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## Life's Requirements

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### Abstract

Life on Earth is molecular in nature, with its lifelike attributes – e.g., information processing and catalysis – emerging as a result of both the specific properties of those molecules and the interactions among them. If this is a general model for life, then life must require (i) a source of energy, with which to build and sustain molecular complexity and information processing; (ii) elemental raw materials,

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from which to construct molecules having specific properties and reactivity; (iii) a solvent that supports the synthesis of the full range of molecules required by life and properly mediates the full range of necessary interactions among those molecules; and (iv) physicochemical conditions in which life's molecules can be synthesized, are appropriately stable, and can interact as needed for lifelike function. For life on Earth, these general requirements, respectively, take the specific form: (i) light energy in visible-to-near-infrared wavelengths or chemical energy as provided by oxidation–reduction disequilibrium, (ii) the “biogenic” elements (carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur) (iii) liquid water, and (iv) specific ranges in temperature, pH, salinity, pressure, and other environmental factors. Our knowledge of these factors relates to cellular life as we observe it now or can infer from the fossil or molecular records. Life's origin may be constrained by a more stringent set of requirements that are, as yet, not fully understood.

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**Keywords**

Habitability · Solvent · Biogenic elements · Energy · Physicochemical conditions

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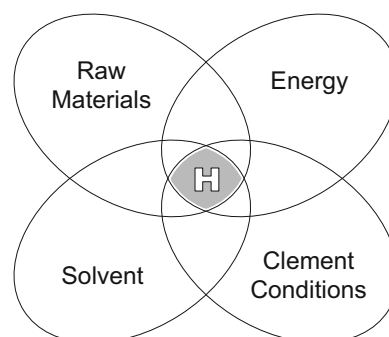
**Introduction**

Consideration of life's requirements provides a basis for evaluating the suitability of different environments to support the origin of life and/or maintain extant life. Such evaluation can be used to ask:

- (i) *What is the full range of environments beyond Earth in which life might be possible?* Inherent in this question is the possibility that life beyond Earth might utilize a different biochemistry that is subject to substantially different requirements and constraints than is Earth's biology. In this reference frame, the requirements, capabilities, and tolerances of life on Earth represent one specific manifestation of a more generic set of biological requirements, and the environments that are habitable with respect to Earth life may represent a subset of a potentially much broader range of habitable environments. *The Limits of Organic Life in Planetary Systems* (Baross and Committee on the Limits of Organic Life in Planetary Systems 2007) considers life in this broad reference frame, and lists the following broad requirements for life, in decreasing order of certainty: (1) thermodynamic disequilibrium; (2) an environment capable of maintaining covalent bonds, especially between carbon, hydrogen, and other atoms; (3) a liquid environment; and (4) a molecular system that can support Darwinian evolution. We consider the first three categories in the discussion of “life's requirements” that follows below (Fig. 1).
- (ii) *Which environments provide the most compelling targets in a search for life beyond Earth?* Here, an understanding of life's requirements provides a basis on which to prioritize environments offering the greatest probability for the emer-

**Fig. 1 Life's requirements.**

Life requires a source of energy, a suitable solvent, specific elemental building blocks, and physicochemical conditions that support life's covalent and non-covalent chemistry. Habitable conditions (H) exist where and when these requirements are all satisfied



gence of life and/or the clearest, most “detectable” signs of life. Limitations in the current understanding of the pathways and events that lead to the origin of life (even for Earth life, let alone for life having a different biochemistry) restrict the ability to think in terms of a probability of life’s emergence. Hence, the focus here is on understanding how nominally habitable environments may differ in the abundance, character, and quantity of biosignature evidence they present by virtue of how scarcely or abundantly they satisfy life’s requirements.

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## Solvent

In the context of exoplanets, it is valuable to understand whether life universally requires a liquid environment and which liquids might suitably support life. The concept of the habitable zone is built upon the idea that life requires a liquid (water) environment and that only planets having stable liquid at the surface could support biospheres robust enough to be detected remotely. Specifying a particular liquid specifies a range of temperatures and pressures in which that liquid is stable and ultimately a range of distances around the host star within which a planet’s radiation budget could provide suitable temperature/pressure conditions at the surface.

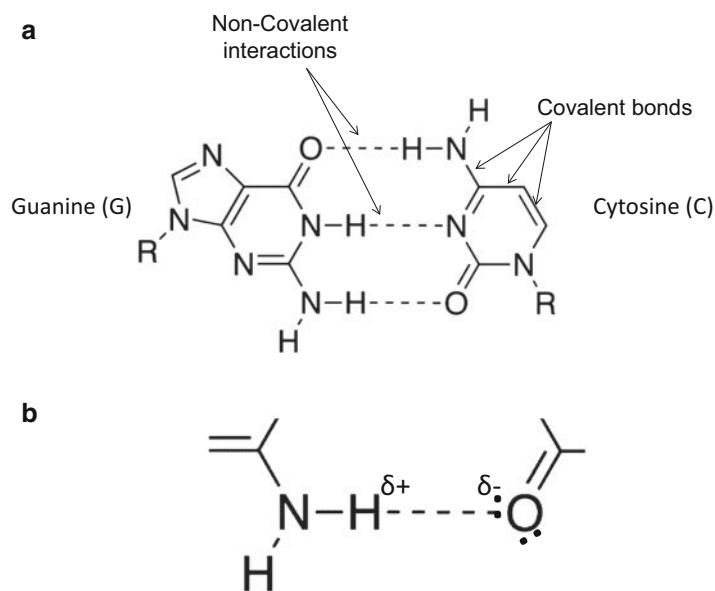
Why does life require a liquid environment? Life as we understand it is characterized by a myriad of interactions among the molecules that comprise its biochemistry – many of which are large and structurally complex – and between those molecules and the chemistry of the environment. Among the possible phases of matter, a liquid (or liquid-like) environment is thought necessary to support these interactions. A solid matrix within and outside an organism would confound the potential for such interactions to occur at meaningful rates because the transport of large molecules through solid matrix is very slow in comparison to that through liquids. Interaction among molecules is possible and occurs readily in the gas phase, but large and structurally complex molecules often thermally decompose before acquiring sufficient kinetic energy to enter the gas phase. Only liquid solvents (or supercritical fluids, which have properties similar to liquid solvents)

appear to support both molecular complexity *and* foster interactions among complex molecules.

