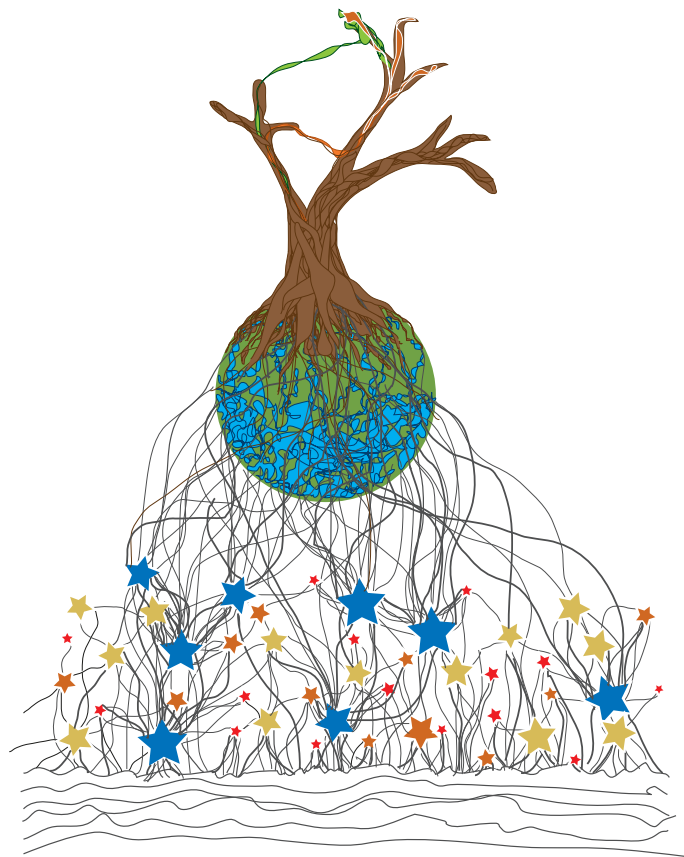


The Origin and Evolution of Life on a Pale Blue Dot

Astrophysical, Geochemical and Biological Constraints on Habitability

Aditya Chopra



A thesis submitted for the degree of Doctor of Philosophy

Research School of Astronomy & Astrophysics
Research School of Earth Sciences



Australian
National
University

November, 2015

Declaration

This dissertation is an account of research undertaken between April 2009 and November 2015 at the Research School of Earth Sciences, The Australian National University, Canberra, Australia.

The work presented in this thesis is that of the candidate alone, except where indicated by due literature reference and acknowledgements in the text. It has not been submitted in whole or in part for any other degree at this or any other university.

This thesis is based on six papers published in refereed scientific journals or books. The development of ideas and research was undertaken with guidance from my supervisor Charles H. Lineweaver and published papers presented in the thesis were written collaboratively with him. Below I describe my contributions to the research in each chapter and associated papers.

- Chapter 1 is the paper [Lineweaver and Chopra \(2012a\)](#). Section 1.1 is my major research contribution to the paper. Research on the distribution of biomass on Earth, the constraints for habitable zones within the Earth, and the energy requirements and sources for the earliest bacteria is my work.
- Chapter 2 is the paper [Chopra and Lineweaver \(2016\)](#) where my research forms a major contribution to all sections of the paper.

Aditya Chopra
15 June 2021

Acknowledgements

Like Sagan's apple pie, this thesis was not put together from scratch, because that would have required me to first create the universe. So to all baryons, wise ancestors and enlightened cousins, eukaryotic or otherwise, thank you.

I am grateful to my supervisor, research school, friends and family.

Thank you Google et al. May the electrons keep following and the entropy keep increasing...

Abstract

Some of the most fundamental questions in astrobiology are: How does life begin and evolve? Does life exist elsewhere in the universe? What is the future of life on Earth and beyond? This thesis approaches these questions by investigating the chemical and energy requirements for life and the conditions that enabled the emergence and proliferation of life on Earth. Understanding how common the necessary physical processes, chemical ingredients and environmental conditions may be on other planets helps us assess the likelihood of finding life beyond our planet and gives us clues about the best targets and detection methods for future search efforts.

Our evaluation of astrophysical and geochemical constraints on the habitability of Earth-like planets tells us that temperature and the presence of water are the main factors that define the limits for life. Our analysis of recent exoplanet detections suggests that the fraction of stars with planets is $\sim 100\%$, and that the fraction with wet rocky planets is likely to be comparably large. We find that the most fundamental free energy redox and photon gradients associated with the earliest life forms on Earth, and the energy-transducing metabolisms they induce, are plausible on other wet rocky planets.

Even if the emergence of life is a common feature of planetary systems throughout the universe, we propose a new Gaian bottleneck hypothesis where we postulate that in addition to water, energy and abiogenesis, the early extinction of planetary life is also a cosmic imperative. We discuss why the vast majority of initially wet rocky planetary environments evolve away from habitable conditions within about a billion years because of the strength, rapidity and universality of abiotic positive feedbacks in the atmospheres of terrestrial planets in traditional circumstellar habitable zones. We argue that the maintenance of planetary habitability is a property more associated with an unusually rapid evolution of biological regulation of surface volatiles, than with the luminosity and distance to the host star. Our model suggests that a planet needs to be inhabited in order to remain habitable and predicts that lifeless habitable planets will be rare. The Gaian bottleneck to the long-term persistence of life may be a better explanation for the non-prevalence of extraterrestrial life than the conventional emergence bottleneck paradigm.

Keywords: habitability, planetary science, astrobiology

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Abbreviations

ANU	Australian National University
BOM	Bureau of Meteorology
CSIRO	Commonwealth Scientific and Industrial Research Organisation
LAH	List Abbreviations Here
WSF	What (it) Stands For

Physical Constants

Speed of Light $c_0 = 2.997\,924\,58 \times 10^8 \text{ m s}^{-1}$ (exact)

List of Symbols

a	distance	m
P	power	W (J s ⁻¹)
ω	angular frequency	rad

For/Dedicated to/To my...

