MATTERS OF ACTIVITY

RAUE REIHE

RAW STUDIES

Regine Hengge

The Biological Foundation of Sustainability: The Essential Role of Microbes in Planetary Metabolism

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DE GRUYTER

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Edited by Horst Bredekamp
for the Cluster of Excellence
Matters of Activity

DE GRUYTER

Horst Bredekamp

VORWORT ZUR RAUEN REIHE / RAW STUDIES

Die *Raue Reihe* ist ein Publikationsorgan des seit 2019 existierenden Exzellenzclusters *Matters of Activity* der Humboldt-Universität zu Berlin. Diese aus mehr als 40 Fächern der Geisteswissenschaften, der Naturwissenschaften, der Medizin und des Design gebildete Institution versucht, die gängige Formel von der Passivität der Materie und der Aktivität des Geistes und mit ihr jedwede Form des Dualismus infrage zu stellen und Alternativen zu bestimmen. *Matters of Activity* zielt auf Antworten für zentrale Fragen, die mit dem Naturverhältnis des Menschen und damit mit den fundamentalen Krisen der Gegenwart zu tun haben.

Der Exzellenzcluster ist aus dem Vorgänger *Bild Wissen Gestaltung* entstanden, der für die bildgebenden Verfahren der Naturwissenschaften und der Medizin, aber auch allen weiteren Wissenschaften, die mit Diagrammen und Visualisierungen aller Art arbeiten, systematisch versucht hat, die Bipolarität von Aktivität und Passivität am Beispiel des Bildes zu überwinden. Vor dem Hintergrund dieses Ansatzes, der dem Bild nicht nur eine passiv wiedergegebene Qualität, sondern einen aus der Formprägung heraus aktiven eigenen Sinn zusprach, ist nun die Materie in ihrer weitesten Form in den Mittelpunkt gerückt, um sich mit dieser Horizonterweiterung der entscheidenden Frage nach der Aktivität an sich zu nähern.

Beide Cluster haben zahlreiche Publikationen und eine Reihe von Ausstellungen samt zugehörigen Katalogen hervorgebracht, so etwa mit der im Berliner Gropiusbau durchgeführten Schau *+ultra. gestaltung schafft*

wissen. Zusammenfassende Darstellungen sind bis heute immer wieder in Sammelbänden, die teils aus zentralen Symposien er hervorgingen, publiziert worden (etwa *Active Materials*, De Gruyter 2021 und *Toward a New Culture of the Material*, De Gruyter 2024).

Die neue Clusterpublikationsreihe soll diesen Veröffentlichungen im Sinne der Schnelligkeit, des Prozesscharakters und auch der möglichen Spontaneität zur Seite stehen. Ein Vorbild war jene *graue Literatur*, wie sie etwa die *Preprints* des Berliner Max-Planck-Instituts für Wissenschaftsgeschichte oder auch die legendären Bände des Merve-Verlages darstellen. Die in unregelmäßigen Abständen erscheinenden Hefte der neuen Zeitschrift stehen unter dem Gesamttitel *Raue Reihe*, um im Sinne des Clusters im digitalen Zeitalter darauf zu verweisen, dass die Widerständigkeit der Materie nach wie vor die entscheidende Bestimmung der Existenz in all ihren Spielarten darstellt. Mit *Rauheit* ist das Poröse, haptisch Spürbare, das Ungeschliffene, dafür aber umso stärker Konturierte verbunden, wodurch auch der Versuchscharakter der vorgelegten Texte betont wird. Im besten Sinn sollen sich diese Publikationen im Avantgardebereich des Tastenden und Erprobenden, das Risiko und Thesenbildung wagt, bewegen.

Thematisch soll es im Sinne des eingangs Beschriebenen um grundlegende Theorien, Begriffe und Fragestellungen gehen, wie sie im Exzellenzcluster regelmäßig erörtert werden. Hierzu gehört etwa, und dies sind mögliche Themen zukünftiger Hefte, der Begriff der *Energeia*; die Distinktionsmöglichkeiten zwischen organischer und nichtorganischer Welt; die Divergenz als mögliche Brücke im Sinne einer allgemeinen Morphologie; die Definition des Lebens als Latenz gerichteter Energie; der Begriff der Aktivität, etwa durch Temperaturschwankung sowie die Bedeutung der Skalierung. Bereits festgelegt sind Nummern zur Theorie des Filterns, zur mathematischen Topologie, zu einer neuen Philosophie des Waldes, zu einer Neubestimmung der Morphologie und der Kategorie der Schönheit sowie einer Definition des Analogen als „aktive Materie".

Das erste Heft stammt von Regine Hengge, die am Exzellenzcluster als Professorin für Mikrobiologie an der Humboldt-Universität arbeitet. Ihre

Ausführungen zum *Metabolismus* von den Bakterien bis zum gesamten Planeten als biologische Grundlage von Nachhaltigkeit berühren einen Kern der Fragestellungen und Themenbereiche des Clusters, und darin haben sie einen programmatischen Charakter.

PREFACE TO RAUE REIHE / RAW STUDIES

The academic journal *Raw Studies* is a publication organ of the Cluster of Excellence *Matters of Activity* at Humboldt-Universität zu Berlin, which has been in existence since 2019. This institution, made up of more than 40 disciplines from the humanities, natural sciences, medicine, and design, endeavors to question the common formula of the passivity of matter and the activity of the spirit and with it, any form of dualism by defining alternatives. *Matters of Activity* aims to find answers to central questions that have to do with human relationship to nature and with the fundamental crises of the present.

The Cluster of Excellence emerged from its predecessor, *Image Knowledge Gestaltung*, which systematically attempted to overcome the bipolarity of activity and passivity for image processing in the natural sciences and medicine, but also for all other disciplines working with diagrams and visualizations of all kinds. Against the background of this approach, which ascribed to the image not only a passively reproduced quality but also a meaning of its own that is active in its form, matter in its broadest form has now taken center stage in order to approach the crucial question of activity itself with this broadening of horizons.

Both clusters have produced numerous publications and a series of exhibitions and associated catalogues, such as the exhibition *+ultra. knowledge & gestaltung* at Gropius Bau in Berlin. To date, overarching publications have repeatedly been published in anthologies, some of which emerged from central symposia (such as *Active Materials*, De Gruyter 2021 and *Toward a New Culture of the Material*, De Gruyter 2024).

The new cluster publication series is intended to support these publications in terms of speed, process character, and spontaneity. One model was the *grey literature*, such as the *preprints* of the Max Planck Institute for the History of Science in Berlin or the legendary volumes of the Merve publishing house. The issues of the new journal, which are published at irregular intervals, have the overall title *Raue Reihe* (*Raw Studies*) in order to emphasize, in the spirit of the cluster in the digital age, that the resistance of matter continues to be the decisive determination of existence in all its varieties. The German word *Rauheit* (roughness, rawness) is associated with the porous, haptically perceptible, with the unpolished yet all the more strongly contoured, stressing the experimental character of the texts presented. In the best sense, they move in the realm of the avant-garde – tactile, experimental, risk-taking, and thesis-forming.

Thematically, in the sense of what was described earlier, *Raw Studies* will deal with fundamental theories, concepts, and questions regularly discussed at the Cluster of Excellence. These include – possibly as topics for future issues – the concept of *energeia*; the possibilities of differentiation between the organic and non-organic world; divergence as a possible bridge in the sense of a general morphology; the definition of life as the origin of latency in directed energy; the concept of activity, for example through temperature fluctuation and the significance of scaling. Issues on the theory of filtering, mathematical topology, a new philosophy of the forest, a redefinition of morphology and the category of beauty, as well as a definition of the analog as *active matter*, have already been determined.

The first issue is by Regine Hengge, who works at the Cluster of Excellence as Professor of Microbiology at Humboldt Universität zu Berlin. Her remarks on *metabolism* from bacteria to the entire planet as the biological foundation of sustainability touch on a core of the Cluster's questions and topics, making it a programmatic series introduction.

