The energy expansions of evolution

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The history of the life–Earth system can be divided into five 'energetic' epochs, each featuring the evolution of life forms that can exploit a new source of energy. These sources are: geochemical energy, sunlight, oxygen, flesh and fire. The first two were present at the start, but oxygen, flesh and fire are all consequences of evolutionary events. Since no category of energy source has disappeared, this has, over time, resulted in an expanding realm of the sources of energy available to living organisms and a concomitant increase in the diversity and complexity of ecosystems. These energy expansions have also mediated the transformation of key aspects of the planetary environment, which have in turn mediated the future course of evolutionary change. Using energy as a lens thus illuminates patterns in the entwined histories of life and Earth, and may also provide a framework for considering the potential trajectories of life–planet systems elsewhere.

Free energy is a universal requirement for life. It drives mechanical motion and chemical reactions—which in biology can change a cell or an organism[1,2]. Over the course of Earth history, the harnessing of free energy by organisms has had a dramatic impact on the planetary environment[3–7]. Yet the variety of free-energy sources available to living organisms has expanded over time. These expansions are consequences of events in the evolution of life, and they have mediated the transformation of the planet from an anoxic world that could support only microbial life, to one that boasts the rich geology and diversity of life present today. Here, I review these energy expansions, discuss how they map onto the biological and geological development of Earth, and consider what this could mean for the trajectories of life–planet systems elsewhere.

In the beginning

From the time Earth formed, around 4.56 billion years ago (Ga), two sources of energy were potentially available to living organisms: geochemical energy and sunlight. Sunlight is a consequence of the planet's position in the Solar System, whereas geochemical energy is an intrinsic property of the Earth. Geochemical energy arises when water reacts with basalts and other rocks[8–10]. These water–rock reactions—which continue today[11]—generate reduced compounds such as hydrogen, hydrogen sulfide, and methane[8–10]. Oxidation of these compounds releases energy, which organisms can capture and store in the form of chemical bonds. Although sources of geochemical energy can be at or near Earth's surface, they need not be: many are deep within the planet, out of reach of sunlight.

Assuming that life did not parachute in, fully formed, from elsewhere, a number of authors[12–15] have argued that the transition from non-life to life took place in the context of geochemical energy, with the ability to harness sunlight evolving later (Fig. 1). Consistent with this, both phylogenetic[16] and biochemical[13,17] evidence suggest that the earliest life forms were chemoautotrophs, perhaps living by reacting hydrogen with carbon dioxide and giving off acetate, methane and water[13,16]. Mounting evidence[18–22] suggests that the transition from non-life to life may have taken place before 3.7 Ga—a time from which few rocks remain[23].

Energy epoch one: geochemical energy

Analysis of biochemical pathways suggests that, under favourable environmental conditions, early autotrophs could readily have adopted a heterotrophic lifestyle, feeding on the contents of dead cells[24]. At this time in Earth history, oxygen was at trace levels[25], so the first ecosystems would have been anaerobic.

Early ecosystems may have quickly diversified to take the form of a microbial mat, where the waste products of one group of life forms feed the metabolism of another[26,27]. Such an arrangement generates layered communities of organisms, each layer having a different metabolic speciality[28,29]. In anaerobic ecosystems of this type, mobile predation is essentially nonexistent: growth rates are so low that hunting and consuming other organisms doesn't yield enough energy[30]. Viruses, however, are likely to have been an important force from early in the history of life[31]. They act as agents of death—and by lysing cells, they would have provided additional sources of organic carbon to heterotrophs. Viruses also transport genes from one host to another, and thus may have enabled the spread of evolutionary innovations. Many of the coevolutionary selection pressures of the modern biosphere would have been minimal (for example, predation and the opportunity to live inside other organisms) or absent (for example, sexual selection).

The niches available would have been those near sources of geochemical energy, suggesting a patchy, local distribution of life. Consistent with this, geochemical models[32–34] suggest that the productivity of the biosphere before it was powered by the sun would have been at least a thousand times less than it is today, and may have been one million times less.

Owing to the scarcity of rocks from Earth's remote past, the impact of early life on the planetary environment is also hard to assess. Life inevitably creates a suite of changes in its environment (Box 1), and the establishment of life would have initiated biogeochemical cycling, but owing to the low productivity of the biosphere, the initial effects are likely to have been small[32–34].