Chapter 1

Habitable Worlds

This chapter was published as

C. H. Lineweaver and A. Chopra (May 2012a). 'The Habitability of Our Earth and Other Earths: Astrophysical, Geochemical, Geophysical, and Biological Limits on Planet Habitability'. *Annual Review of Earth and Planetary Sciences*, 40(1), pp. 597–623. ISSN: 0084-6597. DOI: [10.1146/annurev-earth-042711-105531](https://doi.org/10.1146/annurev-earth-042711-105531)

Abstract

We review the habitability of our Earth and other Earth-like planets. Understanding habitability and using that knowledge to locate the nearest habitable planet may be crucial for our survival as a species. To evaluate remotely the habitability of the increasing number of Earth-like exoplanets, we need to understand which features of our own planet enabled the origin and evolution of life – and if these features are universal. We discuss the habitability of Earth, the habitability of planets orbiting other stars, and the habitability of our galaxy. We profile the 'bioshell' - the $\sim 1\%$ volume of our planet, which is inhabited by life and describe temperature and nutrient deserts where there is little biomass. The inhabited and uninhabited regions on Earth suggest that the presence of liquid water in a narrow temperature range is the main constraint that can be used in a habitability classification scheme for rocky planets.

We review current ideas about the microbiology and bioenergetics of the earliest terrestrial life forms and find that the conditions for life's emergence may be different and more specific than the broader conditions to which life can adapt. Since life and its environment co-evolve, we propose the dynamic concept of an 'Abiogenesis Habitable Zone', where life can get started and which, upon continual modification by life, transitions into a 'Habitable Zone'. Our compilation of recent exoplanet detections suggests that the fraction of stars with planets is $\sim 100\%$ and the fraction of stars with a rocky planet in the habitable zone could be comparably large. Recent discoveries suggest that there are at least 10 times as many Earth-sized planets as Neptune sized planets, which in turn are 10 times more abundant than Jupiter-sized planets. Although the process of rocky planet formation and supply of water to terrestrial planets, seems to be a common product of star formation, the water content of a rocky planet is probably highly variable. This variability can be used to classify their habitability, e.g., ocean planets, Earth-like planets, and desert planets.

*The Sun with all those planets revolving around it
and dependent on it, can still ripen a bunch of grapes
as if it had nothing else in the universe to do.*
— Galileo Galilei

The universe is filled with stars like our Sun (Robles et al., 2008), rocky planets like our Earth (Howard, Marcy, Bryson et al., 2012), water like in our oceans (Mottl et al., 2007), amino acids like those that make up our proteins, and all the other ingredients for life (Pizzarello, 2007). But is the universe filled with anything we would recognize as life (Lineweaver, 2006)? De Duve (1995) has argued that the initial deterministic nature of proto-biochemistry makes life a “cosmic imperative” built into the chemistry of the universe, and we should therefore expect life to be common in the universe.