Regine Hengge

THE BIOLOGICAL FOUNDATION OF SUSTAINABILITY: THE ESSENTIAL ROLE OF MICROBES IN PLANETARY METABOLISM

"We've got ninety-nine percent the same genes as any other person. We've got ninety percent the same as a chimpanzee. We've got thirty percent the same as a lettuce. Does that cheer you up at all? I love about the lettuce. It makes me feel I belong."[1]

INTRODUCTION

The ongoing climate change, rampant biodiversity loss, omnipresent pollution and waste accumulation around the world can no longer be overlooked or denied. As a consequence, "sustainability" has become a buzzword – but what does it actually mean when it comes to the details and practical action? What has to be "sustained"? Obviously, humans need to reduce the production of CO_2, harmful pollutants and waste, with processes of production and consumption somehow becoming "circular". In 2012, the United Nations adopted Sustainable Development Goals (SDG) that became part of the UN 2030 Agenda for Sustainable Development (United Nations, 2015). These goals were essentially defined from an anthropocentric perspective and try to sustain human health and well-being by combining and compromising between economic, social, and environmental sustainability. Throughout the document, nature is still largely seen as a service-providing resource for the lives of humans requiring better management, although a few drastic readjustments might be needed in order to avoid catastrophic consequences of current trends (Leal Filho et al., 2020). In the following, a change of perspective will be proposed, i.e., instead of focusing on what Planet Earth can do for us – or, to put it more drastically, how we can best colonize and exploit Planet Earth – we should ask what we can do to make sure that the planetary biosphere will be able to continue to function and evolve with and for *all* its living inhabitants that depend on each other in this biosphere.

From a general perspective, this requires a fundamental change in our current worldwide dominating relationship with nature. In practical terms,

it calls for the definition of basic criteria and strategies that may guide us in our attempts to create a more integrative and, therefore, more sustainable way of human living – both on a large scale and in our personal lives. Such criteria are also important to prevent strategies or technologies that we might have been devised with the best of intentions from potentially becoming counterproductive and harmful. In general, the attempt to solve problems generated by technology with the help of even more technology is at least questionable. However, the problem may also arise in more specific contexts, e.g., with biomimetic or bio-derived active materials. These materials show intrinsic activities that can be triggered to perform appropriate movements without external energization or that otherwise respond to changing conditions in desirable and apparently more sustainable ways (Fratzl et al., 2021). Such activity may become maximal with miniaturization down to the molecular scale, a principle exploited by nanotechnology. Being focused on the functionality of these intrinsically active designed materials or objects, we tend to forget that they might also have a greater potential to be destructive in comparison to inert or inactive materials precisely because of their activity – in short, there is a potential to unintentionally exacerbate rather than contribute to solving the sustainability problem.

For most of human history, we have focused on understanding and solving local problems. However, what is obviously at stake now is the functioning of Planet Earth as a whole, or, more precisely, the extremely complex self-controlled and self-sustained biosphere occupying only a relatively thin "critical zone" around the Earth's surface (Latour, 2018) where life in all its biodiversity can thrive – including human life and societies. In order to understand destructive human activity and successfully transform it into supportive and re-integrative action, we need to understand how the planetary biosphere operates, which in turn requires understanding its evolution. For billions of years, the exclusive drivers in planetary evolution were microbes. As on modern Earth, they play a major role in planetary material and energy cycles, i.e., in planetary metabolism, and in the lives and health of all macroscopic living beings, including humans, where they

form tightly associated microbiomes. Strikingly, however, this key role of microbes[2] – which by definition are invisible – is still considered niche knowledge and is not sufficiently taken into account even by many scientists, e.g., in our current climate models (Casadevall and others, 2022; Cavicchioli et al., 2019).

EARLY EVOLUTION OF PLANET EARTH AND THE FORMATION OF A MICROBIAL BIOSPHERE

In the early Archaean world almost 4 billion years ago, when the first living cells appeared, which were primitive bacteria, the entire Planet Earth – including its surface – essentially consisted of non-organic[3] matter. Its atmosphere, too, was very different from the atmosphere today (Catling and Zahnle, 2020). Instead of free oxygen, carbon dioxide (CO_2), which originated from strong volcanic activity, was the major atmospheric component[4] besides water vapor (H_2O), nitrogen (N_2) and smaller amounts of hydrogen (H_2) and hydrogen sulfide (H_2S). Due to its greenhouse gas activity, the higher level of CO_2 compensated for sun radiation being approximately 30% less than today (Herwatz et al., 2021). As a result, the planet's surface temperatures were in a range compatible with life (0°C – 105°C).

The first living cells in this Archaean period of the Earth's history were hydrogen and sulfur bacteria, which had a *lithotrophic* lifestyle[5], meaning they derived energy from the high-energy electrons present in the inorganic molecules H_2 or H_2S and used this energy to convert the carbon in CO_2 into their own organic cell material (based on its main atomic composition designated as C/H/O in figs. 1–3; on the basics of energy metabolism, see background 1). In parallel, methanogenic bacteria evolved that used hydrogen and sulfur bacteria's living or dead organic material as energy and carbon sources for building their own cell material in an *organotrophic* manner, thereby generating methane (CH_4) as a waste product (fig. 1A). Overall, the combined activities of these bacteria resulted in a *linear* conversion of CO_2, H_2 and H_2S into living organic matter, CH_4 and free sulfur (S). Over the entire

Archaean period, this process steadily reduced the atmosphere's CO_2 content while its CH_4 level increased, the latter replacing the former as a greenhouse gas such that the planet's temperature remained hospitable to life.

→ BACKGROUND 1
General principles of energy metabolism

All living cells convert environmental energy (either from sunlight or chemicals) into biologically usable energy through chemical reactions, in which electrons (e^-) are transferred (redox reactions). Some redox-active molecules easily give off electrons, i.e., they are readily oxidized and rank highly on the quantitative redox potential (E_o') scale (e.g., H_2 or glucose). Other molecules are avid electron acceptors, i.e., they are readily reduced and rank lower on the redox potential scale (e.g., O_2, which is the best e^- acceptor of all molecules available in biological systems). When electrons flow from good e^- donors to good e- acceptors (both partners do what they "like" best, so to speak), this is, energetically, a downhill reaction, i.e., energy is released. The further apart the two molecules rank on the redox potential scale, the more energy is released – for good reasons, the transfer of 2 e^- from H_2 to O_2, which results in the formation of H_2O, is called the "Knallgas" reaction.[6] However, instead of allowing for an explosive free energy release (heat), living cells divide this electron transfer into many small steps by using intermediate organic electron carriers. These are associated with enzymes that convert the small amounts of energy released at each redox step into the cellular energy currency, i.e., they use it either to form an energy-rich bond in ATP[7] (chemical energy) or to establish a gradient of protons (H^+) over the cellular membrane[8] (electrochemical, i.e., essentially battery energy). These two forms of operative energy are interconvertible thanks to a ubiquitous enzyme, the membrane-associated ATPase[9], and are used to drive the diverse molecular machines (see background 2) that run all the cellular "business". Excess energy not immediately used is stored by synthesizing larger high-energy organic molecules such as starch or glycogen (two kinds of glucose polymers) or lipids (fat). Notably, living systems do not use the thermodynamically most "primitive",

i.e., least organized form of energy, which is the heat generated by combustion, as this would be destructive to their organic constituents. ←

After these processes had continued for roughly one billion years, evolution hit a major jackpot by inventing photosynthesis (PS). For the first time, life processes on Earth could make use of a practically unlimited *extraterrestrial* source of energy – sunlight. This dramatically accelerated the accumulation of organic living material on Earth. It also resulted in an accelerated consumption of CO_2 and, therefore, decreased temperatures. A freezing collapse of the living world was avoided thanks to the equally thriving methanogens still producing large amounts of CH_4. While the initially evolved mode of photosynthesis did not produce oxygen (anoxygenic PS), cyanobacteria optimized the sunlight-driven energization of electrons in this process by coupling it to the cleavage of H_2O into free oxygen (O_2), energized electrons (e^-) and protons (H^+). Despite this production of free oxygen, however, the atmospheric O_2 content did not rise for some hundreds of millions of years, because the O_2 generated was readily absorbed by the abundant iron (generating iron oxides, i.e., rust, resulting in the planetary surface turning brown) and by sulfur in the Earth's crust (fig. 1B). While the production of living matter had gained unprecedented efficiency with the evolution of PS, the accelerated material fluxes associated with it still represented a linear overall process, which implied two dangers that bore the potential for catastrophe: (i) a planetary temperature collapse due to nearly complete consumption of CO_2, and (ii) oxygen poisoning of the existing living cells as soon as the O_2 buffering capacity of the Earth's crust were exhausted, i.e., the available iron and sulfur would be fully oxidized, and free O_2 would then accumulate in the atmosphere.