Energy epoch two: sunlight

At some point early in the history of the Earth—perhaps by 3.7 Ga[18,19,21] (Fig. 1)—organisms evolved to harness the energy in sunlight to drive chemical reactions. Today, several groups of bacteria engage in photosynthesis, using a variety of different pathways[35]. One pathway, oxygenic photosynthesis, gives off oxygen as a by-product; the others, all forms of anoxygenic photosynthesis, do not. Genetic[35], fossil[36], and biochemical[37] evidence all suggest that of the two, anoxygenic photosynthesis evolved first.

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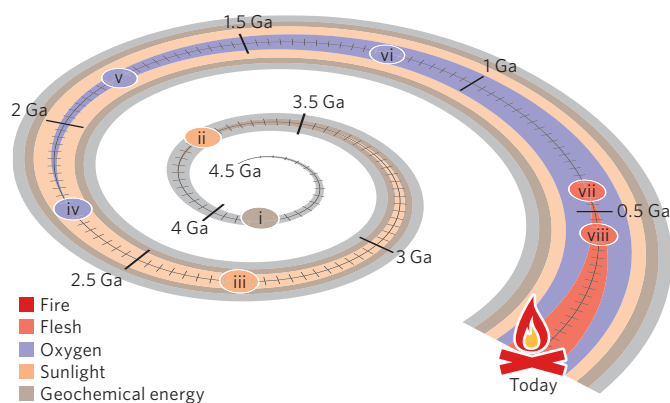
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Figure 1 | Key events during the energy expansions of evolution. (i) Life emerges; epoch of geochemistry begins. (ii) Anoxygenic photosynthesis: start of energy epoch 2, sunlight. (iii) Emergence of cyanobacteria. (iv) Great Oxidation Event: energy epoch 3, oxygen. (v) Probable eukaryotic fossils appear. (vi) Fossils of red algae appear. (vii) Start of energy epoch 4, flesh. (viii) Vascular plants colonize land; fire appears on Earth. Finally, the burning logs indicate the start of energy epoch 5, fire. The dates of (i)–(iii) are highly uncertain. For (i) I have taken the earliest date for which there is evidence consistent with life[20]. For (ii) I have taken the earliest date for which there is evidence consistent with photosynthesis[18,19,21]. For (iii), I have marked the date currently supported by fossil evidence for the presence of cyanobacteria (see main text, 'Cyanobacteria and the oxygenation of the air'). Tick marks represent intervals of 25 million years. Figure drawn by F. Zsolnai.

Because sunlight is abundant across the planet's surface, the ability to use it made far more of the planet available to life. Consistent with this, models of the early Earth suggest that the advent of anoxygenic photosynthesis greatly increased the productivity of early ecosystems[32,33]. At the same time, microbial ecosystems were able to become more diverse. Forms of photoheterotrophy[38] may also have begun to evolve. This lifestyle does not involve fixing carbon—organisms still require a source of organic carbon—but does involve transducing sunshine into ATP, which reduces energy needs from other sources.

During this epoch, the impact of life on the planetary environment expanded too. Structures such as stromatolites[39] and banded iron formations[19] began to appear, and methane may have started to build up in the atmosphere[40]. Indeed, the climate of the early Earth appears to have been temperate[41] despite the fact that, back then, the sun had only about 70% of its current brightness[42]. Methane, along with ethane, which can be produced from methane by photochemical reactions in the atmosphere[43], are greenhouse gases: thus, methane production on the part of living organisms may have helped to keep the early Earth from freezing[25,43].

But the crucial event of this period—the one that would go on to have by far the most biological and geological impact—was the evolution of oxygenic photosynthesis, an innovation that appeared in just one phylum, the cyanobacteria.

Cyanobacteria and the oxygenation of the air. In the absence of a biotic source of oxygen, trace quantities of the gas can be generated abiotically: water molecules can be split by sunlight[44] or radioactive decay[45]. However, these abiotic processes are much less efficient than their biotic equivalent[34,44]. Had cyanobacteria, or something like them, never evolved, oxygen would never have built up in the atmosphere of the Earth.

But build up it did. Between 2.45 and 2.32 Ga (ref. [46]), significant quantities of oxygen began to accumulate in the air, an episode known as the Great Oxidation Event. Before the Great Oxidation, atmospheric oxygen levels were less than 10^{-5} of the present

Box 1 | Transforming life.