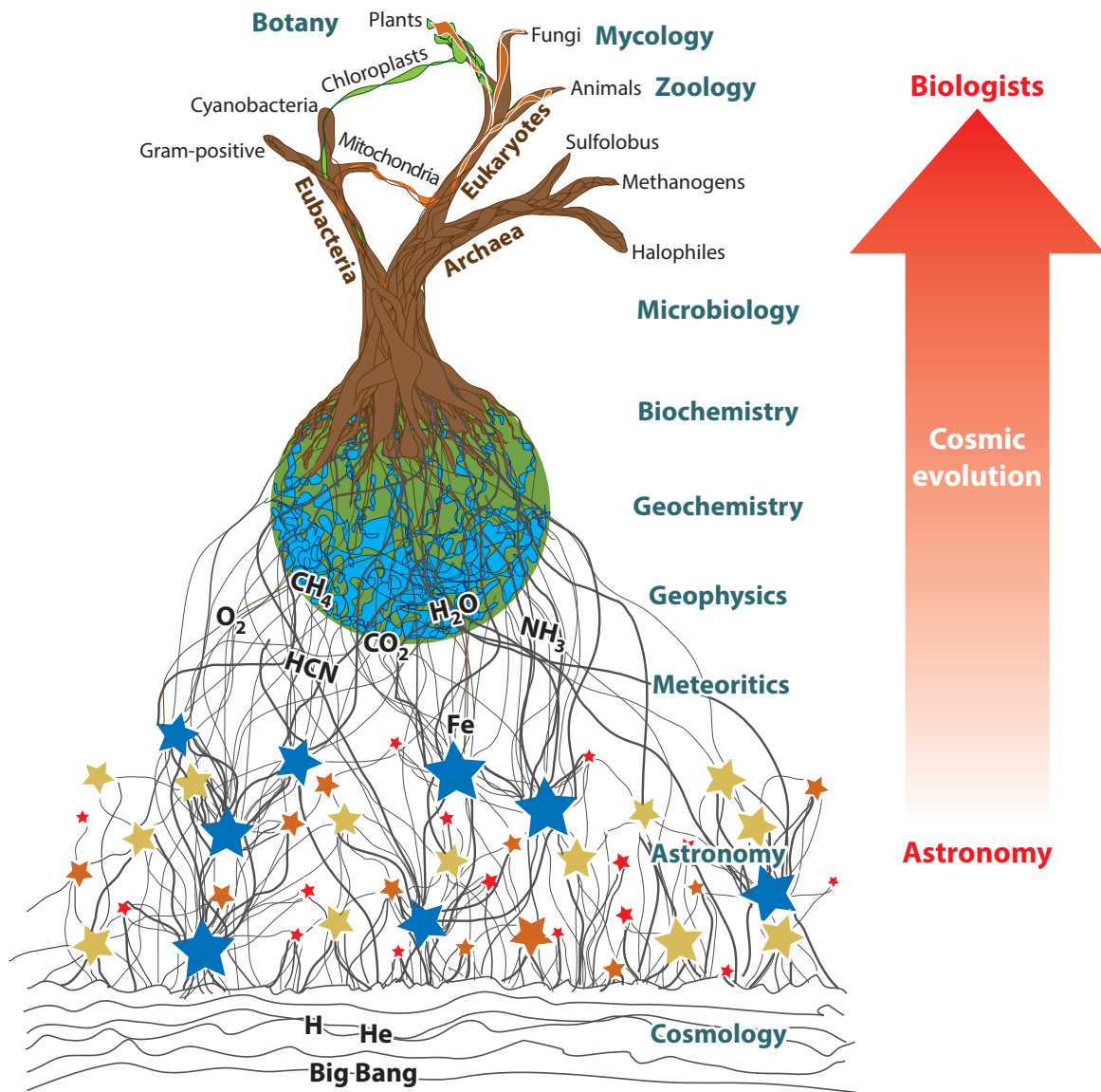


Figure 1.1: The emergence of biologists from astronomy. Starting from the big bang at the bottom, deterministic physical sciences set the context for the emergence of life. The resulting biologists (animals) at the top of the tree (e. g. Hedges and Kumar, 2009; Pace, 1997) have constructed the brown phylogenetic tree based on the molecular fossils inside the DNA of the inhabitants of the biosphere. The terrestrial tree of life took root approximately four billion years ago. We review the features of rocky planets that are implicated in the ability to give root to, and maintain, a tree of life.

Terrestrial life emerged from nonlife approximately four billion years ago (Battistuzzi et al., 2004; Sleep and Bird, 2008) (Figure 1.1). Descriptions of where this happened include warm little ponds (Darwin, 1871), hot hydrothermal vents (Martin, Baross et al., 2008; Wächtershäuser, 2006), and cold little

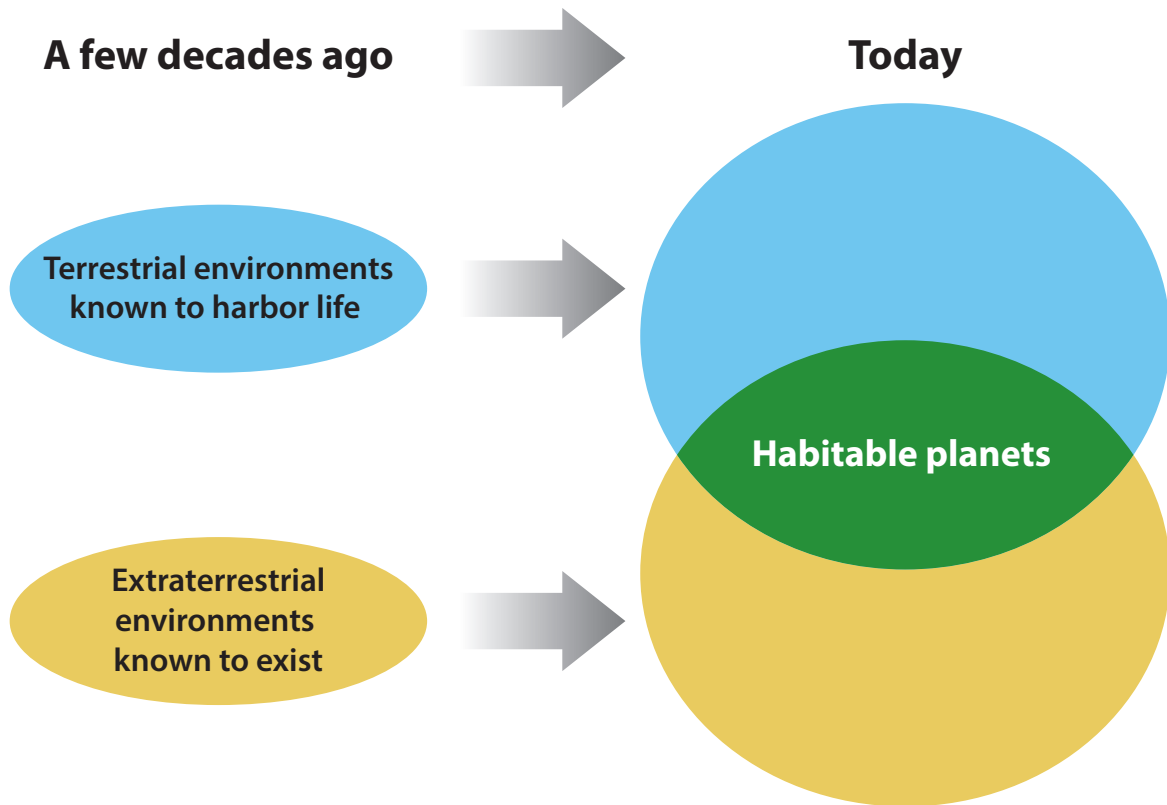


Figure 1.2: Emergence of habitable planets. Habitable planets are emerging from the increasing overlap of two sets of environments: the increasingly large set of terrestrial environments known to harbor life and the increasingly large set of extraterrestrial environments on the newly detected rocky exoplanets. The overlap of these research fields bolsters expectations that the universe may be filled with habitable planets.

ponds (Bada et al., 1994). Scenarios for how life emerged include a prebiotic soup under a reducing atmosphere (Miller, 1953; Oparin, 1924) and some form of semi-deterministic molecular chemistry (Dyson, 1999; Segré and Lancet, 2000) that evolved into auto-catalytic reactions (Eigen, 1971) and produced replicating molecules (Cairns-Smith, 1982; Gesteland and Atkins, 1999), proto-metabolisms (Pascal et al., 2006), and cell membranes (Deamer and Weber, 2010). Despite the variety of these scenarios, some common threads represent our best estimates of what we might expect to share with extraterrestrial life. We can expect extraterrestrial life to be based on Darwinian evolution and the most fundamental features of terrestrial biochemistry (Benner et al., 2004; De Duve, 2007; Feinberg and Shapiro, 1978; Lineweaver and Chopra, 2012b; Morris, 2003; Pace, 2001). Noncoincidentally, these are the same features that are often used to define life (e. g. Joyce, 1994; Leach et al., 2006; Sagan, 1970; Schrödinger, 1944).