Indeed, the second of these catastrophes, also called the *Great Oxygenation Event*, started around 2.8 billion years ago. While bacteria later learned to make good use of oxygen (see below), they were first hit by the "dark side" of free atmospheric oxygen, i.e., its ability to convert into various

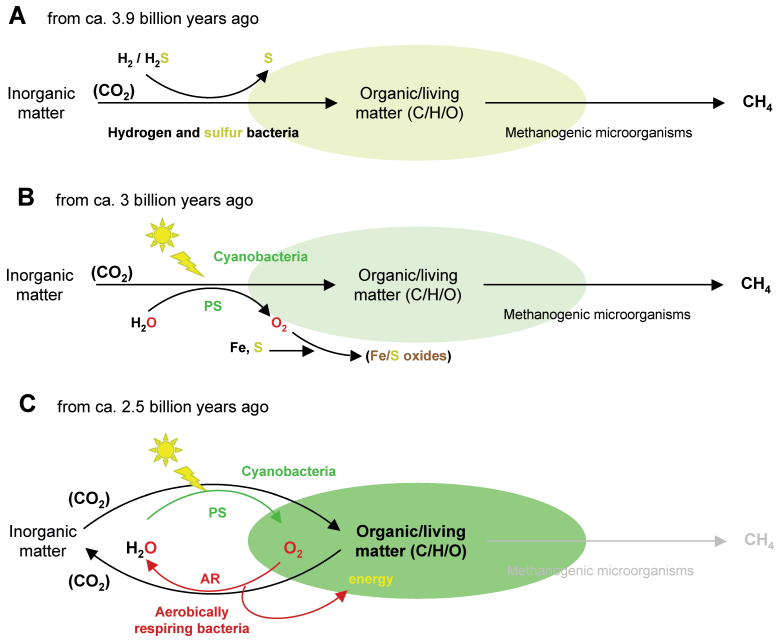

FIGURE 1

Successive stages of evolution of the early planetary biosphere inhabited exclusively by microorganisms. Abbreviations: PS, photosynthesis; AR, aerobic respiration; C/H/O, organic matter, which mainly consists of carbon, hydrogen and oxygen atoms.

reactive oxygen species (ROS), also called oxygen radicals, especially under conditions of UV irradiation, which is a part of sunlight. These ROS attack organic molecules – including cellular macromolecules such as proteins, DNA and lipids – by oxidizing (i.e., withdrawing electrons from) these molecules and thereby damaging essential functions in living cells. But bacteria found solutions to this problem. Many sulfur and hydrogen bacteria, as well as the methanogens, withdrew into deeper, oxygen-free earth layers and sediments, where they can be found to this day, now called anaerobic

bacteria. Others developed an aerobic lifestyle by evolving enzymes with the ability to eliminate ROS, as well as elaborate repair mechanisms capable of reverting oxidative damage of proteins or DNA.

The other disaster, i.e., a potential total exhaustion of CO_2, was avoided by another jackpot event in evolution, the invention of aerobic respiration (AR; fig. 1C). AR depends on an enzyme (terminal oxidase) in the respiratory electron transfer chain, which can dump low-energy electrons derived from organic energy sources (such as sugars) onto O_2, thereby generating H_2O. On the one hand, this allowed for more efficient use of energy sources.[10] In addition, dumping electrons onto O_2 to create H_2O is the reversion of the cleavage of H_2O into O_2 and electrons, which occurs in photosynthetic cyanobacteria. Even better, the organotrophic energy metabolism associated with AR oxidized the carbon atoms in the organic energy sources to CO_2. In other words, life had managed to link photosynthesis and aerobic respiration in a way by which the material fluxes of water/oxygen and CO_2/organic matter had become fully *circular* (fig. 1C).

Overall, this established a power cycle energized by sunlight that drove the conversion of nearly all available CO_2 into organic living matter, which was now able to form a microbial biosphere that slowly covered the planetary surface.[11] In this system, the atmospheric CO_2 was dynamically stabilized at quite a low concentration, with essentially all other carbon equally dynamically bound in living matter, while free oxygen reached a substantial atmospheric concentration (but still somewhat below its current concentration). Thus, the carbon-based planetary biosphere had turned into a gigantic *homeostatic* or *self-sustaining* system that kept on running since the CO_2 required for cyanobacterial photosynthesis was regenerated by aerobically respiring bacteria feeding on other bacteria (fig. 1C). As James Lovelock put it: *Gaia* had awakened (Lovelock, 1988).

EVOLUTION AND FUNCTIONING OF THE MODERN PLANETARY BIOSPHERE

All principal features and functions of life were already fully evolved in this still entirely *prokaryotic* biosphere. Its single-cell inhabitants consisted not only of bacteria, but also the related *archaea*, which had phylogenetically split off from primitive bacteria at a relatively early stage, possibly in niches with extreme environmental conditions (Eme et al., 2017).[12] Prokaryotic cells are surrounded by at least one lipid membrane and additional stabilizing cell wall structures. They spend a considerable part of their available energy to control fluxes of matter and energy across this semipermeable boundary. As a result, an intracellular composition and spatial order is homeostatically maintained that is very different from the outside environment. Thus, living cells are thermodynamically open systems that exist in an actively maintained and highly dynamic state far from the thermodynamic equilibrium. Under good conditions, i.e., when enough nutrients and energy sources are available and physical parameters such as temperature, salt or pH are within tolerable limits, cells also manage to grow and proliferate. In order to do so, they need to know what to maintain and how to repair, rebuild, and properly partition it during cell division. In other words, they contain coded information (in their DNA[13]) and the molecular machinery to duplicate and execute this code (DNA/RNA polymerases and ribosomes). Their versatile energy metabolism converts external energy sources into readily usable or storable cellular energy forms, which are either chemical (e.g., ATP) or electrochemical (i.e., the H^+ gradient over the cellular membrane which serves as a battery). These energy forms power a myriad of elaborate molecular machines that perform the work required for maintenance, building, division and movement of these microscale homeostatic single-cell systems (see background 2).

→ BACKGROUND 2

Enzymes, molecular machines and living systems

Many biological chemical reactions, particularly electron transfer reactions in energy metabolism, can, in principle, occur spontaneously, i.e., they are energetically going "downhill" as they proceed from a state A with a higher energy level to a lower energy level, state B. Nevertheless, many of these chemical processes are actually very slow as they have to pass through an intermittent molecular state A* at an energy level that is higher than that of state A (since chemical bonds have to be disrupted before they can reform in different configurations). The energy difference between states A and A* is called the *activation energy*. *Enzymes* are biological catalysts, which speed up such reactions by reducing this activation energy as they assist in establishing the intermittent state A* – they help to "tunnel" through the activation energy hill.

On the other hand, many biological chemical reactions – including those involved in building the macromolecular cell components or in unfolding and/or degradation of defective proteins in cellular protein quality control – are energetically "uphill", i.e., the final state B is at a higher energy level than the starting state A. These reactions would not occur spontaneously but need *energization*. In addition, many precise material transfers such as the transport of ions, small organic molecules (sugars, amino acids, etc.) or macromolecules (RNAs, proteins, polysaccharides) from location A to location B within the cell or across the cell envelope require energization, just like any cargo transport in the macroscopic world. These tasks are executed by nanoscale *molecular machines*, which are proteins or often complexes of several proteins (plus sometimes also RNAs) with catalytic (enzymatic) or transport activities. Key cellular reactions are performed by even *programmable molecular machines* such as DNA and RNA polymerases, which synthesize new strands of these nucleic acids along an existing template strand, or the ribosomes, which decode the genetic information in mRNA to synthesize a myriad of different proteins. In order to do their job, these molecular machines contain energizing protein domains or subunits, which cleave ATP (ATPases) or other energy-rich molecules or they couple their (transport) activity to the energetically

downhill influx of H^+ across the cellular membrane (or of other ions for which gradients are also established across the membrane). Thus, these molecular machines use chemical or electrochemical energy to perform highly specific mechanical or chemical work – they are the workhorses that build, organize and operate cells. It is noteworthy that, unlike the macroscopic machines invented billions of years later by humans, the tiny molecular machines inside cells are not energized by heat (i.e., combustion or simple fuel burning), but use "smarter" forms of energy.

