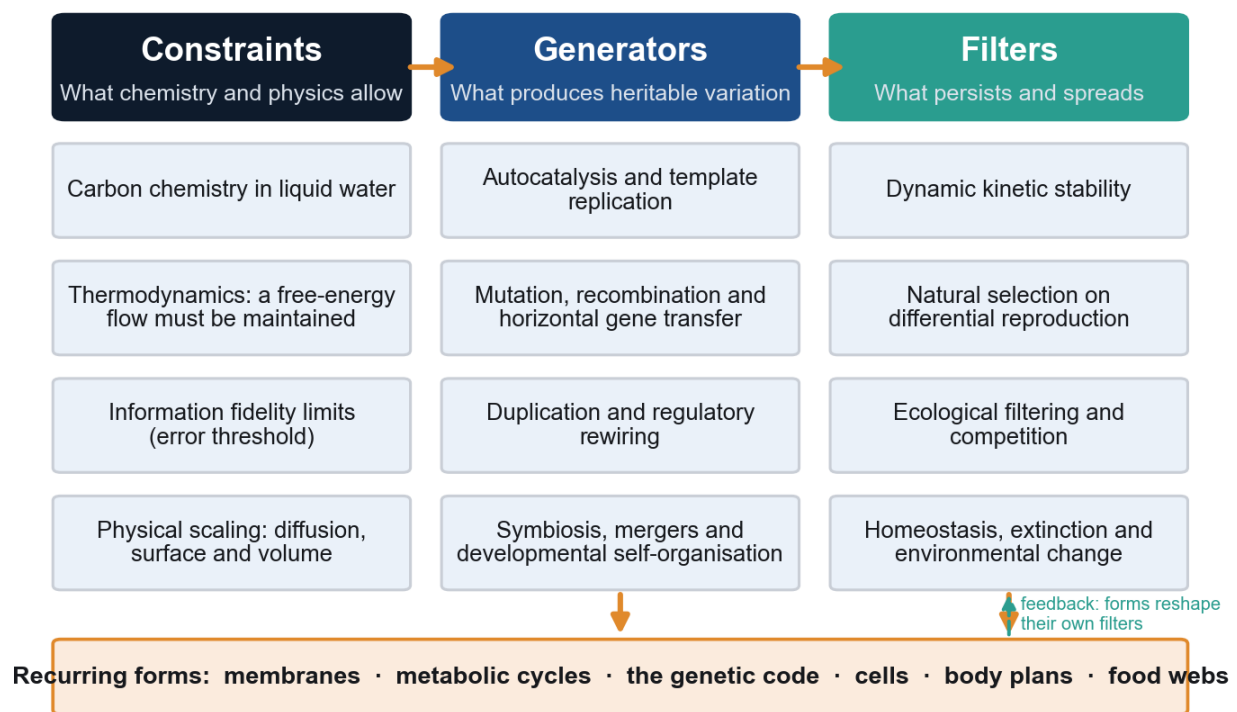


Figure 3. The creation structure for living systems. Constraints set by chemistry and physics define what can exist; generators produce heritable variation; filters select what persists and spreads. Living forms can then change their own filters, a feedback absent from most nonliving systems.

Source: H Heuristics, adapting the framework of *The Architecture of Creation* (2026). Illustrative.

Constraints are what chemistry and physics allow. Carbon forms stable chains, rings and multiple bonds with itself and with hydrogen, oxygen, nitrogen, phosphorus and sulfur, and so supports an almost unlimited variety of molecules. Liquid water dissolves ions and polar molecules, drives oily molecules to assemble into membranes and participates in most biochemical reactions. Thermodynamics requires that

any system maintaining internal order export entropy, so life needs a continuous supply of free energy. Information theory limits how accurately information can be copied for a given cost. Physical scaling sets how fast molecules diffuse, how surface area and volume grow with size, and how heat and nutrients move through bodies.

Generators produce variation. Before heredity, the main generators were chemical: reactions driven by energy sources, catalysis by minerals and by molecules themselves, and autocatalysis, in which a product speeds its own formation. After heredity, the generators are mutation, recombination, horizontal gene transfer, gene duplication and the rewiring of regulatory networks, together with symbiosis, in which separate lineages merge. Development, the process that builds an organism from a single cell, is also generative: it turns genetic changes into changes of form, and its self-organising dynamics bias which forms are easy to produce.

Filters decide what persists. The most basic is what the chemist [Addy Pross](#) calls dynamic kinetic stability: a population of molecules that copies itself persists if it is made faster than it decays, even though no individual molecule lasts. Natural selection is the same filter applied to entities that inherit their properties. At larger scales, competition, predation, ecological filtering and environmental change remove some lineages and favour others. Homeostatic feedback, which holds bodies and possibly planets near an operating point, is a filter on states rather than on lineages.

One feature distinguishes the biological creation structure from its cosmic counterpart. Living systems change their own filters. Organisms modify their environments, a process called [niche construction](#), and those modified environments then select future generations. Photosynthetic microbes created the oxygen that later selected for aerobic respiration. Beavers build dams that select for organisms adapted to ponds. Humans now set many of the filters for the rest of the biosphere.

2.2 Levels of organisation

Life is organised in levels, each built from units of the level below: molecules into molecular machines, machines into cells, cells into organisms, organisms into populations and ecosystems, and ecosystems into the biosphere. Figure 4 places the levels in the space of size and time. Two observations follow. Each level spans a characteristic band of sizes and timescales, separated from the next by roughly one to three orders of magnitude. And the timescale of a level is long compared with the dynamics of the level below, which is what allows each level to be treated, to a good approximation, as a unit with stable properties.

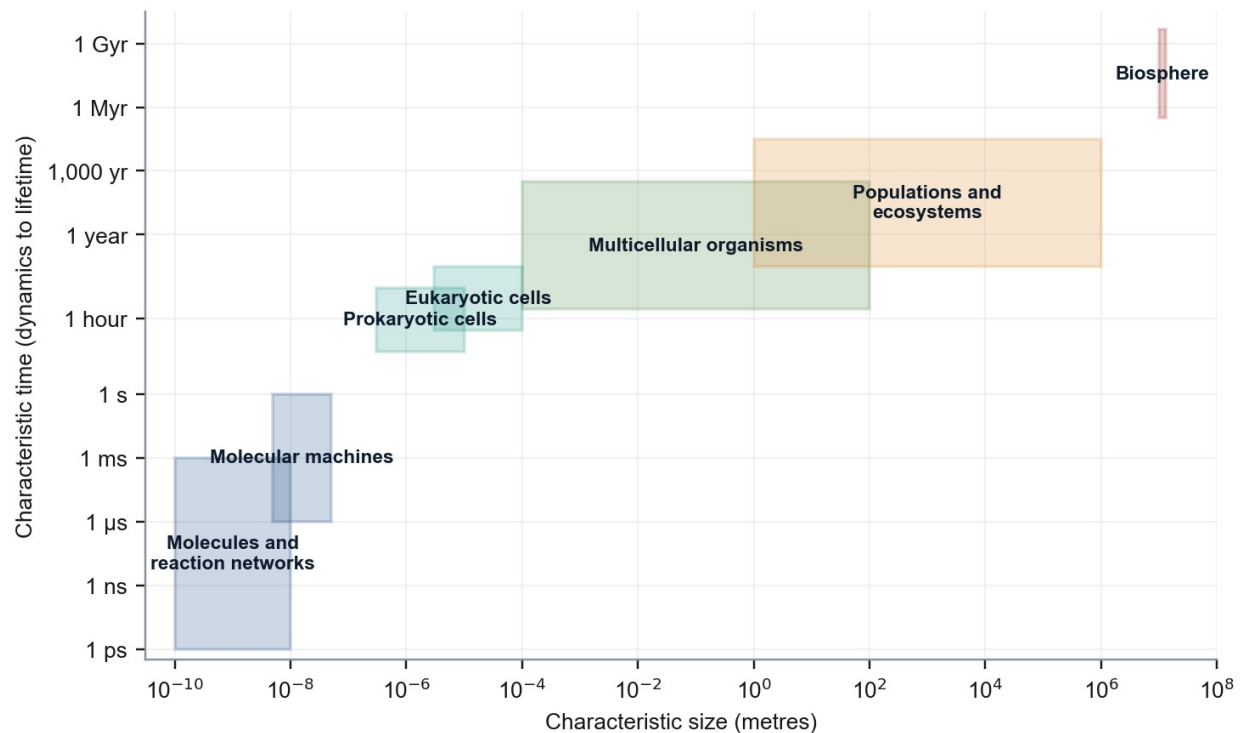


Figure 4. Levels of living organisation in size and time. Each box spans characteristic sizes and the range from typical internal dynamics to typical lifetime. Larger levels change more slowly than the levels they contain, which allows them to be treated as units.

Source: H Heuristics. Ranges are indicative orders of magnitude. Illustrative.

This separation of scales is not unique to life; the cosmic hierarchy shows the same pattern. What is distinctive is that biological levels were assembled historically through a series of major evolutionary transitions, in which units that once reproduced independently became parts of a larger unit that reproduces as a whole (Section 6.7). The hierarchy of life is therefore not only a hierarchy of size but a hierarchy of individuality.

2.3 Eight recurring principles

The prompt for this report asks whether energy flows, molecular networks, compartmentalisation, feedback, heredity, selection, cooperation, adaptation, emergence and hierarchical organisation recur across biological scales. For analysis these can be grouped into eight principles, defined in Table 3. Adaptation is treated as the outcome of selection acting on heritable variation, and molecular networks as one form of the broader principle of feedback-coupled networks.

Table 3. Eight recurring principles of living organisation

Principle	Definition	Mathematical signature	Examples
Energy flow	Free energy is captured from a gradient and dissipated in building and maintaining structure	Free-energy balance; entropy production; scaling of metabolic rate	Chemiosmosis, metabolism, food webs
Information	States of a system that specify other states and are copied or transmitted	Shannon entropy; channel capacity; error thresholds	Genomes, regulatory states, neural codes, culture
Boundaries	Interfaces that separate inside from outside and control exchange	Surface-to-volume scaling; diffusion limits	Membranes, skins, territories, habitat edges
Feedback	Outputs that modify the rate of the process producing them	Negative feedback gives set points; positive feedback gives switches and runaway; delays give cycles	Gene regulation, homeostasis, predator–prey cycles
Heredity and selection	Differential persistence of variants that pass on their properties	Replicator equation; Price equation; fixation probability	Natural selection, immune selection, cultural selection
Cooperation	Interactions in which parts provide benefits to others at a cost	Hamilton's rule; public-goods games	Multicellularity, symbiosis, social insects
Hierarchy	Units nested inside larger units, often as a result of transitions in individuality	Modularity; nested scaling	Organelles in cells, cells in bodies, colonies
Emergence	Properties of a whole that its parts lack, arising from their interactions	Phase transitions; bifurcations; attractors	Autocatalytic sets, development, ecosystem stability

Source: H Heuristics. The list extends the seven cosmic patterns of the companion report with the principles specific to life: information, heredity, selection and cooperation.

2.4 Four equations that frame the rest

Four relationships recur throughout the report. The first is the Gibbs free-energy change of a reaction, which determines whether it can proceed spontaneously:

$$\Delta G = \Delta H - T\Delta S \quad (1)$$

where ΔH is the change in enthalpy, T the temperature and ΔS the change in entropy. A reaction can proceed only if ΔG is negative. Living systems make many reactions with positive ΔG proceed by coupling them to reactions with larger negative ΔG , most often the hydrolysis of ATP. The [second law of thermodynamics](#) is not violated by the growth of biological order, because the organism's internal entropy decrease is more than paid for by the heat and waste it releases.

The second is Claude [Shannon's measure of information](#), the average uncertainty removed by learning which of several states a system is in:

$$H = -\sum p_i \log_2 p_i \quad (2)$$

A DNA base can take four states, so it carries at most two bits. Information in this sense is a property of a channel, not a meaning; biological information acquires meaning because it is used to build and regulate the system that copies it.

The third is the replicator equation, which describes how the share x_i of a type in a population changes when its growth rate f_i differs from the mean growth rate $\bar{f}$:

$$dx_i/dt = x_i (f_i - \bar{f}) \quad (3)$$

Types that grow faster than average increase in share. Equation 3 is the simplest form of selection, and it applies equally to molecules, cells, organisms and, with care, to strategies and ideas. Its generalisation by George Price, the [Price equation](#), splits evolutionary change into a part due to selection and a part due to imperfect transmission, and it is the framework used in Section 6.

The fourth is the [Hamilton's rule](#) condition for cooperation to spread, where r is genetic relatedness, B the benefit to the recipient and C the cost to the actor:

$$r B > C \quad (4)$$

Equation 4 explains why cooperation is common between cells of the same body, which are clones with $r = 1$, and rarer between unrelated organisms. It is one of several mechanisms for cooperation reviewed by [Martin Nowak](#).

2.5 The five layers, read biologically

The foundational report organised creation structures into five layers. In the cosmic report the biological and reproductive layers had only analogues; here they apply in full, as Table 4 shows.

Table 4. The five layers of the Architecture of Creation, applied to living systems

Layer	General meaning	Biological counterpart	Example
Fundamental	Laws and constants that constrain everything	Chemistry of carbon and water; thermodynamics; quantum chemistry of bonds	Hydrophobic molecules self-assemble into bilayers in water
Geometric	Shapes favoured by the constraints	Spheres (cells), helices (DNA, proteins), branching networks (vessels, roots), sheets (tissues)	The double helix; the area-maximising branching of lungs
Biological	How living systems build form	Gene regulation, development, morphogen gradients, mechanical forces in tissues	Turing patterns in skin; segmentation of embryos
Emergent	Order from local rules without a designer	Autocatalytic sets, flocking, colonies, ecosystem dynamics	Termite mounds; predator–prey cycles
Reproductive and evolutionary	Heredity, selection and repetition	Natural selection, drift, symbiosis, major transitions	The repeated evolution of eyes and of multicellularity

Source: *H Heuristics*. In the cosmic report the bottom two layers had only partial analogues; with heredity they become the dominant layers.

03

PART I · PREBIOTIC CHEMISTRY



3. The Architecture of Prebiotic Chemistry

Part I of the core structure examines the chemistry that preceded life: why carbon and water, where the building blocks came from, what supplied the energy and which settings could have concentrated and organised the products. The section ends where chemistry would need to become self-sustaining, which is the subject of Section 4.

3.1 Why carbon and water

Life as we know it is built from six elements: carbon, hydrogen, nitrogen, oxygen, phosphorus and sulfur. All six are among the most abundant reactive elements in the universe, made in stars by the processes described in the companion report. Carbon is singled out because it forms four strong covalent bonds, including bonds to itself, so it can build chains, branches and rings of almost unlimited length and variety. Silicon, often proposed as an alternative, forms weaker bonds to itself and much stronger bonds to oxygen, so in an oxygen-bearing environment it is locked into rock (Section 12).

Water is singled out as the solvent. It is liquid over a wide temperature range, dissolves salts and polar molecules, has a high heat capacity that buffers temperature, and above all forces oily molecules to cluster together. That [hydrophobic effect](#) drives membranes to self-assemble and proteins to fold, and so does a large share of the structural work of biology without any genetic instruction. Water is also a reactant: it is consumed or released in most biochemical reactions, including those that link building blocks into polymers. Linking amino acids or nucleotides releases water, which in bulk water is thermodynamically uphill. This is the 'water paradox' of prebiotic chemistry and one reason many researchers look to environments where water is periodically removed (Section 3.5).

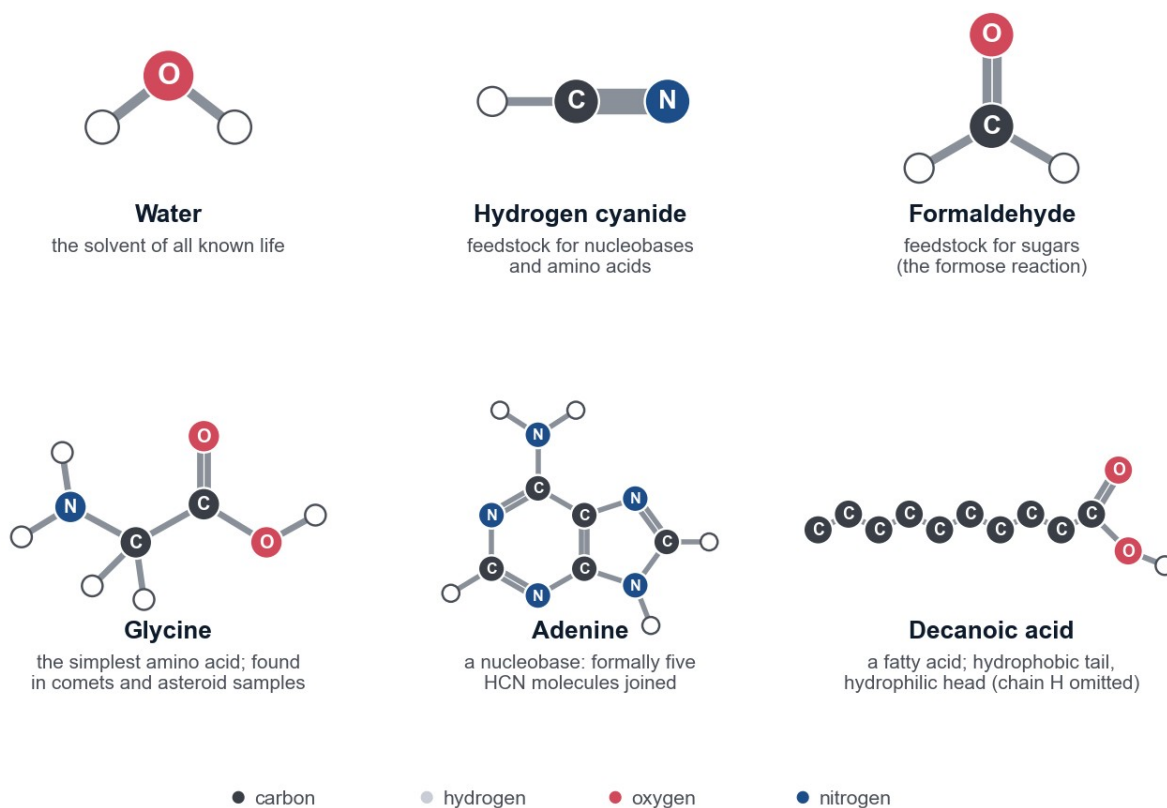


Figure 5. Some molecules of prebiotic chemistry. Hydrogen cyanide and formaldehyde are simple feedstocks that react to give nucleobases and sugars. Glycine is the simplest amino acid. Adenine has the formula of five hydrogen cyanide molecules. Fatty acids such as decanoic acid assemble into membranes in water.

Source: H Heuristics. Ball-and-stick drawings in two dimensions; bond lengths and angles approximate. Illustrative.

3.2 The early Earth as a chemical reactor

The Hadean Earth, between its formation and about four billion years ago, is poorly preserved, but enough is known to set the stage. A giant impact that formed the Moon melted much of the planet. Within about 150 million years the surface had cooled enough for liquid water, as recorded by oxygen isotopes in zircon crystals from the Jack Hills of Western Australia. The atmosphere was probably dominated by carbon dioxide and nitrogen, with little or no free oxygen ([Catling and Zahnle, 2020](#)). The young Sun was about 25 to 30 per cent fainter but emitted more ultraviolet light, and the surface was bombarded by meteorites and comets. Volcanism, hydrothermal circulation and lightning were widespread.

These conditions provided three things life would need: a diversity of chemical environments, sources of energy far from equilibrium, and mineral surfaces of many compositions. The mineralogist Robert Hazen has shown that the number of mineral species on Earth grew from a few hundred to several thousand over its history, in large part because of life ([Hazen and colleagues, 2008](#)); the Hadean surface was mineralogically simpler, but already offered clays, sulfides, borates in some settings and phosphates.

3.3 Where the building blocks came from

The modern experimental study of the origin of life began in 1953, when Stanley Miller passed electric sparks through a flask of methane, ammonia, hydrogen and water and found amino acids in the products ([Miller, 1953](#)). A reanalysis of Miller's archived samples using modern instruments found more than 20 amino acids ([Johnson and colleagues, 2008](#)). Miller's gas mixture is now thought to be more reducing than the early atmosphere, but the experiment established the central point: the molecules of life form readily from simple precursors when energy is supplied.

Since then, routes have been found to most of the major building blocks (Table 5). In 1960 Joan Oró made adenine from ammonium cyanide ([Oró, 1960](#)). The [formose reaction](#), discovered by Aleksandr Butlerov in 1861, makes sugars from formaldehyde, though as an unselective tar. A long-standing obstacle was making nucleotides, the units of RNA, because joining a free sugar to a free base works poorly. In 2009 John Sutherland's group bypassed the problem by building pyrimidine nucleotides from simpler fragments ([Powner, Gerland and Sutherland, 2009](#)), and in 2015 they showed that hydrogen cyanide, hydrogen sulfide and ultraviolet light can give precursors of nucleotides, amino acids and lipids from a common network of reactions ([Patel and colleagues, 2015](#)). Thomas Carell's group later described a unified route to both pyrimidine and purine nucleotides driven by wet–dry cycles ([Becker and colleagues, 2019](#)).

Table 5. Selected landmarks in prebiotic synthesis

Year	Result	Significance	Main limitation
1861	Formose reaction: formaldehyde to sugars (Butlerov)	Sugars from a one-carbon feedstock	Produces a complex mixture; ribose is a minor product
1953	Amino acids from sparked gases (Miller)	Building blocks form spontaneously with energy input	Gas mixture more reducing than now thought likely
1960	Adenine from ammonium cyanide (Oró)	Nucleobases from hydrogen cyanide	Low yields; needs concentrated cyanide
1996	RNA chains up to about 50 units on clay (Ferris and colleagues)	Minerals can template and catalyse polymerisation	Requires pre-activated nucleotides
2009	Pyrimidine nucleotides without free ribose (Powner and colleagues)	Solves a long-standing nucleotide problem	Multi-step; depends on sequencing of conditions
2015	Cyanosulfidic protometabolism (Patel and colleagues)	Common origin for precursors of RNA, protein and lipid	Requires specific geochemical settings
2019	Purines and pyrimidines from one pathway (Becker and colleagues)	Wet–dry cycling as a unifying driver	Laboratory sequencing of steps
2019–20	Metal-driven core-metabolic reactions without enzymes (Muchowska and colleagues ; Preiner and colleagues)	Parts of the citric acid cycle and carbon fixation run on minerals	Networks are not yet self-sustaining

Source: H Heuristics, from the studies linked. Each result shows that a step is chemically possible; none shows that the steps occurred together on the early Earth.

A second source of building blocks was delivery from space. The Murchison meteorite, which fell in Australia in 1969, contains dozens of amino acids and tens of thousands of distinct organic compounds ([Schmitt-Kopplin and colleagues, 2010](#)). All five nucleobases used in DNA and RNA have now been identified in carbon-rich meteorites ([Oba and colleagues, 2022](#)), uracil has been found in samples returned from asteroid Ryugu ([Oba and colleagues, 2023](#)), and samples from asteroid Bennu contain 14 of the 20 amino acids used in proteins together with all five nucleobases ([Glavin and colleagues, 2025](#)).

The prebiotic inventory was therefore not a local accident of Earth. It is a widespread outcome of chemistry in the Solar System (Grade A).

Box 3.1 Chirality. Many biological molecules come in mirror-image forms. Life uses almost exclusively left-handed amino acids and right-handed sugars, but abiotic synthesis produces equal mixtures. How one hand came to dominate is unresolved. Proposed mechanisms include small biases from polarised light or from magnetic mineral surfaces, amplified by autocatalytic reactions that favour the commoner hand, as in the Soai reaction. Some meteorite amino acids show small excesses of the left-handed form. The question is graded C: amplification mechanisms are demonstrated, the original bias is not.

3.4 Energy: the disequilibria life feeds on

Building blocks are not enough. Linking them, sorting them and keeping them away from equilibrium needs a continuous supply of free energy. All known life gets that energy from redox chemistry: the transfer of electrons from a donor, such as hydrogen, hydrogen sulfide, ferrous iron or organic matter, to an acceptor, such as carbon dioxide, sulfate, nitrate or oxygen. The energy released depends on the difference in redox potential between the two couples, as shown in Figure 6.

$$\Delta G^{\circ'} = -n F \Delta E^{\circ'} \quad (5)$$

where n is the number of electrons transferred, F is the Faraday constant (96.5 kJ per volt per mole of electrons) and $\Delta E^{\circ'}$ is the difference in standard potentials at pH 7. Using equation 5, the oxidation of hydrogen by oxygen releases about 238 kJ per mole; the conversion of hydrogen and carbon dioxide to methane, the metabolism of methanogenic archaea, releases about 134 kJ per mole of methane; and the respiration of one NADH, the cell's main electron carrier, releases about 220 kJ. A cell captures this energy in steps of roughly 50 to 60 kJ, the free energy of making one ATP under cellular conditions.