During the past few decades, the exploration of some extreme environments on Earth has uncovered extremophile microbial life in conditions previously thought to be too hostile for life. These discoveries have expanded the variety of terrestrial environments known to harbor life (Baross et al., 2007; Madigan et al., 2010; Pedersen, 2010; Rothschild and Mancinelli, 2001; Shock and Holland, 2007; Stetter, 2006). During the same few decades, progress in the characterization of the planets and moons of our Solar System, and progress in the detection of a wide variety of exoplanets in orbit around an increasingly large fraction of stars, has broadened the range of known extraterrestrial environments (Sections 1.2 and 1.3). The growing overlap of these two sets of environments suggests that habitable planets are abundant (Figure 1.2). This increases the probability of finding some kind of extraterrestrial life.

The number of papers and conferences reporting new exoplanet and extremophile discoveries, and those grappling with the issue of planetary habitability, has enormously increased. Recent reviews of habitability include Kasting and Catling (2003), Gaidos, Deschenes et al. (2005), Hoehler et al. (2007), Fishbaugh et al. (2007), Kopparapu et al. (2013) and Kasting, Kopparapu et al. (2014).

This review provides an overview of habitability and focuses on what we know about the habitability of Earth, the habitability of planets orbiting other stars, and the habitability of our galaxy. It synthesizes facts and current ideas about the microbiology of the earliest terrestrial life and the latest findings of planet hunters. It is organized as follows: Section 1.1 reviews the limits of terrestrial life and illustrates where life is found, and is not found, on the habitable planet that we know best—Earth. We discuss energy constraints on life and how the conditions for life’s emergence may be different and more specific than the broader conditions to which life can adapt. Section 1.2 presents the increasingly compelling evidence that planets in general, and rocky planets in particular, are a common product of star formation. Section 1.3 discusses the habitability of the most Earth-like exoplanets and the traditional circumstellar habitable zone (HZ). Section 1.4 reviews the supply of water to terrestrial planets. Finally, Section 1.5 reviews work on the galactic HZ and discusses a variety of habitability issues.

1.1 The Habitable Zones on Earth

Because habitability is about the complex relationship between life and environment, we start close to home with a discussion of the relationship between terrestrial life and terrestrial environments. The close fit between our requirements and what Earth can provide is not coincidental. Earth and the life on it have coevolved. However, life is not infinitely adaptive. Some parts of Earth are habitable and some, even after approximately four billion years of evolution, are not. Life as we know it has limits, and we can explore these limits most easily on Earth.

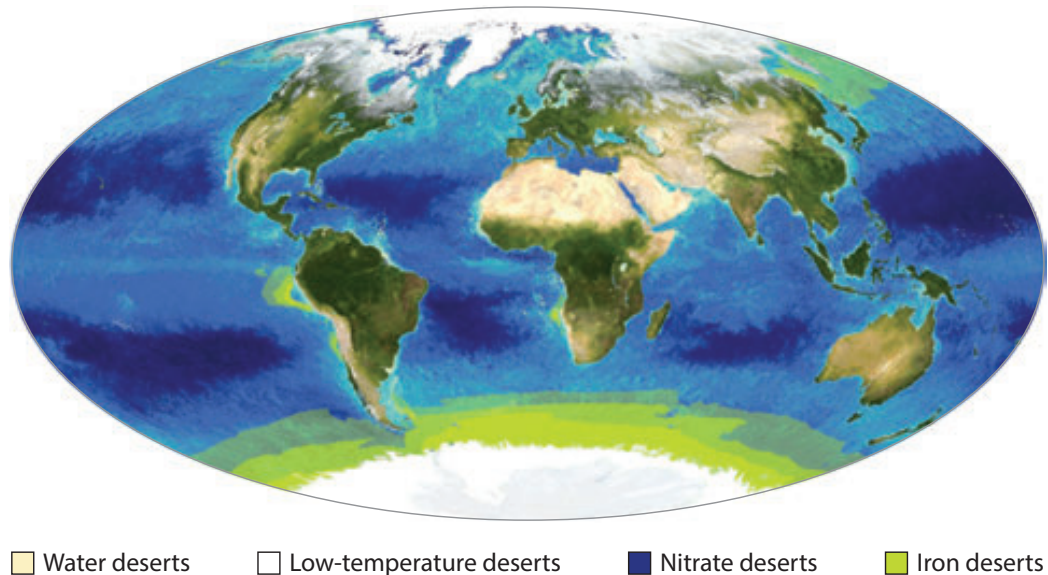


Figure 1.3: Four deserts on Earth's surface. Life is not evenly distributed over the surface of Earth. There are water deserts (sandy brown), low-temperature deserts (white), nitrate deserts (dark blue), and iron deserts (light green), where the abundance of life is significantly lower than in surrounding regions. This map was constructed with data from [McClain et al. \(2006\)](#); [Stöckli et al. \(2005\)](#).

In a specific region, when some requirement for life is outside the optimal range for life, the total biomass in that region is low (Figure 1.3 presents these regions). We generically call such regions deserts. Low rainfall makes water deserts. Low temperatures make low-temperature deserts at Earth's poles. Far from land, in mid-oceanic gyres (where windblown dust and aerosols are at a minimum ([Duce and Tindale, 1991](#))), low nitrate levels produce nitrate deserts.

Chlorophyll maps of the ocean ([McClain, 2009](#); [McClain et al., 2006](#)) show regions where, despite ample water, photons, and nitrates, there are low concentrations of chlorophyll. Iron fertilization experiments in these enigmatic high-nitrate-low-chlorophyll regions found that the biomass was iron limited, rather than phosphate limited or limited by some other nutrient ([Falkowski, Barber et al., 1998](#); [Smetacek and Naqvi, 2008](#)). Such iron deserts have been identified in the Southern Ocean, the northwest Pacific, and the eastern equatorial Pacific. Low-phosphate regions overlap significantly with nitrate deserts ([Garcia et al., 2006](#)). Because the elements H, O, C, N, P, and S make up $\sim 98\%$ (by mass) of life ([Lineweaver and Chopra, 2012b](#)), one might expect analogous C and S deserts.