At the microscale, life *emerged* with the cell as its smallest functional unit. A cell or, finally at the macroscale, a multicellular organism are not machines (note that, vice versa, it also does not make sense to call a protein or a complex molecular machine "alive"). Rather, living cells and organisms are *homeostatic systems* that use energy – in practice this means energy metabolism and molecular machines – to control fluxes of matter, energy and information across their semipermeable internal and external boundaries. In doing so, they self-sustain, self-repair and self-reproduce in a dynamic semi-stable state that is far from the thermodynamic equilibrium (Prigogine and Stengers, 1984 / 2017). Thereby, living systems thrive, grow and proliferate in constant exchange with their environment – with a tendency to change or actually design their environments according to their needs and thereby expand their physiological boundaries, i.e., their zone of homeostasis (Turner, 2016). This process of boundary expansion is thermodynamically favored by a reduction of maintenance energy, which ultimately drives the evolution of living systems, ecosystems and the planetary biosphere to more and more integration and complexity. ←

Yet, unicellular organisms have an Achilles heel: their small size, which results in a very high surface/volume ratio. This makes their maintenance energetically costly and leaves them vulnerable in often toxic and unpredictably changing environments, where potentially life-threatening abiotic and biotic challenges abound. To cope with these, cell envelopes of bacteria (and archaea[14]) are densely packed with diverse molecular sensors that monitor and react to environmental parameters (diverse chemicals, temperature,

pH, etc.). This information is then transduced into the control of synthesis and activity of specific stress response systems that eliminate stress agents or repair existing cellular damage. In addition, a preventive, general stress response confers enhanced multiple stress resilience during beginning nutrient limitation, i.e., before the bacteria completely run out of molecular building blocks and energy sources they would need for repairing the damage (Storz and Hengge, 2011). In most natural environments, nutrients become only sporadically available and are rapidly consumed, which makes starvation quite common. To better cope under these harsh conditions, many of the organotrophic bacteria no longer restricted themselves to make a living from dead organic material, but became predators with active hunting and killing strategies (Munos-Dorado et al., 2016), such as secreting antibiotics and even shooting toxins directly into other bacteria (Coulthurst, 2019).[15] In addition, bacteriophages, which are viruses that attack, replicate within and finally kill bacteria, co-evolved with bacteria (Dion et al., 2020; Hampton et al., 2020).

In summary, life in the prokaryotic biosphere was energetically costly and precarious, with most of the available energy being used for the maintenance of single cells and entire populations (i.e., to replace cells that had been killed). Evolution responded to this selective pressure with various innovations. A multicellular lifestyle turned out to be a highly successful strategy, i.e., the co-living in large aggregates termed *biofilms*, where bacterial cells are embedded in a protective extracellular matrix of self-produced polymeric fibers (Flemming and Wuertz, 2019). These fibers are either proteins (often in the very stable beta-amyloid conformation) or polysaccharides (e.g., cellulose), which bind water, protect from desiccation and confer stability and elasticity to entire biofilms, allowing them to grow and fold in a tissue-like manner (Erskine et al., 2018; Serra and Hengge, 2019). Moreover, building these bacterial "fortresses" not only helps to keep nasty predators beyond the new community boundaries, but also brings large numbers of cells so close together that the surrounding space is no longer significantly larger than their own intracellular space. This situation is

completely different from that of a lonely cell required to passively endure unpredictable changes in a large environment – within these bacterial communities, the extracellular space becomes a *biofilm-internal milieu* that the bacteria are able to control *homeostatically*. Thus, bacteria in a biofilm can actively generate or "design" a cozy home or *niche*, where life is safer, more predictable, and energetically more efficient (Hengge, 2020). Due to this energetic advantage, the multicellular lifestyle obviously evolved early and repeatedly in otherwise very different bacteria, as well as in archaea and the much later appearing unicellular eukaryotes – multicellularity seems an emergent property of life (Flemming et al., 2016; Hengge, 2020; Serra and Hengge, 2021). Furthermore, multicellular community life in biofilms allows for coordinated efforts by many cells that collectively organize via chemical communication (Mukherjee and Bassler, 2019). This includes joint toxin or exoenzyme production, social movement and even social hunting and large-scale community morphogenesis (Munos-Dorado et al., 2016). In addition, it made physiological differentiation into distinct specialized cell types possible, which allowed for division of labor within the community, and bet-hedging[16] as a novel stress survival strategy (Lowery et al., 2017; Veening et al., 2008). In essence, these social prokaryotic microbes had evolved into early multicellular organisms that retained the option to switch back to unicellularity when required.

Another key innovation in the microbial biosphere was *endosymbiosis*, which led to intracellular compartmentalization and increased operative efficiency of single cells (Margulis and Bermudes, 1985; Martin et al., 2015). The origin of endosymbiosis is likely predation, where one cell engulfs another, but the latter manages to resist digestion and may even turn into an intracellular parasite, followed by a long evolutionary path from mutual adaptation to cooperation and finally, symbiotic division of labor. Thus, the descendants of an alpha-proteobacterium engulfed by some archaeon evolved into a cellular organelle called the *mitochondrion*, which became its cellular power facility by optimizing energy metabolism (Roger et al., 2017). Whether this fateful encounter happened before or after the archaeal host

had evolved a membrane around its DNA is currently unclear. In any case, around 1.8 billion years ago, such *eukaryotes* featuring a DNA-containing nucleus and mitochondria appeared that would later on evolve into unicellular fungi (such as yeasts) and protozoa. Eventually, an early eukaryote picked up a cyanobacterium, which started a new round of endosymbiotic evolution that led to *chloroplasts*, which are cell organelles specialized in performing photosynthesis. The result was the first photosynthetic eukaryotes, which were unicellular algae.

With multicellularity and the compartimented eukaryotic cell architecture established, the stage was set for the evolution of larger and more complex life forms, again expanding the boundaries of actively maintained physiological homeostasis. Furthermore, with the invention of sex – the highly organized recombination and redistribution of DNA from two parental cells during the production of offspring – each daughter cell became a new fitness experiment, speeding up evolution dramatically. Multicellular slime molds, which show striking morphological differentiation in their reproductive cycles, and multicellular algae, which may have looked like the green spheres of modern *Volvox*, appeared. The latter further evolved into the first primitive plants, which started to colonize the land around one billion years ago. Somewhat later, individual protozoa became multicellular and gave rise to the first primitive animals. In addition to the ability to produce cellulose, which primitive plants had inherited from their bacterial ancestors, they invented the synthesis of lignin and hemicellulose. The combination of these polymers eventually generated wood as a stabilizing material that allowed plants to grow larger, even against gravity. On land, the planetary surface turned green and plants (as well as algae in the oceans) began to contribute significantly to planetary photosynthesis, binding additional carbon and increasing free O_2 levels further (which eventually stabilized at 21 % in the atmosphere). Fungi and small animals feasted on microbes, but many microbes also discovered new niches by colonizing the external and internal surfaces of their new and much bigger biospheric co-inhabitants. While many of these interactions were at least

initially pathogenic or parasitic, they eventually evolved into symbiotic *microbiomes*.

All these new achievements converged to produce the *Cambrian Explosion* (around 600 to 500 million years ago) with the appearance of most phyla of animals, which for the first time produced a rich fossil record. Complex new ecosystems evolved and merged into a highly diverse biosphere, which again covered the planet, but looked very different from the ancient microbial biosphere. Even though plants and animals, which dominated the land about half a billion years ago, would have appeared quite strange to us today, this biosphere essentially operated in a manner similar to the biosphere of our historic pre-industrial times (fig. 2). Multicellular plants, algae, fungi and animals had become essential players in the originally microbe-invented, sunlight-driven photosynthesis/respiration cycle. Non-photosynthetic organisms consume organic matter (living or dead) both as a source for building their bodies (anabolic metabolism) and as a source of energy, i.e., for respiration (catabolic metabolism). The latter produces CO_2 that is required for photosynthesis – interestingly, this means that plants and photosynthetic microbes "generously" produce excess biomass for consumption by animals, fungi or other microbes to recover fresh CO_2. This means that interlinked biospheric material and energy cycles continue to sustain life in a dynamic balance of growth and death that also drives evolution.

Overall, the biosphere consists of organic matter that is constantly interconverted in *circular fluxes*. But living systems also entertain complex relationships with non-organic matter in their environment. Outside of the biosphere, non-organic matter (such as minerals or metals) is not systematically turned over in circular processes. Nevertheless, living (eco)systems make use of certain non-organic molecules and integrate them into their circular metabolic processes in a highly controlled manner. Thus, many essential enzymes within living cells contain metal ions (e.g., iron, magnesium, manganese, cobalt and others) as key catalytic components of their reactive centers, simply because metal ions are perfectly suited to drive the

numerous electron shift or transfer (redox) reactions required in energy metabolism and many other cellular biochemical reactions. The common role of iron in many enzymes also reflects the fact that water-soluble iron ions (Fe^{2+}) were highly abundant and thus easily accessible in the archaeal anaerobic world, where these enzymes originally evolved. This actually changed during the Great Oxygenation period, because – in the presence of free O_2 – Fe^{2+} becomes oxidized to water-insoluble Fe^{3+} (which precipitates as rust). This resulted in massive iron starvation – a challenge that bacteria countered by evolving amazingly elaborate uptake systems capable of scavenging remaining molecular traces of soluble Fe^{2+} which still operate in today's organisms (including our own bodies).