All known life on Earth requires liquid water as the solvent. Both the chemistry and the physics of water contribute to its importance for terrestrial life (Fraústo da Silva and Williams 1991; Pohorille and Pratt 2012). From a physical perspective, the large range of pressure/temperature space over which liquid water is stable, its high heat capacity (a measure of how much energy is required to raise the temperature by a given amount), and the simple fact that the stable form of low-pressure water ice is less dense than liquid water (ice floats) all contribute to the stability and prevalence of liquid water habitats across a range of environmental conditions. From a chemical perspective, the importance of water as a solvent is not only to mediate covalent bond formation/breaking but also to govern the diverse range of non-covalent interactions on which life depends (Fig. 2). As Stryer (1988) notes, “Reversible [non-covalent] molecular interactions are at the heart of the dance of life. . . . These bonds are profoundly affected in different ways by the presence of water.” Pohorille and Pratt (2012) describe two properties of water as particularly important in this regard:

1. The high dielectric constant of water serves to moderate the strength of electrostatic attraction (the force “felt” between positively and negatively charged entities) and repulsion (the corresponding force felt between two like charges). Specifically, water’s dielectric constant of about 80 means that the strength of electrostatic interactions is weaker by a factor of 80 than it would be in a vacuum. Without this effect, the inter- and intramolecular interactions created by electrostatic attractions would be too strong to serve their practical function in our biochemistry. That is, without a high dielectric solvent such as water, reversible molecular interactions would, from the standpoint of their practical significance in biochemistry, become largely irreversible.
2. The highly polar nature and hydrogen-bonding capabilities of water confer a strong “hydrophobic effect” – the tendency of nonpolar molecules (e.g., methane) or nonpolar groups within molecules to minimize interaction with water and instead associate with one another. The tendency of oil to form droplets in water, rather than dissolving or dispersing, is an example of this effect. The strength of the hydrophobic effect is largely a function of the strength of interaction among water molecules, rather than of any native force of attraction between nonpolar groups. As a result, the apparent strength of attraction among nonpolar groups is much stronger in water than it would be in less polar or non-hydrogen-bonding solvents. This is critical in Earth’s biochemistry, because most forms of intra- or intermolecular self-organization – for example, the formation of lipid bilayer membranes or the folding of proteins that confers catalytic function – depend on the relatively strong associations among nonpolar groups that result from the hydrophobic effect (Stryer 1988).

For completeness, it should be noted that the chemical reactivity of water can also pose challenges in biochemistry (Baross and Committee on the Limits of Organic



**Fig. 2 Covalent versus non-covalent bonds.** (a) Cytosine (C) and guanine (G) are the complementary nucleobases in Watson–Crick DNA base pairing. Covalent bonds, consisting of electrons shared between atoms and denoted here by solid lines, are responsible for primary molecular structure. Non-covalent interactions, consisting of attractive or repulsive forces felt through space without sharing of electrons, are denoted here by dashed lines. These interactions support molecular recognition, tertiary structure (e.g., protein folding), and other intra- and intermolecular interactions essential to life-like function. Solvent properties play a critical role in mediating both covalent and non-covalent bonding. (b) Hydrogen bonding, which in this example supports the pairing of complementary nucleobases, is enabled by the creation of a partial positive charge ( $\delta^+$ ) on a hydrogen atom bonded to a heteroatom (here, N) and the partial negative charge ( $\delta^-$ ) represented in the “lone pair” of electrons on an adjacent heteroatom (here, O). The through-space attraction felt between those partial charges constitutes the hydrogen “bond.” The strength of such bonds depends heavily on the solvent in which the molecules are dissolved

Life in Planetary Systems 2007). Water can serve as both acid and base and as nucleophile or electrophile, and these properties make it reactive (and potentially destructive) toward several of the bond types that are common elements of our biochemistry. For example, the amide bonds that link together individual amino acids to form proteins are subject to hydrolysis (water-induced bond breaking), and several of the bond types within DNA and RNA can be attacked by water (Jarvinen et al. 1991). While this reactivity is overcome by continuous repair in modern life, it may have posed a greater challenge for prebiotic chemistry (Benner et al. 2012).

Is water the only possible solvent for life? The Committee on the Limits of Organic Life in Planetary Systems (Baross and Committee on the Limits of Organic Life in Planetary Systems 2007) “found no compelling reason to limit the environment for life to water as a solvent, even if life is constrained to use carbon as the scaffolding element for most of its biomolecules.” We need look no further than

Saturn's moon Titan to find extensive lakes of liquid methane (Stofan et al. 2007), and the potential diversity of exoplanet compositions and chemistries may offer yet more possibilities. It is presently unclear whether the physical and solvent properties of water are important solely for our specific biochemistry or would also be required by alternative biochemistries. At the least, suggested alternatives to liquid water (e.g., Bains 2004; Schulze-Makuch and Irwin 2004; McKay and Smith 2005) might be categorized or evaluated based on whether these alternative solvents exhibit similar properties to water and so could conceivably support Earth-like biochemistry or whether their properties could only support a biochemistry very different from ours. A further step would be to identify biochemical requirements that can be considered universal to life – for example, the need to process information with high fidelity – consider how these requirements are met by the solvent properties of water, and ask whether/how the same requirements could be met by solvents with different properties.

Solvent availability can limit the abundance and productivity of life and therefore could potentially affect the “detectability” of a biosphere. On Earth, the distribution of biomass on the landmasses is governed to a substantial degree by the availability of liquid water as precipitation, with the difference between the equatorial rainforests and Saharan Desert of Africa serving as a continent-scale example. Even within liquid water-bearing environments, water can be relatively “unavailable” in chemical terms, when high concentrations of solutes (e.g., salts or sugars) effectively compete for water at the molecular level (Harris 1961; Tapia et al. 2007). The availability of water in solutions is quantified as the *water activity*,  $a_w$ , which is defined as the ratio of the vapor pressure of water over the fluid in question to the vapor pressure of pure water at the same temperature. Organisms are sensitive to this parameter, and metabolic activity has not been documented below a water activity of approximately 0.6 (a level tolerated by some fungi, but few other organisms (Harris 1961; Tapia et al. 2007)). A few natural aqueous environments that have lower water activity are known – for example, the calcium chloride-rich Don Juan Pond in Antarctica, which contains nearly 40% salts by weight (Samarkin et al. 2010; Yakimov et al. 2007; Toner et al. 2017) – but metabolic activity has not been observed despite active efforts to do so (Samarkin et al. 2010).