The capacity of life to transform a planetary environment arises from the fact that life automatically generates several epiphenomena. These are: metabolism, evolution, acceleration and redistribution.

Metabolism causes transformations of inanimate matter, as when a methanogen transforms hydrogen and carbon dioxide into methane and water. Metabolism thus mediates the 'bio' part of biogeochemical cycles. Evolution expands metabolic variety, increases the efficiency with which life consumes energy and resources, and over time, expands the breadth of life's grip on the cycling of the elements.

Acceleration arises from the fact that enzymes catalyse reactions that would otherwise happen slowly, if at all. Sometimes the acceleration is extreme, achieving in 18 milliseconds a reaction that would otherwise be expected to take 78 million years, an improvement of 20 orders of magnitude[154]. Many life-mediated accelerations also include huge improvements in the temperatures and pressures at which reactions can occur. For example: the smectite-to-illite reaction, a transformation between two clay minerals. In the absence of microbial involvement, this transformation requires 4–5 months at 300 °C and high pressure (1,000 atmospheres). In the presence of the bacterium *Shewanella oneidensis*, the same reaction takes just two weeks—at room temperature and one atmosphere[155].

Finally, living organisms redistribute and restructure the physical fabric of the planet. For much of Earth history, the effect was one of concentration. For example, living organisms tend to concentrate the lighter isotopes of elements such as carbon or sulfur inside their bodies[156,157]; they can also produce large accumulations of materials such as limestone. But with the advent of energy epoch 4 (see main text, 'Energy epoch four: flesh'), living organisms also began large-scale mixing of sediments and the transport of materials from the land to the sea, and from the sea surface to the deep sea and back again.

These epiphenomena will occur wherever life does. However, the magnitude of their impact will depend on life becoming abundant. If life is limited (whether by the availability of energy, resources, or evolutionary developments), the potential for life to transform a planet will be small.

atmospheric level of ~21%. By ~2 Ga, they had risen to perhaps 0.1–1% of the present atmospheric level[25]. Although the subsequent history of oxygen is complex and many details are uncertain[47,48], Earth's atmosphere has contained an appreciable level of the gas ever since. (Full oxygenation of the oceans, however, would not happen until around 1.8 billion years after the Great Oxidation[47].)

Of all the events in the early history of the Earth, the Great Oxidation is the least controversial. It marks a line across the history of the planet, with a suite of geological markers showing a shift in the prevailing chemistry[44,49]. In contrast, there is enormous uncertainty about when cyanobacteria first evolved, with estimates spanning a period of one billion years[35,47]. However, genetic[50], fossil[51], and geochemical[47,52] evidence all suggest that cyanobacteria evolved at least 300 million years before the Great Oxidation Event.

But if cyanobacteria evolved hundreds of millions of years before the Great Oxidation, why did oxygen take so long to accumulate? This question has been studied extensively, and various hypotheses have been put forward (for a review see refs [25,53]). In essence, though, it's a matter of planetary chemistry. Both the atmosphere and ocean of the early Earth were full of molecules such as hydrogen, methane and ferrous iron that oxygen reacts with; oxygen may thus have been removed as fast as it was produced[25,54]. Until sources

of oxygen began to exceed the sinks, the gas would have been unable to accumulate[25].

Even before the Great Oxidation, the emergence of cyanobacteria would have increased both the productivity and complexity of microbial ecosystems. As well as a variety of heterotrophs, modern microbial mats and stromatolites often contain photosynthetic organisms of several different types[55]. Moreover, in evolving to extract electrons from the hydrogen in water, rather than from substances such as ferrous iron or hydrogen sulfide, cyanobacteria would have been far less constrained in the habitats they could occupy. Cyanobacteria may even have been among the first organisms to colonize land surfaces[56], increasing the weathering of rocks, and thus the flow of nutrients into the oceans[57]. But these impacts are dwarfed by those that resulted from the accumulation of oxygen in the air.

Oxygen and the planetary environment. The Great Oxidation Event had a dramatic impact on the planetary environment. First, the transition to an oxygen-rich atmosphere took place in tandem with the establishment of the ozone layer[54,58,59], thus changing the physical context in which organisms, especially those on land, evolve. Second, the diversity of minerals at the Earth's surface began to increase[60], eventually more than doubling[61].