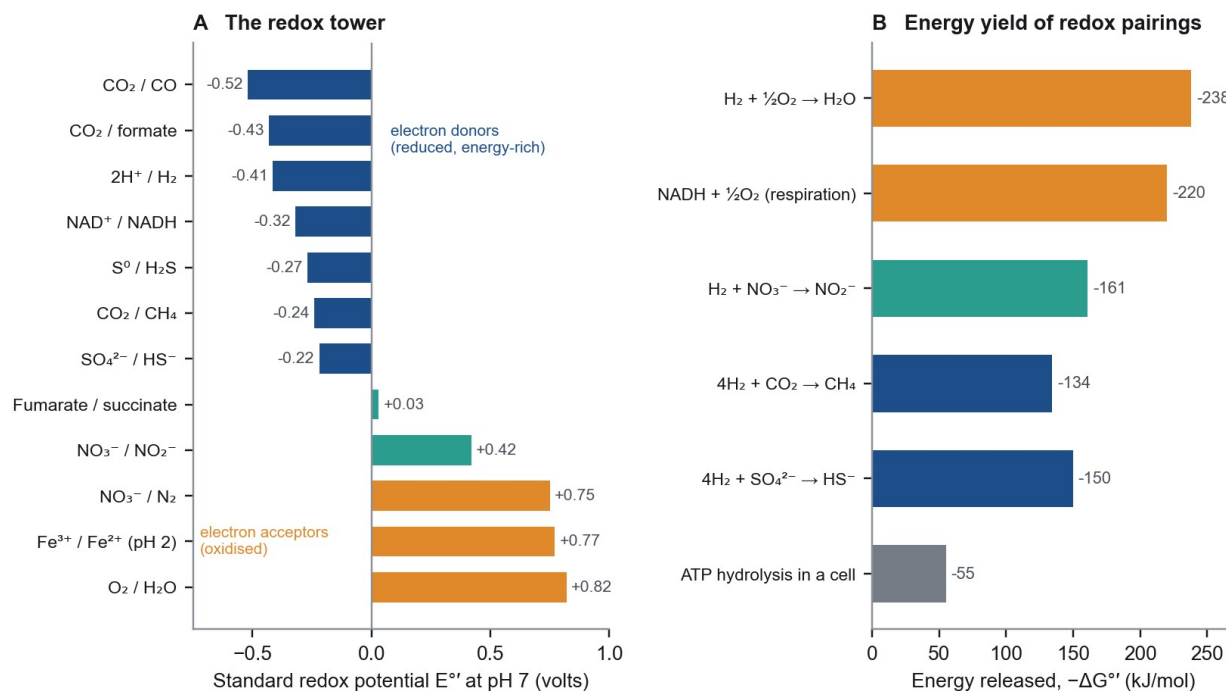


Figure 6. The redox tower. A: standard redox potentials of electron donor and acceptor couples used by living things; electrons flow downhill from couples near the top to those near the bottom. B: free energy released by selected pairings, calculated from panel A with equation 5, compared with the energy of ATP hydrolysis in a cell.

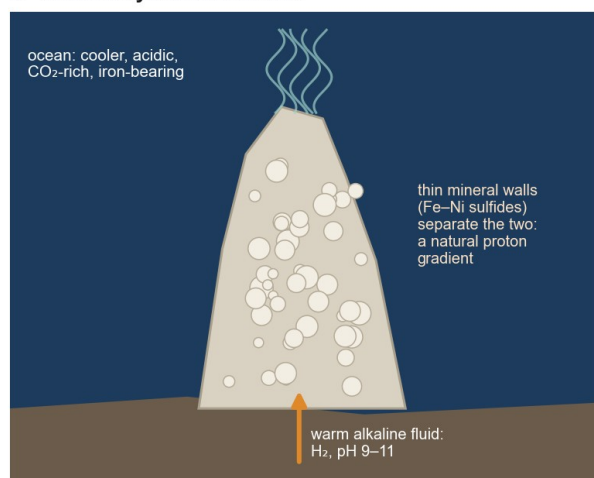
Source: H Heuristics calculation from standard biochemical values (Thauer, Jungermann and Decker, 1977, and standard texts). Values are for standard conditions at pH 7 and differ in real environments.

Two features of the redox tower matter for the origin of life. First, the early Earth offered several large disequilibria without oxygen. Hydrothermal systems release hydrogen when water reacts with iron-rich rock in a process called serpentinisation; the ocean held dissolved carbon dioxide; and the difference between them is the energy source still used by methanogens and acetogens, the microbes many researchers regard as the most ancient. Second, modern cells harvest redox energy indirectly. They use it to pump protons across a membrane and then let the protons flow back through a rotary enzyme, ATP synthase, that makes ATP. This [chemiosmotic coupling](#), proposed by Peter Mitchell in 1961, is universal and therefore probably very ancient (Section 5.2).

3.5 Settings: vents, ponds and surfaces

Where did prebiotic chemistry become organised? Two families of settings dominate current debate, illustrated in Figure 7 and compared in Table 6.

A Alkaline hydrothermal vent



B Warm little pond on volcanic land

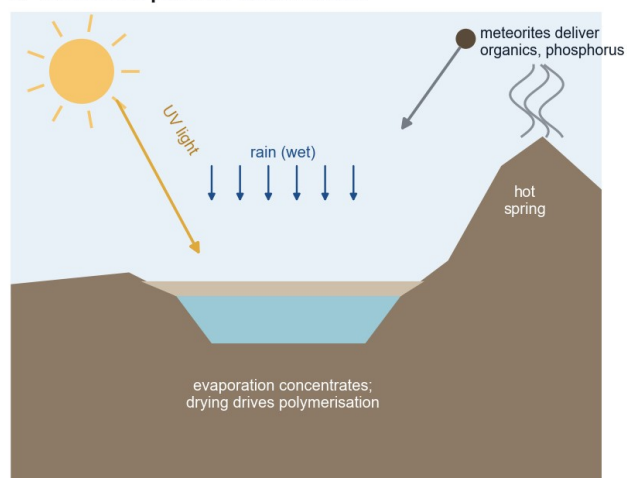


Figure 7. Two candidate settings for the origin of life. A: an alkaline hydrothermal vent, where warm hydrogen-rich fluid meets acidic, carbon dioxide-rich seawater across thin mineral walls, creating natural gradients of pH and redox potential. B: a pond on volcanic land, where wet-dry cycles, ultraviolet light, hot springs and meteoritic input concentrate and transform organic molecules.

Source: H Heuristics, after Martin and Russell (2003), Lane and Martin (2010) and Damer and Deamer (2020). Illustrative; not to scale.

The **alkaline hydrothermal vent** hypothesis, developed by Michael Russell, William Martin and Nick Lane, places the origin in porous chimneys like those of the Lost City field in the Atlantic ([Martin and Russell, 2003](#); [Lane and Martin, 2010](#)). Its strengths are a continuous supply of hydrogen and carbon dioxide, mineral catalysts resembling the iron-sulfur clusters at the heart of ancient enzymes, and natural proton gradients across thin walls that resemble the chemiosmotic gradients of modern cells. Its main weakness is dilution: in an ocean it is hard to concentrate building blocks enough to polymerise them, and water drives polymers apart.

The **surface pond** hypothesis, often traced to Charles Darwin's remark about a 'warm little pond', places the origin on land. Its modern forms emphasise cycles of wetting and drying in volcanic hot-spring pools ([Damer and Deamer, 2020](#)), delivery of organics by meteorites ([Pearce and colleagues, 2017](#)) and ultraviolet-driven cyanosulfidic chemistry ([Sasselov, Grotzinger and Sutherland, 2020](#)). Drying concentrates molecules and drives the condensation reactions that water opposes. Its weakness is that early land was limited and exposed to impacts and radiation.

Table 6. Candidate settings for the origin of life compared

Feature	Alkaline hydrothermal vent	Volcanic surface pond	Other proposals
Energy source	H ₂ -CO ₂ redox disequilibrium; pH gradient	Ultraviolet light; heat; wet-dry cycling	Lightning; impacts; radioactivity
Concentration mechanism	Thermal gradients in pores; mineral adsorption	Evaporation; drying on mineral surfaces	Freezing (eutectic ice); clay surfaces
Polymerisation	Difficult in bulk water	Favoured by drying	Favoured by freezing or surfaces
Link to modern biology	Iron-sulfur enzymes; chemiosmosis; ancient carbon-fixation pathway	Cyanosulfidic chemistry yields nucleotide, amino-acid and lipid precursors	Varies
Key open problem	Making and keeping polymers	Availability and stability of early land	Linking to metabolism
Grade	C	C	C–D

Source: H Heuristics, from the reviews linked in the text. The settings are not mutually exclusive; several researchers argue for chemistry distributed across environments, connected by transport.

Neither setting has been shown to produce a living system, and they may not be alternatives. Different steps could have happened in different places, linked by rivers, rain and tides. What the comparison shows is that the early Earth offered several environments in which the main obstacles, energy, concentration and polymerisation, could be overcome, though not all at once in any single one.

3.6 From mixtures to networks

The step that prebiotic chemistry has not yet achieved is the transition from a mixture of useful molecules to a network that maintains itself. Most prebiotic reactions give mixtures, often dominated by tars, and the useful products decay. A living system needs reactions to be organised: products of one reaction must feed the next, some products must catalyse the reactions that make them, and the whole must run faster than it decays. Systems chemistry, a field that studies networks of reactions rather than individual reactions, has made progress on each element ([Ruiz-Mirazo, Briones and de la Escosura, 2014](#)), and recent work has found that iron, nickel and other metals can drive many of the reactions of the citric acid cycle and of carbon fixation without enzymes ([Muchowska, Varma and Moran, 2019](#)). The next section examines what happens when such networks begin to catalyse and copy themselves.

3.7 What the evidence shows and where it stops

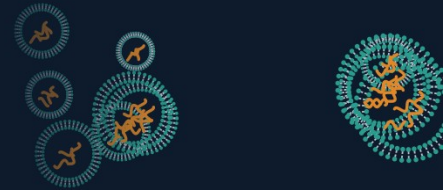
Table 7. Graded conclusions on prebiotic chemistry

Claim	Grade	Basis
Life's main building blocks form readily from simple precursors	A	Hundreds of experiments; meteorites; asteroid samples
Liquid water was present on Earth by about 4.4 billion years ago	A to B	Oxygen isotopes in zircons
Early Earth had abundant redox and pH disequilibria	A	Geochemistry; modern analogues
Plausible routes exist to nucleotides and to activated building blocks	B	Laboratory syntheses since 2009
Prebiotic routes ran together in one setting on the early Earth	C	Geochemical scenarios; no direct record
Life began at vents, or in ponds, or elsewhere	C to D	Competing scenarios, each with gaps

Source: H Heuristics.

04

PART II · THE FIRST LIVING SYSTEMS



4. The Emergence of the First Living Systems

Part II examines the hypotheses for how chemistry became biology: molecular replication, catalytic networks, compartments and their coupling into systems capable of sustained evolution. Because none of these hypotheses has been confirmed, the section relies more than any other on models. Each model is simple, standard and computed here so that its implications can be seen directly.

4.1 Replication and the kinetics of competition

The simplest form of heredity is a molecule that serves as a template for its own copying. Non-enzymatic self-replication has been demonstrated in the laboratory, first by Günter von Kiedrowski in 1986 with short DNA strands and since then with RNA, peptides and other molecules. A surprising feature of these systems is their kinetics. Because product strands stick to each other and must separate before they can serve as templates again, they grow not exponentially but parabolically, in proportion to the square root of their concentration. That difference turns out to matter for whether Darwinian selection can operate at all.

Consider replicators that compete for shared resources and grow at a rate proportional to x^p , where x is concentration. Figure 8 shows the outcome of competition for three values of p , computed for this report. With exponential growth ($p = 1$), the fastest replicator wins and the others go extinct, the 'survival of the fittest' that natural selection requires. With hyperbolic growth ($p = 2$), whichever type starts commonest wins regardless of its rate. With parabolic growth ($p = \frac{1}{2}$), all three types coexist indefinitely, with shares proportional to the square of their rate constants: in the simulation, 45, 33 and 22 per cent. This 'survival of everybody', identified by [Eörs Szathmáry and Irina Gladkih](#), means that the simplest chemical replicators may not undergo selection in the usual sense.

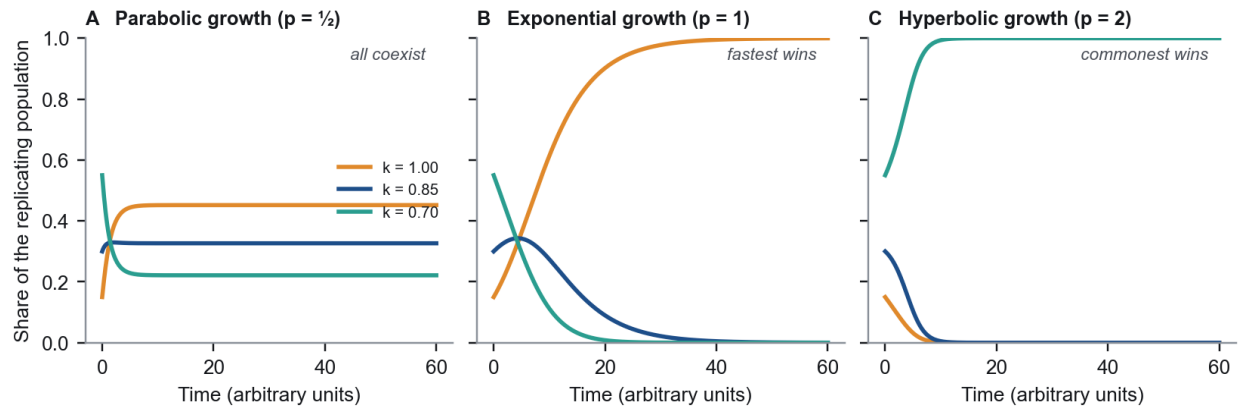


Figure 8. Competition between three replicators with different growth laws. Growth rate is kx^p , with total concentration held constant. Parabolic growth leads to coexistence; exponential growth to survival of the fastest; hyperbolic growth to survival of the commonest, whatever its rate.

Source: H Heuristics simulation of the selection equation $dx_i/dt = k_i x_i^p - x_i \sum_j k_j x_j^p$. Rate constants 1.00, 0.85 and 0.70; initial shares 15, 30 and 55 per cent.

The implication is that heredity alone does not guarantee evolution. For selection to favour better replicators, something must break parabolic coexistence: an enzyme that separates strands, a mechanism that removes products, or compartments that turn the competition among molecules into competition among groups (Section 4.5).

4.2 Autocatalytic networks

A second route to self-maintenance does not require a template. In a network of reactions, a set of molecules is collectively autocatalytic if every reaction that makes a member of the set is catalysed by some member of the set, and every member can be built from a supply of simple 'food' molecules. Stuart Kauffman argued in the 1980s that such sets would arise spontaneously in sufficiently diverse chemistry ([Kauffman, 1986](#)). Critics replied that the required level of catalysis was unrealistic. Wim Hordijk and Mike Steel formalised the idea as a reflexively autocatalytic and food-generated set, or RAF, and found that the required level is modest: on average, each molecule needs to catalyse only one or two reactions ([Hordijk and Steel, 2004](#)).

Figure 9 reproduces this result. In the binary polymer model, molecules are strings of two monomer types up to a maximum length n , reactions join or split strings, and each molecule catalyses each reaction at random with a fixed probability. The food set is all strings of length one or two. For each network, the simulation searches for the largest autocatalytic set. As the average number of reactions catalysed per molecule, f , rises past about one, the probability that an autocatalytic set exists jumps from near zero to near one, and the jump gets sharper as networks get larger. The value of f needed for a 50 per cent chance rises only from about 1.06 to 1.26 as the number of reactions grows sixfold, from 516 to 3,076 reversible pairs.

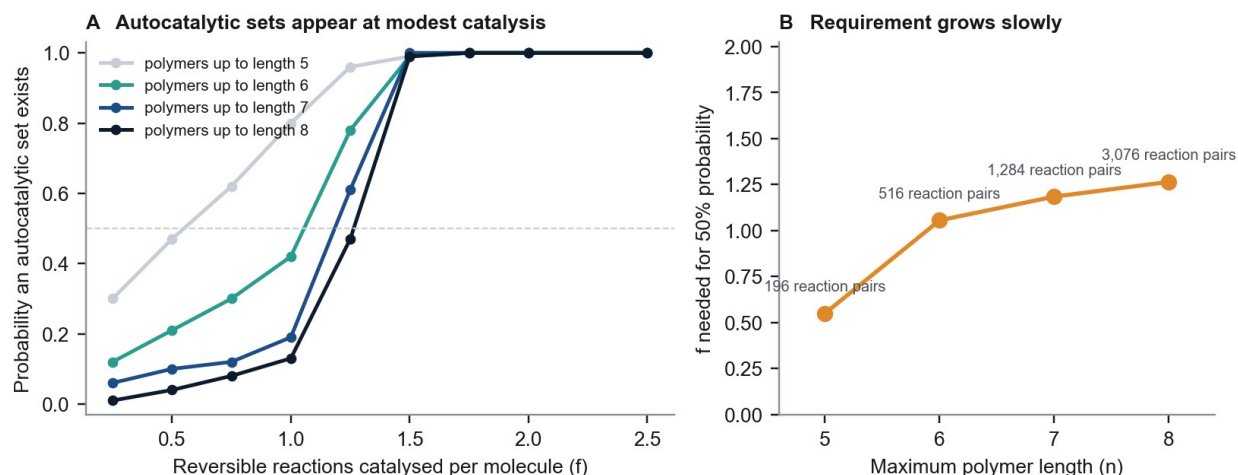


Figure 9. Emergence of autocatalytic sets in random chemical networks. A: probability that a reflexively autocatalytic, food-generated set exists, as a function of how many reactions each molecule catalyses on average. B: the level of catalysis needed for a 50 per cent chance grows only slowly with network size.

Source: H Heuristics simulation of the binary polymer model of Kauffman (1986) and Hordijk and Steel (2004), with the maximal-RAF algorithm. 100 random networks per point; food set is all strings of length 1 and 2.

The result is a clear example of emergence in the sense used in this series: a qualitative property of a whole, collective self-maintenance, appears abruptly when a quantitative property of its parts crosses a threshold. Autocatalytic sets have since been identified in the metabolic network of *E. coli* and in the reconstructed metabolism of early prokaryotes (Xavier and colleagues, 2020). Whether such networks could evolve before templates appeared is debated, because without a genome their variations are poorly inherited (Grade C).

4.3 The RNA world

Modern cells divide labour between DNA, which stores information, and proteins, which do almost everything else. But DNA cannot be copied without proteins, and proteins cannot be made without the information in DNA. The circle is broken if an earlier stage used a single kind of molecule for both roles. RNA is the leading candidate. It stores information in the same way as DNA, and it can fold into shapes that catalyse reactions, as Thomas Cech and Sidney Altman showed in the early 1980s with ribozymes. Walter Gilbert named the hypothetical stage the [RNA world](#) in 1986.

The strongest evidence is the ribosome, the machine that makes every protein. Its structure, solved in 2000, showed that the site where amino acids are joined consists entirely of RNA, with no protein nearby (Ban and colleagues, 2000; Nissen and colleagues, 2000). The ribosome is therefore a ribozyme, and the machine that makes proteins appears to be a relic of a time before proteins. Many essential cofactors, such as ATP, NAD and coenzyme A, are built from RNA nucleotides, which is also suggestive. In the laboratory, ribozymes have been evolved that copy RNA templates nearly 100 nucleotides long (Wochner and colleagues, 2011) and that replicate each other in a cross-catalytic pair indefinitely (Lincoln and Joyce, 2009).

The RNA world remains a hypothesis with gaps. RNA is chemically fragile, the prebiotic synthesis of its nucleotides is demanding (Section 3.3), and no ribozyme yet copies itself in full. Many researchers now favour a messier picture in which RNA, peptides, lipids and metabolism co-evolved from the start. The case that RNA played a central early role is graded B; the case for a stage in which RNA did everything is graded C.

4.4 The error threshold

Copying is never perfect, and errors set a limit on how much information can be maintained. Manfred Eigen showed in 1971 that a population of replicators maintains a 'master' sequence only if the copying error rate per site, u , is below a threshold set by the genome length L and the selective advantage σ of the master sequence (Eigen, 1971):

$$u < \ln(\sigma) / L \quad (6)$$

Above the threshold, the master sequence is lost and the population drifts as a cloud of mutants with no stable identity. Figure 10 computes the effect for this report. For $\sigma = 10$, a genome of 50 sites survives error rates up to about 4.6 per cent per site, but a genome of 200 sites only up to about 1.2 per cent. The consequence is a catch-22: a longer genome could encode a better copying enzyme, but a long genome cannot be maintained without a good copying enzyme. The earliest replicators were therefore limited to short sequences, perhaps tens of nucleotides, unless something improved fidelity or helped cooperating short sequences persist together.

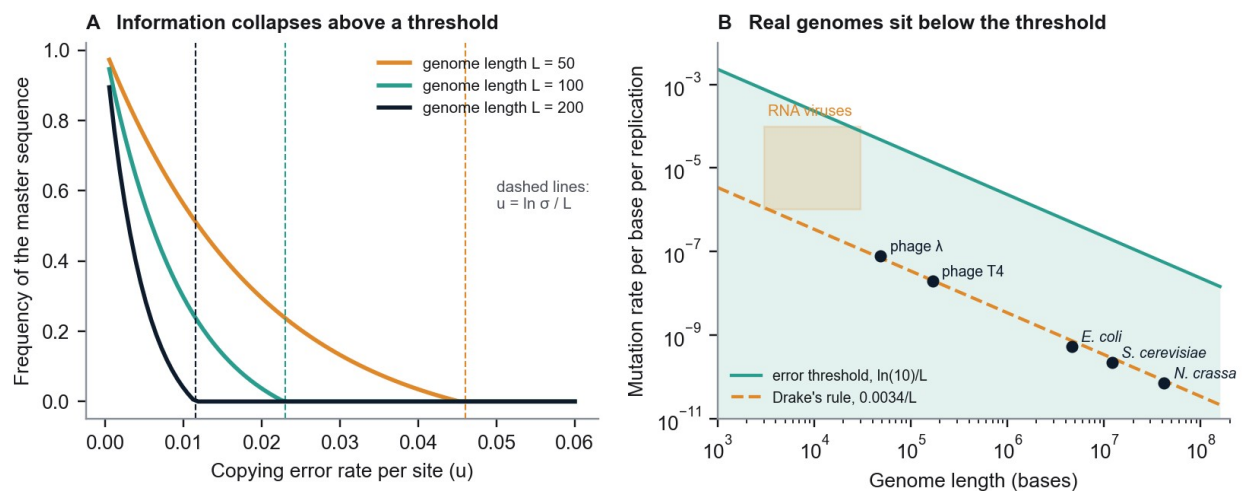


Figure 10. The error threshold. A: equilibrium frequency of the master sequence in Eigen's quasispecies model, for three genome lengths; the master sequence is lost near $u = \ln \sigma / L$. B: per-base mutation rates of real organisms lie below the threshold and close to Drake's rule, which holds that DNA-based microbes make about 0.003 mutations per genome per replication.

Source: Panel A, H Heuristics calculation of the single-peak quasispecies model with $\sigma = 10$, solved exactly on error classes. Panel B: mutation rates from Drake (1991); RNA virus range from Sanjuán and colleagues (2010).

Panel B of Figure 10 shows that real organisms respect the threshold. Across DNA-based microbes, from bacteriophage λ with about 48,500 bases to the fungus *Neurospora* with 42 million, the mutation rate per base falls in proportion to genome length, so that the rate per genome stays close to 0.003, a regularity known as [Drake's rule](#). RNA viruses, which lack proofreading, have short genomes and mutation rates close to the threshold (Sanjuán and colleagues, 2010). The constraint identified by Eigen for the origin of life still shapes genomes today (Grade A for the regularity; B for its interpretation).

4.5 Compartments

Every known cell is enclosed by a membrane. Compartments solve several problems at once. They keep the products of a reaction network together so that they are not lost by diffusion. They link the fate of a molecule to the success of the system it belongs to, so that a gene that helps its compartment grow

spreads with that compartment. And they provide a boundary across which gradients can be built and used.

The membranes of modern cells are made of phospholipids, which are complex to synthesise. Simpler fatty acids, which form under prebiotic conditions and are found in meteorites, also assemble spontaneously into vesicles. Jack Szostak's laboratory has shown that such vesicles can grow by absorbing fatty acids from micelles, divide when stretched into filaments, and hold RNA inside while letting small nucleotides through ([Szostak, Bartel and Luisi, 2001](#); [Hanczyc, Fujikawa and Szostak, 2003](#)). Figure 11 illustrates the cycle. It is a physical, not a genetic, mode of reproduction, but it shows that the boundary of a protocell could grow and divide without any enzymatic machinery.

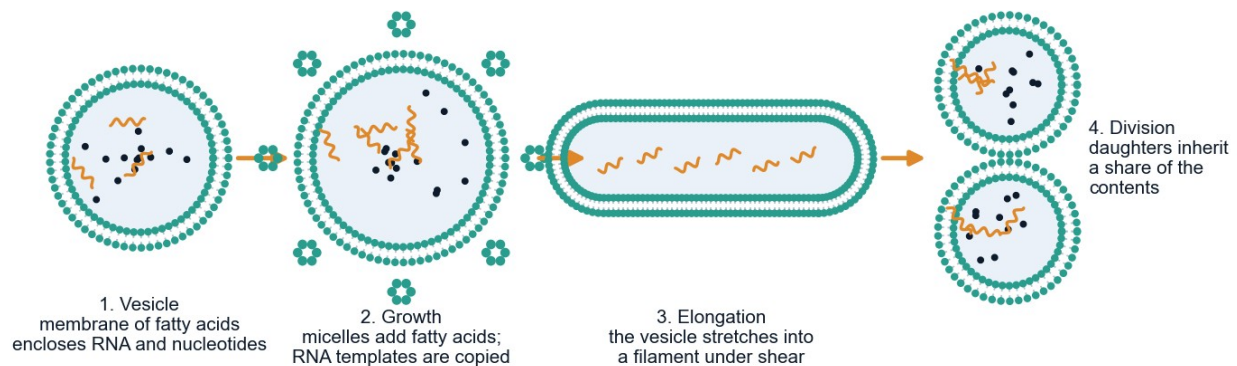


Figure 11. A model protocell cycle. A vesicle of fatty acids encloses RNA and nucleotides; it grows by absorbing fatty acids from surrounding micelles, while internal templates are copied; it elongates into a filament; and gentle shear divides it into daughter vesicles, each inheriting a random share of the contents.