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## Elemental Raw Materials

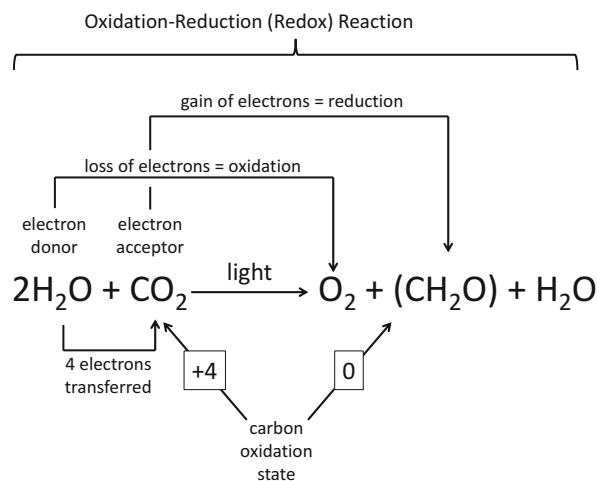
The committee identified a requirement for “an environment capable of maintaining covalent bonds, especially between carbon, hydrogen, and other atoms.” Inherent in this statement is the idea that life is molecular in nature (covalent bonds are the “glue” that holds these molecules together), and this in fact defines two requirements: one for the elemental raw materials from which the molecules are made (the atoms between which the covalent bonds form) and the other for environmental conditions in which the molecules are stable over biologically meaningful time scales. The first of these requirements is considered here and the second in the section that follows.

Several tabulations of the wide range of elements utilized in Earthly biochemistry have been published (Fraústo da Silva and Williams 1991; Silver and Phung 2005). Here, we focus on the six “biogenic elements” – carbon, hydrogen, nitrogen, phosphorus, and sulfur – that appear to be required in the biochemistry of every known organism.

*Carbon.* Carbon forms the backbone of the molecules of Earth’s biochemistry. Underpinning this key role are the capability of carbon to (a) form four bonds – either as four single bonds or as combinations of single, double, and triple bonds – and (b) form stable bonds to itself, to the other biogenic elements, and to a wide range of other elements. By virtue of these capabilities, an extraordinarily large number of possible carbon-based molecules exist, and these possibilities encompass a broad range of both structural and functional diversity. This vast chemical space represents a virtually limitless “library” of possible structures and functions from which to construct a functional biochemistry (Bains and Seager 2012).

Within the library of possible carbon-containing compounds, the greatest structural diversity is represented in molecules that have extensive networks of carbon–carbon bonds and thus in molecules in which carbon has an average oxidation state close to zero (Bains and Seager 2012). (Oxidation state is a measure of the number of electrons lost or gained by an element when it forms a compound or an ion. In actuality, electrons in covalent bonds are shared between the bonded atoms but, for the purposes of calculating an oxidation state, are formally “assigned” to the element that attracts them with greater strength. The oxidation state of carbon when bonded to itself is zero, because the two carbons share the electrons with equal strength.) The average oxidation state of carbon in our biochemistry is slightly less than zero, because the number of instances in which C bonds to H (and thereby decreases its oxidation state) outweighs the number of instances in which C bonds to O or N (and thereby increases its oxidation state). This simple fact that the greatest structural and functional diversity is achieved when the average oxidation state of carbon is near or slightly below zero is important in the context of searching for life on exoplanets:

The most diagnostically biogenic feature of Earth’s atmosphere, its 21% oxygen, arises because biochemistry requires carbon in an average oxidation state near zero, but the predominant form taken up by photosynthetic organisms (the primary producers in Earth’s ecosystems) is CO<sub>2</sub>, in which carbon has an oxidation state of +4. To construct carbon-based biomolecules from CO<sub>2</sub> thus requires an environmental source of electrons in addition to a source of carbon. Oxygen-producing photosynthesis represents a solution to this resource requirement. Specifically, the required electrons are extracted from the H–O bonds in water (H–O–H), with O<sub>2</sub> liberated as a by-product (Fig. 3). That by-product, and the associated “detectability” of Earth’s photosynthetic biosphere, is a result of a biochemical necessity (molecular diversity as achieved through carbon in intermediate oxidation states) expressed within a specific environmental context (one in which C has a +4 oxidation state). It is not an obligate product of photosynthesis and therefore not a certain outcome of a biosphere that evolves photosynthetic energy capture. On Earth, H<sub>2</sub>, H<sub>2</sub>S, Fe<sup>2+</sup>, and other species can serve as electron donors for a form of photosynthesis (“anoxygenic” photosynthesis) that produces no oxygen



**Fig. 3 Anatomy of a “redox” reaction.** The example reaction is a simplified scheme for oxygen-producing photosynthesis, where “(CH<sub>2</sub>O)” represents generic carbohydrate (e.g., sugar). Oxidation–reduction chemistry is the transfer of electrons (“reducing power”) from one atom or molecule to another. The source of electrons is called the “electron donor” or “reductant.” It is “oxidized” in the process of transferring electrons and its “oxidation state” increases. The atom or molecule to which electrons are transferred is called the “electron acceptor” or “oxidant.” It is “reduced” in the process of receiving electrons and its oxidation state decreases. The tendency of a compound to donate electrons is measured by the “oxidation potential” and the tendency to accept electrons by the “reduction potential.” Note: In the actual conduct of photosynthesis, the oxidation of water to oxygen and the reduction of carbon dioxide to carbohydrate are biochemically distinct. They are presented as a single reaction here only for illustrative purposes

(Blankenship 2014). Moreover, for example, it can be envisioned that biosynthesis in an environment in which CH<sub>4</sub> (carbon oxidation state = −4) is the prevailing carbon source would require dumping electrons (e.g., as H<sub>2</sub>) rather than scavenging. Thus, an understanding of environmental context is important in predicting and interpreting potential chemical biosignatures.

*Heteroatoms.* Heteroatoms (anything other than carbon and hydrogen but, in this specific context, O, N, P, and S) confer reactivity, solubility, tertiary structure, and hydrogen-bonding capability to the carbon molecules that incorporate them. Oxygen and nitrogen are strongly electronegative (strongly attract to themselves the electrons shared in a bond with another atom) and thus can impart partial positive charges to atoms with which they bond. Carbon becomes more reactive (is “activated”) through this process, and such reactivity underlies many of the fundamental cycles and synthetic pathways on which our biochemistry depends. Hydrogen bonded to either O or N acquires a partial positive charge, while the heteroatom acquires a partial negative charge (Fig. 2), and this “polarity” serves as the basis for the solubility of many biomolecules in water. For example, sugars are highly soluble in water because the majority of carbons within the molecule have polar −OH groups attached to them. The highly polar H–N and H–O bonds also



play a key role in “hydrogen bonding,” which is the electrostatic attraction between a partially positive H and an unoccupied set of electrons on an N or O to which the H is not covalently bound (Fig. 2). These interactions, which are strong and spatially directional, are a critical element in molecular recognition (e.g., the correct pairing of DNA bases) and other non-covalent interactions upon which biochemistry is based. Key roles for N, P, and S in Earth’s biochemistry are discussed briefly, but not comprehensively, below. Oxygen is sufficiently pervasive in the molecules of our biochemistry – perhaps unavoidably so, given that that biochemistry plays out in the solvent H<sub>2</sub>O – that it is not tractable to succinctly summarize a set of specific roles.