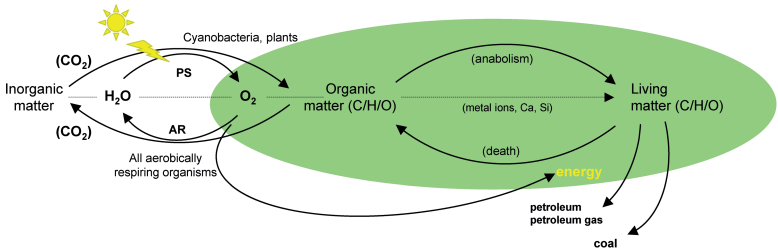

FIGURE 2
The principle functioning of the biosphere after the evolution of macroorganisms. Abbreviations and symbols are as in fig. 1.

Metal ions, however, are also a double-edged sword, as they are not only indispensable for numerous metabolic enzymatic reactions, but also promote many redox reactions that are destructive and toxic to organic matter. An example is the famous Fenton reaction,[17] in which Fe^{2+} drives the production of hydroxyl radicals (OH), which are the most reactive and therefore most toxic of all oxygen radicals (ROS). To reconcile this toxicity with their need for certain metal ions, bacteria evolved intricate systems of metal homeostasis, which tightly control the uptake and efflux of metal

ions as well as their intracellular storage and incorporation into enzymes (Rosen, 2002). Some even learned to use the antimicrobial activity of metals and metalloids to kill their microbial competitors (Li et al., 2021). Related metal homeostasis systems are still functioning even in our own cells.

Non-organic matter in larger amounts is also found in organisms (biomineralization), including calcium (e.g., in coral reefs, shells of marine invertebrates, or bones of vertebrates) and silicon (e.g., in diatoms). During evolution, cells managed to detoxify the originally toxic calcium ions by precipitating them as calcium carbonate (calcite) or calcium phosphates – and then discovered how to integrate this hard, stiff material into their cellular and organismic structures as a stabilizing skeleton or protective shell (Ehrlich et al., 2021; Murdoch, 2020). This, again, required a homeostatic control of calcium fluxes in often specialized cells, which in turn allowed the evolution of signal transduction systems that use calcium ions as signaling molecules (Carafoli and Krebs, 2016).

Most importantly for what would happen later, the biosphere did not, in fact, operate in a fully circular way; rather, some organic matter elapsed (fig. 2). When living organisms die, they are consumed by organotrophic animals, fungi and bacteria, whose aerobic energy metabolism oxidizes part of the carbon contained in dead organic material back to CO_2. However, during the Earth's long history, large amounts of organic matter, primarily from dead algae, became confined in sedimental locations where not enough oxygen was available to allow full oxidation of this organic carbon to CO_2. This resulted in the formation of extended subterranean deposits of still energy-rich petroleum and petroleum gas (C/H) as well as coal (essentially pure C) – a sleeping chemical time bomb that would eventually blow up, driving the transition into the *Anthropocene*.

For the longest time in human history, the activities of a slowly growing human population around the world remained integrated in the biosphere's material and energy cycles. To today, many indigenous cultures – no matter whether they live as hunter-gatherers or from agriculture – still use and transform mainly organic materials and see themselves as a part of and nourished by the biosphere (Ingold, 2000). With the advent of industrialization in Western countries, this perspective changed entirely. The biosphere and non-organic matter from the Earth's crust were now regarded as an apparently unlimited resource for making products that could be "consumed", which basically means their transformation into "waste". As a consequence, the economy changed from a circular to a linear processing of matter, literally fueled by the discovery of a seemingly unlimited new energy resource that the planet provided in the form of petroleum and coal. This new human economy has been affecting the biosphere in three essential ways that are all massively toxic and thus destructive (fig. 3):

(1) Massive burning of fossil and newly grown organic matter

For the recent about one and a half centuries, the initially Western and then worldwide human economy has been energized by burning coal and petroleum. In addition, burning is the standard method of "waste" disposal, i.e., non-used agricultural or post-consumption materials. The latter in particular are usually already in a state of high disorder or entropy, where burning represents the only terminal use (if any use is intended at all). Moreover, humankind is burning tropical and other forests at an ever-increasing rate. Burning constitutes the final oxidation of carbon atoms in organic materials to CO_2, which releases the bulk energy stored in C-H bonds in the form of heat, some of which we convert into electrical energy or use directly as kinetic energy to drive different engines or, on much smaller scales, chemical reactions. For thermodynamic reasons, this conversion of heat into other forms of energy is rather inefficient, and its high

temperatures structurally destroy organic matter – which is why heat from burning processes is very rarely used in and by biological systems. As a result of this massive combustion of fossil and newly grown organic matter by humans, the atmospheric CO_2 content has been rising at a speed unprecedented in planetary history (from about 280 ppm in pre-industrial times to >400 ppm in the 21st century). It is now literally firing back – due to the greenhouse gas effect of CO_2 – as a no longer deniable climate change and global warming with all its disastrous consequences.

(2) Massive conversion of fossil organic matter (petroleum) into plastic and non-natural organic chemical products that are toxic to the biosphere

Petroleum is also *the* raw material for the production of (i) plastics, i.e., highly stable artificial polymers, and (ii) most industrial organic chemicals. These chemical conversions are energetically costly, indirectly contributing to massive CO_2 production. Moreover, most of these chemical products currently generated are toxic to biological systems. Discarded macroplastic either gets burned to CO_2 or ends up polluting the planet's land and oceans where it kills wildlife. In addition, mechanical or chemical stress, heat and irradiation turn plastics into physiologically harmful microplastic particles and fibers that are now found in all organisms and ecosystems, i.e., essentially anywhere in the biosphere. Organic chemicals that we produce as drugs to combat human or animal diseases, as well as omnipresent food preservatives and additives, turn out to be massively detrimental to the microbiome that our bodies depend on for long-term health (Maier et al., 2018). Moreover, after drugs and other compounds are shed, they accumulate in ecosystems where they damage other living organisms and – via our food and drinking water – find their way back into our own bodies. The same happens with a myriad of industrial organic chemicals, including PCBs, chemical dyes, and many others – the list is endless. Most notably, many of these organic chemicals used in medicine or agriculture are produced with the very intention to be biologically toxic – just think of antibiotics (killing

not only pathogenic bacteria, but also our own beneficial microbiota) and all kinds of "pesticides", which include insecticides (killing insects, including those that pollinate many of our crop plants), herbicides (killing "weeds", i.e., essentially all plants except single desired crops), fungicides (also killing mycorrhizal fungi that most plants need for efficient nutrient uptake) and other "biocides". Even when human-produced organic chemicals are not designed to be immediately toxic, they are designed – often by introducing fluorine or chlorine atoms into ring structures – to be highly stable, which means they are not subject to biological degradation. As a consequence, these molecules slowly accumulate within the environment and organisms until they interfere with essential biological processes and become toxic.

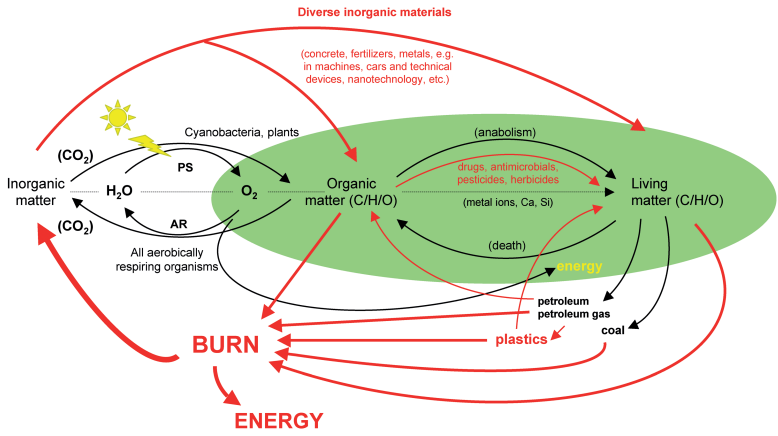

Figure 3
Human activities (highlighted in red) affecting the integrity and functioning of the planetary biosphere. Abbreviations and symbols are as in fig. 1.

(3) Massive extraction, processing and introduction into the biosphere of non-organic matter from the Earth's crust

In the course of our technological "revolutions", humans have indeed been turning the Earth's crust upside down by extracting non-organic raw materials through hugely energy-intensive procedures. This started in prehistoric times with the discovery that metals could be used to make weapons and tools to transform human surroundings mechanically. These activities, however, remained without large-scale ecological consequences since the necessary energy supply – consisting of human and animal muscle force and local fire – was severely limiting. Again, this changed fundamentally with the discovery of fossil fuels as an apparently limitless energy source, which has scaled up the extraction of non-organic matter from the Earth's crust at an ever-increasing pace. The resulting technological transition from organic to non-organic matter can be seen at a particularly large scale and with devastating consequences in human building and agriculture.