Source: *H Heuristics*, after Hanczyc, Fujikawa and Szostak (2003) and Zhu and Szostak (2009). Illustrative; not to scale.

Compartments also solve the problem of cooperation among molecules. Suppose a protocell needs two kinds of gene, A and B, but B copies faster than A. In free solution, B will take over and the system will fail. Inside compartments, a group with too much B grows slowly, so selection between compartments can counter selection within them. This 'stochastic corrector' model of [Szathmáry and Demeter \(1987\)](#) is simulated in Figure 12. In free solution the faster template reaches fixation within a few generations. In compartments, the population settles to a stable mix, with the faster template making up about 68 per cent and mean compartment fitness about 71 per cent of the maximum, because random division continually produces compartments with balanced contents that grow fastest.

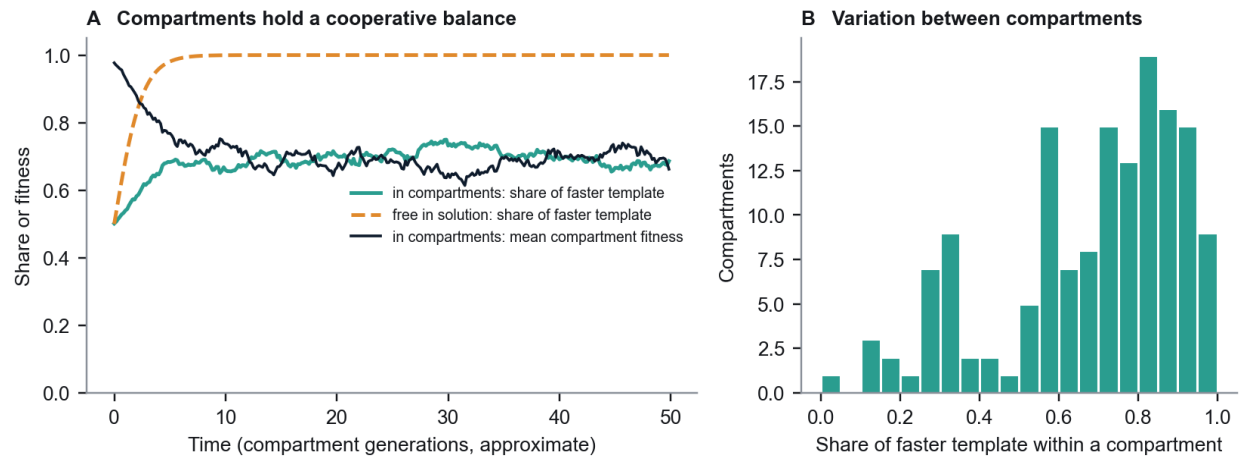


Figure 12. The stochastic corrector. A: two essential templates, one replicating 30 per cent faster, maintained in 150 compartments that divide at 40 templates; the faster template is held in check by selection between compartments, whereas in free solution it takes over. B: the composition of compartments at the end of the run.

Source: H Heuristics simulation after Szathmáry and Demeter (1987). Compartment growth is proportional to $4 \cdot f_A \cdot f_B$; division is random; the free-solution curve is the deterministic outcome without compartments.

The stochastic corrector is a first example of a theme that recurs throughout this report: a new level of organisation can arise when selection between groups overcomes selection within them. The same logic applies to chromosomes, to cells in a body and to colonies of social insects (Sections 6.7 and 7.2).

4.6 Coupling metabolism, information and compartments

The hypotheses above are often presented as rivals: metabolism first, genetics first or compartments first. Figure 13 shows why each is incomplete on its own. A metabolism without heredity cannot accumulate improvements. A replicator without metabolism depends on an external supply of activated building blocks. A compartment without either is an empty bubble. Tibor Gánti's chemoton model of 1971 defined the minimal living system as the coupling of all three, and most researchers now treat the origin of life as the problem of how that coupling arose.

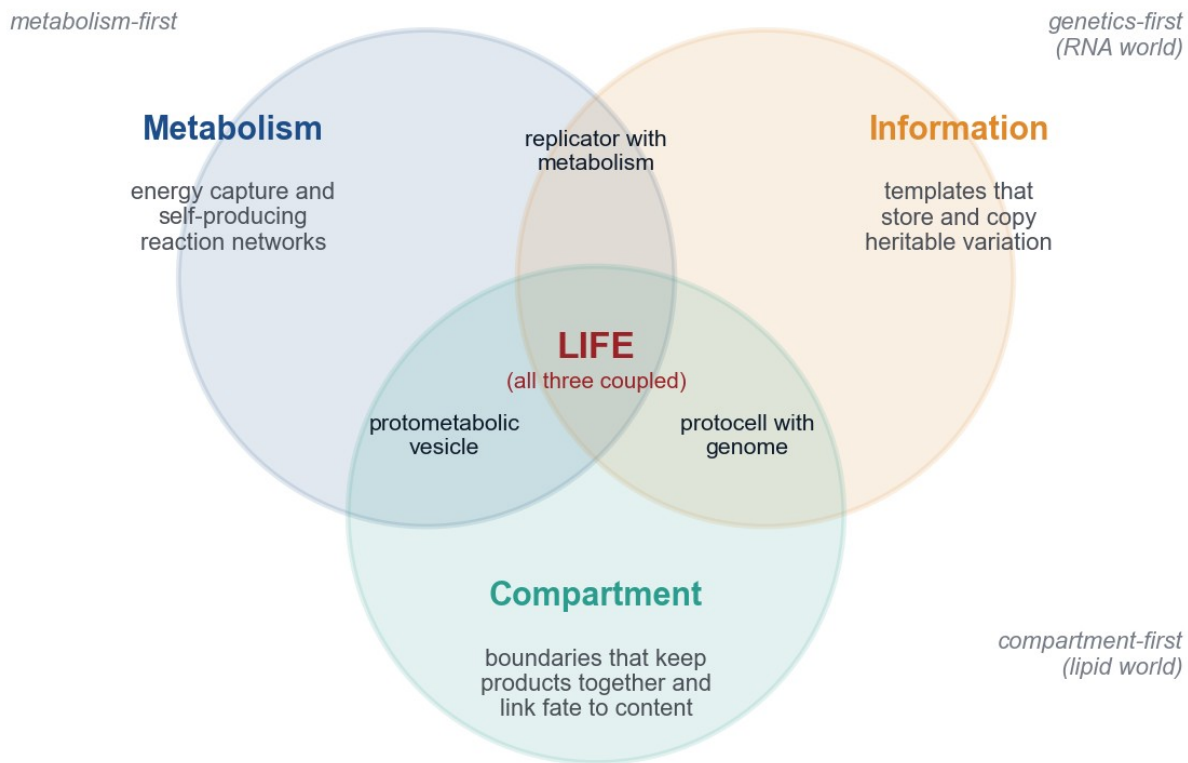


Figure 13. Three subsystems of a minimal living system. Each origin-of-life hypothesis begins in one subsystem; life in the full sense requires all three to be coupled, so that metabolism builds the compartment and the templates, the templates specify the catalysts, and the compartment keeps them together.

Source: H Heuristics, after Gánti's chemoton model and Ruiz-Mirazo, Briones and de la Escosura (2014). Illustrative.

The coupling is where the creation structure becomes fully biological. Before it, the filters acting on chemical systems are physical: which molecules are stable, which networks persist. After it, the filter is natural selection: which systems leave more descendants. The transition is plausibly gradual, through stages in which heredity was partial and selection weak, which makes it hard to name a moment at which life began. That difficulty is a feature of the problem, not a failure of definition.

4.7 The last universal common ancestor

Comparing the genomes of living organisms allows a partial reconstruction of LUCA, the most recent population from which all life descends. LUCA was not the first living thing; it was already a sophisticated cell, the survivor of an unknown period of earlier evolution. [Weiss and colleagues \(2016\)](#) identified 355 protein families probably present in LUCA, pointing to an anaerobic organism that used hydrogen, fixed carbon dioxide by the Wood–Ljungdahl pathway and lived at high temperature. A broader analysis by [Moody and colleagues \(2024\)](#) estimated that LUCA lived about 4.2 billion years ago, had a genome of perhaps 2.5 million bases encoding about 2,600 proteins, and possessed an early immune system against viruses, implying that it lived in an ecosystem with other organisms. Both reconstructions are contested in detail (Grade B to C), but they agree that by the time of LUCA the core architecture of the cell, described in Section 5, was already in place.

4.8 How likely was it?

If life appeared on Earth soon after conditions allowed, does that mean it arises easily? The intuition is strong, but the inference is weak. [David Spiegel and Edwin Turner \(2012\)](#) showed why with a Bayesian analysis, which Figure 14 reproduces. Suppose life arises on a habitable planet as a random event at an unknown rate λ per billion years. Life on Earth appeared within about 0.6 billion years of habitability. But observers like us could exist only if life began early enough to leave time for evolution, perhaps within 1.4 billion years. The likelihood of the observation must be conditioned on that selection effect.

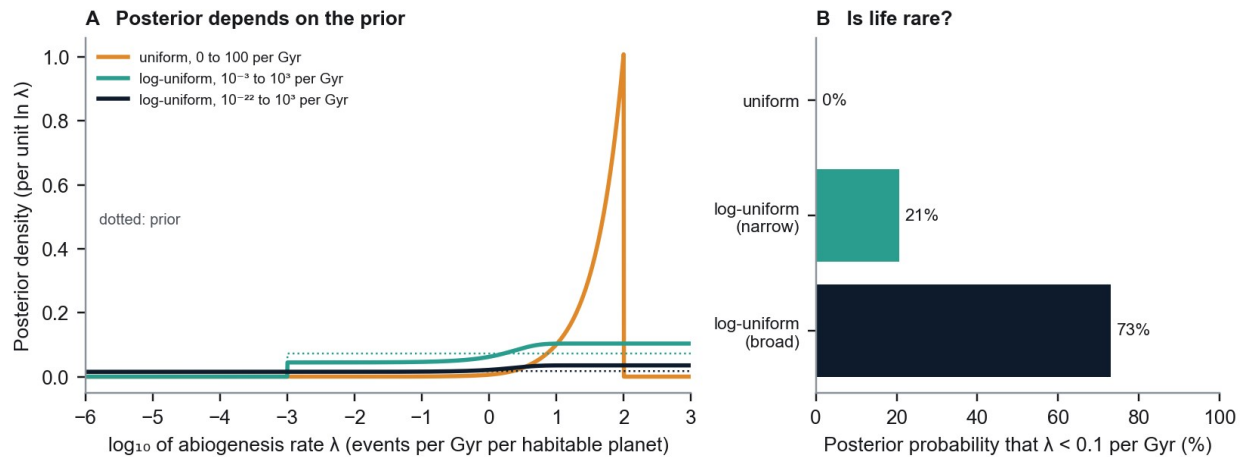


Figure 14. What the early appearance of life implies about its probability. A: posterior distribution of the rate of abiogenesis λ under three priors, given that life arose within 0.6 billion years and that it must have arisen within 1.4 billion years for observers to exist today. B: posterior probability that λ is below 0.1 per billion years, meaning life is rare.

Source: H Heuristics calculation after Spiegel and Turner (2012). Likelihood $(1 - e^{-\lambda \cdot 0.6}) / (1 - e^{-\lambda \cdot 1.4})$.

The result depends almost entirely on the prior. With a prior that treats all rates up to 100 per billion years as equally likely, the posterior strongly favours easy abiogenesis, and the chance that life is rare is under 0.1 per cent. With a prior uniform in the logarithm of λ over six orders of magnitude, that chance rises to about 21 per cent; over 25 orders of magnitude, which reflects genuine ignorance about the chemistry, it is about 73 per cent. The early appearance of life on Earth is encouraging but cannot, by itself, show that life is common (Grade A for the logic; the frequency of life is Grade D). Section 12 returns to the question.

4.9 What the evidence shows and where it stops

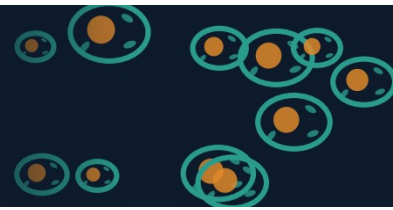
Table 8. Graded conclusions on the emergence of the first living systems

Claim	Grade	Basis
All life descends from a common ancestral population	A	Shared code, machinery and phylogeny
Self-replication, autocatalytic sets and protocell division are chemically possible	A	Laboratory demonstrations
Copying fidelity limits genome size (error threshold)	A	Theory; Drake's rule
RNA played a central early role, and the ribosome is a relic of it	B	Ribosome structure; cofactors; ribozymes
LUCA was an anaerobic, hydrogen-using cell living about 4.2 billion years ago	B to C	Phylogenetic reconstruction; molecular clocks
A specific pathway from chemistry to life has been identified	D	Not achieved
The early appearance of life implies that life is common	D	Inference depends on the prior

Source: H Heuristics.

05

PART III · THE CELL



5. The Architecture of the Cell

Part III turns from the origin of life to life as it exists. The cell is the smallest unit that has all the properties listed in Section 1.3, and every organism is either a cell or a collection of cells. This section asks how membranes, metabolism, genetic information, molecular machinery and regulatory feedback combine to sustain biological organisation, and which features of the cell are constrained by chemistry and physics rather than by history.

5.1 Two designs, one core

Cells come in two basic designs, shown in Figure 15. Prokaryotic cells, the bacteria and archaea, are typically one or two micrometres long, have no nucleus and keep their DNA in a single circular chromosome in the cytoplasm. Eukaryotic cells, which make up animals, plants, fungi and protists, are typically ten to a hundred times larger in diameter and a thousand times or more in volume. They keep their DNA in a nucleus and contain internal membranes and organelles, including mitochondria, which descend from bacteria (Section 6.6).

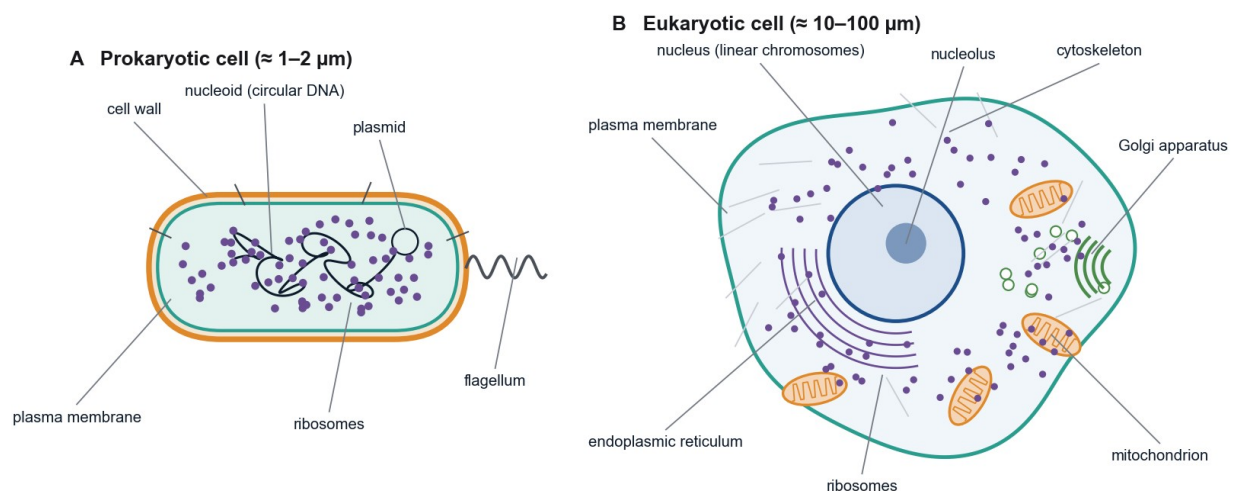


Figure 15. Prokaryotic and eukaryotic cells. The prokaryote (A) has a cell wall, a single membrane, a nucleoid of circular DNA, ribosomes and often a flagellum. The eukaryote (B) has a nucleus, an endomembrane system, mitochondria and a cytoskeleton. Both share the same core machinery for information and energy.

Source: H Heuristics. Schematic; the two cells are not drawn to the same scale. Illustrative.

Beneath the differences lies a shared core. Every known cell uses DNA to store information, RNA to transmit it, ribosomes to translate it into proteins, the same 20 amino acids, a nearly identical genetic code, ATP as an energy currency and a lipid membrane across which ion gradients are maintained. This shared core is the strongest evidence for common ancestry. It also shows how conservative evolution is

with respect to the deepest layer of cellular architecture: once the core was established, changing it would have broken too many interdependent parts.

Figure 16 gives a sense of what a cell is made of, using the bacterium *Escherichia coli*, the best-studied organism. Proteins make up more than half of its dry mass, and RNA, mostly in ribosomes, about a fifth. A single cell contains about 2.4 million protein molecules, 22 million lipid molecules and about 19,000 ribosomes when growing fast. The quantitative study of such numbers, collected in resources such as [BioNumbers](#) and [Cell Biology by the Numbers](#), has become a field in its own right.

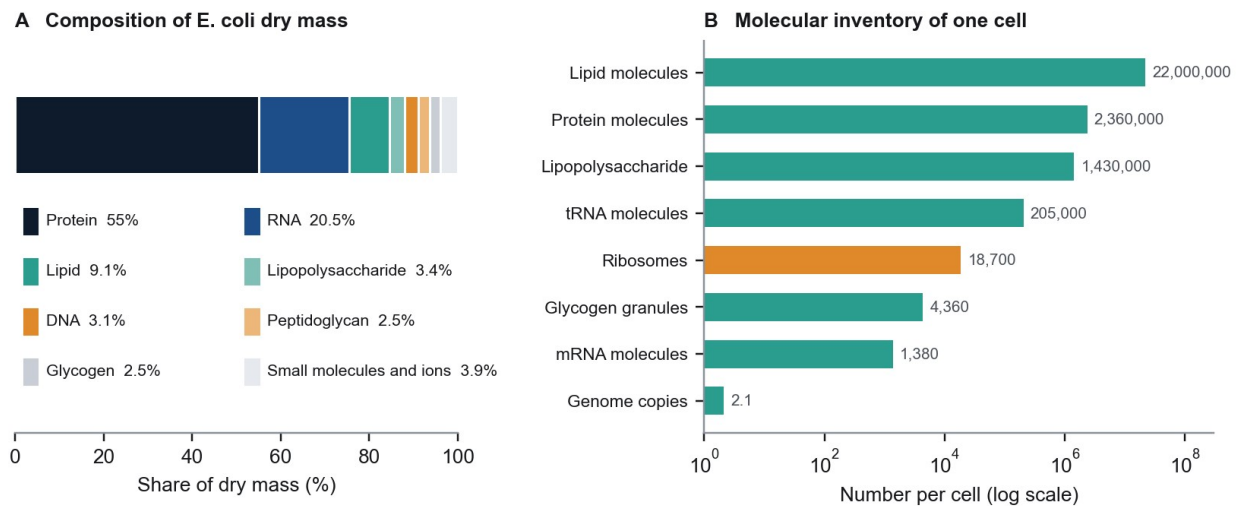


Figure 16. What a bacterial cell is made of. A: composition of the dry mass of *E. coli*. B: approximate number of molecules of each kind in one cell growing with a doubling time of about 40 minutes.

Source: Neidhardt and colleagues, *Physiology of the Bacterial Cell* (1990), as compiled in *BioNumbers*. Values vary with growth rate.

5.2 Membranes and the energy of gradients

The membrane is the cell's boundary and its power supply. Phospholipids, molecules with a water-loving head and two oily tails, assemble spontaneously in water into a bilayer about five nanometres thick that is nearly impermeable to ions. Proteins embedded in it act as pumps, channels, sensors and transporters. Because the membrane resists ion flow, energy can be stored as a difference in ion concentration and electrical charge across it.

Mitchell's chemiosmotic mechanism (Section 3.4) uses that stored energy. Electron-transport chains in the membrane use redox energy to pump protons out; ATP synthase lets them back in and uses the flow to make ATP. The proton-motive force across a bacterial membrane is typically 150 to 200 millivolts, which across a membrane five nanometres thick amounts to an electric field of about 30 million volts per metre. Every known cell uses chemiosmosis or a sodium-based variant, which suggests it was present in LUCA. Nick Lane and William Martin have argued that this universality reflects an origin in the natural proton gradients of hydrothermal vents ([Lane and Martin, 2012](#)); the argument is graded C.

Archaea and bacteria build their membranes from chemically different lipids, with mirror-image glycerol backbones and different tail chemistries. One interpretation is that LUCA did not yet have a modern lipid membrane and that the two domains evolved theirs independently. This 'lipid divide' is one of the puzzles any reconstruction of early cells must explain.

5.3 Metabolism as a network

A cell's metabolism is a network of a few thousand chemical reactions, each catalysed by an enzyme, that converts food into energy and building blocks. Its architecture has three recognisable features. First, a small core of central reactions, glycolysis, the citric acid cycle and the pentose phosphate pathway, produces 12 precursor metabolites from which almost all other cell components are built. Second, the network has a 'bow-tie' shape: many nutrients feed into the core, and many products flow out of it, so the core acts as a narrow waist. Third, a few metabolites, such as ATP, NADH and coenzyme A, participate in a large share of all reactions, so the network has a small number of highly connected hubs ([Jeong and colleagues, 2000](#); [Ravasz and colleagues, 2002](#)).

Each feature has a functional interpretation. The core is old and conserved because everything depends on it. The bow-tie lets a cell switch food sources without rebuilding its biosynthesis. Hub metabolites act as common currencies that couple energy-releasing and energy-requiring reactions, in the same way that money couples transactions in an economy. Whether these features are optimal or simply the outcome of history is debated, but they recur across all domains of life (Grade A for the structure; B for its interpretation).

5.4 Biological information: storage, transmission and expression

The flow of information in a cell, often summarised as the central dogma, runs from DNA to RNA to protein (Figure 17). DNA stores information in a sequence of four bases, which pair specifically, A with T and G with C, so that each strand carries the information to rebuild the other. Transcription copies a gene into messenger RNA. The ribosome reads the messenger RNA three bases at a time and adds the corresponding amino acid to a growing chain, which then folds into a protein. Some RNAs are not translated but act directly, as parts of the ribosome or as regulators.

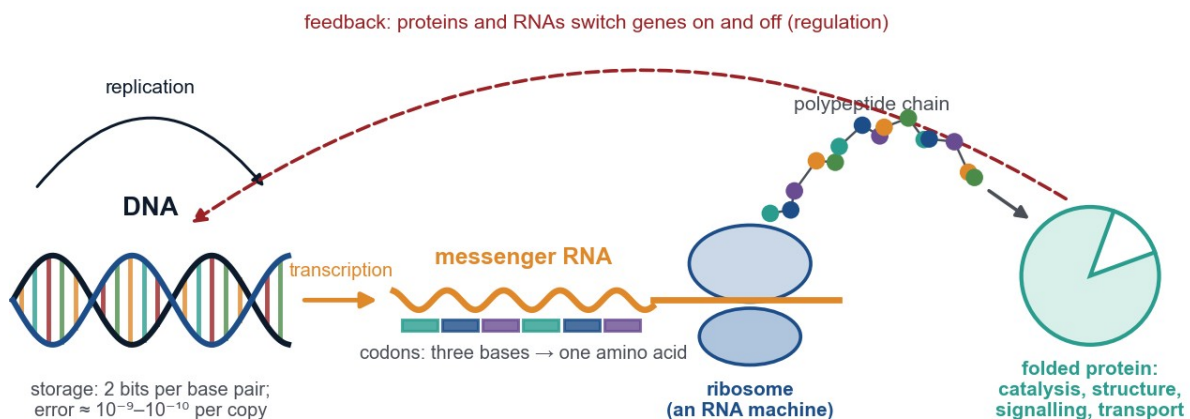


Figure 17. The flow of information in the cell. DNA is copied by replication and transcribed into messenger RNA; ribosomes translate the RNA into a chain of amino acids that folds into a functional protein. Proteins and RNAs in turn regulate which genes are expressed, closing a feedback loop.

Source: *H Heuristics*, after Crick (1970). Illustrative; not to scale.

The information content of genomes is large but finite. The human genome has about 3.1 billion base pairs, or about 6.2 billion bits, but most of it does not code for proteins; the roughly 20,000 protein-coding genes occupy about 1.5 per cent. The *E. coli* genome has 4.6 million base pairs and about 4,300 genes.

Genome size does not track organismal complexity: some amoebae and lungfish have genomes many times larger than ours, a pattern known as the [C-value paradox](#), which Michael Lynch and John Conery attributed largely to the weakness of selection against extra DNA in small populations ([Lynch and Conery, 2003](#)).

Fidelity has a price

Each step in the information flow has a characteristic error rate, shown in Figure 18. DNA replication is the most accurate: polymerases select the right base about 99,999 times in 100,000, proofreading improves this by about a hundredfold, and mismatch repair by about a hundredfold more, giving net error rates of around one in a billion to one in ten billion bases per copy ([Kunkel, 2004](#)). Transcription and translation are much less accurate, with errors of around one in 10,000 to one in a million for transcription and one in 1,000 to one in 10,000 for translation. The difference makes sense: an error in DNA is inherited by every descendant, whereas an error in one protein molecule affects only that molecule.