*Nitrogen.* The bonding pattern of nitrogen – three covalent bonds, plus an unoccupied pair of electrons – combined with its ability to support hydrogen bonding, underpins a key role in several aspects of biochemistry:

1. The “bases” of DNA and RNA incorporate multiple nitrogen atoms that form the basis for Watson-Crick base pairing through hydrogen bonding (see Fig. 2).
2. The amide group,  $-(CO)-N-$ , is the linkage by which individual amino acids are assembled into proteins. Hydrogen bonded to the N in this linkage bears a partial positive charge that, combined with the O, creates a repeating dipole within the molecule. This provides a basis for the protein molecule to fold upon itself and thereby acquire catalytic activity. It has been suggested that such a repeating dipole may be a universal feature of life’s catalytic molecules (Benner et al. 2004).
3. By virtue of its bonding pattern, N plays the key role in the redox activity of molecules such as NAD and FAD, which are essential components of both energy metabolism and biosynthetic pathways.

*Phosphorus.* Phosphorus, in the form of phosphate, occupies two main roles in our biochemistry. Both appear to be based upon the trivalent nature of the phosphate anion ( $PO_4^{3-}$ ); specifically, phosphate can form two bonds while simultaneously retaining a single negative charge:

1. The nucleic acid polymers DNA and RNA are based upon a sugar–phosphate backbone. In this context, phosphate bonds to two sugar molecules, leaving a repeating negative charge within the backbone. Benner et al. (2004) argued that this repeating charge is critical in conferring the primary physical properties, such as solubility, on nucleic acid polymers, and that such a repeating charge may be a critical feature of any genetic system.
2. In Earth’s biochemistry, energy metabolism is based upon the phosphate-phosphate bond in adenosine triphosphate (ATP). This bond is easily formed and unmade, and its high-energy content is in large part attributable to the repeating negative charge in the bonded phosphate groups (Stryer 1988). The electrostatic repulsion between these adjacent charges makes it highly favorable for the terminal phosphate group to “leave” and be solvated by water.

*Sulfur.* Sulfur is a component of the protein-forming amino acids cysteine and methionine, where it plays a role in two aspects of protein structure and function. Sulfur forms weak covalent bonds with itself, such that sulfur-containing amino acids within different regions of a protein may bond to one another. The resulting “disulfide bridge” serves as a structural element that, by virtue of its effect on protein folding, can directly impact the catalytic potential of the protein (Sevier and Kaiser 2002). Sulfur can also play a role in complexing metals at the catalytic center of proteins, such as in the formation of the widespread “iron–sulfur clusters” (Johnson et al. 2005).

Arguments have been offered that the biogenic elements as we know them are uniquely suitable for life (Pace 2001), while others suggest that alternatives even to carbon could meet some of the basic requirements for functionality in biochemistry (Bains 2004; Benner et al. 2004). The incorporation of specific elements in the core biochemistry of Earth life must be dictated, at some level, by the resources available in a given environment. To play a useful role, such elements must be both sufficiently abundant in bulk and accessible in the liquid medium occupied by life (i.e., either soluble or extractable without too high an energetic cost; Fraústo da Silva and Williams 1991). This raises the possibility that inclusion of specific elements in specific roles of our biochemistry may simply reflect availability in the Earth system, rather than unique suitability for a given function. This may indeed be true for some transition metals, which typically play roles in enzyme or coordination chemistry (Ulmer and Vallee 1971). Similar considerations would apply to alien worlds, and resource mobility/availability would be an important criterion by which to evaluate the potential for alternative solvents or elements for life.

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## Physicochemical Environmental Conditions

Along with elemental raw materials from which to construct the molecules of biochemistry, life also requires physical and chemical conditions that are conducive to the stability and interaction of those biomolecules. Extremes of temperature and pH, high salinity, radiation, high pressure, and chemical toxicity can all threaten the integrity of these molecules. A variety of sources have reviewed the tolerances and capabilities of terrestrial life with respect to physicochemical extremes (e.g., Baross and Committee on the Limits of Organic Life in Planetary Systems 2007; Rothschild and Mancinelli 2001), and currently known physicochemical limits to life are presented in Table 1. The potential of the cell membrane to serve as a barrier against some environmental extremes and not against others allows and suggests a basis for grouping environmental conditions into either of two categories (Baross and Committee on the Limits of Organic Life in Planetary Systems 2007):

The first category includes components of the environment against which the cell membrane represents a viable barrier. For example, the cell interior can be held at near-neutral pH even when the external environment is more acidic or alkaline (Krulwich et al. 1996) or limited to salinities much less than those in the environment (Oren 1999). This mechanism depends on the relative impermeability

**Table 1** Currently known physical and chemical limits to life

Variable	Activity observed at	Example references
Temperature (high)	122 °C	Takai et al. (2008)
Temperature (low)	−15 °C	Deming (2002)
Acid pH	0	Edwards et al. (2000)
Alkaline pH	13	Horikoshi (1999)
Water activity	0.6	Tapia et al. (2007)
Radiation	10,000–11,000 gray (gamma)	Cox and Battista (2005)
Pressure <sup>a</sup>	200–1200 MPa?	Daniel et al. (2006), Lauro and Bartlett (2008), and Sharma et al. (2002)

<sup>a</sup>A variety of organisms thrive at ocean trench pressure of 110 MPa. Sharma et al. (2002) report metabolic activity of organisms in diamond anvil cells at pressures up to 1200 MPa; however, other observations indicate that oligomeric proteins begin to dissociate at pressures in the range of 200 MPa and that monomeric proteins denature at pressures in the range of 400–800 MPa

of the cell membrane with respect to large or charged species (e.g., H<sup>+</sup>, OH<sup>−</sup>, Na<sup>+</sup>). However, because the membrane cannot provide a perfect barrier and a thermodynamic drive exists to equilibrate the internal and external environments, such mechanisms require continuous expenditure of energy to maintain the disequilibrium state that is represented in internally different conditions. In “category 1,” adaptation to extreme conditions need not require alteration of an organism’s core biochemistry; rather, it can be based on expenditure of energy combined with specific adaptations to sustain transmembrane chemical gradients.