Third, the appearance of atmospheric oxygen created a variety of new abiotic niches. As well as the anoxic and micro-oxic niches that had existed from the outset, the oxygenation of the atmosphere created an abundance of oxygen-rich niches, too. Today, aerobic prokaryotes show an enhanced ability to tolerate extremes of salinity and pH compared to their anaerobic counterparts[62], suggesting that the availability of oxygen might also have allowed for the colonization of other, previously inaccessible, abiotic niches. At the same time, the availability of oxygen would have increased the availabilities of oxidants such as nitrate and sulfate—and thus would also have increased the productivity of chemotrophic life forms.

Fourth, the Great Oxidation seems to have coincided with a series of extreme ice ages[63]. The reasons for this are unresolved[63], but some authors[25,64,65] have suggested it could have been due to a decline in the flux of biogenic methane reaching the atmosphere, and a corresponding decline in the contribution of methane and its byproducts to keeping the climate warm.

But the most significant environmental impact of the Great Oxidation was a change in the prevailing chemistry, and the ready availability of oxygen gas as a source of energy for living organisms.

Energy epoch three: oxygen

Oxygen is a rich source of energy: the use of oxygen as an electron acceptor releases more energy per electron transfer than that of any other element except for chlorine and fluorine[66]. (Neither chlorine nor fluorine is cosmically abundant, however, and both are so reactive as to be an unlikely foundation for any kind of biology[66].) The diversification of the biosphere that would ultimately take place was, to a large extent, enabled by the growing abundance of oxygen.

The emergence of the ability of living organisms to use oxygen as an energy source is shrouded in at least as much mystery as the emergence of cyanobacteria. At issue is whether early life forms could have evolved to use trace oxygen or hydrogen peroxide produced through abiotic processes[67]—and thus whether aerobic respiration originated before the advent of cyanobacteria, or whether it evolved in conjunction with them. Whatever the case, long before the Great Oxidation Event, aerobic organisms, if they existed, could have prospered in oxygen-rich oases generated by cyanobacteria[68,69].

As well as being a source of energy, oxygen is both a biological problem and an opportunity. Problem: the presence of oxygen inactivates some enzymes, and oxygen derivatives such as hydrogen peroxide and the superoxide ion are reactive compounds that damage both DNA and proteins[70,71]. To survive in the presence of oxygen, organisms need a superstructure of protective enzymes. Opportunity: the availability of oxygen permits the construction of new molecules, such as collagen[72].

During this epoch, two momentous events took place: the emergence of eukaryotes and the emergence of the lineage that would eventually produce land plants. Both events represent fusions between two previously independent lineages, an archaeon and an alphaproteobacterium in the case of eukaryotes[73,74], and a eukaryote and a cyanobacterium in the case of the plant lineage[75]; the alphaproteobacterium evolved to become the mitochondrion, the cyanobacterium, the chloroplast. Both events thus also represent important shifts in the capacity for organisms to transduce energy. Fossils of red algae show that both events had taken place by ~1.2 Ga (ref. [76]), and microfossils that are probably eukaryotic in origin date to 1.8 Ga (ref. [77]).

In extant eukaryotes, organelles of mitochondrial origin take several different, but related, forms[78]. Notably, only one—the 'standard' mitochondrion found, for example, in humans—requires oxygen. Three others are involved in forms of anaerobic metabolism; of these, two produce hydrogen. These observations fit with the hypothesis, advanced by Martin and colleagues[74,79], that the ancestral eukaryote resulted from a prior symbiotic association between a hydrogen-dependent archaeon and a metabolically flexible alphaproteobacterium that, in the absence of oxygen, lived anaerobically producing hydrogen, and in the presence of oxygen, lived aerobically. If this hypothesis is correct, the ancestral eukaryote could have been a facultative anaerobe, able to live in both oxic and anoxic environments. Such a scenario not only accounts for the different types of mitochondria seen in extant eukaryotes[78], but also for the fact that, today, species with mitochondria that produce ATP through anaerobic pathways are sprinkled across the eukaryotic tree while exhibiting a similar underlying biochemistry[78,80].

Eukaryotes differ from prokaryotes in many respects, from meiosis and syngamy to the presence of a cell nucleus, as well as a suite of other features. In addition, complex multicellularity and large size has evolved only in eukaryotes—which Lane and Martin[81] have attributed to an enhanced capacity to generate energy owing to the possession of mitochondria (Box 2). From the point of view of the biosphere, the emergence and diversification of eukaryotes provided a new set of niches for prokaryotes to occupy—which in turn allowed eukaryotes to occupy a far wider variety of niches. Today, most, perhaps all, eukaryotes have symbiotic dependencies on consortia of prokaryotes—microbiomes—that give them access to a greater variety of energy sources and metabolic capabilities[82].