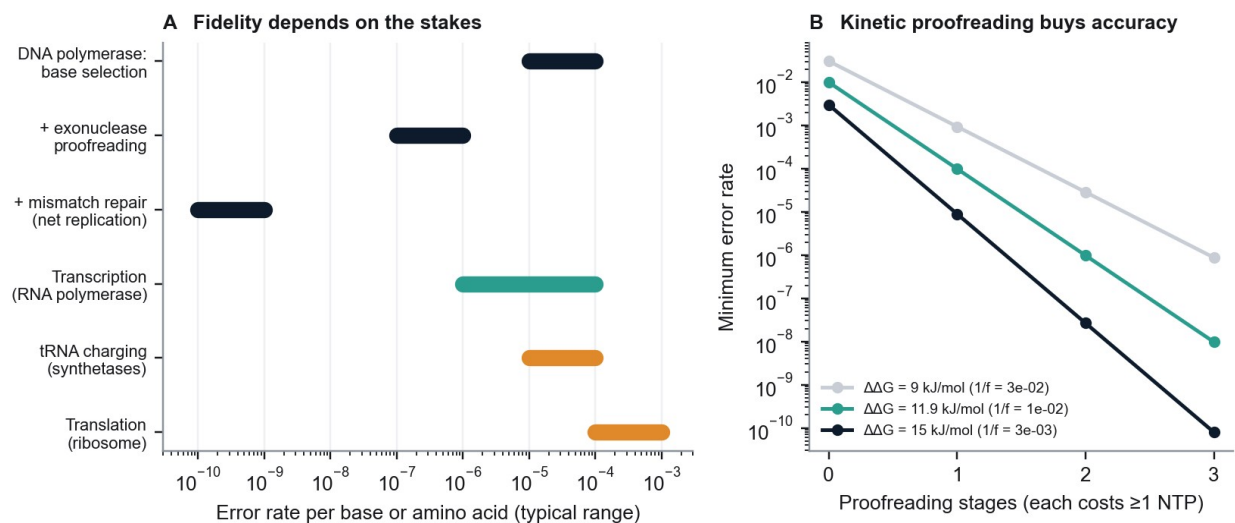


Figure 18. The accuracy of biological information transfer. A: typical error rates at each step, with DNA replication orders of magnitude more accurate than transcription or translation. B: Hopfield's kinetic proofreading; each additional proofreading step, paid for with the hydrolysis of a nucleotide triphosphate, multiplies accuracy by the basic discrimination factor.

Source: Panel A, ranges from Kunkel (2004) and reviews of transcriptional and translational fidelity. Panel B, H Heuristics calculation of the Hopfield (1974) limit, $\text{error} = f^{m+1}$, with $f = \exp(\Delta\Delta G/RT)$ at 37 °C.

How can a polymerase discriminate so well when the energy difference between correct and incorrect base pairs is small? John Hopfield showed in 1974 that cells buy accuracy with energy. If a step that discriminates by a factor f is followed by an irreversible, energy-consuming step that gives the enzyme a second chance to reject a wrong substrate, accuracy rises to f squared, and with m such steps to f^{m+1} ([Hopfield, 1974](#)). Kinetic proofreading is an example of a general principle that recurs in this report: maintaining information against noise costs free energy.

The genetic code is not arbitrary

The genetic code assigns 64 three-base codons to 20 amino acids and a stop signal. Francis Crick once described it as a 'frozen accident', an assignment that was fixed early and could not later change. But the code has a striking structure: codons that differ by one base usually encode the same amino acid or a chemically similar one, so that many point mutations and translation errors are harmless or mild. To test how unusual this is, this report compared the standard code with one million random codes that keep the

same block structure but shuffle which amino acid goes with which block, as in [Haig and Hurst \(1991\)](#). Each code was scored by the mean squared change in amino-acid polarity, measured by Woese's polar requirement, caused by all possible single-base substitutions.

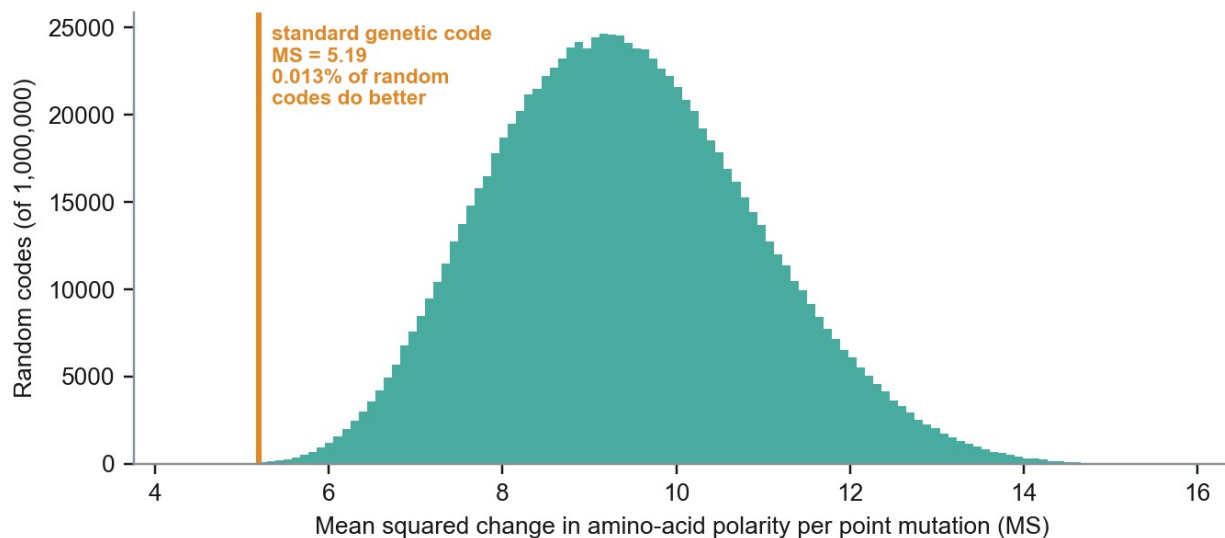


Figure 19. How well the genetic code buffers mutations. The distribution shows the error score of one million random genetic codes with the same block structure as the standard code; lower scores mean point mutations cause smaller changes in amino-acid polarity. Only 131 random codes, about one in 7,600, score better than the standard code.

Source: H Heuristics calculation following Haig and Hurst (1991) and Freeland and Hurst (1998), using Woese's polar requirement scale. All single-base substitutions between sense codons weighted equally.

The result, in Figure 19, is that only about one in 7,600 random codes does better. When the calculation is refined to weight the kinds of error that are commonest in practice, [Freeland and Hurst \(1998\)](#) found the standard code better than about a million in a million random alternatives. Whether the code was shaped by selection for error minimisation, by the chemistry of early codon–amino acid interactions or by the order in which amino acids were added is still debated (Grade B for the optimality; C for its cause). Either way, the code illustrates the interplay of constraint, generation and filtering: chemistry constrains the possible assignments, history generated the candidates, and selection filtered out codes in which errors were more damaging.

5.5 Regulation and feedback

A cell does not express all its genes all the time. Gene regulatory networks, in which transcription factors switch genes on and off, decide which proteins are made, in what amounts and when. Uri Alon and colleagues found that these networks are built from a small set of recurring circuits, called network motifs, that appear far more often than in random networks ([Milo and colleagues, 2002](#); [Alon, 2007](#)). Each motif performs a recognisable function.

Figure 20 shows two of them, simulated for this report. In negative autoregulation, a protein represses its own gene. That lets the cell switch the gene on at full strength and then brake it near the target level, so the protein reaches half its final level about six times faster than with simple regulation, 0.11 compared with 0.70 protein lifetimes in the simulation. The speed-up was confirmed experimentally by [Rosenfeld, Elowitz and Alon \(2002\)](#). In the second circuit, three repressors inhibit each other in a ring. Michael

Elowitz and Stanislas Leibler built this 'repressilator' into *E. coli* in 2000 and showed that it oscillates ([Elowitz and Leibler, 2000](#)), a founding result of synthetic biology.

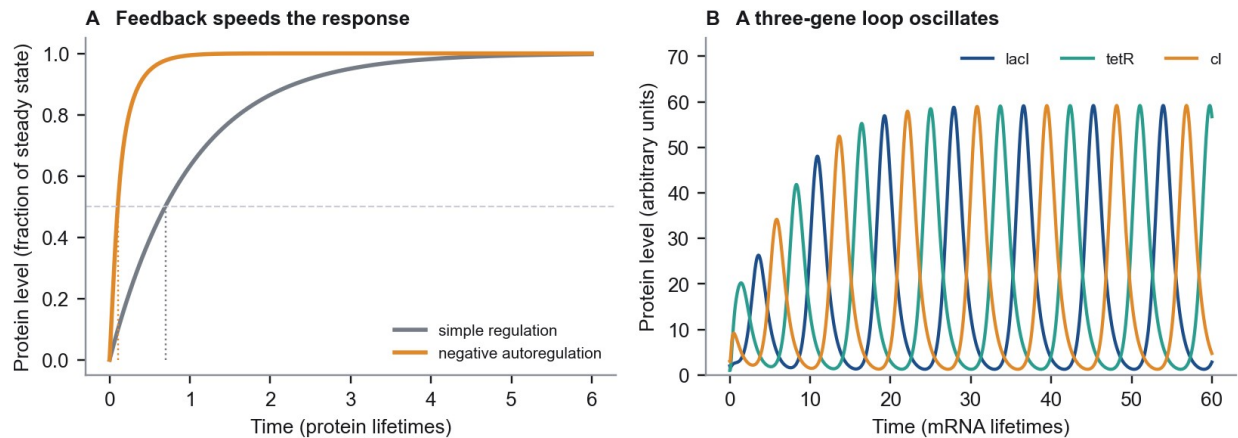


Figure 20. Feedback in gene regulation. A: negative autoregulation, in which a protein represses its own production, reaches its steady level much faster than simple regulation with the same final level. B: three genes that repress each other in a ring produce sustained oscillations, as in the synthetic repressilator.

Source: H Heuristics simulation. Panel A, $dx/dt = \beta/(1 + (x/K)^4) - x$ versus $dx/dt = 1 - x$; panel B, the dimensionless repressilator model of Elowitz and Leibler (2000) with $\alpha = 216$, $\alpha_0 = 0.216$, $\beta = 5$, $n = 2$.

Feedback is everywhere in the cell. Negative feedback holds concentrations near set points and speeds responses; positive feedback creates switches that commit a cell to one fate or another; delayed negative feedback produces oscillations, including the circadian clocks found in organisms from cyanobacteria to people. These are the same dynamical motifs that recur in ecosystems and in the climate system (Sections 8 and 10), which is why feedback is graded as a shared principle across scales in Section 11.

5.6 How simple can a cell be?

In 2016 the J. Craig Venter Institute reported JCVI-syn3.0, a bacterium with a synthetic genome reduced to 473 genes, the smallest genome of any self-replicating organism grown in the laboratory ([Hutchison and colleagues, 2016](#)). It was built by stripping genes from a previous synthetic genome derived from *Mycoplasma mycoides* ([Gibson and colleagues, 2010](#)). Most of the retained genes deal with expressing and preserving genetic information, building the membrane and running a pared-down metabolism; strikingly, 149 genes, nearly a third, had unknown functions when the work was published. The minimal cell depends on a rich growth medium that supplies many building blocks, so a free-living cell in the wild would need more. The lesson is that even the simplest cell is complex, and that the gap between the most elaborate prebiotic chemistry and the simplest living cell is very large.

5.7 Size, scaling and the pace of life

Physical scaling constrains cells and organisms. A cell's surface area grows with the square of its size but its volume with the cube, so a large cell has less membrane per unit of cytoplasm through which to exchange nutrients and waste. Diffusion is fast over a micrometre but slow over a millimetre. Prokaryotes are small partly because their energy is generated at the outer membrane. Eukaryotes escaped this limit by internalising their energy-generating membranes in mitochondria, which, Lane and Martin argued, gave them orders of magnitude more energy per gene and made large genomes and complex cells

affordable ([Lane and Martin, 2010](#)). The size of the advantage is debated ([Lynch and Marinov, 2015](#)), but the role of mitochondria in eukaryotic complexity is widely accepted (Grade B).

At the level of whole organisms, metabolic rate scales with body mass with a remarkable regularity first described by Max [Kleiber \(1932\)](#):

$$B \approx B_0 M^{3/4} \quad (7)$$

With B in watts and M in kilograms, B_0 is about 3.4 for mammals. Figure 21 shows the consequences. A 25-gram mouse runs at about 0.2 watts and a 70-kilogram person at about 80 watts; a 4-tonne elephant needs about 1.7 kilowatts, far less than 160,000 mice of the same total mass. Per kilogram, the mouse burns energy 20 times faster than the elephant, and its heart rate, breathing rate and lifespan scale accordingly. Geoffrey West, James Brown and Brian Enquist proposed that the three-quarter exponent arises from the geometry of space-filling branching networks such as blood vessels ([West, Brown and Enquist, 1997](#)). The explanation, and whether the exponent is exactly three-quarters, remain debated (Grade A for the approximate relationship; C for its explanation).

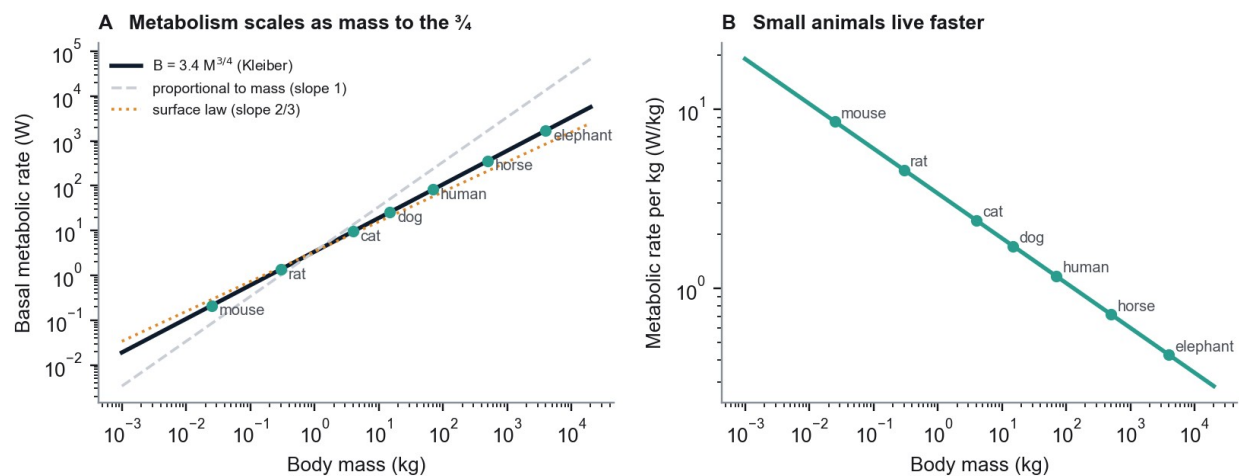


Figure 21. Metabolic scaling. A: basal metabolic rate of mammals rises as the three-quarter power of body mass, between proportionality and a surface-area law. B: metabolic rate per kilogram therefore falls with size, so small animals live faster.

Source: H Heuristics calculation from Kleiber's relation $B = 3.4 M^{0.75} W$. Reference animals are placed on the fitted relation; measured values scatter around it by tens of per cent.

06

PART IV · EVOLUTION

6. Evolution as a Generative Process

Part IV examines the engine that turned the first cells into the living world: variation, heredity, natural selection, drift, symbiosis and ecological interaction. Evolution is often described as a filter, natural selection removing the unfit. This section argues that it is better understood as a full creation structure in which generators and filters are equally important, and in which the products of evolution change the process itself.

6.1 The algorithm

Charles Darwin's [On the Origin of Species](#) (1859) set out an argument that Richard Lewontin later condensed into three conditions ([Lewontin, 1970](#)). If individuals in a population vary in some trait, if that variation affects survival or reproduction, and if the trait is heritable, then the population will change over generations, with the traits that improve reproduction becoming commoner. The argument is general. It applies to any population of entities that meet the three conditions, whether genes, cells, organisms, viruses or, in modified form, cultural practices.

George Price gave the argument an exact mathematical form. For any trait z , the change in its average value from one generation to the next is

$$\bar{w} \Delta \bar{z} = \text{Cov}(w, z) + E(w \Delta z) \quad (8)$$

where w is fitness, the number of offspring. The first term is selection: the trait increases if it covaries with fitness. The second is transmission: the change in the trait between parent and offspring, including mutation and developmental noise. Equation 8 is an identity, not a hypothesis; its value lies in partitioning change into its causes, and in applying at any level, from genes within a cell to groups within a population ([Price, 1970](#)).

6.2 The generators: sources of variation

Selection can act only on variation that exists. The generators of variation are more diverse than the textbook image of random point mutation suggests (Table 9).

Table 9. Generators of heritable variation

Generator	What it does	Typical rate or scale	Evolutionary role
Point mutation	Changes a single base	About 10^{-10} to 10^{-8} per base per generation in DNA organisms	Fine-tuning; raw material for all change
Recombination and sex	Shuffles existing variants into new combinations	One or more crossovers per chromosome per meiosis	Combines beneficial mutations; removes harmful ones
Horizontal gene transfer	Moves genes between unrelated organisms	Common in prokaryotes; a large share of genes in many bacterial genomes	Rapid acquisition of new functions, such as antibiotic resistance
Gene duplication	Copies a gene, freeing one copy to change	About 0.01 per gene per million years in many animals	Origin of new gene families
Regulatory change	Alters when and where genes are expressed	Frequent; often small effects	Changes in form during development
Symbiosis and merger	Combines whole lineages	Rare but transformative	Mitochondria, plastids, lichens, corals
Transposable elements	Mobile DNA that copies itself into new locations	About half of the human genome derives from them	Raw material for regulatory and genomic innovation

Source: H Heuristics, from standard evolutionary genetics texts and the studies cited in this section. Rates are order-of-magnitude.

The generators are not neutral with respect to form. Development channels genetic changes into a limited range of outcomes: some changes in form are easy to produce and others almost impossible. Marc Kirschner and John Gerhart called this capacity to generate useful variation 'evolvability' and argued that it is itself shaped by evolution, through modular body plans, weak regulatory linkages and robust core processes ([Kirschner and Gerhart, 1998](#)). François Jacob described evolution as a [tinkerer](#) rather than an engineer: it builds new structures by modifying old ones, which is why the same genes and proteins are reused in very different roles across the tree of life.

6.3 The filters: selection and drift

The fate of a new mutation depends on two forces. Selection favours mutations that increase reproduction and removes those that decrease it. Genetic drift, the random sampling of which individuals happen to reproduce, changes frequencies regardless of effect. Their relative strength is set by the product of population size N and selection coefficient s . Motoo Kimura derived the probability that a single new mutation eventually spreads through the whole population:

$$u = (1 - e^{-2s}) / (1 - e^{-2Ns}) \quad (9)$$

for a haploid population ([Kimura, 1962](#)). A neutral mutation fixes with probability $1/N$. A beneficial mutation with $s = 0.01$ in a population of 100 fixes with probability about 0.023, only twice the neutral value; most beneficial mutations are lost by chance while still rare. Figure 22 confirms equation 9 by direct simulation for this report.

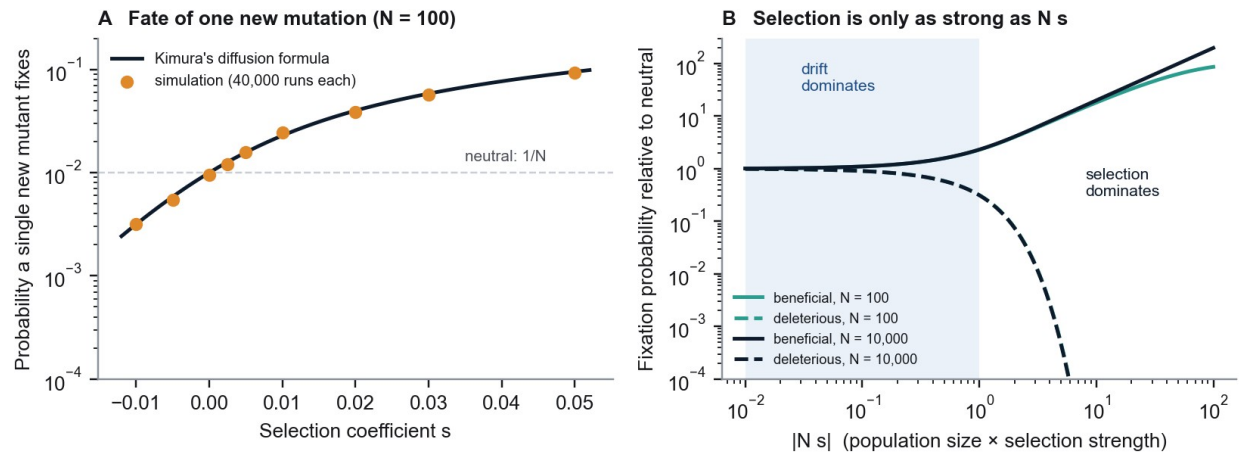


Figure 22. Selection and drift. A: probability that a single new mutation spreads through a population of 100, from simulation and from Kimura's formula. B: the same probability relative to the neutral value, as a function of $N \cdot s$. When $|N s|$ is below about 1, drift dominates and harmful mutations can spread; when it is above about 1, selection dominates.

Source: H Heuristics Wright–Fisher simulation, 40,000 replicate populations for each selection coefficient, compared with Kimura (1962).

Panel B of Figure 22 shows a principle with wide consequences. When $|N s|$ is much less than one, a mutation behaves almost neutrally, whether its effect is good or bad. Kimura's [neutral theory](#) and Tomoko Ohta's [nearly neutral theory](#) built on this to explain why much molecular evolution proceeds at a steady clock-like rate. Michael Lynch has argued that small population sizes in large multicellular organisms weakened selection enough to let genomes accumulate introns, mobile elements and regulatory complexity that would have been purged in bacteria ([Lynch, 2007](#)). If so, some of the complexity of animal and plant genomes is a consequence of weak selection, not of strong selection for complexity (Grade B to C).

6.4 Fitness landscapes

Sewall Wright pictured evolution as movement on a [fitness landscape](#), a map from genotypes to fitness on which populations climb toward peaks. The shape of the landscape depends on epistasis, the extent to which the effect of one mutation depends on others. Stuart Kauffman's NK model captures this with N genes, each of whose fitness contribution depends on its own state and on K others ([Kauffman and Levin, 1987](#)).

Figure 23 shows the model computed exactly for this report, with 14 genes and therefore 16,384 genotypes. With $K = 0$, genes act independently and there is one peak, which any uphill walk reaches in about seven steps. As K rises, the landscape becomes rugged: with $K = 4$ there are about 80 peaks, and with $K = 13$, the maximum, about 1,100. Uphill walks become short, ending after about one and a half steps on a nearby local peak, and the average height of the peaks reached falls. Modest epistasis gives the highest peaks reached; very high epistasis gives a 'complexity catastrophe' in which selection becomes ineffective at finding good solutions.

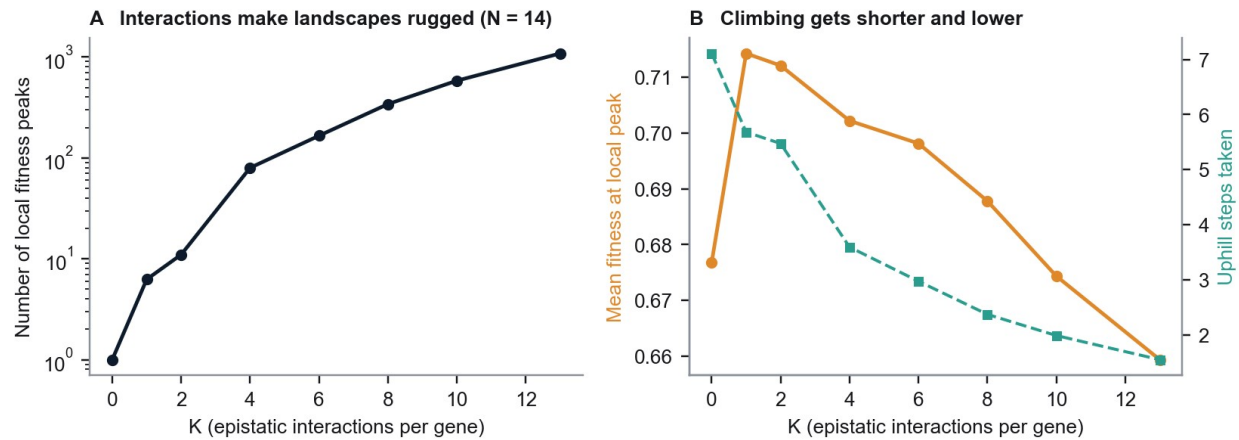


Figure 23. Rugged fitness landscapes in the NK model. A: number of local fitness peaks among 16,384 genotypes rises steeply with the number of interactions per gene. B: adaptive walks reach peaks after fewer steps, and the peaks reached are lower on average once interactions are strong.

Source: H Heuristics exact computation of NK landscapes with $N = 14$; four random landscapes per K and 200 greedy adaptive walks per landscape.

Real landscapes are mapped experimentally by constructing all combinations of a few mutations. [Weinreich and colleagues \(2006\)](#) showed that of the 120 possible orders in which five mutations could produce a highly antibiotic-resistant enzyme, only 18 are accessible by steps that each increase resistance. Epistasis thus makes evolution partly predictable, by restricting the paths available, and partly contingent, by making the outcome depend on which mutations happened first.

6.5 Evolution observed

Evolution is not only inferred from the past; it is observed. The longest-running experiment is Richard Lenski's Long-Term Evolution Experiment, in which 12 populations of *E. coli* have been propagated in a glucose-limited medium since 1988, now for more than 75,000 generations. Samples frozen every 500 generations allow ancestors and descendants to be competed directly. Fitness has risen throughout. [Wiser, Ribeck and Lenski \(2013\)](#) found that the trajectory over the first 50,000 generations is described by a power law with no upper bound, not by a curve that approaches a ceiling.