The second category encompasses conditions, such as pressure and temperature, that are “felt” within the interior of a cell regardless of the presence of membranes and therefore require adaptation at the biomolecular level. Temperature only falls cleanly into this category for small organisms: By virtue of their size, large organisms have the potential to maintain an internal temperature different from that of the environment. However, physiologically meaningful temperature gradients cannot be maintained at the size scale of microorganisms; the temperature outside is, effectively, the temperature inside. In cases of biochemical-level adaptation to temperature or pressure, it is necessary that both molecular stability (the stability of covalent bonds) and molecular interactions (non-covalent bonding) be supported, and the latter could potentially prove more restrictive. Specifically, non-covalent bonds are typically weaker than covalent bonds and thus may be more sensitive to disruption as temperatures or pressures increase. For example, the strength of the non-covalent bonds that underlie the proper folding of proteins (and thereby confer catalytic activity) or base pairing in DNA (and thereby allow high fidelity information processing) must increase as the temperature increases, and this is indeed observed. For example, the strength of bonding between the complementary DNA bases cytosine and guanine (“C” and “G,” Fig. 3) is greater than that between adenosine and thymine (“A” and “T”), and the relative proportion of G–C pairs in

DNA is generally higher in organisms that live at higher temperatures (Jaenicke and Sterner 2002).

The concept of “extremes” is relative and depends on the biochemistry in question. For example, our biochemistry depends on hydrolyzable polymers (proteins and nucleic acid polymers) and nucleic acid base pairing whose functions are optimized at near-neutral pH, and alkaline or acidic conditions are extreme in this context (Krulwich et al. 1996). But alternative biochemistries could optimize in a different pH range, such that near-neutral pH would be extreme. The same principle is generally true in each dimension of physicochemical space, although with limits. Ultimately, temperatures can increase to a point at which thermal motion overcomes even the strongest bonds, and neither covalent nor non-covalent interactions remain to viably support life that is molecular in nature. Baross and Committee on the Limits of Organic Life in Planetary Systems (2007) suggested that carbon-based chemistry would probably be nonviable at temperatures much above 600 K, and it is likely that the weaker and more water-labile bonds represented in our biochemistry (e.g., the carbon-nitrogen “amide” bonds that form the backbone of our proteins) would become nonviable at even lower temperatures. Similarly, high pressures or intense/high-energy radiation will ultimately overcome any chemistry.

*Environmental conditions and the origin of life.* The range of conditions tolerated by modern organisms could be significantly broader than the range of conditions conducive to the origin of life. Modern organisms employ a variety of sometimes complex and energy-intensive mechanisms for adapting to the broad range of conditions reflected in Table 1 (Krulwich and Ivey 1990; Jaenicke and Sterner 2002; Hoehler 2007), and such mechanisms would likely not be available to prebiotic chemistry or early organisms. The origin of life on Earth is not understood sufficiently to predict what reduced portion of physicochemical space could suitably give rise to Earth-like life, much less to alternative biochemistries. Absent that understanding, it should simply be borne in mind that environments capable of supporting extant life are not necessarily equivalent to environments where life can emerge.

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## Energy

Thermodynamic disequilibrium (Gibbs free energy) may be the only absolute requirement for life (Baross and Committee on the Limits of Organic Life in Planetary Systems 2007). While such disequilibrium is virtually ubiquitous and takes a variety of forms, life on Earth appears to utilize only light energy within the visible-to-near-infrared portion of the electromagnetic spectrum and chemical energy associated with oxidation-reduction (“redox”) reactions. What these forms of energy have in common is that they can drive a flow of electrons, either by the chemically spontaneous transfer of valence electrons from one atom to another (redox chemistry) or via the excitation of electrons out of the ground state by

absorption of a photon (light energy), followed by transfer to another atom or molecule. On Earth, biological energy capture – the process by which life harnesses energy from the environment and stores it in a biochemically useful form – fundamentally depends on this flow of electrons. Light wavelengths insufficient to excite ground state electrons and chemical processes that release energy but do not drive a flow of electrons (e.g., crystallization, dissolution, or hydration reactions) are not known to support biological energy capture. Whether the restricted set of biologically useful energy sources is specific to Earth life, or represents a more general constraint on energy utilization, has not been well established and remains an open research topic in astrobiology.

In order to be useful to biology, “acceptable types” of energy must also be of a magnitude that is compatible with biochemical mechanisms of energy capture. This requirement is expressed in two measures: energy delivered per unit of energy carrier (e.g., energy per photon or per mole of chemical reacted) and energy delivered per unit of time.

The first measure, which can be thought of as similar to voltage (e.g., volts, joules per coulomb of electrons), is represented in the Gibbs energy change ( $\Delta G$ ) of chemical reactions and in the wavelength of light. In either case, the energy delivered per unit of energy carrier must be sufficient to drive the synthesis of ATP, the universal molecular carrier of energy in Earth's biochemistry (Schink 1988). In the case of redox chemistry, this requirement can be a tangible constraint on energy utilization, and some redox processes that liberate energy can nonetheless be useless to biology because they fail to satisfy this requirement (Schink 1988; Hoehler et al. 2001; Hoehler 2004). In contrast, the energy represented in visible-to-near-infrared photons (the wavelength range used in photosynthesis) significantly exceed the energy required for ATP synthesis, such that the Gibbs energy requirement is not a tangible constraint on photosynthetic biology.

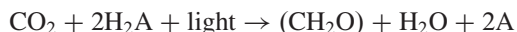
The second measure has units of energy per time or power (e.g., watts, joules per second) and has a lower limit derived from the need to expend energy to maintain a metabolically viable and orderly state against the tendency of systems toward more disordered states (as reflected in the second law of thermodynamics) (Hoehler and Jørgensen 2013). For example, life must expend energy to repair or newly synthesize damaged biomolecules. The collective energy required for such functions has been termed “maintenance energy” (Pirt 1965). Because the rate of acquired damage or the rate at which a system tends toward disorder can be affected by environmental conditions such as temperature, maintenance energy can be expected to depend on both biochemical specifics and environmental conditions.

It should be noted that both “voltage” and power can reach levels that overwhelm the biochemical machinery that serves to capture energy and then becomes destructive – as, for example, when sunlight is focused through a magnifying glass onto a leaf. Thus, the utility of energy sources to biology is constrained not only to specific types but also to defined ranges of power and voltage (Hoehler 2007).