For the purposes of this Perspective, however, one feature of eukaryotes is particularly important. This is the ability to engage in phagocytosis—the engulfment of particles and, sometimes, other life forms. The wholesale engulfment of other beings appears to be a eukaryotic invention[83], and it whets the appetite for:

Energy epoch four: flesh

Around 575 million years ago (Ma), during the Ediacaran Period, a new form of life began to become abundant: animals[84]. And with animals would soon come a powerful new force of nature: the acquisition of energy through the active hunting and eating of other life forms, especially, other animals. This would produce a radical shift that, within a mere 40 million years, transformed the Earth. Before this epoch, ecosystems were microbial. The advent of widespread flesh-eating launched the Phanerozoic, triggering an enormous increase in organism size[85], a new tempo of macroevolutionary change[86,87], new kinds of ecosystems[86–88], and an increased impact of life on the fabric of the planet[87].

As in the case of oxygen, however, flesh-eating has a prehistory. Predation by single-celled eukaryotes may have caused the evolution of the first armoured algae, around 770 Ma[89–91], as well as a major increase in eukaryotic diversity[92]. Moreover, animals represent one

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Box 2 | Life and energy.

Living organisms gather energy from external sources and transduce it into ATP molecules. By breaking the bonds in ATP, they can use energy in the cell to do work such as copying DNA, building proteins, maintaining their cellular structures, growing, powering their flagellae, and so on. Of these activities, building proteins is particularly expensive, accounting for a significant proportion of a cell's total energetic costs.

Lane and Martin[81] argue that the fundamental difference between prokaryotes and eukaryotes is one of energy limitation. They suggest that, owing to the mechanics of ATP synthesis, prokaryotes are intrinsically limited in the amount of ATP they can manufacture—and thus, in the number of proteins they have the power to build.

Eukaryotes, they argue, are not limited in this way because their cells contain large numbers of mitochondria—the sites of ATP synthesis. Mitochondria are the descendants of the alphaproteobacterium that, long ago, fused with an archaeon to form the ur-eukaryotic cell. Today, mitochondrial genomes are highly reduced compared with that of their bacterial ancestor, but the genes they have kept are those important for the local regulation of ATP production[158]. With so much more ATP available at so little extra expense, the evolution of mitochondria released the ancestral eukaryote from an energetic constraint, allowing for the episode of proteome expansion[159] that coincides with the emergence of the eukaryotic cell. This difference in energetic potential, Lane and Martin suggest, is the reason that prokaryotes have remained small and morphologically simple, while eukaryotes have been able to radiate through a landscape of complex shapes and extreme bigness.

More generally, the need to use energy efficiently can mould the finest details of living organisms. For example, life forms often evolve to reduce the costs of building particular proteins[160–162]. The reason is that amino acids vary in how much energy they take to make[163]. Especially when a protein is made in large quantities, such differences add up. Thus, over time, mutations that cause 'expensive' amino acids to be replaced by 'cheaper' ones tend to be favoured—so long as the replacement does not interfere with the protein being able to function.

Box 3 | Oxygen and the evolution of animals.

No one disputes that ample oxygen is a prerequisite for the evolution of large, mobile animals—that no other substrate provides enough energy to power them. But a major point of contention concerns the role of oxygen in the early evolution of animals[164]. The question has two parts: how much oxygen was required for their initial evolution, and how much for their spectacular and rapid diversification, more than 200 million years later, at the start of the Cambrian?

The answer to the first part is: not much[165]. Like the earliest eukaryotes, the earliest animals may well have had mitochondria that were facultatively anaerobic[78,165], and thus would have been able to persist in environments where oxygen levels were low or unstable.

However, low oxygen limits animal ecology in several ways. Without a good supply of oxygen, animals cannot grow big or move fast: they cannot get enough power. A neat demonstration of this comes from work by Sperling and colleagues[166]. Using data from modern oceans, these authors showed that in low oxygen regions, there can be plenty of animals, but they tend to be small and passive. Active predators—flesh eaters—only appear once oxygen levels become more moderate. Another point to note is that without access to oxygen, animals cannot make collagen, one of their main connective tissues. Without collagen, they cannot leave body fossils[72].