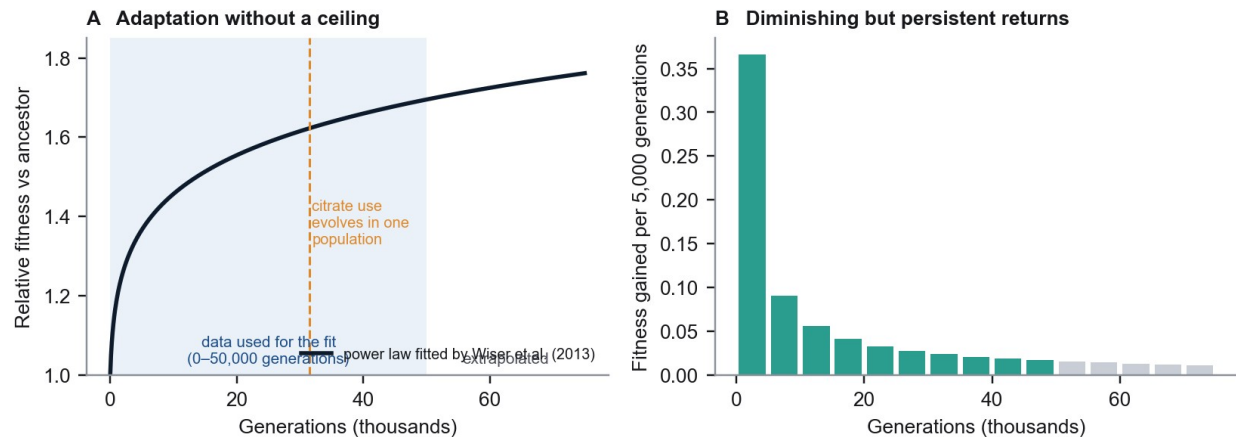


Figure 24. Open-ended adaptation in the Long-Term Evolution Experiment. A: fitness relative to the ancestor follows a power law with no asymptote; at 50,000 generations it is about 1.70. B: gains per 5,000 generations fall steadily but never reach zero. Around 31,500 generations one population evolved the ability to use citrate, a novel function.

Source: *H Heuristics*, plotting the power-law model $w = (b t + 1)^a$ with $a = 0.0950$ and $b = 0.00515$ fitted by Wisser, Ribeck and Lenski (2013) to 0–50,000 generations; beyond 50,000 generations the curve is an extrapolation. Citrate innovation from Blount, Borland and Lenski (2008).

Figure 24 shows the fitted curve. The gain in the first 5,000 generations was about 0.37; the gain between 45,000 and 50,000 generations was about 0.017, more than 20 times smaller but still positive. In one population, a qualitatively new ability appeared: around generation 31,500 it evolved the capacity to use citrate, present in the medium but unusable by the ancestor in the presence of oxygen ([Blount, Borland and Lenski, 2008](#)). Replaying that population from frozen samples showed that the innovation depended on earlier, apparently neutral mutations, an experimental demonstration of historical contingency.

Outside the laboratory, evolution is observed in antibiotic and pesticide resistance, in the beaks of Darwin's finches across wet and dry years, in the colour of peppered moths, and in viruses such as influenza and SARS-CoV-2, whose evolution is tracked in real time by genome sequencing (Grade A).

6.6 Symbiosis and the shape of the tree

The tree of life is not purely a tree. Lynn Margulis argued in 1967 that mitochondria and chloroplasts descend from free-living bacteria engulfed by other cells ([Sagan, 1967](#)). The idea was resisted but is now established: both organelles have their own small circular genomes, bacterial-type ribosomes and double membranes, and their genes place them within the alphaproteobacteria and cyanobacteria respectively ([Archibald, 2015](#)).

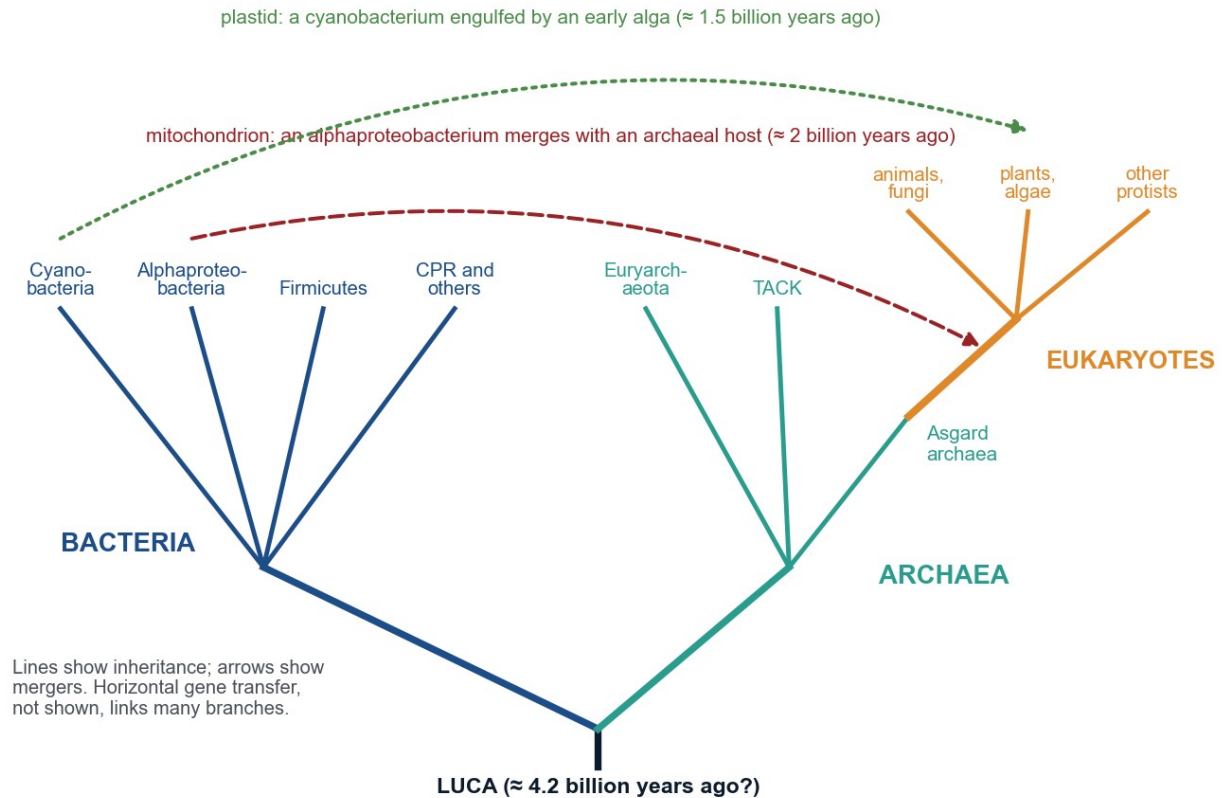


Figure 25. The tree of life with its two great mergers. Life divides into bacteria and archaea. Eukaryotes arose from within the Asgard archaea after a merger with an alphaproteobacterium that became the mitochondrion; plants and algae arose after a later merger with a cyanobacterium that became the plastid.

Source: *H Heuristics*, after Hug and colleagues (2016), Spang and colleagues (2015) and Eme and colleagues (2023). Branch lengths and dates are schematic.

Carl Woese's sequencing of ribosomal RNA revealed in 1977 that prokaryotes comprise two deeply separate groups, the bacteria and the archaea ([Woese and Fox, 1977](#); [Woese, Kandler and Wheelis, 1990](#)). Since 2015, discoveries of the Asgard archaea, first from environmental DNA and then in culture, have shown that eukaryotes emerged from within the archaea, as shown in Figure 25 ([Spang and colleagues, 2015](#); [Imachi and colleagues, 2020](#); [Eme and colleagues, 2023](#)). The eukaryotic cell is therefore a chimera of an archaeal host and a bacterial partner. The most complex cell type on Earth arose not by gradual elaboration of one lineage but by merger, a generator of variation unavailable to cosmic structures.

Horizontal gene transfer adds a network of cross-links to the tree, especially among prokaryotes. Genomic surveys such as that of [Hug and colleagues \(2016\)](#) have also revealed that most of life's genetic diversity is microbial and that a large share belongs to lineages known only from their DNA.

6.7 The major transitions

John Maynard Smith and Eörs Szathmáry identified a series of major transitions in evolution in which entities that could reproduce independently came to reproduce only as part of a larger whole, and in which new ways of storing and transmitting information arose ([Szathmáry and Maynard Smith, 1995](#)). Figure 26 lists them.

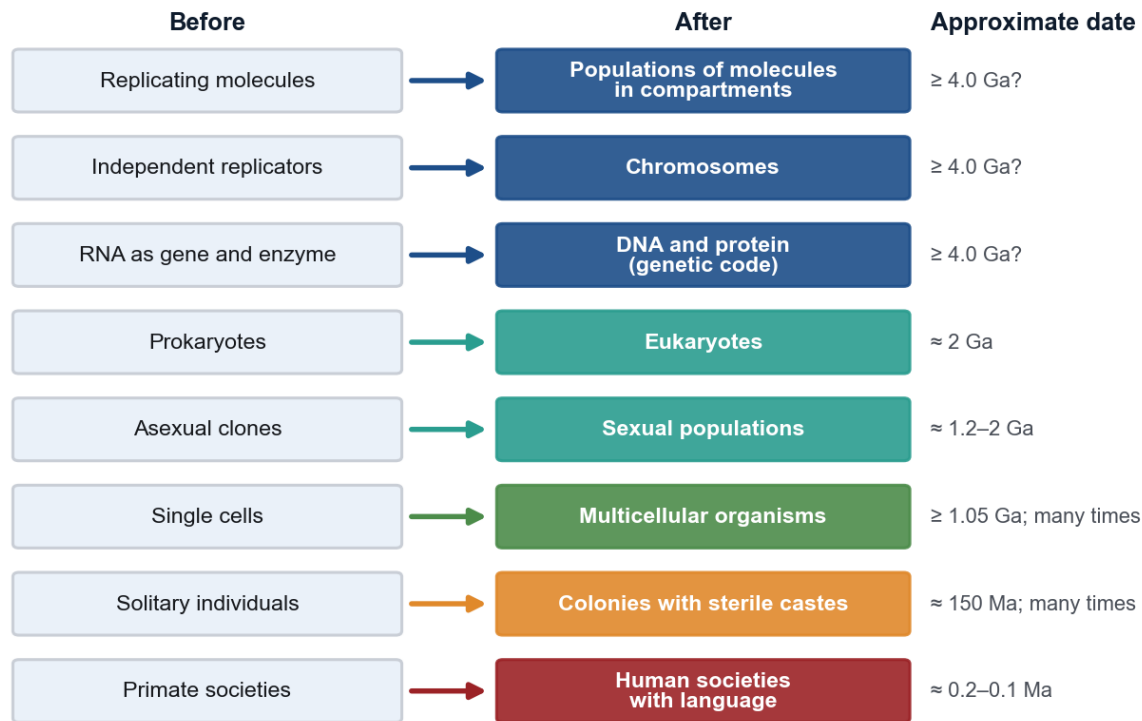


Figure 26. The major transitions in evolution. In each, previously independent units became parts of a new, higher-level individual, or a new system for storing and transmitting information arose. Several transitions happened more than once.

Source: *H Heuristics*, after Maynard Smith and Szathmáry (1995). Dates are approximate; the first three are inferred, not observed.

The transitions share a common logic. Each required the lower-level units to cooperate, which created an opportunity for cheats: a gene that replicates without contributing to the cell, a cell that proliferates without contributing to the body, a worker that lays her own eggs. Each was stabilised by mechanisms that align the interests of the parts with those of the whole. Compartments did this for early genes (Section 4.5), chromosomes linked genes so that they replicated together, a single-cell bottleneck at the start of each generation does it for multicellular organisms (Section 7.2), and sterile castes and policing do it for social insect colonies. Recognising this common logic is one of the strongest arguments for a general architecture of life: the same problem, conflict between levels, is solved repeatedly with recognisably similar mechanisms (Grade B).

6.8 Contingency and convergence

If the tape of life were replayed, would the outcome be similar? Stephen Jay Gould argued that it would not, because history is shaped by unpredictable events such as mass extinctions. Simon Conway Morris argued that it would, because the same solutions evolve repeatedly. The evidence supports both, at different levels ([Blount, Lenski and Losos, 2018](#)).

- **Convergence is common for functions with strong physical constraints.** Camera-type eyes evolved separately in vertebrates and cephalopods. Echolocation evolved in bats and toothed whales. Streamlined bodies evolved in fish, ichthyosaurs and dolphins. C_4 photosynthesis evolved more than 60 times in plants. In each case physics leaves few good solutions.

- **Contingency is common for particular lineages and body plans.** No other lineage has evolved anything like a vertebrate skeleton, an insect's body or a human language. The particular species that exist reflect the survivors of particular extinctions.
- **The framework predicts this pattern.** Where constraints narrow the space of viable forms, different lineages converge on the same forms, as in the cosmic report's discs and spheres. Where the space is large, history decides which of many viable forms appears.

6.9 Does evolution make things more complex?

The largest organisms and the most complex cells, bodies and brains have appeared progressively later in the history of life. It is tempting to conclude that evolution drives life toward complexity. The evidence does not support a general drive. Daniel McShea's survey found no consistent trend in complexity within lineages ([McShea, 1996](#)). Many lineages have simplified, including parasites, which lose organs and genes, and the reduced genomes of endosymbiotic bacteria. Most life, by number of individuals and by number of species, remains microbial, and bacteria have not become more complex in any obvious way in billions of years.

A simpler explanation fits the evidence. Life began near a lower bound of complexity, below which nothing can live. Variation in both directions then spreads the distribution, and because it cannot spread below the lower bound, the maximum rises over time even if no lineage is pushed upward. Gould called this a passive trend, the 'left wall' effect. Some transitions, such as those that create new levels of individuality, do appear to be one-way, which may add a weak ratchet. But complexity is not the goal of evolution, and the framework makes no assumption that it is (Grade B).

07

PART V · MULTICELLULARITY

7. The Emergence of Multicellular Complexity

Part V examines how single cells became organisms composed of many differentiated cells. The transition requires cooperation, specialisation, communication and a developmental programme that builds a body from one cell each generation. It is a central test case for the framework, because it happened many times, independently, and so allows recurring principles to be distinguished from historical accidents.

7.1 Many origins

Multicellularity is not a single event. Richard Grosberg and Richard Strathmann counted at least 25 independent origins ([Grosberg and Strathmann, 2007](#)), and complex multicellularity, with many cell types and three-dimensional tissues, evolved at least six times: in animals, land plants, red algae, brown algae and two or more groups of fungi ([Knoll, 2011](#)). Simple multicellularity, such as filaments of cyanobacteria, appeared more than two billion years ago. The oldest well-dated complex multicellular organism, the red alga *Bangiomorpha*, is about 1.05 billion years old ([Gibson and colleagues, 2018](#)).

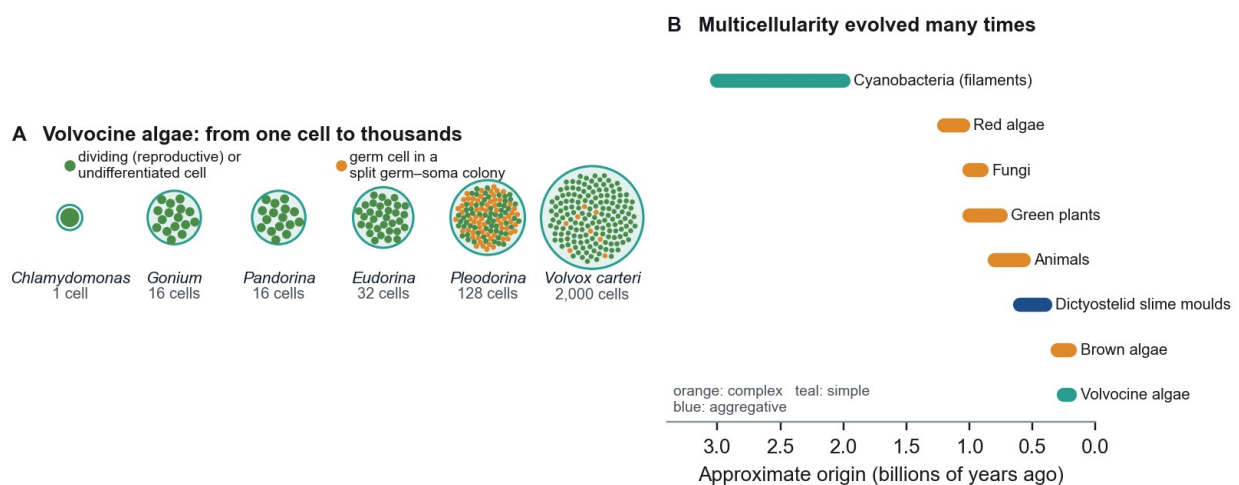


Figure 27. Multicellularity as a repeated transition. A: the volvocine green algae span single cells, colonies of identical cells and Volvox, with thousands of cells divided into a few reproductive germ cells and many sterile somatic cells. B: approximate times of origin of multicellularity in selected lineages.

Source: Panel A, H Heuristics illustration after Kirk (2005) and Herron and Michod (2008); cell numbers are typical values. Panel B, approximate ranges from Knoll (2011), Grosberg and Strathmann (2007) and the studies cited in the text; molecular-clock and fossil dates differ.

The volvocine green algae, shown in Figure 27, offer a living sequence of the steps involved. *Chlamydomonas* is a single cell. *Gonium* is a flat plate of 8 to 16 identical cells, each able to reproduce. *Eudorina* forms a sphere of 32. In *Pleodorina* some cells are small and sterile. *Volvox carteri* has a few thousand cells, of which only about 16 are germ cells; the rest are somatic cells that swim but never reproduce (Kirk, 2005). The lineage diverged from single-celled ancestors only about 200 million years ago (Herron and Michod, 2008).

Multicellularity can also evolve in the laboratory. William Ratcliff and colleagues selected brewer's yeast for rapid settling to the bottom of a tube, which favours large clusters. Within 60 days, 'snowflake' clusters evolved in which daughter cells stay attached to their mothers, and the clusters soon evolved a division of labour in which some cells die to release offspring clusters (Ratcliff and colleagues, 2012). The repeated, rapid and experimentally reproducible emergence of multicellularity shows that the transition is not improbable once the right ecological conditions arise (Grade A).

7.2 Cooperation and the problem of cheats

A multicellular organism is a society of cells that has largely suppressed conflict. Somatic cells give up reproduction to support germ cells, and the arrangement is stable because the cells of a body are genetically identical: by Hamilton's rule (equation 4), with relatedness $r = 1$, any cost to a somatic cell that brings a larger benefit to the germ line is favoured. Most complex multicellular organisms pass through a single-cell bottleneck, the fertilised egg or spore, at the start of each generation, which resets relatedness to one and purges any cheating lineage that arose in the previous generation.

Where relatedness is lower, cooperation is more fragile. In the social amoeba *Dictyostelium discoideum*, thousands of free-living cells aggregate when starved to form a fruiting body, in which about a fifth of the cells die to form a stalk that lifts the others as spores. Because aggregating cells can come from different genetic lineages, cheater strains that contribute less to the stalk evolve readily. Aggregative multicellularity has arisen several times but has never produced complex organisms, consistent with the view that clonal development is needed to suppress conflict at scale (Grade B).

Box 7.1 Cancer as a breakdown of multicellular cooperation. Cancer occurs when cells escape the controls that keep them cooperating: they divide without signals, ignore signals to stop, evade programmed cell death, recruit blood supply and invade other tissues. From the framework's perspective, cancer is selection at the level of cells overriding selection at the level of the organism. Bodies counter it with layered defences, including tumour-suppressor genes, limits on cell division and immune surveillance. Larger, longer-lived animals have more cells at risk, yet whales and elephants do not have higher cancer rates than mice, a puzzle known as Peto's paradox; elephants, for example, carry about 20 copies of the tumour suppressor gene TP53.

7.3 Division of labour

Once cells cooperate, specialisation becomes advantageous. A cell that both swims and divides does both less well than two cells that each do one. Theoretical work by Richard Michod and others shows that specialisation is favoured when the trade-off between functions is convex, so that a specialist is more than twice as good at its task as a generalist that splits its effort. Larger groups favour more specialisation, which is consistent with the correlation between colony size and germ–soma differentiation in the volvocine algae.

The number of cell types is a rough measure of organismal complexity. Sponges have perhaps a dozen, fruit flies dozens and humans several hundred; the Tabula Sapiens atlas, built by sequencing the RNA of individual cells, catalogued more than 400 types across 24 human organs ([Tabula Sapiens Consortium, 2022](#)). Detlev Arendt has argued that cell types evolve like species, by duplication and divergence of the gene regulatory programmes that define them ([Arendt, 2008](#)).

7.4 Communication and adhesion

A multicellular body needs cells that stick together and talk to each other. Many of the genes for adhesion and signalling that animals use predate animals. The genome of the choanoflagellate *Monosiga brevicollis*, a single-celled relative of animals, contains cadherins, receptor tyrosine kinases and other proteins once thought to be specific to multicellular animals ([King and colleagues, 2008](#)). The transition to animal multicellularity thus involved co-opting existing tools for new purposes, a clear example of Jacob's tinkering ([Brunet and King, 2017](#)).

Cells communicate by secreted molecules, by contact between membrane proteins, by electrical coupling through gap junctions and by mechanical forces. A handful of signalling pathways, among them Wnt, Hedgehog, Notch, TGF- β and receptor tyrosine kinases, account for most cell-to-cell communication during animal development and are shared by all animals with differentiated tissues.

7.5 Development: building a body from one cell

Development turns a single fertilised cell into an organism with a reproducible form. It relies on three main mechanisms. First, gradients of signalling molecules called morphogens give cells positional information: a cell reads the local concentration and adopts a fate accordingly, an idea formalised by Lewis Wolpert as the [French flag model](#). Second, gene regulatory networks convert these signals into stable cell states, often through positive feedback loops that lock in a decision. Third, self-organising processes generate pattern from initially uniform conditions.

The third mechanism was proposed by Alan Turing in 1952. He showed that two chemicals that react and diffuse at different rates can spontaneously form stable spots or stripes from an almost uniform starting state, if a short-range activator is combined with a longer-range inhibitor ([Turing, 1952](#)). For decades the idea was a mathematical curiosity, but Turing-type mechanisms have now been implicated in the stripes of tropical fish ([Kondo and Asai, 1995](#)), the spacing of hair follicles and feathers, and the ridges of the palate. Figure 28 shows the range of patterns a single reaction-diffusion model produces as two parameters change.

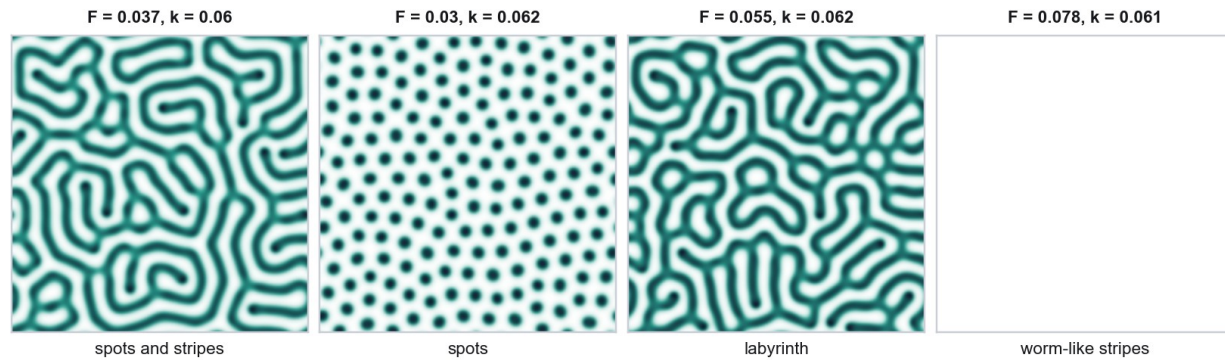


Figure 28. Turing patterns. The same pair of reaction-diffusion equations, started from nearly uniform conditions with small random perturbations, produces spots, stripes or labyrinths depending on the feed rate F and removal rate k . Similar mechanisms pattern skin, hair follicles and feathers.

Source: H Heuristics simulation of the Gray–Scott model on a 160×160 grid, 9,000 time steps, diffusion rates 0.16 and 0.08. The cover image uses the same model.

The development of animals is coordinated by a conserved set of regulatory genes. The Hox genes, discovered in fruit flies by Edward Lewis, specify the identity of body segments along the head-to-tail axis ([Lewis, 1978](#)). Similar genes, arranged in the same order on the chromosome and expressed in the same order along the body, pattern the axes of vertebrates. The discovery that animals as different as flies and mice use a shared genetic toolkit, and that evolution changes form mainly by changing when and where toolkit genes are switched on, is the central result of evolutionary developmental biology ([Carroll, 2008](#)).

7.6 The Cambrian and the origin of body plans

Large animals appear in the fossil record with the Ediacaran biota about 575 million years ago, and most major animal groups appear during the Cambrian, between about 539 and 515 million years ago. The suddenness of this radiation has been debated since Darwin. Current explanations combine several factors ([Erwin and colleagues, 2011](#)): rising oxygen in the late Neoproterozoic (Section 10.2), which allowed larger and more active bodies; the prior evolution of the developmental toolkit; and ecological feedbacks once predators, burrowers and eyes appeared, which created new filters and new opportunities. Molecular clocks place the origins of many animal lineages earlier than their first fossils, implying a period of cryptic evolution among small, soft-bodied animals (Grade B).