## Photosynthesis

Photosynthesis has particular relevance in the context of exoplanets because it is thought that photosynthetic biospheres offer a higher probability of remote detection. For this reason, we focus the further discussion of life's energy requirements primarily on the utilization of light energy in photosynthesis. At a conceptual level, the general biological requirements for voltage and power correspond, respectively, to requirements for the wavelength and intensity of light that can support photosynthesis. Wavelength determines the amount of energy delivered per unit of energy carrier (photon). For example, a wavelength of 500 nm corresponds, by Planck's law, to an energy of  $4 \times 10^{-19}$  J-photon<sup>-1</sup> or 239 kJ·(mol photons)<sup>-1</sup>. Intensity (photon flux) thus specifies the amount of energy delivered through time. To understand the light energy requirements of photosynthesis and their implications for exoplanet biospheres, it is helpful to review the basic concepts of photosynthesis:

Photosynthesis is the conversion of light energy into chemical energy that can fuel metabolic processes, including the synthesis of biomolecules (Blankenship 2014). Most photosynthetic organisms utilize CO<sub>2</sub> as the source of carbon for biosynthesis, in which case a source of electrons (an electron-donating molecule or reductant) is also required, and the overall photosynthetic reaction can be generalized as (Kiang et al. 2007b):



Here, "H<sub>2</sub>A" is a reductant or electron-donating species, "A" is its oxidized equivalent, and "CH<sub>2</sub>O" is a generic representation of carbohydrate organic matter (e.g., the sugar glucose, C<sub>6</sub>H<sub>12</sub>O<sub>6</sub>, is (CH<sub>2</sub>O)<sub>6</sub>). When the reductant-oxidant pair is H<sub>2</sub>O/O<sub>2</sub>, the process is termed "oxygenic" (oxygen-producing) photosynthesis, which is familiar to us as green plant photosynthesis and is also utilized by algae and by cyanobacteria, the microbial innovators of this metabolism (Blankenship et al. 2007). "Anoxygenic" (non-oxygen-producing) photosynthesis utilizes reductant-oxidant pairs such as H<sub>2</sub>S/S, H<sub>2</sub>/H<sup>+</sup>, and Fe<sup>2+</sup>/Fe<sup>3+</sup> (Blankenship 2014). A key difference between these two broad categories is that anoxygenic photosynthesis uses electron donors that generally yield electrons easily, while water electrons are tightly held and can only be extracted by a highly oxidizing molecule. As a result, oxygenic photosynthesis has both shorter wavelength requirements and greater biochemical complexity than anoxygenic photosynthesis.

*Mechanism.* Photosynthesis proceeds using "photosystems," which are networks of molecules that absorb light (e.g., *pigments* like chlorophyll) and transfer energy and electrons to be captured in chemically stable forms. The known anoxygenic metabolisms proceed using single photosystems that in each case are driven by absorption of a single photon. Oxygenic photosynthesis uses two photosystems ("PS I" and "PS II," which absorb photons of differing wavelengths) that are connected in series by the passage of an electron from one to the other. Owing to this highly coordinated, two-photon scheme, oxygenic photosynthesis is mechanistically and

biochemically more complex and appears to have evolved later than anoxygenic photosynthesis (Blankenship et al. 2007).

*Wavelength requirements.* Understanding the wavelength requirements for photosynthesis is important, given that the spectral quality of light available to a surface biosphere can differ considerably as a function of both stellar temperature and planetary atmospheric composition (gases and aerosols in the atmosphere may absorb and/or scatter heavily and thus significantly diminish photon flux in specific wavelength regions, e.g., Arney et al. 2016). In particular, relative to our sun, the availability of short wavelength light is limited in cooler stars, which emit primarily at longer wavelengths (e.g., Segura et al. 2005; Kiang et al. 2007a).

On Earth, oxygenic photosynthesis is driven by photon absorptions at visible wavelengths and anoxygenic photosynthesis by absorptions in the visible through near-infrared.

What factors constrain the longest wavelengths that are useful in photosynthesis? *Mechanistically*, photon absorption promotes the electrons in pigment molecules from the ground state to an excited state, which renders the pigments highly reducing (the pigments easily yield or “donate” an electron from this excited state). The energy difference between ground and excited states in the pigment is referred to as the “bandgap” energy and determines the wavelength of light required to drive the excitation. Excited pigment electrons are donated into and flow sequentially through a series of redox active biomolecules called an “electron transport chain.” *Functionally*, the energy represented in the flow of electrons through the electron transport chain can be used to do “biological work,” such as making ATP, just as we capture the energy in electrical currents to do mechanical work. The long wavelength requirements for photosynthesis could conceivably be set by the energy requirements of either the mechanistic (electron exciting) or functional (work performing) aspects of the process, whichever is more stringent.

From a mechanistic perspective, light is only useful if it has energy sufficient to promote electrons from ground to excited states. This appears to be possible at wavelengths at least as long as 1015–1023 nm, which are shown to be used by the anoxygenic photosynthesizer *Blastochloris viridis* (Scheer 2003). Kiang et al. (2007b) suggest that wavelengths longer than about 1100 nm may fail to produce electronic transitions in organic molecules and would therefore be unsuitable for photosynthesis in mechanistic terms. However, as the exact energy required for electronic transitions is a function of specific molecular structure and properties, there is no precise long wavelength limit to what biological molecules could allow (Kiang et al. 2007a, b).