→ EXAMPLE 1: Building with concrete

For a long time, the building of human shelters, huts, and, finally, houses relied on organic materials such as wood, reed, bamboo, or mud. Later on, these organic materials were widely replaced by stone, and, most recently, by concrete. The worldwide production of cement and concrete contributes a substantial part to the current global CO_2 release and threatens to deprive coastal shores worldwide of sand (Habert et al., 2020). Concrete buildings and asphalt roads produced from sand and petroleum derivatives now seal a no longer negligible part of the planetary surface, which destroys biological habitats, diminishes agricultural areas, and promotes catastrophic flooding.

→ EXAMPLE 2: Modern agriculture

The transition from organic procedures to using products of inorganic chemistry is a hallmark of modern agriculture. It started with the hugely energy-intensive procedure invented by Fritz Haber to synthesize ammonium (NH_4^+) from intrinsically inert nitrogen (N_2) in the atmosphere. This tech-

nology is still the basis for producing inorganic chemical nitrogen fertilizers (mostly nitrate, i.e., NO_3^-) that have largely replaced traditional organic practices maintaining complex soil life and fertility. Inorganic fertilizers (including phosphate and potassium) alongside herbicides, fungicides and insecticides essentially turn the organic soil ecosystem with all its living micro-inhabitants into a nearly mineral substrate (Jacobsen and Hjelmsø, 2014). As a result of this loss of organic content and microbial biomass and diversity, soil water retention capacity becomes severely compromised. In addition, such impoverished soil can switch from acting as a substantial carbon sink to carbon emission, thus contributing to climate change instead of counteracting it (Ren et al., 2024). Furthermore, inorganic fertilizers need to be used at high concentrations since their uptake by plant root systems no longer works efficiently when fungal root networks (mycorrhiza) have been destroyed (Sosa-Hernández et al., 2019). These excess quantities of nitrogen fertilizers (mainly NO_3^-) are also transformed into the superactive greenhouse gas N_2O in a bacterial process called denitrification – or, along with excess phosphate, reach ground water, rivers and marine shores, where they promote deadly toxic cyanobacterial blooms.

Today, we have also littered the planetary surface with cars, trains, ships and airplanes while living amidst countless technical devices mainly made of tightly mixed and intertwined non-organic materials. The fact that these non-organic materials are not naturally integrated into biospherical material cycles actually lies at the origin of our modern material processes operating in a linear manner – production and consumption are converting resources into products into waste. As a result, we are now faced with massive planetary waste and an environmental pollution crisis. In making and using our technological devices, we fully focus on the desired function, but are strikingly insensitive to toxicity and biological damage – an anthropocentric perspective and priority that, unfortunately, has remained unchanged, especially with new technologies such as digitalization and nanotechnology, which are considered highly innovative but, again, largely depend on non-organic materials.

All of these activities and their resulting waste and pollution have interrelated, detrimental effects on local and global ecosystems. Since the beginning of agriculture and, above all, of the use of fossil fuels allowing mass extraction of non-organic matter – two innovations one might call the first and second fall of humankind –, human activity has destroyed about half of the Earth's overall plant biomass. The anthropogenic mass, i.e., non-organic human-made items such as buildings, roads, and machines – in short, the "technosphere" –, has now surpassed the organic mass of all living beings on Earth, i.e., the biosphere (Elhacham et al., 2020). One of the consequences is a massive reduction in worldwide biodiversity and an accelerating mass species extinction that is associated with a loss of overall stability and robustness of ecosystems.

In a nutshell, modern human activity on this planet has been burning and intoxicating our highly evolved and intricately self-sustained biosphere, replacing it with a non-organic technosphere and suffocating what has remained of it in non-biodegradable waste. By destroying the organic integrity of the biosphere, driving biological species into extinction and massively reconverting organic biomass back into CO_2, current human activity is essentially reversing planetary evolution.

FUNDAMENTAL STRATEGIES TO SUSTAIN AND REBUILD, RATHER THAN DESTROY THE PLANETARY BIOSPHERE

Is anybody still surprised that we have entered the *Anthropocene*, i.e., the period in planetary history from when on the "traces" of human activities will remain detectable forever? In fact, humankind will leave much more than traces or "footprints" if we do not re-integrate our activities into the organic material and energy cycles that have generated and are (still) operating the planetary biosphere. Strategies and directions in doing so may be directly derived from the summary of human destructive activities outlined above, with the following list focusing on general principles illustrated with just a few important examples:

(1) Avoid burning organic matter

The fact that today's planetary CO_2 emission exceeds its fixation is not only a result of the massive burning of fossil resources such as coal, petroleum and gas, but also of the worldwide burning of living or newly grown organic matter, i.e., a reduction in the biosphere's mass. Thus, it is obvious that global deforestation or large-scale burning of agricultural "waste" needs to be drastically reduced. In addition to the reduction of burning, we should try to preserve carbon as much as possible once it is fixed by choosing carbon sink solutions over carbon neutrality. Thus, instead of burning "biogas" – produced from agricultural waste and household bio-waste – or "biofuel" produced from crop plants – which theoretically is carbon-neutral and remains an option for special purposes –, non-used plant material should be composted and/or used to increase organic content in the soil wherever possible. Similarly, we should see oil produced by algae not as fuel, but rather as a precious resource (replacing petroleum) for chemical syntheses of useful organic molecules – this way, large-scale biotechnological oil production by algae from sunlight, CO_2, and water as well as new enzymatic pathways for CO_2 fixation, which use and improve natural enzymes by synthetic biology (Bierbaumer et al., 2023), may even become a significant sink for CO_2. Also, current ideas of carbon capturing by burning newly grown plant matter (e.g., for heating buildings) while filtering out, compressing and storing CO_2 below ground look promising only on paper, since the huge amount of energy required for CO_2 storage (for simple thermodynamic reasons) is usually left out of the picture. Overall, *biological* carbon capture – via the growth of photosynthetic organisms, i.e., plants, algae, or cyanobacteria, which could also be improved through synthetic biology – is more efficient than *technical* carbon capture, as the former happens in living cells that retrieve the necessary (chemical) energy from sunlight, whereas the latter requires extra energy input.

(2) Promote the growth of organic life instead of destroying it

The growth of photosynthetic organisms is based on the fixation of atmospheric CO_2 and thus constitutes the direct natural carbon sink. Plants actually represent >80% of the entire planetary biomass (Bar-On et al., 2018). Therefore, a wide range of plant-based activities should be promoted, ranging from the planting of trees to growing crop plants that are not burned later. Another important strategy is the revitalization of agricultural soil, which involves restoring and actively caring for soil microbiota that include mycorrhizal fungi as well as typical soil bacteria, protozoa and tiny soil-dwelling animals. This requires switching to more organic forms of agriculture that increase the organic content of soil (by adding back plant "waste" directly or in a fermented form, i.e., as compost, which is enriched for the relevant microbes) and use fewer or no pesticides and inorganic fertilizer. This would not only counteract the danger of agricultural soil changing from a globally significant carbon sink to emitting carbon, which renders climate change mitigation almost impossible (Ren et al., 2024). Thus, restoring the natural organic content of agricultural soil worldwide could, in fact, contribute fundamentally to counteracting climate change (Certini and Scalenghe, 2023). It would also slow down biodiversity decline, including that of soil microbes (Jacobsen and Hjelmsø, 2014) and pollinating insects, and it would reduce the pollution of water environments that leads to algal blooms that are deadly for other organisms. Generally speaking, instead of remaining "anti-biotic" (meaning "counteracting life") by burning and intoxicating the biosphere and replacing it with the technosphere, human practices need to become "probiotic" in a broad sense (Lorimer, 2020). These probiotic practices would not only set in motion multiple interlinked positive effects but also build upon microorganisms, whose essential role in all natural material cycles and the health of organisms and ecosystems has not been sufficiently appreciated, if not ignored, for too long (Casadevall et al., 2022).

(3) Transition to renewable energy, i.e., solar energy or natural energy forms derived from solar energy

Given our current mainly CO_2-driven climate change, there is obviously no alternative to the transition to renewable energy.[18] As a consequence, a worldwide general agreement on the necessity to phase out of fossil energy and its associated CO_2 release finally seems to be emerging even though actual strategies, technologies and time frames remain under controversial debate. Sunlight, wind, tides, geothermal heat and – in many countries for a certain duration – nuclear fission will provide electricity and H_2 under eventually carbon-neutral conditions. However, risks imposed by the used technology, which may endanger ecosystems and biodiversity, need to be taken into account – from excessive extraction of necessary resources (e.g., from the arctic sea floor) to accumulating radioactive waste.