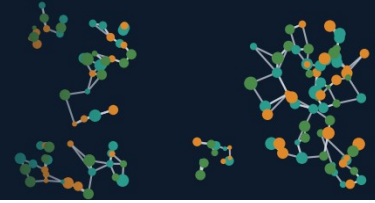
Table 10. Requirements for complex multicellularity and how they were met

Requirement	Problem	Typical solution	Shared across lineages?
Adhesion	Cells must stay together	Cell walls (plants, algae, fungi); adhesion proteins (animals)	Function shared; mechanisms differ
Communication	Cells must coordinate	Secreted signals; contact signalling; plasmodesmata in plants	Function shared; toolkits largely lineage-specific
Conflict suppression	Cheating cells must not spread	Single-cell bottleneck; early germ-line separation; programmed death	Bottleneck widely shared
Division of labour	Specialised cells must be produced reliably	Gene regulatory networks that stabilise cell types	Logic shared; genes differ
Patterning	Cells must adopt fates by position	Morphogen gradients; reaction-diffusion; mechanical cues	Mechanisms recur
Transport	Large bodies need internal supply	Vascular systems in plants and animals; diffusion in thin forms	Branching geometry recurs

Source: *H Heuristics*, from Knoll (2011), Grosberg and Strathmann (2007) and Brunet and King (2017).

08

PART VI · ECOSYSTEMS



8. The Architecture of Ecosystems

Part VI rises above the organism to communities and ecosystems: food webs, nutrient cycles, population dynamics, succession, biodiversity, interdependence and the feedback relationships connecting organisms to their environments. Ecosystems are not organisms; they do not reproduce as units and are not shaped by selection in the same way. The question is which principles of organisation still apply at this level.

8.1 Energy through food webs

Almost all ecosystems run on sunlight captured by photosynthesis. Producers convert light into chemical energy; herbivores eat producers; carnivores eat herbivores; decomposers recycle the dead of every level. Raymond Lindeman described this flow in 1942 and observed that only a fraction of the energy at one level reaches the next ([Lindeman, 1942](#)). Transfer efficiencies typically lie between 5 and 20 per cent, with about 10 per cent a common rule of thumb; the rest is used in respiration or not eaten.

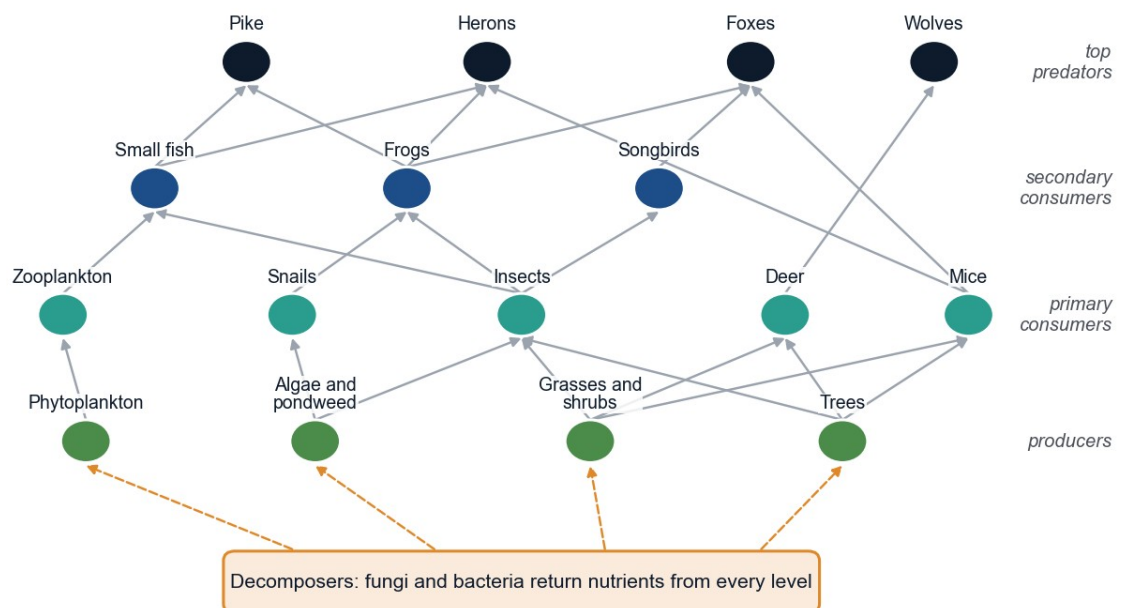


Figure 29. An illustrative food web linking a lake and its shore. Arrows point from food to consumer. Producers capture sunlight; consumers are arranged by trophic level; decomposers return nutrients to producers from every level, closing the cycle of matter while energy flows through once.

Source: H Heuristics. A generic temperate example; real food webs contain hundreds of species and many more links. Illustrative.

The consequence, shown in panel A of Figure 30, is that energy falls geometrically with each step. At 10 per cent efficiency, the fifth trophic level receives one ten-thousandth of primary production. This is why food chains rarely exceed four or five links, why top predators are rare and range widely, and why a diet low on the food chain requires less land.

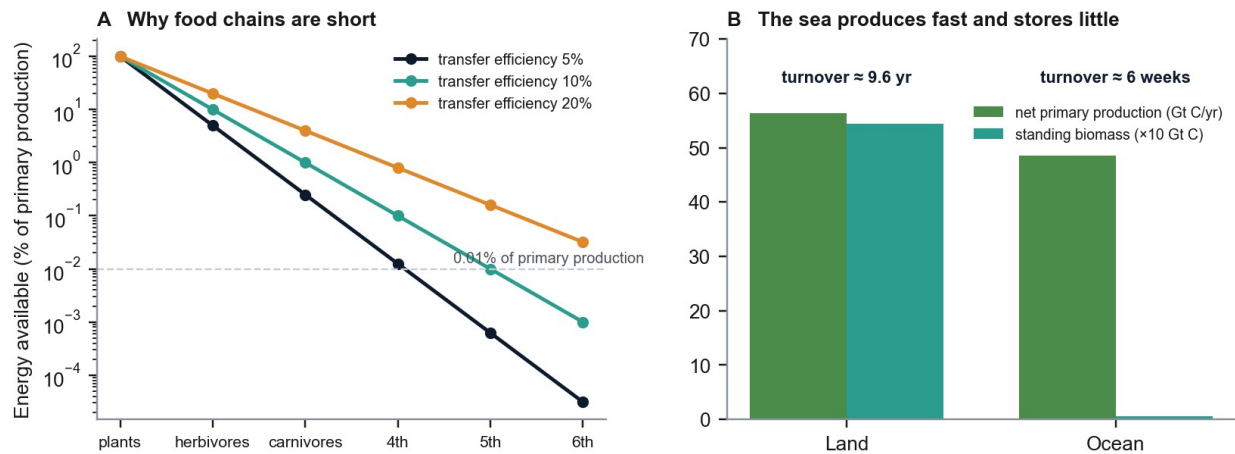


Figure 30. Energy and turnover in ecosystems. A: energy available at each trophic level for three transfer efficiencies. B: the land and the ocean produce similar amounts of new biomass each year, but the ocean stores about a hundredth as much, because its producers are microscopic and short-lived.

Source: Panel A, H Heuristics calculation. Panel B, net primary production from Field and colleagues (1998); biomass from Bar-On, Phillips and Milo (2018); turnover is biomass divided by production.

Panel B of Figure 30 shows a striking contrast. Land and ocean each fix roughly 50 billion tonnes of carbon a year (Field and colleagues, 1998). But land plants store most of their carbon in long-lived wood, giving a turnover time of about ten years, whereas the ocean's producers are mostly single-celled phytoplankton that are eaten or die within days, giving a turnover time of about six weeks. Similar energy flows can support very different structures, a reminder that energy flow constrains but does not determine form.

8.2 Where life's mass is

Yinon Bar-On, Rob Phillips and Ron Milo estimated the total biomass of Earth at about 550 billion tonnes of carbon (Bar-On, Phillips and Milo, 2018). Figure 31 shows the distribution. Plants account for about 80 per cent and bacteria for about 13 per cent, much of it deep underground. Animals make up only about 2 billion tonnes, less than 0.5 per cent, and most of that is arthropods and fish. Humans account for about 0.06 billion tonnes and livestock for about 0.1 billion tonnes; together they outweigh all wild mammals more than twentyfold.

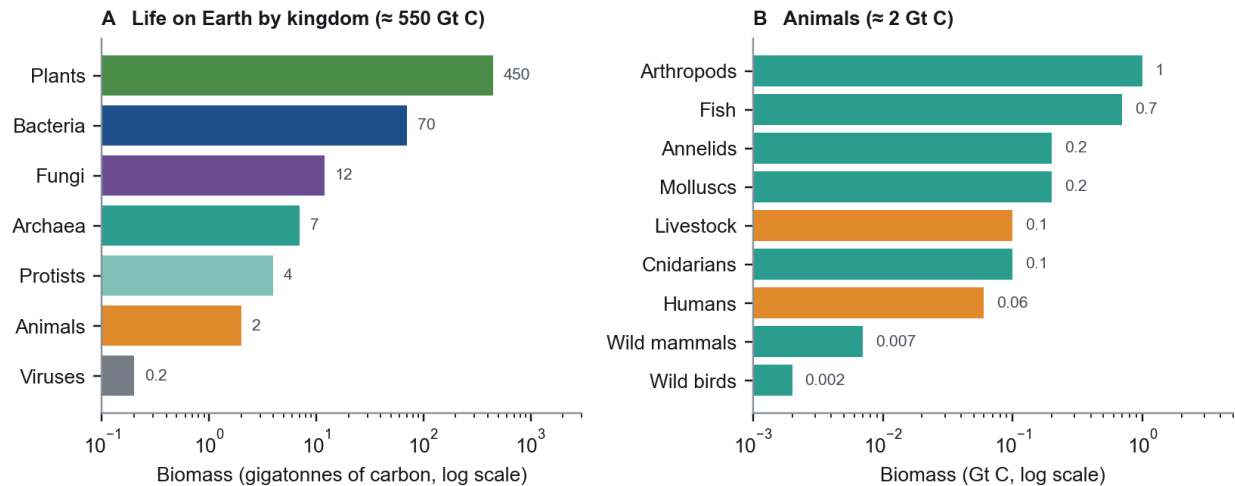


Figure 31. The distribution of biomass on Earth. A: by kingdom; plants dominate, followed by bacteria. B: animals, which make up less than half a per cent of the total; humans and their livestock far outweigh wild mammals and birds. Source: Bar-On, Phillips and Milo (2018). Values in gigatonnes of carbon; uncertainties are large, especially for bacteria and archaea.

8.3 Nutrient cycles

Energy flows through ecosystems once and leaves as heat. Matter cycles. Carbon, nitrogen, phosphorus, sulfur and water are taken up by producers, passed through consumers and returned to the environment by decomposers and by geological processes. The cycles are driven largely by microbes: a small set of microbial metabolisms, including photosynthesis, respiration, nitrogen fixation, nitrification and denitrification, and sulfate reduction, link the elements in a global network that Paul Falkowski and colleagues called Earth's 'microbial engines' (Falkowski, Fenchel and Delong, 2008). Each metabolism exploits a step on the redox tower of Figure 6, so the same thermodynamic constraint that powered the first cells organises the chemistry of the planet.

8.4 Population dynamics and feedback

Populations of predators and prey are coupled by feedback. More prey supports more predators; more predators reduce prey; fewer prey cannot support the predators, which decline, letting prey recover. With a delay in the loop, the populations cycle. The classic Lotka–Volterra model produces cycles of arbitrary size; a more realistic version, in which prey growth is limited and predators become satiated, produces either a stable equilibrium or a stable cycle.

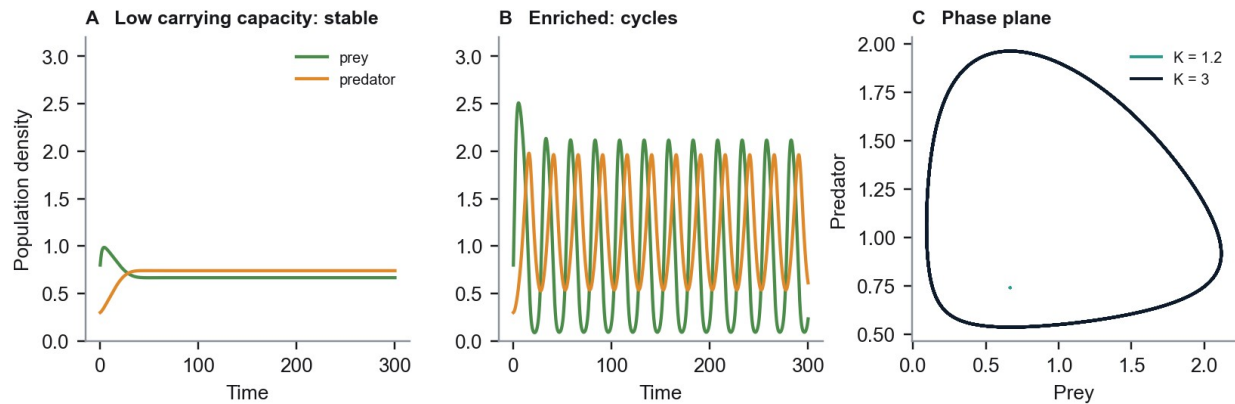


Figure 32. Predator–prey dynamics and the paradox of enrichment. A: with a modest carrying capacity, populations settle to equilibrium. B: raising the prey's carrying capacity destabilises the system into large cycles. C: the same dynamics in the phase plane; the stable point becomes a limit cycle.

Source: H Heuristics simulation of the Rosenzweig–MacArthur model with logistic prey growth and a saturating predator response ($r = 1$, $a = 1$, $h = 1$, $e = 0.5$, $m = 0.2$). Equilibrium is stable for carrying capacity K below 2.33.

Figure 32 shows a counterintuitive result, simulated for this report. Increasing the food available to the prey, by raising its carrying capacity from 1.2 to 3.0, does not simply produce more of both species. Above a threshold, at $K = 2.33$ for these parameters, the equilibrium becomes unstable and the populations swing through large cycles that carry prey numbers close to zero at each trough, where in a real population chance events could cause extinction. Michael Rosenzweig called this the [paradox of enrichment](#). It illustrates a general property of feedback systems: adding more energy to a system can destabilise it.

8.5 Complexity and stability

Ecologists long assumed that more diverse, more connected communities are more stable. In 1972 Robert May showed that in randomly assembled communities the reverse is true ([May, 1972](#)). If S species interact with probability C and interactions have typical strength σ , a random community is almost certainly stable when $\sigma\sqrt{SC}$ is below one and almost certainly unstable above it.

$$\sigma\sqrt{SC} < 1 \quad (10)$$

Figure 33 reproduces the result. For communities of 25 to 200 species, the probability of stability falls from near one to near zero as $\sigma\sqrt{SC}$ passes one, and the transition sharpens with size. Panel B shows why: the eigenvalues of a large random interaction matrix fill a circle of radius $\sigma\sqrt{SC}$ centred on -1 , and the community becomes unstable once the circle crosses zero.

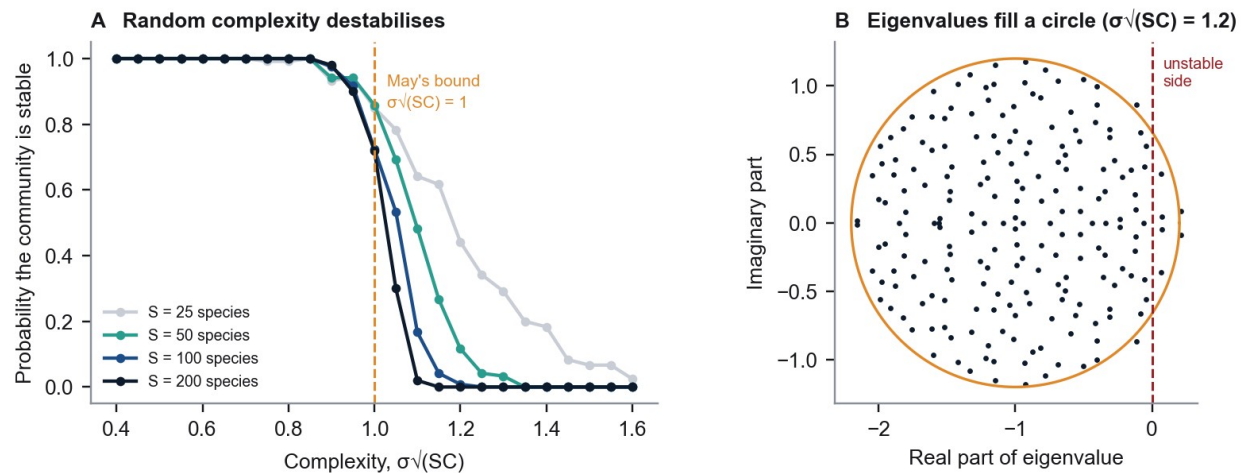


Figure 33. May's complexity–stability bound. A: probability that a random community of S species returns to equilibrium after a disturbance, as a function of complexity $\sigma\sqrt{SC}$. B: eigenvalues of one random community of 200 species fill a circle; the community is unstable if any lie to the right of zero.

Source: H Heuristics simulation of May (1972); connectance $C = 0.3$, self-regulation -1 , normally distributed interaction strengths; 50 to 120 random communities per point.

Real ecosystems are both complex and persistent, so they cannot be random. May's result therefore became a question: what structures allow complex ecosystems to persist? Answers include weak interactions, which are common in real food webs; modularity, in which species interact mostly within compartments; and particular combinations of predator–prey, competitive and mutualistic interactions, whose effects on stability were analysed by [Allesina and Tang \(2012\)](#). Empirically, more diverse grasslands vary less in total productivity from year to year, even though individual species fluctuate more ([Tilman and Downing, 1994](#)): diversity stabilises the aggregate even when it does not stabilise the parts ([Cardinale and colleagues, 2012](#)).

8.6 Biodiversity and area

Larger areas hold more species, following the species–area relation $S = c A^z$, with z typically between about 0.15 within continents and 0.35 across islands. Robert MacArthur and Edward O. Wilson explained the pattern on islands as an equilibrium between the arrival of new species, which slows as the island fills, and extinction, which rises as more species share limited space ([MacArthur and Wilson, 1963](#)). Figure 34 shows both ideas. The relation has a sobering corollary: with $z = 0.25$, reducing a habitat by 90 per cent eventually removes about 44 per cent of its species, though the losses may take decades or centuries to play out.

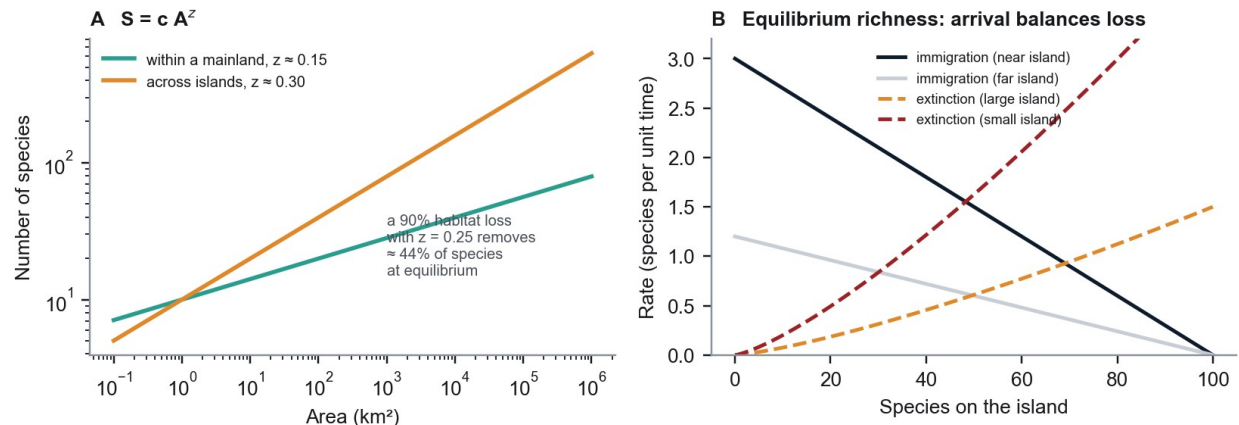


Figure 34. Area and diversity. A: the species–area relation for two values of the exponent z . B: the MacArthur–Wilson equilibrium; island species richness settles where the immigration and extinction curves cross, higher for near and large islands.

Source: H Heuristics calculation. Panel A, $S = 10 A^z$; panel B, illustrative linear immigration and convex extinction curves after MacArthur and Wilson (1963).

How many species are there? About two million have been described. Statistical extrapolation suggests about 8.7 million eukaryotic species ([Mora and colleagues, 2011](#)), and scaling arguments for microbes have produced estimates as high as a trillion ([Locey and Lennon, 2016](#)), though such numbers depend heavily on how microbial species are defined (Grade C).

8.7 Keystones, engineers and regime shifts

Not all species matter equally. Robert Paine removed the starfish *Pisaster* from rocky shores and found that diversity collapsed as mussels took over, introducing the idea of a [keystone species](#) whose effect is far larger than its abundance. The decline of sea otters in Alaska let sea urchins multiply and destroy kelp forests ([Estes and colleagues, 1998](#)). Ecosystem engineers such as beavers, corals and earthworms physically build the habitats others use ([Jones, Lawton and Shachak, 1994](#)).

Ecosystems can also switch abruptly between alternative states. Shallow lakes flip between clear water dominated by plants and turbid water dominated by algae; savannas flip between grassland and forest; coral reefs flip to algal dominance. Each state is maintained by its own reinforcing feedbacks, and a gradual change in conditions can push the system past a tipping point ([Scheffer and colleagues, 2001](#)). C. S. Holling described the capacity to absorb disturbance without changing state as [resilience](#). These are the same nonlinear dynamics of feedback and bifurcation found in cells and in the climate system.

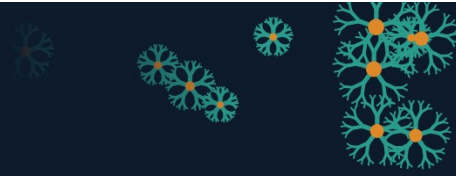
Table 11. Principles of ecosystem organisation

Principle	Ecological expression	Quantitative signature	Grade
Energy flow	Trophic levels; short food chains	Transfer efficiency 5–20% per level	A
Matter cycling	Microbially driven biogeochemical cycles	Redox steps of the redox tower	A
Feedback	Predator–prey cycles; density dependence; regime shifts	Limit cycles; bifurcations; hysteresis	A
Constrained complexity	Structured, not random, interaction networks	May's bound $\sigma\sqrt{(SC)} < 1$	A for the bound; B for the escape routes
Diversity and area	More area, more species	$S = c A^z$ with $z \approx 0.15\text{--}0.35$	A
Diversity and stability	Diverse communities have steadier aggregate function	Portfolio and insurance effects	B

Source: H Heuristics, from the studies cited in this section.

09

PART VII · INTELLIGENCE



9. Intelligence and the Evolution of Information Processing

Part VII explores sensory systems, nervous systems, learning, cognition and intelligence as biological capacities built upon earlier forms of information processing. The section treats intelligence as one solution among several to a general problem, acting on information about a changing world, and not as the destination of evolution.

9.1 Information processing before nerves

Every living cell processes information. A bacterium such as *E. coli* swims in runs, punctuated by tumbles that randomly reorient it. Receptors in its membrane measure the concentration of attractants such as sugars and amino acids; a chemical network compares the present concentration with that of about a second earlier; and if conditions are improving, the cell tumbles less often. The result is a biased random walk up chemical gradients ([Berg and Brown, 1972](#)). The system adapts to the background level, so it responds to changes over a range of concentrations spanning about five orders of magnitude, and it has a form of short-term memory.

Single cells also communicate and anticipate. Many bacteria measure their own population density by releasing and detecting signalling molecules, a process called quorum sensing, and switch on collective behaviours such as bioluminescence or biofilm formation only when numerous enough for them to pay ([Miller and Bassler, 2001](#)). *E. coli* entering a mammalian gut experiences a rise in temperature before a fall in oxygen, and it has evolved to switch toward anaerobic metabolism in response to temperature alone, in effect predicting what comes next ([Tagkopoulos, Liu and Tavazoie, 2008](#); [Mitchell and colleagues, 2009](#)). The slime mould *Physarum polycephalum*, a single giant cell, can find the shortest path through a maze ([Nakagaki and colleagues, 2000](#)) and builds transport networks with efficiency comparable to the Tokyo rail system ([Tero and colleagues, 2010](#)).

These examples establish an important point for the framework. Sensing, memory, decision and anticipation are not unique to brains. They are general properties of systems that use feedback-controlled chemistry to couple internal states to external conditions, and they are as old as cells (Grade A).

9.2 The nervous system

Chemical signalling is slow over distances larger than a cell. Neurons solve that problem with electrical signals that travel along thin extensions at up to about 100 metres per second, and chemical synapses that pass signals between cells in about a millisecond. Figure 35 shows the basic plan: dendrites collect inputs, the cell body integrates them, and the axon carries an all-or-nothing output to many targets.