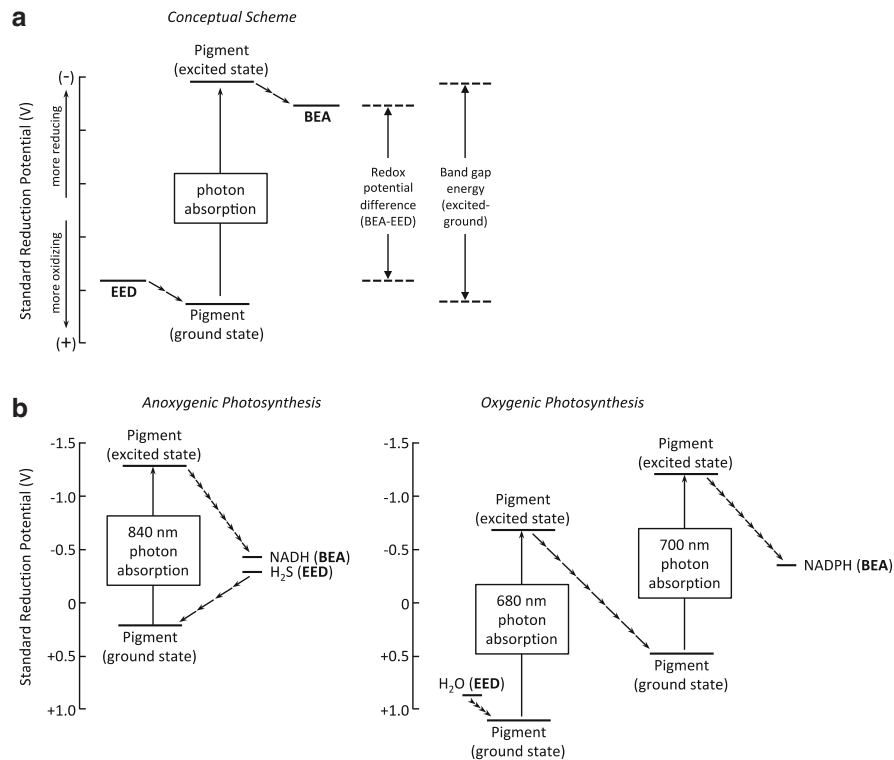
The functional requirements of photosynthesis – to provide for the storage of energy and reducing power – can set more stringent constraints on required photon energy and thus shorter wavelength limits. It is the sum of the energies associated with these two functions, plus the necessity that some photon energy be lost to heat in order to drive the process forward, that constrains the required photon energy.

The minimum Gibbs energy change shown to drive energy capture and storage in the biological energy carrier ATP (about 10–20 kJ·mol<sup>-1</sup> in non-photosynthetic organisms; Schink 1988; Hoehler et al. 2001) is small in comparison to the energies

delivered by visible and near-IR photons. Even the 1015–1023 nm wavelengths used by *B. viridis* correspond to Gibbs energies of about  $118 \text{ kJ}\cdot\text{mol}^{-1}$ , so that the energy storage requirement by itself does not impose a stringent constraint on long wavelength limit. The additional requirement that photon absorption drive the capture, and storage in biologically useful form, of electrons from external sources can add significantly to the overall photon energy requirement, depending on the nature of the external electron donor. This function requires that a pigment molecule have a reduction potential in the ground state that is sufficient to accept an electron from an external electron donor and an oxidation potential in the excited state (following photon absorption) sufficient that it can donate an electron to a biological electron acceptor (Fig. 4a). The minimum bandgap energy (the minimum energetic difference between ground and excited state) and the associated excitation wavelength must span at least the difference in redox potential between external electron donor and biological electron acceptor (Fig. 4a). To extract electrons from water, a very poor electron donor, the pigment must be much more oxidizing in ground state than is needed for anoxygenic electron donors, which yield electrons more readily. Because the initial biological electron acceptors in both oxygenic and anoxygenic systems have similar redox potential, the bandgap energy is larger in the case of oxygenic photosynthesis relative to anoxygenic photosynthesis (Fig. 4b), and the associated excitation wavelength is correspondingly shorter. Specifically, the excitation wavelength for the primary event in photosynthesis is about 680 nm, and a second excitation occurs at about 700 nm, whereas anoxygenic photosynthesis uses wavelengths generally in the range of 800–1000 nm. Until recently, it was assumed that photosystems I and II were maximally efficient in photon energy use and that two-photon oxygenic photosynthesis could not be achieved with longer wavelength photons. However, the cyanobacterium *Acaryochloris marina* has now been shown to use a structural variant of the chlorophyll used by green plants, in which the primary (PS II) excitation occurs in the range of  $723 \pm 3 \text{ nm}$  and the secondary (PS I) excitation occurs at  $740 \pm 5 \text{ nm}$  (Mielke et al. 2013; Miyashita et al. 1997; Renger and Schlodder 2008). Could oxygenic photosynthesis be driven by considerably longer wavelengths? It has been proposed that a coupled network of three photosystems could theoretically achieve oxygenic photosynthesis using wavelengths in the near-IR (approx. 1000 nm) (Wolstencroft and Raven 2002). However, such a system would require even greater molecular coordination and biochemical complexity than is represented in the (already remarkably complex and highly coordinated) two-photon system utilized for oxygenic photosynthesis on Earth.

Whether short wavelength limits exist for the light energy that can be used in photosynthesis may be specific to the biochemistry in question. On Earth, wavelengths as short as about 400 nm are captured and used in photosynthesis. However, the energy content of these shorter wavelength photons is effectively dissipated as heat so that the remaining energy is equivalent to the bandgap (excitation) energy. Ultraviolet wavelengths are inhibitory or destructive to photosynthetic organisms on Earth. UV-B (280–315 nm) and shorter wavelengths cause damage to DNA (Caldwell 1979), while both UV-B and UV-A (315–400 nm) inhibit photosynthesis





**Fig. 4** Flow of electrons from an external electron donor (EED) to a biological electron acceptor (BEA) during photosynthesis. (a) Generalized scheme showing the change in reduction potential of electrons as they flow through the photosystem. An upward trajectory on this plot requires input of energy (e.g., via photon absorption); a downward trajectory is thermodynamically spontaneous. The required bandgap energy (pigment excitation wavelength) must span from a ground state reduction potential more positive than that of the EED to an excited state reduction potential more negative than that of the BEA. Here and in panel (b), multiple arrows indicate that electron transfer may occur through multiple intermediate carriers. (b) Electron flow in anoxygenic photosynthesis as observed in green sulfur bacteria (left panel) and oxygenic photosynthesis (right panel). Relative to anoxygenic photosynthesis, oxygenic photosynthesis has a larger difference in redox potential between BEA and EED, a larger bandgap energy/shorter excitation wavelength, and is driven by successive absorption of two photons versus one

due to generation of reactive oxygen intermediates (White and Jahnke 2002). Photosynthetic organisms combat these effects through production of UV-screening pigments and antioxidants (White and Jahnke 2002), but these are mechanisms that limit damage by short wavelength radiation rather than enable it to be used directly in photosynthesis. Direct utilization of UV and shorter wavelengths would require both “antenna” molecules capable of capturing and transferring high photon energies *and* a biochemistry that is compatible with exposure to such radiation.

## Light Intensity Limits for Photosynthesis

Life's need to receive a minimum flux of energy through time ("maintenance energy") is expressed in photosynthetic biology as requirement for photon flux (light intensity). Conceptually, this flux should be sufficient to support a viable metabolic state. Mechanistically, it must also be capable of driving electron flow through the sequence of reactions that define the photosystem. The mechanistic constraint is important given that oxygenic photosynthesis couples the events driven by absorption of two photons in short (nanosecond) succession (Rappaport and Diner 2008). Theoretically, this could impose a more stringent constraint on photon flux than the maintenance energy requirement.