The subtle variations of biomass over the horizontal surface (Figure 1.3) are dwarfed by the nonsubtle variations of biomass in the vertical direction. The terrestrial biosphere is a thin bioshell whose thickness (~ 10 km) is $\sim 1/600$ of Earth's $\sim 6,400$ km radius. Figure 1.4 is a vertical profile of terrestrial biomass. Low temperatures and low densities prevent life from living permanently in air or on the highest mountains (low-temperature deserts). High temperatures prevent life from existing more than ~ 5 kilometers underground, because the average continental geothermal gradient of $20\text{--}30^\circ\text{C per km}$ reaches the upper temperature limit of life (122°C , ([Takai et al., 2008](#))) at approximately that depth. (Shield gradients and those above subduction zones can be as low as $\sim 10^\circ\text{C per km}$.) Thus, the interior of Earth is a spherical high-temperature desert. The bioshell is thin because life is kept squeezed into a narrow HZ between a high-temperature desert below and a low-temperature desert above (Figures 1.4 and 1.5).

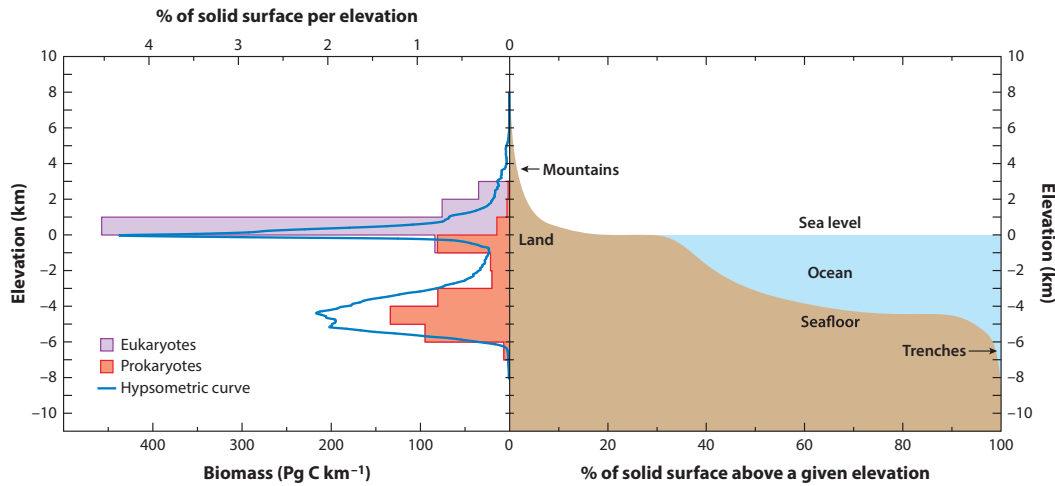


Figure 1.4: Vertical profile of biomass in the thin terrestrial bioshell (± 10 km). The hypsographic curve on the right shows the fraction of Earth's solid surface above a given elevation. For example, 30% of the solid surface is above sea level, whereas the remaining 70% is below sea level. The hypsometric curve on the left (blue line) [Perotti and Rinaldi \(2011\)](#) shows the fraction of Earth's solid surface at any given elevation. The histogram on the left shows our estimate of the vertical profile of terrestrial biomass (total carbon in terrestrial life forms) derived from combining data from [Houghton \(2003\)](#); [Whitman et al. \(1998\)](#). Since the publication of the paper presented in this chapter, [Kallmeyer et al. \(2012\)](#) analysed a more diverse range of sediment samples and estimate that the biomass in sub-seafloor sediments is 10-45% lower than estimates used by [Whitman et al. \(1998\)](#). [Hinrichs and Inagaki \(2012\)](#); [Jorgensen \(2012\)](#) and further analysis by [McMahon and Parnell \(2014\)](#) confirm the overestimation by [Whitman et al. \(1998\)](#). However, we find that even with the new estimates our main conclusions of the relative distribution of prokaryotic and eukaryotic life is not challenged.