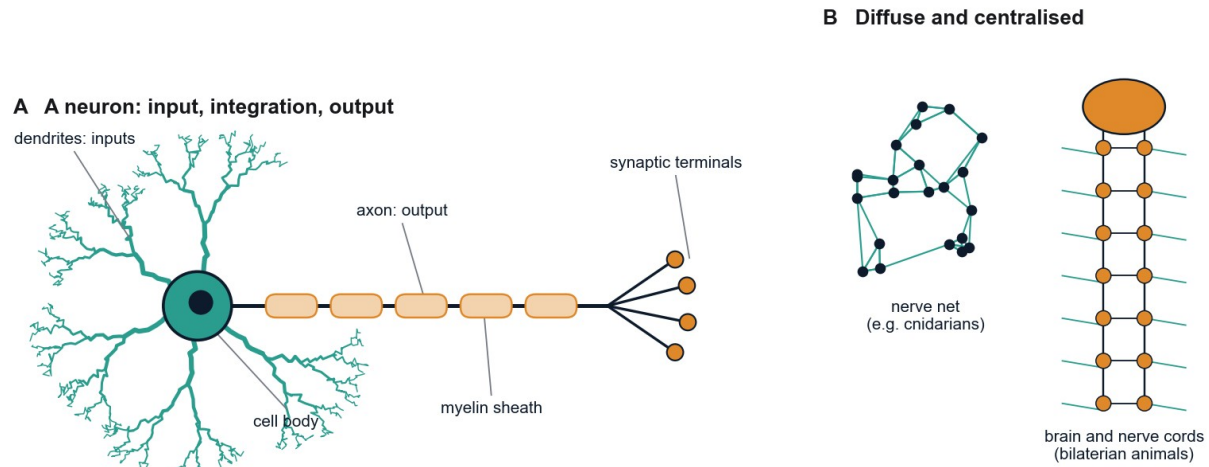


Figure 35. Neurons and nervous systems. A: a neuron collects inputs on branching dendrites, integrates them in the cell body and sends an output along an insulated axon to synaptic terminals. B: two architectures; a diffuse nerve net, as in cnidarians, and a centralised brain with nerve cords, as in bilaterian animals.

Source: H Heuristics. Schematic; not to scale. Illustrative.

Many components of neurons are older than nervous systems. Ion channels that generate electrical signals exist in bacteria; proteins of the synapse are found in sponges and choanoflagellates, which have no neurons. Nervous systems may have evolved more than once: comb jellies, or ctenophores, have neurons built from a partly different molecular toolkit, and a 2023 study found that their nerve net consists of cells fused into a continuous network rather than separate cells joined by synapses ([Moroz and colleagues, 2014](#); [Burkhardt and colleagues, 2023](#)). Gáspár Jékely, Fred Keijzer and Peter Godfrey-Smith have argued that early nervous systems evolved as much to coordinate the movement of a multicellular body as to process sensory information ([Jékely, Keijzer and Godfrey-Smith, 2015](#)). On that view the first job of a nervous system was internal: to make many cells act as one.

9.3 Brains of many designs

Nervous systems range from 302 neurons in the nematode *Caenorhabditis elegans*, whose complete wiring diagram was published in 1986 ([White and colleagues, 1986](#)), to about 139,000 in the brain of the fruit fly, mapped synapse by synapse in 2024 ([Dorkenwald and colleagues, 2024](#)), to about 86 billion in the human brain ([Azevedo and colleagues, 2009](#)) and about 257 billion in the African elephant, most of them in the cerebellum ([Herculano-Houzel and colleagues, 2014](#)). Figure 36 compares them.

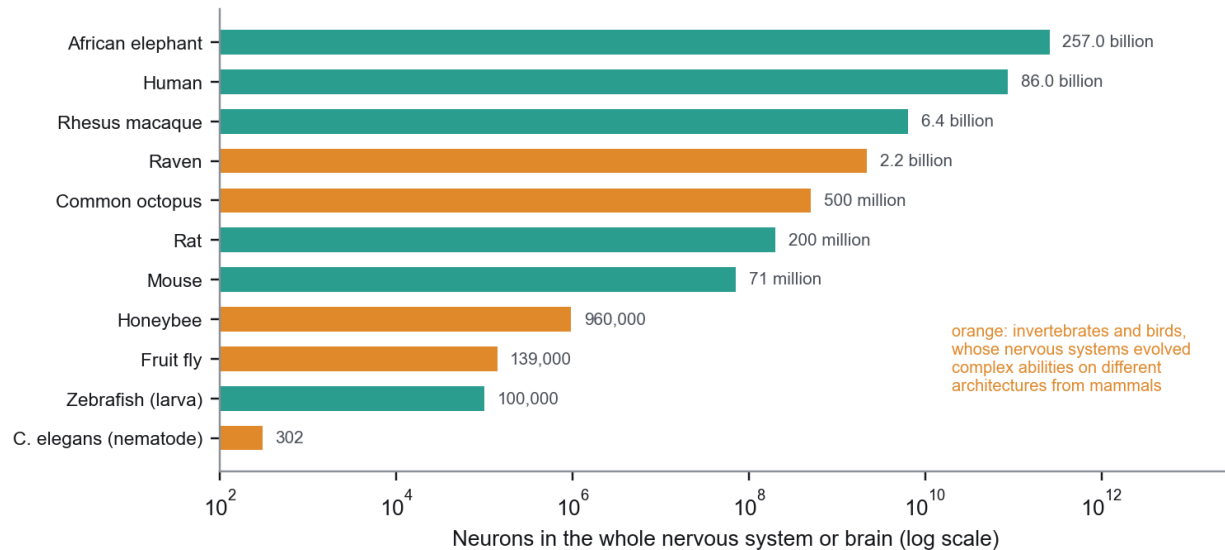


Figure 36. Neurons in nervous systems of selected animals, on a logarithmic scale. Complex behaviour appears across a wide range of neuron numbers and on different architectures; birds pack neurons densely, and an octopus has most of its neurons in its arms.

Source: White and colleagues (1986); Dorkenwald and colleagues (2024); Menzel and Giurfa (2001); Herculano-Houzel (2009); Azevedo and colleagues (2009); Olkowitz and colleagues (2016); Herculano-Houzel and colleagues (2014). Zebrafish larva and octopus values are approximate.

Neuron number alone does not determine ability. Birds pack neurons much more densely than mammals; a raven has about 2.2 billion neurons in a brain weighing about 15 grams, comparable in number to many monkeys with larger brains (Olkowitz and colleagues, 2016), and corvids plan, use tools and remember the past (Emery and Clayton, 2004). Octopuses have about 500 million neurons, two-thirds of them in the arms, and solve problems with a nervous system organised on entirely different principles from that of vertebrates (Albertin and colleagues, 2015). The last common ancestor of octopuses, crows and humans lived more than 550 million years ago and probably had a simple nervous system. Complex cognition therefore evolved at least three times independently, a striking case of convergence (Grade A).

9.4 The cost of information

Processing information costs energy. Rolf Landauer showed that erasing one bit of information must dissipate at least $kT \ln 2$ of energy, about 3×10^{-21} joules at body temperature (Landauer, 1961). Biological information processing is far above this limit. Laughlin, de Ruyter van Steveninck and Anderson (1998) estimated that transmitting one bit costs between about ten thousand and ten million ATP molecules, depending on the component, and the human brain, about 2 per cent of body mass, uses about 20 per cent of resting energy, roughly 20 watts (Raichle and Gusnard, 2002; Attwell and Laughlin, 2001).

The high cost of neurons is a filter. Large brains are found mainly in animals whose diet or social life gives a high return on information, and brain tissue is lost readily in lineages where it does not pay, as in many parasites and cave-dwelling animals. Intelligence is therefore not a free good that evolution accumulates by default; it is an expensive adaptation favoured only in particular ecological circumstances (Grade B).

9.5 Nested adaptive systems

Life has evolved several systems for acquiring and storing information about the environment, each faster than the one before it and each built on the one before it. Figure 37 places them on a common scale. Genetic adaptation responds over generations and stores information for millions of years. Gene regulation and epigenetic marks respond within minutes to hours and can persist for a lifetime or a few generations. The adaptive immune system learns to recognise new pathogens within days and remembers them for decades. Nervous systems respond in milliseconds and learn within seconds to years. Culture transmits learned information between individuals and across generations, accumulating it over thousands of years.

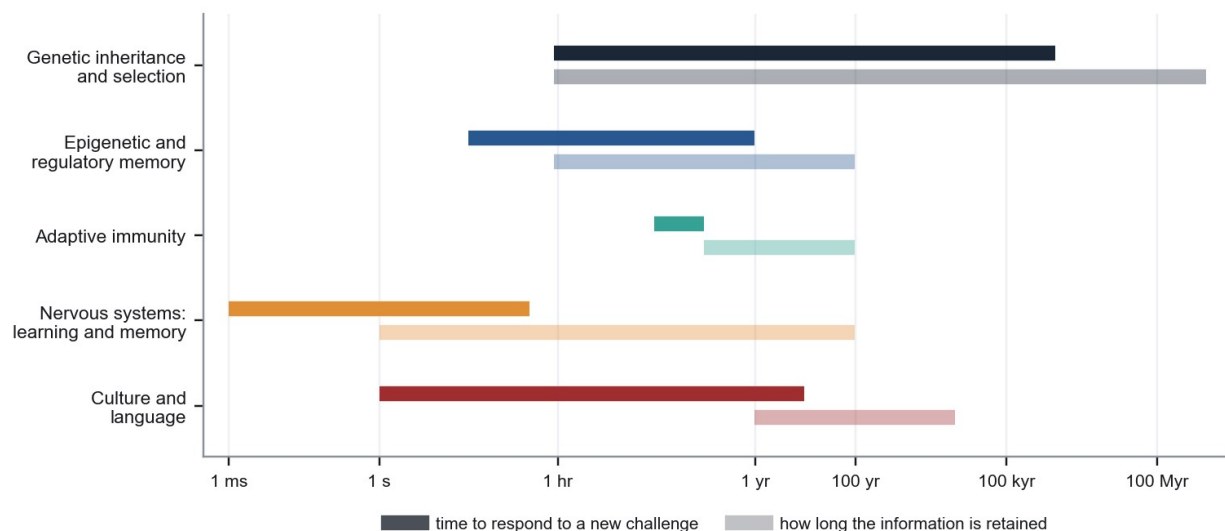


Figure 37. Life's nested information systems. Each bar spans the typical time to respond to a new challenge (dark) and the time over which information is retained (light). Faster systems evolved later and are built on slower ones; each lets organisms track changes too quick for the system beneath it.

Source: *H Heuristics. Indicative orders of magnitude. Illustrative.*

The pattern has a simple logic. Each new system allows organisms to track environmental changes that are too fast for the system below. Each is also controlled by the system below: genes build brains, and brains carry culture. This nesting is the informational counterpart of the hierarchy of individuality described in Section 6.7, and it is perhaps the clearest example in biology of the framework's claim that new generators emerge from earlier ones. The neuroscientist Karl Friston has proposed a general account in which all such systems minimise the surprise of their sensory inputs by building predictive models of their environment ([Friston, 2010](#)). The proposal is influential but contested and is graded C.

9.6 Culture

Social learning is widespread in animals: chimpanzee communities differ in tool-use traditions that are learned, not inherited ([Whiten and colleagues, 1999](#)), and birdsong dialects pass between generations. Human culture differs in degree and perhaps in kind, because it is cumulative: innovations build on earlier innovations until no individual could invent the whole from scratch. Robert Boyd, Peter Richerson and Joseph Henrich have argued that cumulative culture created a new inheritance system, subject to selection, that co-evolved with human genes and transformed the species' ecology ([Boyd, Richerson and Henrich, 2011](#)). In the terms of this report, language was the last of the major transitions in Maynard

Smith and Szathmáry's list: a new system for storing and transmitting information that created a new kind of collective individual.

9.7 No ladder

The evidence does not support a ladder of intelligence with humans at the top and all evolution leading up to it. Information processing evolved early and in every lineage; neurons evolved once or twice; complex cognition evolved at least three times on different architectures; and cumulative culture on the human scale evolved once, in the last few hundred thousand years, out of more than four billion years of life. The framework predicts that information-processing systems will appear wherever environments vary in ways that reward tracking them. It does not predict that technological intelligence is a likely outcome, and the single human case cannot establish how likely it is (Grade D).

10

PART VIII · THE PLANETARY SYSTEM



10. Life as a Planetary System

Part VIII investigates how biological activity transforms planetary environments, influences atmospheric chemistry, and interacts with climate and geological processes over time. Life is not merely a passenger on Earth. Over four billion years it has changed the composition of the air, the chemistry of the oceans and the minerals of the crust, and those changes have in turn redirected evolution.

10.1 The biosphere as a layer

The biosphere is the thin shell of Earth in which life is found. Figure 38 shows how thin it is: from microbes several kilometres down in the crust to spores and bacteria in the upper troposphere, it spans perhaps 20 kilometres on a planet 6,371 kilometres in radius. Yet within that film life processes energy on a planetary scale. Earth absorbs about 120,000 terawatts of sunlight. Global net primary production of about 105 billion tonnes of carbon a year corresponds to roughly 130 terawatts of captured chemical energy, about 0.1 per cent of the absorbed sunlight and nearly seven times humanity's total primary energy use of about 19 terawatts.

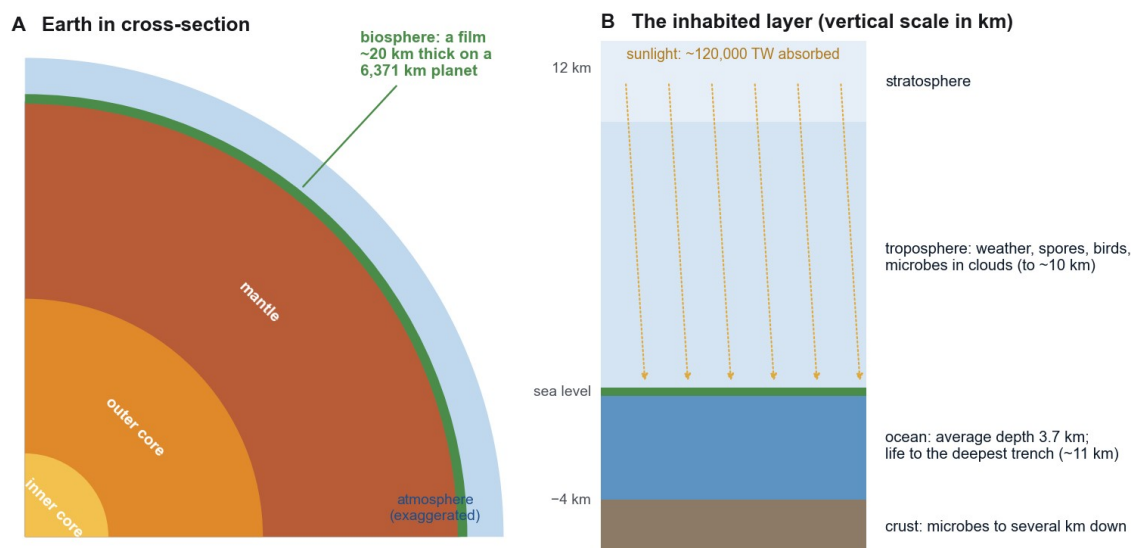


Figure 38. The biosphere as a thin planetary layer. A: Earth in cross-section, with the inhabited layer shown green; at true scale it would be thinner than the line. B: the inhabited layer in detail, from the deep subsurface to the upper troposphere.

Source: H Heuristics. Panel A is schematic, with the atmosphere and biosphere exaggerated; panel B is to vertical scale in kilometres. Illustrative.

10.2 Oxygen: a planet remade

The most dramatic example of life changing its planet is the oxygenation of the atmosphere (Figure 39). Cyanobacteria evolved oxygenic photosynthesis, which splits water and releases oxygen, perhaps by 3 billion years ago. For hundreds of millions of years the oxygen was consumed by reduced iron, sulfur and volcanic gases. Between about 2.43 and 2.22 billion years ago, oxygen accumulated in the atmosphere for the first time in the Great Oxidation Event ([Luo and colleagues, 2016](#); [Poulton and colleagues, 2021](#)). Levels then stayed low, perhaps one per cent of today's or less, for more than a billion years, before rising again in the Neoproterozoic Oxygenation Event between about 800 and 540 million years ago ([Lyons, Reinhard and Planavsky, 2014](#)).

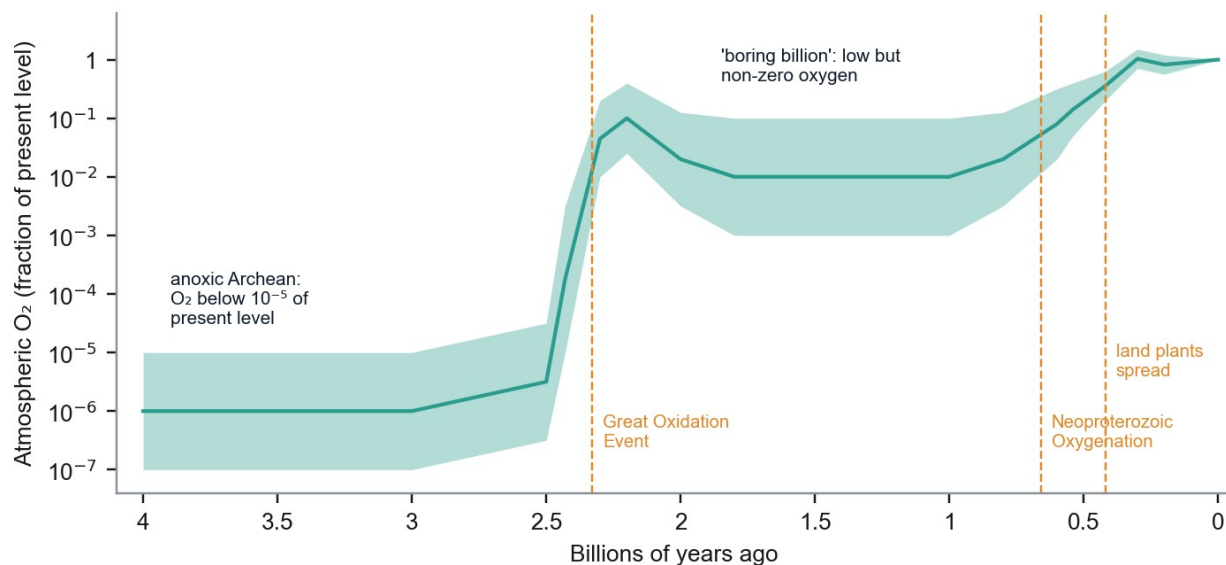


Figure 39. Atmospheric oxygen through Earth's history. Oxygen was virtually absent for the first half of Earth's history, rose in the Great Oxidation Event, remained low through the mid-Proterozoic and rose to near-modern levels in the late Neoproterozoic and Palaeozoic.

Source: H Heuristics, schematic envelope after Lyons, Reinhard and Planavsky (2014), Holland (2006) and Poulton and colleagues (2021). Uncertainty spans orders of magnitude for most of the record.

The consequences cascaded. Oxygen allowed aerobic respiration, which yields more than ten times as much ATP per glucose as fermentation, and later supported large, active animals. It formed an ozone layer that shields the surface from ultraviolet light. It oxidised iron and sulfur in the oceans and on land, and Robert Hazen and colleagues estimated that about two-thirds of known mineral species could not have formed without it ([Hazen and colleagues, 2008](#)). The rise of oxygen may also have contributed to the 'Snowball Earth' glaciations, by removing methane, a greenhouse gas ([Hoffman and colleagues, 1998](#)). Oxygen was, for most life then existing, a toxic pollutant. The organisms that produced it changed the filters that every later lineage faced.

10.3 The co-evolution of Earth and life

Oxygen is one of many links between life and the rest of the Earth system (Figure 40). Marine organisms build shells of calcium carbonate and silica, which sink and become rock, controlling ocean chemistry and storing carbon for millions of years. Land plants, which spread from about 470 million years ago, accelerated the chemical weathering of silicate rocks, which draws down carbon dioxide; their spread is associated with a large fall in carbon dioxide and with the late Palaeozoic glaciation ([Berner, 1997](#)).

Microbes drive the nitrogen and sulfur cycles. Subduction carries biologically processed carbon and water into the mantle, and volcanoes return them.

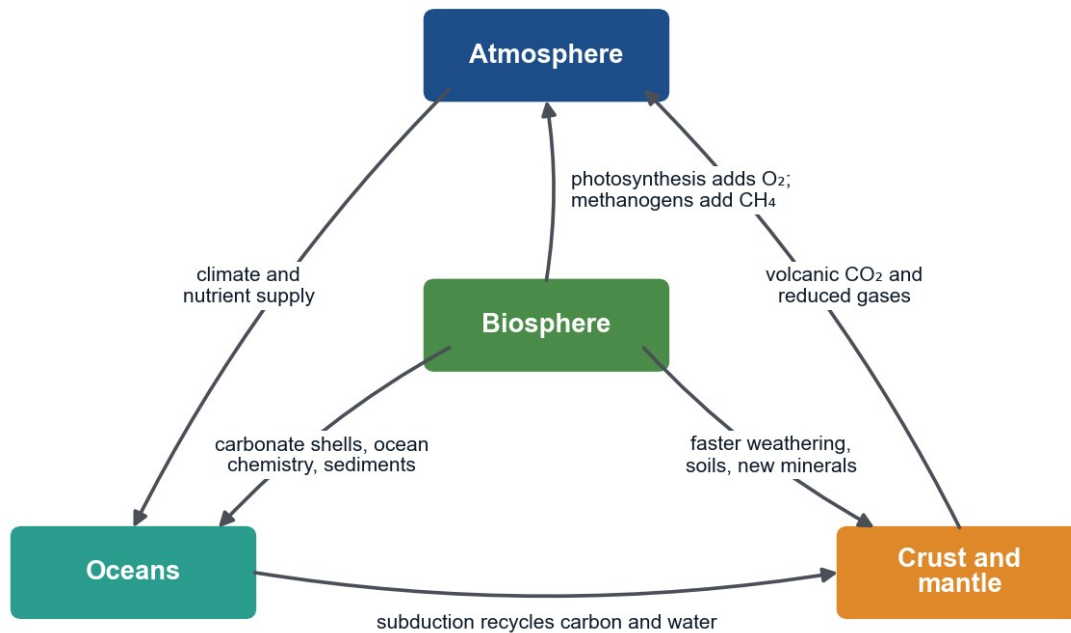


Figure 40. Feedbacks between life and the Earth system. The biosphere changes the composition of the atmosphere and oceans and the weathering of the crust; those changes alter climate and nutrient supply, which in turn select which life persists.

Source: H Heuristics. Illustrative.

Table 12. Milestones in the co-evolution of Earth and life

Approximate time	Biological event	Planetary consequence
≥ 3.5 Ga	Anaerobic microbes, including methanogens	Methane may have warmed the early Earth under a fainter Sun
~3.0–2.7 Ga	Oxygenic photosynthesis evolves	Local oxygen oases in shallow seas
2.43–2.22 Ga	Oxygen accumulates (Great Oxidation Event)	Ozone layer; oxidised minerals; possible global glaciation
~2.0–1.6 Ga	Eukaryotes with mitochondria	New ecological roles; larger cells
0.8–0.54 Ga	Neoproterozoic Oxygenation; animals radiate	Oxygenated deep ocean; bioturbation of sediments
~0.47–0.36 Ga	Land plants and forests	Faster weathering; soils; lower CO ₂ ; coal deposits
~0.1 Ga	Calcareous plankton dominate open-ocean carbonate	Ocean carbonate chemistry stabilised
Last ~10,000 years	Agriculture and industry	Land transformation; rising CO ₂ ; novel materials

Source: H Heuristics, from the studies cited in this section. Dates are approximate and several are debated.

10.4 Does life regulate the planet?

James Lovelock and Lynn Margulis proposed in the 1970s that life, together with the atmosphere, oceans and rocks, forms a self-regulating system that keeps conditions habitable, the [Gaia hypothesis](#). Critics objected that natural selection acts on individuals, not on planets, so there is no mechanism by which a biosphere could evolve to regulate itself ([Kirchner, 2002](#)). Andrew Watson and Lovelock replied with [Daisyworld](#), a model planet on which black and white daisies compete. Each daisy grows best at the same temperature, and each simply follows its own growth rate. But because black daisies absorb more sunlight and warm their surroundings while white daisies reflect it, their combined growth stabilises the planet's temperature.

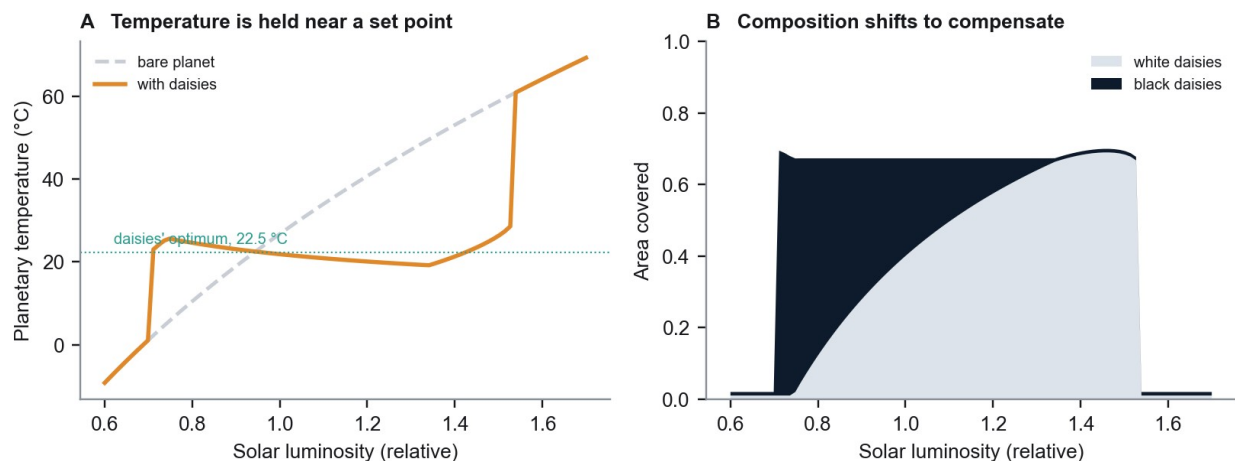


Figure 41. Daisyworld. A: as the sun brightens, a bare planet warms steadily, but a planet with black and white daisies holds its temperature between about 19 and 29 °C over a wide range of luminosity. B: the balance shifts from black to white daisies as the sun brightens, until regulation fails.