The lowest photon fluxes that appear to support a metabolically viable state have been quantified in a species of red algae (Littler et al. 1986) and in several anoxygenic phototrophs (e.g., Marschall et al. 2010). These fluxes are five to six orders of magnitude lower than the average photon flux at Earth's surface and are equivalent to the solar flux at a distance of approximately 500–1000 AU. By comparison, the water worlds of our solar system are frozen at the surface from Jupiter's orbit (5 AU) outward. Thus, it seems unlikely that photon flux would be limiting at the organism (maintenance energy) level for any world on which the radiation budget allows liquid surface water. Rather, low light intensities may be more likely to affect whether a photosynthetic biosphere can be sufficiently productive to yield a detectable signal (e.g., Kiang et al. 2007a).

## Photosynthesis and the Detectability of Biospheres

For exoplanets, photosynthetic biospheres may be more or perhaps uniquely detectable in comparison to non-photosynthetic biospheres, for two reasons:

*Photosynthetic life is capable of creating gaseous products that are far from equilibrium relative to the contextual chemistry*, as reflected in large  $\Delta G$  values for the production of such species. For example,  $O_2$  is created during photosynthesis when electrons from water are extracted and ultimately used to reduce  $CO_2$  to organic compounds, such as glucose:  $CO_2 + H_2O \rightarrow O_2 + 1/6 C_6H_{12}O_6$ . The large disequilibrium represented in the gaseous product  $O_2$  is reflected in the standard Gibbs energy change for this reaction,  $\Delta G = +478 \text{ kJ} \cdot (\text{mol } O_2)^{-1}$  (and thus  $-478 \text{ kJ} \cdot (\text{mol } O_2)^{-1}$  for the reaction of  $O_2$  back to equilibrium with respect to glucose), which closely approximates the standard oxidation potential for water:  $2H_2O \rightarrow O_2 + 4H^+ + 4 \text{ electrons}$ ,  $\Delta G = +475 \text{ kJ} \cdot (\text{mol } O_2)^{-1}$  and  $+119 \text{ kJ} \cdot (\text{mol electrons})^{-1}$ . It is the significant energy content of visible photons that enables the establishment of such large Gibbs energy changes: The primary excitation wavelength in oxygenic photosynthesis, 680 nm, is equivalent to a photon energy of  $176 \text{ kJ} \cdot \text{mol}^{-1}$ .

It is important to note that non-photosynthetic life can also invest energy that results in the creation of disequilibrium products, for example, when (energy-

yielding) ATP hydrolysis is coupled to (energy-requiring) biosynthesis (McCollom and Amend 2005). However, the energy represented in ATP under physiological conditions is approximately  $50 \text{ kJ}\cdot\text{mol}^{-1}$ , so that multiple instances of ATP hydrolysis would have to be coupled to the synthesis of a single product in order to achieve disequilibria such as that represented in  $\text{O}_2$ . Although this occurs routinely in biochemistry, the products of such reactions are often large, complex molecules – for example, proteins and nucleic acid polymers – that are not volatile.

*Photosynthesis has potential to yield and sustain a globally larger and more productive biosphere than is possible in its absence.* On Earth, biosynthesis requires energy, elemental raw materials (carbon, nitrogen, phosphorus, and sulfur), and a source of electrons with which to reduce  $\text{CO}_2$  carbon to an intermediate oxidation state. Non-photosynthetic life is reliant on planetary chemistry (including atmospheric chemistry resulting from stellar radiation) to fill each of these needs, and energy availability can be encountered as a significant limitation. Photosynthesis eliminates the reliance on planetary chemistry to provide energy, through provision of an external source. Oxygen-producing photosynthesis also effectively alleviates the potential for electron supply to be limiting, by making (widely abundant) water accessible as a source of electrons. Our biosphere is thus overall limited by availability of elemental raw materials (in the oceans) or water (on the continents), rather than by energy or electrons. It has been estimated that, by virtue of the capability for oxygenic photosynthesis and the corresponding alleviation of resource requirements, the modern biosphere is more productive by three or more orders of magnitude than was the pre-photosynthetic biosphere (Canfield et al. 2006).

Could light energy be limiting to the global productivity of a photosynthetic biosphere and thereby diminish the detectable signal of life? As discussed above, it seems unlikely that low light flux could be prohibitive to photosynthetic life in absolute terms, for any body that receives sufficient light to support liquid water at the surface. Moreover, on Earth, the productivity of the photosynthetic biosphere is overall limited by availability of water and elemental resources or “nutrients” rather than by light flux. Indeed, Earth’s biosphere utilizes only a few percent of the available light energy, such that photon fluxes would have to fall well below the levels required to sustain liquid water before they proved limiting to photosynthesis. However, for cooler stars that emit a much smaller fraction of their light in visible wavelengths than does our sun, it might be possible for stellar flux to prove limiting to photosynthetic productivity. This could be true particularly for planets near the outer edge of the habitable zone and/or those in which atmospheric absorption or scattering significantly diminishes the flux of photons to the surface. In this context, it is particularly important to understand the long wavelength limits for photosynthesis and for oxygenic photosynthesis in particular. The shorter the wavelength requirement and the cooler the star, the greater the chance that light flux could prove limiting to overall biospheric productivity. This stands as an important question to evaluate in quantitative terms.

## Summary

Assessment of life's requirements can help to assess both the full range of environments beyond Earth in which life might be possible and which among those environments provide the most compelling targets in a search for life. As we currently understand it, life requires a source of energy, with which to build and sustain molecular complexity and information processing; specific elemental raw materials, from which to construct molecules having specific properties and reactivity; a solvent that supports the synthesis of the full range of molecules required by life and properly mediates the full range of necessary interactions among those molecules; and physicochemical conditions in which life's molecules can be synthesized, are appropriately stable, and can interact as needed for lifelike function. Life on Earth expresses specific forms of these general requirements: light energy in visible-to-near-infrared wavelengths or chemical energy as provided by oxidation-reduction disequilibrium, the "biogenic" elements (carbon, hydrogen, oxygen, nitrogen, phosphorus, and sulfur), liquid water, and specific ranges in temperature, pH, salinity, pressure, and other environmental factors. Understanding how well different environments meet these requirements – for example, how much energy or how much of a given element is available – will allow us to move from a binary (yes/no) to a more quantitative approach to habitability. This, in turn, can inform our sense of both possibility and priority as we begin to search for life beyond Earth.

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