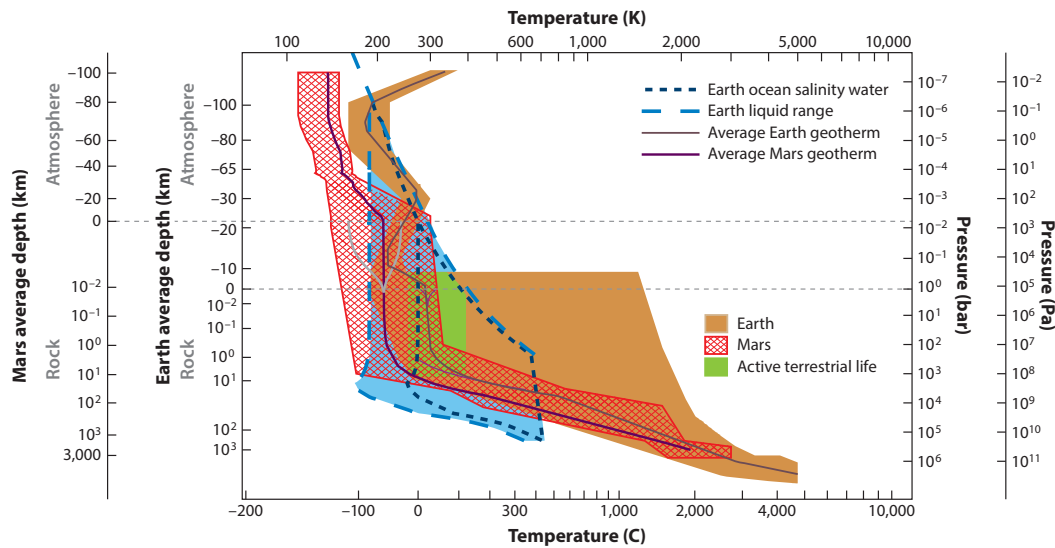


Figure 1.5: Uninhabited water on Earth and the potential biosphere of Mars. This pressure-temperature phase diagram is a superposition of the region where H_2O is liquid (blue), all terrestrial environments (brown), inhabited terrestrial environments (green), and all Martian environments (hatched red). Notice the large regions of uninhabited terrestrial liquid water that is either too cold ($-80^\circ C < T < -20^\circ C$) or too hot ($122^\circ C < T < 400^\circ C$) for life. The ± 10 km vertical extent of the green area corresponds to the elevation range of the biomass profile in [Figure 1.4](#). The shape of the green area shows that the presence of liquid water and the $-20^\circ C$ to $+122^\circ C$ temperature range are the dominant variables determining habitability. These inhabited and uninhabited terrestrial environments, set by the need for liquid water and a specific range of temperature, are our best guides to exoplanet habitability. Figure from [Jones, Lineweaver and Clarke \(2011\)](#). See also [Cockell \(2011\)](#); [Jones and Lineweaver \(2010, 2012\)](#); [Mottl et al. \(2007\)](#).

Terrestrial biomass is approximately evenly divided between eukaryotes (55%; Figure 1.4, light purple) and prokaryotes (45%; Figure 1.4, orange). Biomass is also roughly evenly divided between above sea level (56%) and below sea level (44%). Of Earth's eukaryotic biomass, 99.5% is on land (Sundquist and Ackerman, 2014). About 96% of prokaryotic biomass is below sea level, mostly in seafloor sediments (Whitman et al., 1998). The oxygenic photosynthesis that powers most of the eukaryotic life on land was a relatively late adaptation (Kiang et al., 2007; Sleep and Zoback, 2007), as was the ability to colonize the land (Battistuzzi et al., 2004). Five hundred million years ago, there was land but little eukaryotic life on it. Thus, for approximately the first three billion years, the profile of terrestrial biomass may have resembled the current prokaryotic profile (Figure 1.4, orange).

1.1.1 The Abiogenesis Habitable Zone

As we learn more about the origin of life, we can start to define an abiogenesis habitable zone (AHZ) where the requirements for life's emergence are met. The habitability requirements for the origin of life may be substantially different from, and more specific than, the requirements to maintain life on a planet—think of the difference between a spark plug to start an engine and a carburetor to supply it with fuel. If you shine light onto a vat of HOCNPS, or bubble molecular hydrogen through a flask of amino acids, life does not spontaneously emerge. For a planet to manage the transition from the nonliving to the living - to qualify as an AHZ - juxtapositions and flows of specific combinations of molecules are needed to produce auto-catalytic reactions and proto-metabolisms that can tap into either the flow of redox pairs or photons (De Duve, 1995; Lane et al., 2010).

Once life begins, organisms do not just passively adapt to preexisting environments. They actively change and construct the world they live in (Odling-Smee et al., 2003). The evolutionary history of life on Earth can be written in terms of how organisms have modified their environments. From the oxygenation of the atmosphere to the creation of beaver dams, life modifies its environment. But life also modifies itself and adapts to fit the environment—evolving, for example, spores to survive dry conditions, antifreeze for survival at low temperatures, and salt pumps to survive at high salinity. Whether life adapts to fit an environment or modifies an environment to be able to survive, the result is the same: The initial specific AHZ is widened (Figure 1.6). Through its management of the greenhouse and its partitioning of reductants and oxidants, the activity of life increases the range of inhabited environments (Hazen et al., 2008; Nisbet, Zahnle et al., 2007).

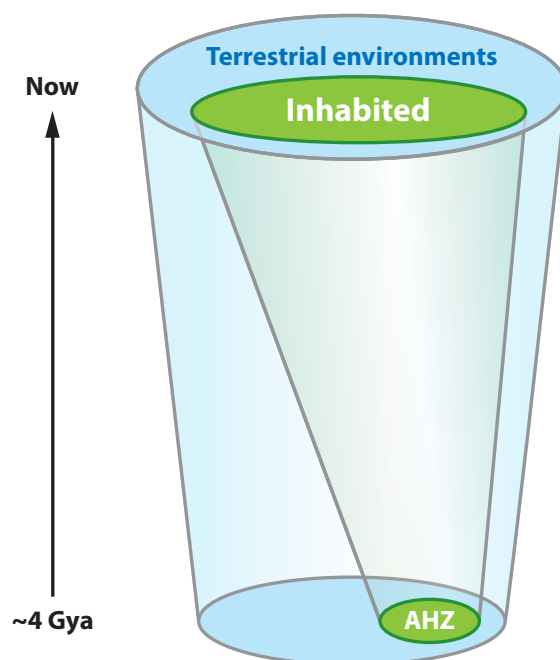


Figure 1.6: Abiogenesis habitable zone (AHZ). The conditions needed for the origin of life (before life could adapt) are narrower than the broader conditions to which life can adapt.

Environments change life-forms, and life-forms change environments. This feedback between life and environment may be so strong that, for a planet to be habitable, it might have to be inhabited. Thus, planetary habitability becomes a dynamic concept with different stages. Habitability begins as a relatively narrow AHZ, completely dependent on the chemistry and other physical characteristics of the planet. Once life emerges and passes the “Darwinian threshold” (Woese, 2002) habitability shifts to a dependence on both the characteristics of the planet and the adaptability of its life-forms. Finally, habitability becomes predominantly dependent on the ability of the inhabitants to regulate their environment. The thermoregulation of Earth over the past four billion years, despite a 30% increase in solar luminosity, is a possible example of such Gaian regulation (Lovelock, 1965, 2000; Lovelock and Margulis, 1974; Schneider, 2004; Schneider and Boston, 1991). It may be that natural negative-feedback processes, such as the carbon-silicate cycle (Walker et al., 1981), without Gaian regulation, are not conducive to life any more than a nonevolving body would be (Schwartzman and Volk, 1989). Thus, eventually, habitability becomes a property of life, as much as, or perhaps more than, it is a property of a planet.