Such observations have led a number of authors[167–170] to wonder whether a rise in oxygen permitted the Cambrian Explosion by releasing an important evolutionary constraint. Although evidence for a rise in atmospheric oxygen towards the end of the Proterozoic is mixed (and disputed), it seems that parts of the deep ocean became well oxygenated around this time, leading Lenton and colleagues[171] to suggest that—even in the absence of a rise in atmospheric oxygen—the activities of the earliest animals could have facilitated the oxygenation of the oceans, which in turn could have facilitated the evolution of larger, faster, hungrier animals.

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of several transitions to complex multicellular life[93]—transitions that Stanley[86] suggested might, in part, have resulted from single-celled eukaryotes engulfing and consuming each other. Indeed, molecular clocks show that the first animals also evolved around this time[94,95] (Box 3), leading Knoll and Lahr[92] to propose that tiny animals might have helped drive the diversification of eukaryotic protists.

Today, animals influence diversity at all levels of an ecosystem, with grazers such as slugs[96] or zooplankton[97] maintaining the diversity of plants or phytoplankton, and carnivores such as wolves[98] maintaining the diversity of plants through their predation on herbivores. This kind of ecology—complex food webs with many types of eaters—was absent from Earth until around 550 Ma, when the first animals that eat animals evolved. Their appearance seems to have triggered the rapid diversification of animal life sometimes referred to as the Cambrian Explosion.

In addition to their effects on the structure of ecosystems, the flourishing of flesh-eating animals heralded a step-change in both biomass and biodiversity[87]. In the oceans today, for example, Butterfield[87] has estimated that animals may comprise as much as 80% of the biomass in the pelagic zone. Furthermore, with the evolution of animals, new coevolutionary selection pressures—in particular, arms races between the eaters and the eaten—appeared, accelerating the pace of macroevolution[99]. At the same time, animal

guts and external surfaces provided new niches for other life forms, both symbiotic and hostile.

On the geological side, the flourishing of animals had at least four major impacts. First, the evolution of predation rapidly led to the evolution of armour—shells, scales, spikes and carapaces built from materials such as calcite and silica[100]. Although, as noted above, the first protective coverings (on algae) date back to around 770 Ma (ref. [90]), it's not until the evolution of flesh-eating animals that shells and other forms of protection became widespread. This development would eventually result in vast deposits of materials such as radiolarite[101], limestone[102], coquina[103] and chalk[104] and would also produce changes in ocean chemistry, as organisms removed dissolved materials such as silica and calcium and used it for themselves[105,106].

Second, animals produce faeces, which have important effects on the way that nutrients are distributed around the globe. For example, in the ocean, zooplankton faecal pellets sink more rapidly than individual algal or bacterial cells, and thus transport organic matter from the surface to the seabed[107]. Today, the faeces of sperm whales bring iron from the deep sea to the ocean surface[108]; the faeces of birds like cormorants transport nutrients from the ocean onto land, sometimes in fantastic quantities[109].

A third geological impact of animals is caused by their ability to burrow. Simple, horizontal burrows appear in the fossil record around 555 Ma (ref. [110]); by the early Cambrian, the abundance, size, depth and complexity of burrows had increased considerably[110].

Widespread burrowing creates a mixing of sediments known as bioturbation. As Darwin[111] observed with respect to earthworms, burrowing is analogous to ploughing: it redistributes nutrients as well as sifting, irrigating, and aerating sediments and soils.

Finally, from bioturbation, faeces, and the evolution of armour, a fourth major impact of flesh-eating life forms emerges: a reorganization of Earth's biogeochemical cycles[105,112–114].

Energy epoch five: fire

Of all the planets and moons in the Solar System, Earth is the only one to have fire. This is because, to have fire, all of three conditions must be met. (1) Fire needs a source of ignition—such as lightning strikes. Throughout Earth history, these have been abundant; today, there are more than 1.4 billion lightning strikes per year (ref. [115]), of which an appreciable number ignite wildfires[116]. Lightning occurs on other planets[117], but none of these meets the other two conditions. (2) Fire needs oxygen. Assuming current atmospheric pressure, Earth's air must contain at least 16% of the gas[118,119]. For most of Earth's history, oxygen levels have been lower than this threshold. (3) Fire needs fuel. So it is not until the evolution of vascular plants on land, around 420 Ma, that all three conditions were met[120].