Source: H Heuristics simulation of Watson and Lovelock (1983), with their published parameters; daisy death rate 0.3, optimum 22.5 °C.

Figure 41 reproduces the model. Over a range of solar luminosity from about 0.71 to 1.53 times the reference value, the daisies hold the planet's temperature between about 19 and 29 °C, while a bare planet over the same range would vary from about 2 to 60 °C. Regulation emerges without foresight or planetary selection, from local growth plus a coupling between organisms and environment. Daisyworld shows that self-regulation is possible; it does not show that Earth's biosphere does regulate climate. The evidence is mixed. Some feedbacks, such as plant-enhanced weathering, are stabilising over millions of years; others, such as methane release from warming wetlands, amplify change. Tim Lenton has argued that stabilising feedbacks are favoured because unstable configurations tend to eliminate themselves ([Lenton, 1998](#)). The hypothesis that life has kept Earth habitable is graded C.

10.5 Mass extinctions and recovery

The planet also acts on life. Five mass extinctions in the past 540 million years each removed a large fraction of species ([Raup and Sepkoski, 1982](#)). The largest, at the end of the Permian 252 million years ago, eliminated roughly 80 to 90 per cent of marine species and was triggered by massive volcanism in Siberia, which disrupted the carbon cycle and acidified and deoxygenated the oceans ([Burgess, Bowring and Shen, 2014](#)). The end-Cretaceous extinction 66 million years ago, caused by an asteroid impact ([Alvarez and colleagues, 1980](#)), ended the age of dinosaurs and opened ecological space for mammals.

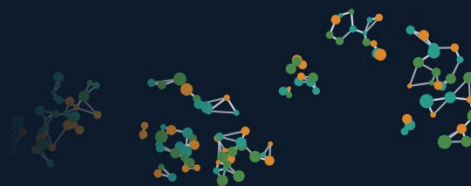
Recovery takes time. Diversity typically took about ten million years to rebound after major extinctions, regardless of their size ([Kirchner and Weil, 2000](#)). Mass extinctions illustrate the framework's filter acting at the largest scale. They are not selective in the usual sense: survivors are often those that happened to be widespread, small or in the right place, not those best adapted to normal conditions. History therefore shapes the living world as much as adaptation does.

10.6 Humans as a planetary force

One species now rivals geological processes. Humans appropriate roughly a quarter of the planet's terrestrial net primary production through harvest and land-use change ([Haberl and colleagues, 2007](#)). Industrial nitrogen fixation through the Haber–Bosch process supports about half of the world's population ([Erisman and colleagues, 2008](#)). In about 2020 the mass of human-made objects, from concrete to plastic, exceeded the dry mass of all living things ([Elhacham and colleagues, 2020](#)). Species are being lost at rates far above the background rate ([Ceballos and colleagues, 2015](#)). From the perspective of the framework, humanity is the latest instance of a pattern that began with the cyanobacteria: a lineage whose activity changes the filters for all other life. The difference is that this lineage can model the consequences. The H Heuristics reports on the [polycrisis](#) examine those consequences in detail.

11

SYNTHESIS



11. The Recurring Architecture of Life

This section tests the central claim of the framework: that several structural principles recur across biological scales. It asks, principle by principle, whether the recurrence reflects a shared mechanism, an analogous mechanism that performs the same role by different means, or only a resemblance. The distinction matters. A shared mechanism allows results from one level to be carried to another; an analogy can guide questions but not answers; a resemblance can mislead.

11.1 Six principles at three scales

Table 13 sets out how six of the principles of Section 2.3 appear at the molecular, organismal and ecosystem scales. The first three columns describe; the last gives this report's verdict.

Table 13. The recurring architecture of life: six principles across three scales

Principle	Molecular systems	Organisms	Ecosystems	Verdict
Information	Genetic and molecular states; templates; regulatory states	Heredity and gene regulation; nervous systems; immune memory	Environmental signals; ecological relationships; no inherited ecosystem genome	Shared up to organisms; analogous for ecosystems
Energy	Chemical reactions; redox gradients; chemiosmosis	Metabolism; Kleiber scaling	Food webs; trophic transfer; nutrient cycles	Shared mechanism at every scale
Boundaries	Membranes; molecular compartments	Cell membranes; skins; immune self–non-self	Habitat edges; territories; watersheds	Shared to organisms; analogous for ecosystems
Feedback	Reaction networks; autocatalysis; regulatory motifs	Homeostasis; development; hormones	Predator–prey cycles; density dependence; regime shifts	Shared mathematics at every scale
Selection	Differential persistence of molecular systems	Natural selection of heritable variation	Ecological filtering and community change	Shared for organisms; analogous below and above
Emergence	Autocatalytic sets; self-assembly	Multicellular organisation; development; cognition	Ecosystem-level properties such as stability and productivity	Shared as a phenomenon; mechanisms differ

Source: H Heuristics assessment. 'Shared' means the same mechanism or mathematics operates; 'analogous' means a different mechanism performs a comparable role.

Figure 42 extends the assessment to eight principles and five scales, adding cellular and planetary levels and the principles of cooperation and hierarchy. Three patterns stand out.

	Molecular	Cellular	Organismal	Ecological	Planetary
Information	shared	shared	shared	analogous	weak
Energy flow	shared	shared	shared	shared	shared
Boundaries	analogous	shared	shared	analogous	weak
Feedback	shared	shared	shared	shared	analogous
Selection	analogous	shared	shared	analogous	weak
Cooperation	analogous	shared	shared	analogous	weak
Hierarchy	analogous	shared	shared	shared	analogous
Emergence	shared	shared	shared	shared	shared

Figure 42. Recurrence of eight principles across five scales. 'Shared' indicates that the same mechanism or mathematics operates; 'analogous' that a different mechanism performs a comparable role; 'weak' that the resemblance is largely metaphorical.

Source: H Heuristics assessment, based on the evidence reviewed in Sections 3 to 10. The judgements in the ecological and planetary columns are the most uncertain.

- 1. Energy flow, feedback and emergence are shared at every scale.** These are physical principles, not specifically biological ones. The same thermodynamics governs a redox reaction, a body's metabolism and a food web; the same mathematics of feedback describes a gene circuit, a hormone system and a predator–prey cycle; and emergence, in the sense of collective properties appearing at thresholds, is found from autocatalytic sets to ecosystem stability. These principles are the strongest part of the case for a coherent architecture (Grade A).
- 2. Information, heredity, selection, cooperation and boundaries are shared from molecules to organisms but become analogies above.** The cell and the organism are the levels at which information is inherited and natural selection acts most clearly. Ecosystems have no genome and do not reproduce, so 'ecosystem selection' and 'ecosystem memory' are analogies. They can be useful analogies, because ecological filtering does change community composition and some ecosystems do retain legacies of past states, but they lack the mechanism that makes natural selection cumulative (Grade B).
- 3. The planetary scale is the most debated.** The biosphere processes energy and contains feedbacks, so those principles apply. Whether the biosphere selects, cooperates or regulates in a sense stronger than metaphor is the Gaia question of Section 10.4, graded C.

11.2 Shared, analogous and unique

The brief for this report asks which mechanisms are shared, which are analogous and which are unique to particular biological systems. Table 14 summarises the answer.

Table 14. Mechanisms that are shared, analogous or unique

Category	Examples	Why it matters
Shared across all scales	Free-energy flow and dissipation; negative and positive feedback; thresholds and bifurcations; hierarchical nesting; power-law scaling	Results transfer between levels; the same models can be used
Shared from molecules to organisms	Template-based heredity; error thresholds; natural selection; kin selection; membranes and compartments; regulatory networks	The core of biology; explains adaptation and design-like complexity
Analogous at higher levels	Ecological filtering as 'selection'; habitat edges as 'boundaries'; ecological legacies as 'memory'; cultural evolution as 'heredity'	Useful for generating questions; results do not transfer automatically
Unique to particular levels	The genetic code (molecular); development from a single cell (multicellular organisms); trophic transfer (ecosystems); cumulative language-based culture (humans); oxygenation of an atmosphere (planetary)	Each level has mechanisms that cannot be reduced to a general principle

Source: *H Heuristics assessment.*

11.3 The core triad: boundary, energy, information

If one combination lies at the heart of the architecture of life, it is the coupling of a boundary, an energy flow and heritable information, the three subsystems of Figure 13. Each major level of biological individuality re-creates the triad at a larger scale. A cell has a membrane, a metabolism and a genome. A multicellular organism has a skin, a circulatory and digestive system, and a germ line. A social insect colony has a nest, a foraging economy and a queen. At each level, the three are coupled so that the system's information specifies its boundary and its energy capture, and the boundary and energy capture protect and propagate the information.

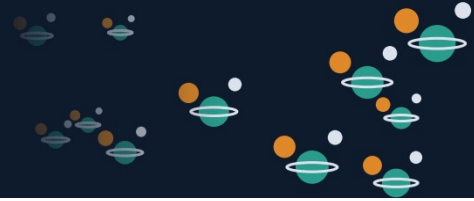
This is the framework's main proposition about life, and it is offered as a proposition, not an established result (Grade B to C). It explains why the major transitions of Section 6.7 recur, why conflict between levels must be suppressed at each one, and why ecosystems, which have energy flows and boundaries but no shared heritable information, do not become individuals.

11.4 What the architecture does not explain

- **The origin of life itself.** The framework describes what a living system must contain, not how the first one formed.
- **The particular forms that exist.** Constraints and filters narrow the space of possibilities, but history, contingency and mass extinctions decide which of many viable forms appear.
- **Why complexity sometimes increases.** The architecture is compatible with increases and decreases; it does not supply a trend.
- **Consciousness.** The report treats information processing and cognition as biological capacities but makes no claim to explain subjective experience.
- **Quantitative laws at every level.** Some scaling laws, such as Kleiber's, are well established; others proposed as universal, such as a single law of biodiversity, are not.

12

BEYOND EARTH



12. Life Beyond Earth and Alternative Architectures

If the architecture of life rests on general principles, it should say something about life elsewhere. This section asks which features of terrestrial life are likely to be universal, which are probably accidents of history, and how life might be recognised if its chemistry differed from ours. It is necessarily the most speculative section of the report, and its claims are graded accordingly.

12.1 What might be universal

Steven Benner and colleagues asked whether there is a common chemical model for life in the universe and concluded that some features are probably required by chemistry while others are contingent ([Benner, Ricardo and Carrigan, 2004](#)). The framework sorts terrestrial features into three groups.

Table 15. Which features of terrestrial life might be universal

Feature	Likely status	Reason	Grade
Energy from chemical or light disequilibrium	Universal	Thermodynamics requires free-energy input to maintain order	A
Boundaries separating inside from outside	Very likely	Without them, products diffuse away and selection cannot act on systems	B
Heritable information with error correction	Very likely for evolving life	Darwinian evolution needs heredity; the error threshold limits genome size without correction	B
Linear polymers as information carriers	Likely	One-dimensional sequences are easy to copy; Benner argues a repeating charged backbone is needed	C
Carbon as the structural element	Likely	Carbon's bonding versatility is unmatched; silicon is a poor substitute in oxygen-rich settings	C
Water as solvent	Likely but not certain	Water's properties are exceptional, but other liquids exist on other worlds	C
DNA, RNA, the 20 amino acids, the genetic code	Probably contingent	Many alternatives work in the laboratory; the specific set reflects history	C
Cells, multicellularity, nervous systems	Plausible but not required	Recurrent on Earth, but each depends on particular histories	D

Source: H Heuristics assessment, drawing on Benner, Ricardo and Carrigan (2004) and Schwieterman and colleagues (2018).

Laboratory work supports the view that the specific molecules of terrestrial life are not the only possibilities. Synthetic biologists have built genetic systems with six or eight nucleotide letters, polymers

with different backbones that can store and evolve information, and organisms that incorporate non-standard amino acids. The architecture of a heritable, error-corrected information polymer appears to be required for evolution; the particular polymer does not.

12.2 Other solvents, other worlds

Water is liquid on Earth's surface but not on most worlds. Figure 43 compares the liquid ranges of candidate solvents with the temperatures of possible habitats. Titan, Saturn's largest moon, has lakes and seas of liquid methane and ethane at about -179°C ; ammonia is liquid at temperatures found on some moons and cold planets; sulfuric acid is liquid in the clouds of Venus. Known life is active between about -20°C and 122°C , the latter recorded for the methanogen *Methanopyrus kandleri* ([Takai and colleagues, 2008](#)).

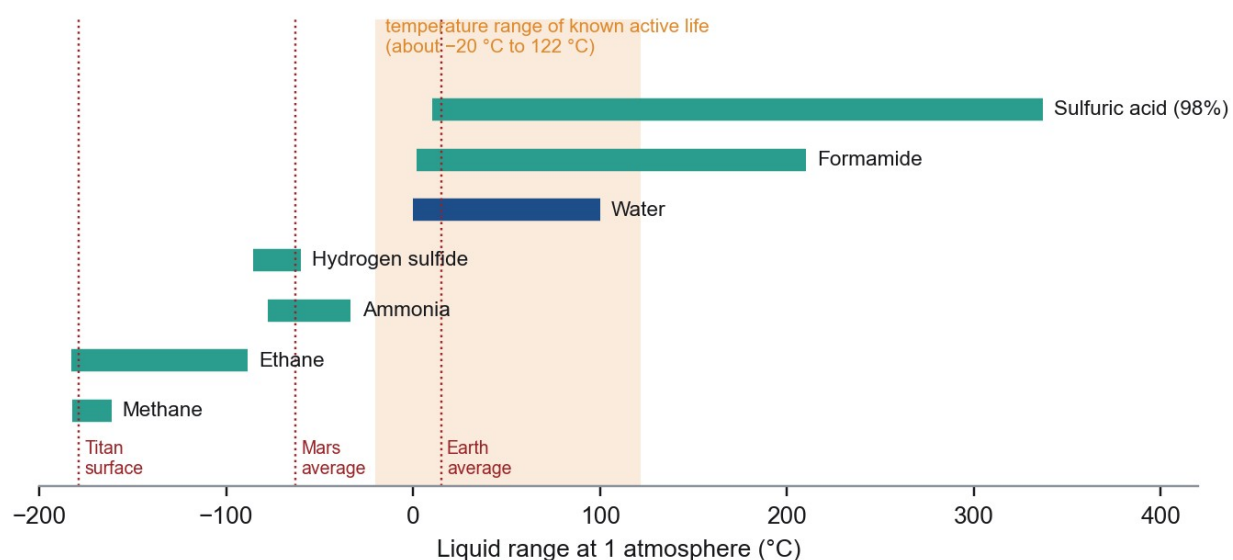


Figure 43. Candidate solvents for life. Bars show the liquid range of each substance at one atmosphere; the shaded band shows the range of temperatures at which known life is active. Water's range overlaps the conditions on Earth; methane and ethane those on Titan's surface.

Source: *H Heuristics*, from standard physical data. Liquid ranges shift with pressure and mixture; Titan's surface pressure is about 1.5 atmospheres.

Each solvent has drawbacks. Hydrocarbons do not dissolve ions or drive the hydrophobic effect that builds membranes in water, though theoretical work has proposed membrane-like structures that could form in liquid methane. Chemistry at -179°C is very slow. Sulfuric acid destroys most organic molecules familiar to biochemists. Water remains the best candidate by a wide margin, but the question is open (Grade C).

12.3 Where to look

Table 16. Targets in the search for life beyond Earth

Target	Why it is interesting	Key evidence or mission
Mars	Liquid water on the surface more than three billion years ago; organic molecules in mudstones; possible subsurface brines today	Curiosity and Perseverance rovers; planned sample return
Europa (Jupiter)	Global salty ocean beneath an ice shell, in contact with a rocky floor	Europa Clipper , launched 2024
Enceladus (Saturn)	Plumes from a subsurface ocean contain molecular hydrogen, organic molecules and phosphates	Cassini: Waite and colleagues (2017) ; Postberg and colleagues (2023)
Titan (Saturn)	Rich organic chemistry; methane lakes; subsurface water ocean	Dragonfly rotorcraft, planned launch 2028
Venus clouds	Temperate cloud layer, though extremely acidic	Contested phosphine detection; proposed probes
Exoplanets	Thousands known; rocky planets in habitable zones are common	JWST atmospheric spectra; future Habitable Worlds Observatory

Source: H Heuristics, from the studies and missions linked. No target has yet yielded accepted evidence of life.

Enceladus stands out because it already meets the three requirements identified in this report for a setting where life could arise: liquid water, an energy source in the form of molecular hydrogen from water–rock reactions resembling those at Earth's alkaline vents, and the six main biological elements, including phosphorus ([Postberg and colleagues, 2023](#)). Whether life is there is unknown.

12.4 Recognising life we do not know

Searches for life on exoplanets will rely on biosignatures: gases or surface features that are hard to explain without life. Oxygen together with methane is a classic example, because the two react and must be continuously replenished; Carl Sagan and colleagues showed that the Galileo spacecraft could detect life on Earth by such signs ([Sagan and colleagues, 1993](#)). But any single gas can have non-biological sources, and reviews stress the need to interpret biosignatures in the context of the whole planet ([Schwieterman and colleagues, 2018](#); [Seager, Bains and Petkowski, 2016](#)). Claims of possible biosignatures on the sub-Neptune [K2-18 b](#) illustrate the difficulty: the detections have been disputed in follow-up analyses.

A different approach looks for the architecture of life rather than its chemistry. Lee Cronin, Sara Walker and colleagues have proposed assembly theory, which measures how many steps are needed to build a molecule from simple parts; molecules that need many steps and are found in many copies are argued to require a selective process such as life ([Marshall and colleagues, 2021](#); [Sharma and colleagues, 2023](#)). The proposal is contested, but its logic aligns with this report: life is recognisable by the signatures of selection and accumulated information, whatever its chemistry (Grade C to D).

12.5 What a single example can tell us

All of biology so far is based on one example of life. That limits what can be inferred about life elsewhere. Section 4.8 showed that the early appearance of life on Earth is weak evidence about its frequency. The architecture of life explains why the ingredients and conditions for life are common, why certain features

are probably required for any evolving system and why others are contingent. It does not tell us how often the transition from chemistry to biology occurs. A single discovery of independently originated life, on Mars, an icy moon or an exoplanet, would transform that question; a long series of careful non-detections would constrain it. Either outcome would test the framework.

13

TESTS

13. Testable Propositions

A framework that cannot fail is not useful. This section states the report's main claims as propositions that could be tested, together with the evidence that would count against them. Propositions marked as H Heuristics propositions are original to this series; the others restate established or widely discussed hypotheses in a form that makes their tests explicit.

Table 17. Testable propositions

#	Proposition	Test	Would count against it
1	Building blocks of life form wherever carbon, nitrogen, water and energy meet	Analyse returned samples (Bennu, Ryugu, future Mars and icy-moon samples) and comet dust	Pristine primitive bodies lacking amino acids and nucleobases
2	A self-sustaining, evolving chemical system can be assembled from prebiotically plausible components	Laboratory systems chemistry; long-run evolution experiments with RNA, peptides and vesicles	Persistent failure despite exhaustive exploration of plausible conditions (weak evidence only)
3	Autocatalytic sets arise at modest levels of catalysis in diverse chemical mixtures (Section 4.2)	Screen random mixtures of peptides or RNA for collective self-maintenance	Catalysis rates in real mixtures far below about one reaction per molecule
4	Copying fidelity limits information content in all evolving systems (Section 4.4)	Mutation rates and genome sizes in newly sequenced lineages, synthetic replicators and any alien life	Stable genomes far above the error threshold without error correction
5	H Heuristics proposition: every level of biological individuality couples a boundary, an energy flow and heritable information (Section 11.3)	Comparative study of colonies, symbioses, holobionts and candidate new transitions	A stable, reproducing individual that lacks one of the three
6	Major transitions require mechanisms that suppress conflict among lower-level units	Experimental evolution of multicellularity; genomics of social insects and symbioses	Stable higher-level individuals with unchecked lower-level competition
7	Convergence is strongest where physical constraints are tightest (Section 6.8)	Compare the frequency of convergence for physically constrained and unconstrained traits across the tree of life	Equal convergence regardless of constraint
8	Complexity shows no general driven trend; maximum complexity rises passively	Measure trends in complexity within many lineages	A consistent upward bias within most lineages
9	Random complex ecosystems are unstable; persistent ones are structured (Section 8.5)	Compare interaction structures of real food webs with randomised versions	Real webs no more stable than random ones of the same size and connectance

#	Proposition	Test	Would count against it
10	Complex cognition evolves where environments reward tracking rapid change, on varied architectures	Comparative ecology and neuroanatomy of birds, cephalopods, mammals and insects	Complex cognition unrelated to ecological or social demands
11	The biosphere has net stabilising effects on climate over millions of years (Section 10.4)	Earth-system models and geochemical proxies across the Phanerozoic	Biological feedbacks found to be net destabilising over long timescales
12	Life elsewhere, if found, will use energy from disequilibria, boundaries and heritable polymers, but not necessarily DNA or our amino acids (Section 12.1)	Biochemistry of any independently originated life	Life without compartmentalisation or without a heritable information carrier
13	Signatures of selection, such as abundant molecules of high assembly complexity, distinguish life from abiotic chemistry	Measure assembly complexity across abiotic and biological samples	Abiotic processes producing equally complex molecules in abundance
14	H Heuristics proposition: energy flow, feedback and emergence are shared mechanisms at every scale; information, selection and cooperation become analogies above the organism (Section 11.1)	Formal models testing whether ecological and planetary processes meet Lewontin's conditions	Ecosystems or biospheres shown to have heritable variation in fitness

Source: H Heuristics.

14

VERDICT



14. Conclusion: Is There a Coherent Architecture of Life?

14.1 The verdict

This report set out to evaluate whether a coherent architecture of life can explain recurring patterns across molecular, cellular, organismal, ecological and planetary scales while respecting the distinct mechanisms operating at each level. The answer is a qualified yes.

There is a coherent architecture, and it has a clear structure. At its base are physical principles that operate at every scale: free energy must flow for order to persist, feedback creates set points, switches and cycles, and collective properties emerge when quantitative thresholds are crossed. On that base sits the specifically biological core: boundaries, energy capture and heritable information coupled into self-maintaining systems that natural selection can act on. The core was first assembled in the origin of life, by processes still not understood, and was then re-created at larger scales in the major transitions, each time with mechanisms to suppress conflict between parts. Above the level of the organism, the biological core gives way to analogies: ecosystems and the biosphere have energy flows, feedbacks and emergent properties, but not heredity in the full sense.

The qualification is that the architecture is a family of related mechanisms, not a single law. The same principle is implemented differently at each level, and each level has mechanisms of its own, from the genetic code to trophic transfer to language. Treating resemblances as identities would mislead. The framework's value lies in asking, for each level, which principles are shared in mechanism and which only in role.

Answer to the defining question. Life emerged from nonliving chemistry when energy-driven reaction networks, heritable templates and self-assembling boundaries became coupled into systems that natural selection could act on. Thereafter, a recurring architecture of energy flow, compartmentalisation, feedback, heredity, selection, cooperation and hierarchical assembly built cells, organisms, ecosystems and a biosphere. The architecture is real and recurrent, but it is implemented by distinct mechanisms at each level, and it explains how life builds complexity, not that it must.

14.2 What the evidence shows, and where it stops

Table 18. Summary of graded conclusions

Question	Answer	Grade
Are life's ingredients and settings common?	Yes; prebiotic building blocks form readily and are found across the Solar System	A
Do we know how life began?	No; key steps are demonstrated separately, none together	C–D
Does all known life share one ancestor and one core architecture?	Yes	A
Is evolution generative as well as selective?	Yes; generators of variation are diverse and themselves evolve	A
Do major transitions share a common logic?	Yes; cooperation stabilised by conflict suppression	B
Is there a built-in trend toward complexity or intelligence?	No; maximum complexity rises passively; intelligence evolved rarely and late	B
Does life regulate its planet?	Life transforms the planet; whether it stabilises it is contested	A / C
Do the same principles recur across scales?	Energy, feedback, emergence: yes. Information, selection, cooperation: within organisms, otherwise as analogies	B
Is life common in the universe?	Unknown; one example cannot decide	D

Source: H Heuristics.

14.3 Ten heuristics for reading a living system

The working heuristics below translate the architecture into questions that can be asked of any biological structure, from a molecule to an ecosystem.

- 1. Find the energy.** Identify the free-energy gradient the structure lives on and what it costs to maintain.
- 2. Find the boundary.** Ask what separates inside from outside and what crosses it.
- 3. Find the information.** Ask what is inherited, how accurately, and at what cost.
- 4. Find the loops.** Identify the negative feedbacks that hold it steady and the positive feedbacks that could tip it.
- 5. Name the generator.** Ask what produced the variants among which this one was chosen.
- 6. Name the filter.** Ask what removed the alternatives: selection, drift, ecology, physics or history.
- 7. Check the level.** Ask at which level selection is acting, and whether lower levels are in conflict with it.
- 8. Separate constraint from contingency.** Ask whether the form is one of few that physics allows, or one of many that history happened to produce.
- 9. Distrust purpose language.** Translate 'for' into 'favoured by selection because'; if the translation fails, the explanation is incomplete.
- 10. Grade the claim.** Ask whether the evidence is direct, inferred, contested or speculative, and say so.

14.4 Closing

The first report in this series asked why the same forms recur across unrelated systems. The second showed how physical law generates the structures of the cosmos. This report has followed the story into the one domain where structures copy themselves. Copying changes everything. Once information is inherited, the filters of the creation structure become cumulative, and a process with no foresight can assemble cells, bodies, ecosystems and minds. Yet the same physical principles that built stars and planets still govern every step: energy must flow, boundaries must hold, and feedback decides what persists. Life is not an exception to the architecture of creation. It is that architecture, given memory.

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