The persistence of life on Earth requires liquid water, an appropriate temperature range, nutrients, and an energy source. Self-assembly is an example of an additional requirement for abiogenesis that would be relaxed once life got started (making the AHZ narrower than the HZ). For example, origin-of-life chemists are trying to understand how RNA could self-assemble in the presence of water (e.g. Szostak et al., 2001). To self-assemble, dehydration reactions are needed. Cyclic evaporative dehydration could happen near continental hot springs or in warm tidal pools as the kilometer-high tides came in and out every few hours (e.g. Lathe, 2004). On ocean planets (Section 1.3), there could be no dehydration reactions because there would be no evaporation from solid surfaces. Thus RNA would not self-assemble and life might not be able to get started on ocean planets. If the self-assembly of RNA required cyclic evaporation, and this assembly was critical to the emergence of life, ocean planets would be lifeless. They would be habitable but uninhabited planets.

1.1.2 Habitable Energies

On Earth today, ~60% of the biomass is phototrophic and ~40% is chemotrophic (Figure 1.4). Thus, the dominant energy source for life is the solar photon flux. However, when life emerged approximately four billion years ago there may have been much less dry land (Taylor and McLennan, 2009) and no eukaryotes. The terrestrial biomass distribution thus may have more closely resembled the current prokaryotic distribution in which the majority of the biomass is not necessarily in the photic zone but at hydrothermal vents at various depths, which were more common approximately four billion years ago (Sleep, 2010; Southam et al., 2007). Studying the earliest and most fundamental metabolisms of terrestrial life is our best hope for understanding how likely such energy-transducing metabolisms (and thus life) are to emerge elsewhere. Candidates for the earliest metabolisms include two broad categories of primary producers: anoxygenic phototrophs and chemolithotrophs. Chemolithotrophs live off inorganic redox pairs supplied by chemical disequilibria at hydrothermal vents (Kelly and Wood, 2006; Nisbet and Sleep, 2001).

Hyperthermophiles are the deepest- and shortest-branched organisms on the phylogenetic tree of life (e.g. Lineweaver and Grether, 2003; Pace, 1997). Hyperthermophiles gain energy by inorganic redox reactions employing compounds such as H_2 , CO_2 , S^0 , Fe^{2+} , and Fe^{3+} (Stetter, 2006). Redox reactions in hydrothermal vents and hot springs probably played a dominant role in early metabolism. The earliest life forms were probably chemoheterotrophs that evolved in high-temperature, low-pH, and high-salinity environments resembling hydrothermal vents (Martin, Baross et al., 2008) or hot springs. The transition of life from a redox-only energy source to a redox and photon energy source is suggested by comparing the energies of different metabolic reactions in Figure 1.7 (Sleep and Bird, 2008). The earliest redox reactions – pyrite formation, sulfur reduction, methanogenesis, and acetogenesis (Blank, 2009; Ljungdahl, 1986; Martin and Russell, 2007; Wächtershäuser, 1998) – provide less energy than photosynthesis. However, these early reactions do provide enough energy to charge transmembrane potentials in a chemiosmotic coupling and convert low-energy molecules such as ADP, NAD^+ , and NADP^+ to higher-energy molecules such as ATP, NADH, and NADPH (Mitchell, 1961). These molecules are universal energy currencies and likely to have been adopted by the earliest organisms.