From the start, fire has had both geological and biological impacts. Fire regimes drive the evolution of plant traits[121]; fires affect soils and air quality; and although, each year, a significant amount of biomass goes up in smoke, fire can promote biodiversity[122]. Fire may even have driven the initial spread of flowering plants[123]—an event that led to radiations of many other groups, including ants[124], bees[125] and mammals[126]. Furthermore, fire contributes new material to the Earth—charcoal, ash and soot—and may also act as a control on planetary oxygen levels[127]. But as an energy source, per se? That's a more recent development, and has come in two phases.

The first phase began with the evolution of a fire creature. This creature—a member of the genus *Homo*[128]—began to control the use of fire, deliberately setting fires alight and using fire for cooking. Exactly when cooking began remains controversial, with possible dates ranging from 1.5 Ma to 0.4 Ma (ref. [129]). The important point, though, is that cooking is a kind of predigestion: cooked food, be it meat[130], vegetable[130] or lipid[131], delivers more energy than the same food eaten raw. In using fire to cook food, hominins thus developed a way to extract more energy from their diets, and to eat a wider variety of food.

The second phase of fire as an energy source is even more recent—but the onset is nonetheless difficult to pinpoint. Does it start with the use of fire to manufacture labour-saving tools? With the smelting of iron, something otherwise energetically impossible? With the burning of fossil fuels such as coal to generate heat and light? With the invention of the internal combustion engine? Or with the discovery of the Haber–Bosch process for fixing nitrogen—which, in 1925, Alfred Lotka[132] described as the start of "a new cosmic epoch"? Perhaps these last three are the most important contenders, as together, they have transformed the planet[7]. In particular, the human input of energy to manufacture and deliver an otherwise limiting nutrient has produced far higher crop yields, enormously larger human populations, and gigantic populations of human-associated animals such as pigs, cows, horses and chickens[133]. Erisman and colleagues[134] estimate that between 1908 and 2008, industrially produced nitrogen fertilizer supported an additional four billion people and that by 2008, nitrogen fertilizers were responsible for feeding 48% of the human population. Meanwhile, Pimm and colleagues[135] judge that extinction rates are now 1,000 times greater than the typical background rate. In sum, in this epoch of fire, total biomass has remained high, but biodiversity has begun to fall.

The geological impacts of the age of fire are also poised to be dramatic, with rising levels of carbon dioxide and other greenhouse gases in the air, rising sea levels, increasing levels of nitrogen and plastic pollution, a remaking of the landscape with mines, tunnels, dams and cities, the introduction of new chemical compounds, and massive shifts in several biogeochemical cycles. However, the full geological effects of this epoch are, as yet, unknown.

Implications

Different schemata for considering the history of life allow different types of insights. For example, de Duve[136] identified a series of (mostly) biochemical events that happened just once, and discussed to what extent they would be likely to happen again were the tape of life to be replayed. Knoll and Bambach[137] put forward six 'megatrajectories' in the history of life, where each megatrajectory corresponds to the ecological diversification of a new type of life form (prokaryotes, unicellular eukaryotes, land plants, etc), thus linking evolutionary change with ecological complexity. And famously, Maynard Smith and Szathmáry[138,139] proposed a framework based on transitions between different replicating units (genes, chromosomes, individuals, and so on); this has been profoundly helpful in generating a deeper understanding of the levels at which natural selection operates[140].

In recent work, Lenton and colleagues[7] developed a schema for thinking about 'revolutions' in the history of life and Earth. As in the Perspective presented here, their focus is energy. But rather than considering expansions in the types of energy underpinning the biosphere, the authors examined a series of changes in free energy inputs and how these have altered global material cycles. On the basis of their analyses, they conclude that human sustainability will not only require a shift from fossil fuel to solar power, but also a far more active effort to recycle materials such as metals.

Here, I have taken a more bottom-up approach. In considering expansions in the types of energy underpinning the biosphere, I have sought to describe the step-wise construction of a life–planet system. Using energy expansions as the lens reveals a fundamental, recursive interplay between events in the evolution of life and the development of the planetary environment. From this viewpoint, a number of insights emerge.