(4) In technology and design, use or at least mimic biological processes as much as possible

By switching to renewable energy, we are already learning from nature. This applies not only to sunlight as the major direct and indirect energy source, but also to the production and use of hydrogen. Thus, photolytically or electrolytically cleaving H_2O into O_2 and energy-rich H_2 and then burning it back to H_2O directly mimics the biological photosynthesis/respiration cycle (fig. 2; H_2 corresponds to the two energy-rich electrons generated by photosynthesis plus two protons which are ubiquitous). Besides using these natural energy sources, we could also benefit from looking to nature for a more efficient usage. Our current energy production, including renewable energy, is centralized, involves large-scale power plants and devices, and requires far-reaching nets for energy distribution to places of use. By contrast, the energy forms used by cells within an organism are generated locally and on-demand, regardless of whether this is chemical energy (ATP) driving chemical reactions and molecular machines, electrochemical energy used for membrane-associated functions (the membranes surrounding cells essentially function as batteries) or electrical energy as the basis of

signaling processes (e.g., in nerve cells). The source of these forms of energy is, again, chemical energy that is stored either locally directly in the cells for short-term use (glycogen) or in specific tissues for long-term use (fat, starch). In light of these strategies that were optimized by evolution, we might consider using electricity predominantly for signaling purposes (in electronics) and driving smaller machines and devices, hydrogen as a chemical energy/fuel for long-range locomotion and transport, and different types of interconnected local and centralized energy storage systems in our future tightly integrated "energyscapes".

Moreover, not only the energy sector but the production and use of chemicals for drugs and countless other purposes should be more biologically inspired. For instance, humans, animals, and plants are interconnected with microbes in complex webs of antagonistic, supportive, or communicative interactions that operate via highly specific organic chemicals. These chemical compounds have been optimized by evolution and could serve as lead structures for developing more specific drugs with fewer side effects. Another example could be natural plant or microbial pigments, whose colour often depends on oxidation (i.e., a loss of electrons), which means they are also antioxidants (i.e., their released electrons can counteract oxidative damage of other biomolecules). Using such organic pigments in fabric dyeing may result in health-promoting textiles and a reduction of environmental pollution, in contrast to the frequently toxic chemical dyes currently in use. The chemical synthesis of many compounds has been and can be further replaced by biotechnological production procedures based on the genes and enzymes of natural biological synthesis pathways, which are more specific and efficient and generate less or no toxic waste during production. This can make a drastic difference even for single compounds – if they are used in large amounts worldwide.[19]

(5) Replace passive non-organic with active organic materials

Due to their biological origin, organic materials are part of natural turnover cycles, i.e., they are biodegradable and less prone to accumulate as stable waste. In addition, they represent carbon sinks, not only because they are biologically grown materials, but also because their biodegradation is associated with the generation of novel microbial biomass (which remains as stable organic matter in soil or enters the biological food chain) with only some CO_2 release (serving the microbes' energy metabolism). Furthermore, organic materials tend to have intrinsic activities, including the ability to mechanically respond to environmental stimuli (e.g., changes in humidity, temperature, osmolarity, electrical current, etc.) without the need for external energy input (Fratzl and Barth, 2009). The intrinsic activity of these materials relates to their hierarchically organized biological structure or "architecture" that ranges from the nano-scale of the molecules to the micro-scale of multicellular arrangements, to which designed patterning at the visible meso-scale can be added, all of which allows for the storage and triggered release of energy (Fratzl et al., 2021). With this inner architecture often based on entangled fibers or tesselation of flexibly connected small units, these active organic materials may have elastic, shock-absorbent, or other favorable mechanical properties (Fratzl et al., 2016; Hengge and Krauthausen, 2022). Some organic materials, such as bacterial cellulose or fungal mycelia, can be biotechnologically grown directly into desired forms for architectural, medical or design applications (Beyer and Resetar, 2024; Klemm et al., 2011; Meyer et al., 2020). Agricultural or wood waste may serve as nutrients for such microbial growth, which is not only cheap, but also recycles organic waste, maintaining fixed carbon (Cohen et al., 2023; Meyer et al., 2020).

While organic materials of microbial origin are grown in biotechnological facilities (or sometimes under simple workshop conditions), materials derived from plants require agricultural land for growth. This seems to raise a problem of competition with feeding the still increasing world population. However, considering that almost 80 % of the currently used agricultural

land serves for producing just 11% of the calories consumed by humans (which are in fact meat and dairy calories) and the remaining 89 % of the calories (in the form of vegetal food) are grown on the remaining roughly 20% of the available land (Ritchie, 2021), the problem seems to be one of political allocation rather than direct resource competition. Theoretically, reducing worldwide average meat consumption by just 50 % would allow the use of almost 40% of the available land for diverse other crops or partial rewilding. And even if it were just half of this area for various reasons of feasibility (e.g., not all land currently used for pasture is suitable as cropland), this would make the transition to organic agriculture easier, strongly reduce greenhouse gas release (both CO_2 and methane) and environmental pollution caused by intensive animal farming, counteract biodiversity loss and, last but not least, improve human health (Berners-Lee et al., 2018; Ritchie, 2021).

(6) Get inspired by traditional practices and further develop these with modern science

Traditional crafts all over the world evolved long before the discovery of apparently limitless fossil energy that enabled the extraction of non-organic resources at a large scale. Therefore, they depend on empirically developed procedures that not only make use of specific organic materials, but also often rely on dynamic biological processes such as complex natural antagonistic or cooperative interactions between microbes and plants. To name just a few examples: traditional plant-based medicine can harness plant defense mechanism against microbes for therapy of human infectious diseases (Francia and Stobart, 2014; Hengge, 2019; Nunes Silva et al., 2016; Pruteanu et al., 2020); vegetal food fermented by microbes provides significant health benefits (Melini et al., 2019; Soukand et al., 2015); and traditional "fermentative" textile dyeing involves environmental microbes in mixed soil-plant preparations (Douny et al., 2023). Joint anthropological and scientific investigations of these processes (the latter at the microbial/cellular and even molecular level) yield a deep, multi-perspective knowl-

edge (Douny et al., 2023) and could lead to a new biotechnology of "human-curated interspecies interactions" that may be flexibly applied to finding sustainable solutions, for old and new problems in medicine, food production, and technology.

(7) When extracting and utilizing non-organic resources, minimize their introduction into the biosphere, confine, recycle, and give preference to proven non-toxic materials

Much non-organic matter, e.g., most metals, are toxic to biological processes. However, since life evolved in an initially non-organic environment, cells came up with strategies to not only protect themselves, but to actually make use of such substances' interesting properties. The result is an intricate control system for uptake, secretion, confinement, or conversion into non-toxic useful derivatives (e.g., by biomineralization). Again, these biological strategies may serve as a blueprint for human activities. Of course, humankind will continue to use metals in electronic devices, batteries, catalysts, and a myriad of other products. Also, future buildings will still use concrete (though hopefully less and less). But extraction, confinement, and processing procedures can be improved to protect natural environments, and technological advances will provide less toxic alternatives in many cases. For instance, regarding concrete, cement can be generated from raw materials that emit less CO_2 during production and, depending on its composition, concrete can actually even bind CO_2 (Juenger et al., 2010; Winnefeld et al., 2022). By mixing in biochar particles produced from plant waste, it is even possible to generate net-zero-emission concrete (Wyrzykowski et al., 2024). Apart from the huge CO_2 emission problem during extraction and processing, non-organic matter is not subject to sunlight-driven biological turnover, but it is doomed by the second law of thermodynamics to eventually end up as disordered "waste".[20] A circular economy is essential, but we need to keep in mind that building it is hugely energy-intensive, and re/upcycling non-organic materials will only slow down their final transformation into waste. For all these reasons, we should prioritize any potential

replacement of non-organic materials with materials of biological origin, which store carbon and are less energy-intensive in production, less biotoxic, and biodegradable.

(8) Regarding newly produced non-natural materials, minimize their use, increase their efficiency of use, re-use and align their lifespan with the duration of their use

All over the world, a myriad of non-natural materials and substances are chemically produced and used in medicine, agriculture, building, technology or just our daily lives – e.g., think of pharmaceutical drugs, pesticides, or plastic polymers. Not only are many of these designed to be biotoxic (antibiotics, disinfectants, herbicides, fungicides, insecticides, etc.), but most chemicals are also designed for long-term stability, meaning nothing other than non-biodegradability. After the use and decay of products containing such chemicals, these toxic substances are released, spread, and accumulate within the biosphere, including in our own bodies. Even if materials are initially non-toxic, such as many kinds of plastic, their miniaturization by environmental impact results in micro- or even nanofibers, which become biotoxic. It is obvious that – just as with natural non-organic materials – we need to reduce the utilization of these anthropogenic materials and substances and, where they remain essential, maintain them in a circular economy as much as possible. In addition, we should make an effort to adapt their stability and lifespans to their duration of use in relevant products. For instance, highly stable plastic is, in principle, a great material for products of long-term usage – but just a few decades of using it for the most ephemeral purpose of short-term packaging has resulted in flooding our planet with plastic and in the intoxication of all living beings with microplastic. An example from the other end of the spectrum of a mismatch between the lifespans of materials and their products are modern buildings, which should and could last for centuries, but which are often torn down after a few decades due to concrete deterioration – even though the Romans already knew how to build their still existing Pantheon and

other large buildings from self-repairing, durable concrete (Seymour et al., 2023).