First, increasing the types of energy sources available to life has led to a far more complex biosphere. Although only geochemical energy and sunlight can power the *de novo* transformation of inorganic carbon into living tissue, the complexity of the current biosphere rests on multiple levels of energy use. Cyanobacteria, for instance, often require the presence of non-light-using consort organisms in order to grow well[141–143]. Conversely, owing to the metabolic capacities of their prokaryotic symbionts and endosymbionts, eukaryotes are able to live in a far wider range of environments than they could otherwise access[82]. The step-wise diversification of the biosphere has, in turn, led to an expansion of possible niches, from more complex microbial mats to old shells and abandoned burrows. At the same time, the capacity of life to impact the planetary environment—and thereby the environment in which future life will evolve—has expanded dramatically with each epoch.

Because the construction of the biosphere has depended on these energy expansions, the vanishing of an energy source, even temporarily, could cause a corresponding contraction in the biosphere. In the context of the Phanerozoic, some authors have attributed large-scale patterns of both biospheric expansion and contraction to corresponding fluctuations in oxygen availability, with expanding ocean anoxia corresponding to mass extinction events (end-Permian[144,145]; end-Triassic[146]). Likewise, Kring[147] has suggested that one factor in the mass extinction at the end of the Cretaceous may have been dust ejected by the Chicxulub asteroid impact, which may have blocked out the sun long enough to cause a global collapse in photosynthesis. Quantifying this pattern further would be an interesting line for future research.

A related avenue for future research would be an examination of macroevolutionary trends of energy use. For example, Vermeij[148]

argued that the Phanerozoic has been characterized by the repeated replacement of low-energy life forms by those able to harness larger amounts of energy. Among the trends he identified were endotherms tending to replace ectotherms, and angiosperms tending to replace gymnosperms. (The lower-energy form does not always become extinct; sometimes its range is just restricted to a low-energy environment.) Investigating this trend for earlier epochs—or even applying it to human societies[149]—might be enlightening.

A second insight that emerges from this Perspective is that the two clear inflection points in the history of Earth—the Great Oxidation Event and the emergence of mobile animals—also coincide with expansions in the kinds of energy sources available to, and consumed by, living beings. The Great Oxidation shifted the prevailing chemistry of the atmosphere and upper ocean and made oxygen gas abundant. The emergence of life forms that eat one another transformed the nature of ecosystems, and introduced a powerful new set of evolutionary interactions, thus accelerating the pace of macro-evolutionary change. From this point of view, the familiar observation that Earthly life is powered by the sun takes on a more nuanced aspect: the modern biosphere is powered not merely by sunshine but by the oxygen that results from using sunshine in a particular way.

This Perspective further suggests that, through the harnessing of fire as a source of energy, Earth has now arrived at a new inflection point. Considering life–Earth history through the lens of energy expansions supports the view that the Anthropocene is a genuinely novel phase of the planet's geological and biological development—a conclusion independently reached by Lenton and colleagues[7]. The technology of fire may also, perhaps, mark an inflection point for the Solar System and beyond. Spacecraft from Earth may, intentionally or not, take Earthly life to other celestial objects (though whether any Earthly life forms can thrive elsewhere remains unknown).

As this is the only life–planet system we currently know of, it is impossible to know how representative it is of life–planet systems in general. But if the development of other life–planet systems requires a similar series of energy expansions, the framework presented here suggests a way to anticipate the paths that such systems might take. For instance, if a planet has only geochemical energy—perhaps because it is far from its star, or because it is a nomad[150,151] and has no star at all—any life present may have "a limited future in terms of the heights it could achieve"[152]. Or suppose a planet is unable to accumulate oxygen. This could happen if living organisms never evolve a way of splitting water to produce the gas in the first place[6,153]; but even if they do, the planet itself may have characteristics that prevent oxygen from ever building up[6,66]. Without oxygen, the geological, ecological and evolutionary potential of a life–planet system is likely to be constrained, even if life forms analogous to eukaryotes in their energy-harnessing power (Box 2) were to evolve. Conversely, some planets might be able to accumulate new forms of energy, and life forms able to take advantage of them, much faster than Earth has[66].

In short, this Perspective of energy expansions suggests that the likely development of a life–planet system will depend on the interplay between the planet's cosmic situation, its intrinsic properties, and the paths that evolving life can potentially take. The example of this life–planet system suggests that the development of a flourishing, complex biosphere depends on a virtuous circle between evolving life forms and transformations of their planetary home.

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Competing interests

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