CONCLUSIONS

Trying to follow these strategies as much as we can – both as societies and as individuals – should establish a human utilization of matter and energy that will make our activities more compatible with the functioning of the biosphere. In doing so, we will also become more aware of the crucial difference between organic and non-organic matter – only organic matter is part of the natural sunlight-driven material cycles of growth and microbe-mediated decay. This again reminds us to appreciate the fundamental role of microbes on this planet. Microbes have driven the evolution of the biosphere and the planetary metabolism that keeps it going, tightly interlinking it with the atmosphere (fig. 2). The health of ecosystems (such as fertile soil or aquatic habitats), as well as all plants, animals and humans, depends on their interconnected microbiomes (Banerjee and van der Heijden, 2023). Many traditional "fermentative" practices rely on microbes, as do contemporary biotechnology and synthetic biology, which yield products more specifically than chemistry and other technologies while producing less or even no waste. Overall, instead of killing microorganisms or perturbing natural microbiomes, human activities on this planet need to become "probiotic" again.

Some of the criteria or required changes listed above may seem challenging or even radical, especially in our modern world built on a capitalist economy that clearly has other priorities, which, in fact, are at the origin of the current anthropocenic crisis of the biosphere. However, capitalist systems and societies have the freedom to choose their incentives, e.g., to put a price on environmentally destructive products and practices and to hold liable global actors who have sought and keep seeking short-term, extreme private profit at the expense of long-term global destruction. Instead of insisting on perpetuating biosphere-destructive business practices (sometimes

in green-washed disguise), corporations should focus on the many less detrimental new opportunities. The ability to sustain itself in the long run will hopefully be enough of a motivation for humankind to choose incentives and thereby change the economic system in a manner compatible with the survival and health of our biosphere (Dasgupta, 2021; Kemp et al., 2022). Intriguingly, with the fully circular flow of all matter in the biosphere, nature also shows us that continuous growth actually does not depend on material increase – the continuous energy input by sunlight, which is reliably available, has enabled the evolving biosphere to grow in complexity, information content, and functionality over billions of years.

In summary, what needs to be sustained is the self-sustaining planetary biosphere as a whole – keeping in mind that nature or the biosphere is not just a "stakeholder" whose interests need to be balanced with those of other global stakeholders such as human societies or the economy. Rather, a functioning, healthy biosphere is the *foundation* of everything else. We need to understand that humans – along with all non-human beings – are a part of this living biosphere, instead of seeing us and our culture as active opponents to a passive nature that we can exploit or even overcome. In the end, we belong – but a functioning healthy biosphere is also the only possible place where humankind can decently survive on a long-term basis.

NOTES

1 A final statement by Michael, a character in the theatre play *A Number* by Caryl Churchill (2002), after discovering that he is a human clone.

2 Important parts of the following sections summarize fundamental knowledge in microbiology and chemistry, which I present here with a readership of very mixed expertise in mind, ranging from various science and engineering disciplines to the humanities and even art and design. As this knowledge can be found in standard academic textbooks, not every statement is referenced. Also, cited books are mostly suggested for broader reading, whereas journal publications or book chapters are usually cited for more specific information.

3 'Organic' matter or materials are defined here as being of biological origin, with anything else being 'non-organic'; while this definition of 'organic' originally also gave its name to 'organic' chemistry, 'non-organic' as used here is not identical to 'inorganic' as used in chemistry, since it also includes artificial polymers, i.e., plastics, or artificial organic chemicals that are not made by living cells, e.g., PCB or PFAS.

4 The actual CO_2 concentration at this time is not entirely clear (estimates vary between 10x and 2500x the current concentration).

5 From the ancient Greek word *lithos* meaning 'stone' (which stands here for 'inorganic').

6 H_2 -> 2 e^- + 2H^+ and 2e^- + O_2 -> O_2^{2-} combine to H_2 + O_2 -> H_2O (H_2O is formed when O_2^{2-} binds 2H^+, which happens readily due to attraction between the opposite electrical charges).

7 Linking free phosphate (P_i) to ADP, which generates ATP.

8 This is performed by an entire chain of membrane-located proteins (the *respiratory chain*), which couple the flow of e^- through them with pumping H^+ out of the cell.

9 ATPase is a multiprotein complex that can either cleave energy-rich ATP to pump H^+ out of cells or let H^+ flow in and couple this flow to the formation of ATP from ADP and P_i. Which direction the reaction of ATPase takes, depends on how abundant ATP is and/or how steep the H^+ gradient is.

10 This is because O_2 has by far the lowest position on the redox potential scale (or most positive redox potential; see background 1).

11 Traditionally, it is assumed that this bacterial planetary biosphere developed in aequous environments only, i.e., mainly in the oceans. However, in light of our current knowledge of bacterial stress responses and biofilms, it seems likely that large bacterial biofilms also covered the planetary land masses, in which bacteria were protected from desiccation by an extracellular matrix

containing strongly water-binding polysaccharides – the planet must have been a strange place then.

12 Although archaea have now been found in all kinds of environments (including our own gut), many modern archaea are still extremophiles living at extreme temperatures (>100 °C) or salt concentrations.

13 This DNA is structurally highly organized, yet directly accessible in the cytosol – hence the name of *prokaryotes*, i.e., cells that do not yet have a nucleus (*karyon*), which encloses the DNA within a membrane in the much later evolving *eukaryotic* cells.

14 Since research on archaea is dramatically lagging behind in comparison to our knowledge of bacteria, the following description of prokaryotes generally refers to bacteria.

15 Many bacteria have so-called type-VI secretion systems (T6SS), which operate like molecular harpoons that are triggered by cell contact or other signals to shoot and deliver deadly toxins directly into neighbouring cells.

16 *Bet-hedging* means a physiological differentiation of a population into different subpopulations, some of which might not even grow, but instead are better equipped to cope with potentially lethal stress. For instance, a small minority of cells in growing bacterial populations are dormant *persisters*, which would survive the sudden presence of an antibiotic and eventually grow into a new population, whereas the actively growing majority fraction of the population would be killed by the antibiotic.

17 $Fe^{2+} + H_2O_2 + H^+ \rightarrow Fe^{3+} + H_2O + OH^-$. Hydrogen peroxide ($H_2O_2$) is actually produced as a side product in all actively aerobically respiring cells. Since all cells also need and therefore take up iron, the Fenton reaction is a constant threat to cells – using oxygen for energy metabolism is thus not only an energetic blessing, but comes at a price.

18 For several reasons the technical carbon capture storage and/or utilization (CCS/CCU) cannot be a general solution. First, principal thermodynamic and chemical laws result in huge energy requirements for capture, compression and storage of CO_2, as well as for chemically mobilizing CO_2, which has a very low inherent potential energy (this is quite analogous to N_2 and its chemical mobilization in the Haber-Bosch procedure). This high-energy requirement reduces efficiency and impedes large-scale use of CSS/CCU technology. Furthermore, high-concentration storage under high-pressure underground is prone to leakage. The same applies to metal pipelines as metal is corroded by CO_2. Since high CO_2 concentrations are biotoxic, leakage has the potential to wreak havoc on living beings and the environment. Overall, CCS seems a prototypical example of a problematic technological attempt to counteract a

massive problem generated by technology in the first place. Also, CCS/CCU seems to be promoted and provided by those who are mainly responsible for high atmospheric CO_2 content, i.e., the fossil oil industry. It looks like a perfect business model – first, profit from generating a mess and then from offering to clean it up.

19 A striking example is the approximately 50.000 tons of indigo currently used annually for textile dyeing (mainly for an estimated number of 4 billion jeans). It has been shown that replacing the conventional highly energy-consuming and toxic practices of indigo dyeing with a fully developed biotechnology-based procedure would not only be economically competitive, but could reduce annual global CO_2 emission by 3.5 megatonnes and drastically decrease the toxic impact on workers and the environment (Bidart et al., 2024).

20 Interestingly, whether such a disordered non-organic end product is classified as "waste" seems to depend on where it accumulates. For instance, breaking down a concrete building results in a heap of concrete waste in a place different from where its raw materials originated – by contrast, a crumbling stone house basically releases stones into its natural environment, where they immediately serve as a new resource.

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