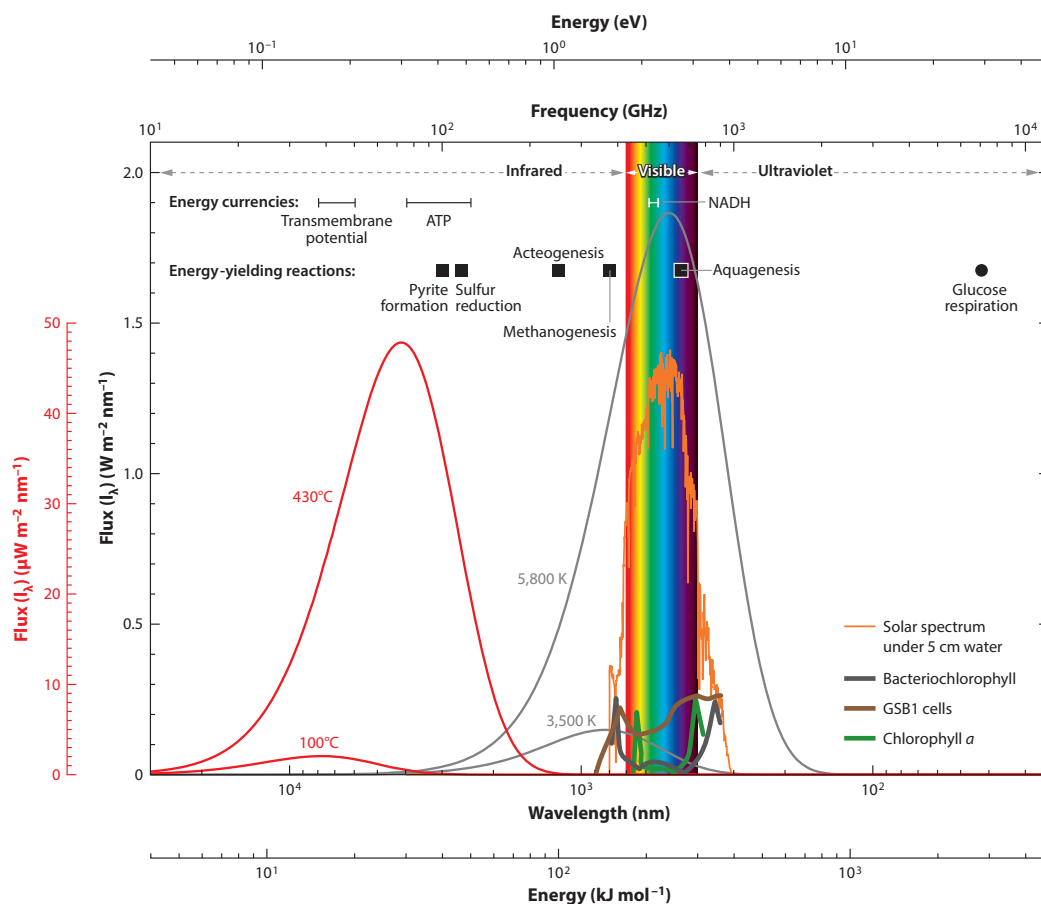


Figure 1.7: Comparison of the photon and redox energy sources of early life with the dominant energy currencies of life. The two sources of energy available to early life were solar photons (represented by the solar spectrum as seen from beneath 5 cm of water (orange)) and inorganic redox pairs available at hydrothermal vents (black squares). The energy obtained from both these sources was converted into the currencies life uses to store or circulate energy (transmembrane potential, ATP, and NADH). Uncertainties indicate the common range of energies associated with these currencies under physiological conditions. Five redox reactions are shown that are candidates for the sources of energy for the first chemolithotrophs (see Table 1.1 and Blank (2009)). Blackbody curves are shown for Sun-like G stars and for the most common star in the universe, low-mass M stars such as Gl581 (Section 1.3). On the left, using a different y-axis, the blackbody spectra of a 430°C hydrothermal vent (or hot spring) fluid and a 100°C fluid represent the native environment of hyperthermophiles. Absorption spectra are shown for two candidates for the earliest anoxygenic photosynthesis: bacteriochlorophyll (Frigaard et al., 1996; Madigan, 2006) and the spectra of intact cells of an obligately photosynthetic bacterial anaerobe (green sulfur bacterium, GSB1) isolated from a deep-sea hydrothermal vent environment (Beatty et al., 2005). The absorption spectrum of eukaryotic chlorophyll a (Cinque et al., 2000) and the maximum energy available from oxic glucose respiration are shown for comparison.

Energy sources based on a redox gradient may have been ubiquitous on the early Earth, particularly because hydrothermal activity may have been more widespread than it is today (Sleep and Zoback, 2007). The similar energies of the earliest metabolic pathways and the availability of the reactants in environments such as hydrothermal vents bolster the case that life began by using energy sources based on redox gradients and over time evolved to perform higher-energy reactions such as oxygenic photosynthesis and oxic respiration. Canfield et al. (2006) claim that the most-active, earliest ecosystems were probably driven by the cycling of H₂ and Fe²⁺ through primary production conducted by anoxygenic phototrophs.

The absorption spectra of bacteriochlorophylls, which are considered to be more ancient than chlorophylls (Blankenship, 2010; Hohmann-Marriott and Blankenship, 2011), and the photosynthetic pigments in green sulfur bacterium (GSB1) peak outside the visible region of the spectrum in the near-IR, where photons can penetrate to some degree through murky water. Although the blackbody emission

Table 1.1: Free energies (ΔG) of redox chemistry of some of the earliest terrestrial energy yielding reactions plotted in Figure 1.7 (Amend and Shock, 2001; Chang, 2005; Martin, Baross et al., 2008; Nicholls and Ferguson, 1992). Oxidic respiration of glucose is included for comparison.

Energy currency	ΔG (kJ/mol)		Example
Trans-membrane potential	12-20		all organisms
ATP	30-50		all organisms
NADH	210-220		all organisms

Energy yielding reaction	ΔG (kJ/mol)		Example
$\text{FeS(s)} + \text{H}_2\text{S(g)} \rightarrow \text{FeS}_2\text{(s)} + \text{H}_2\text{(g)}$	pyrite formation	40	Iron-sulphur world (Wächtershäuser, 1998)
$\text{S(s)} + \text{H}_2\text{(aq)} \rightarrow \text{H}_2\text{S(aq)}$	sulphur reduction	45	<i>Sulfurospirillum</i> , <i>Pyrodicticum occultum</i> , <i>Thermococcus</i> spp.
$4\text{H}_2\text{(aq)} + 2\text{CO}_2\text{(aq)} \rightarrow \text{CH}_3\text{COOH(aq)} + 2\text{H}_2\text{O(l)}$	acetogenesis	100	<i>Acetogenium kivui</i> , <i>Acetobacterium</i> spp., <i>Clostridium thermoaceticum</i>
$\text{CO}_2\text{(aq)} + 4\text{H}_2\text{(aq)} \rightarrow \text{CH}_4\text{(aq)} + 2\text{H}_2\text{O(l)}$	methanogenesis	130	<i>Methanococcus</i> , <i>Methanobacterium</i>
$\text{H}_2\text{(aq)} + 0.5\text{CO}_2\text{(aq)} \rightarrow \text{H}_2\text{O(l)}$	aquagenesis	250	<i>Aquifex aeolicus</i>
$\text{C}_6\text{H}_{12}\text{O}_6 + \text{O}_2 \rightarrow \text{CO}_2 + \text{H}_2\text{O}$	oxic respiration	2870	Many bacteria, archaea and eukaryotes including <i>Homo sapiens</i>

of hot hydrothermal fluids has far fewer photons in the near-IR than in the mid-IR, they are in sufficient numbers and of high enough energy that GSB1 can photosynthesize and live in a dark environment. Photons of even lower energies ($\sim 1,000$ nm) are used by purple anoxygenic bacteria (Kiang et al., 2007). Note that all redox reactions in Figure 1.7 are above the peak energy of the 100°C ambient temperature of a hyperthermophile environment. Any redox reaction that is used by life must satisfy the constraint that the activation energies must be higher than what is available as background energy in the environment (Shock and Holland, 2007). An upper limit for the temperature at which metabolic activity can take place is set by the temperature at which the molecular dissociation of proteins and membranes takes place.

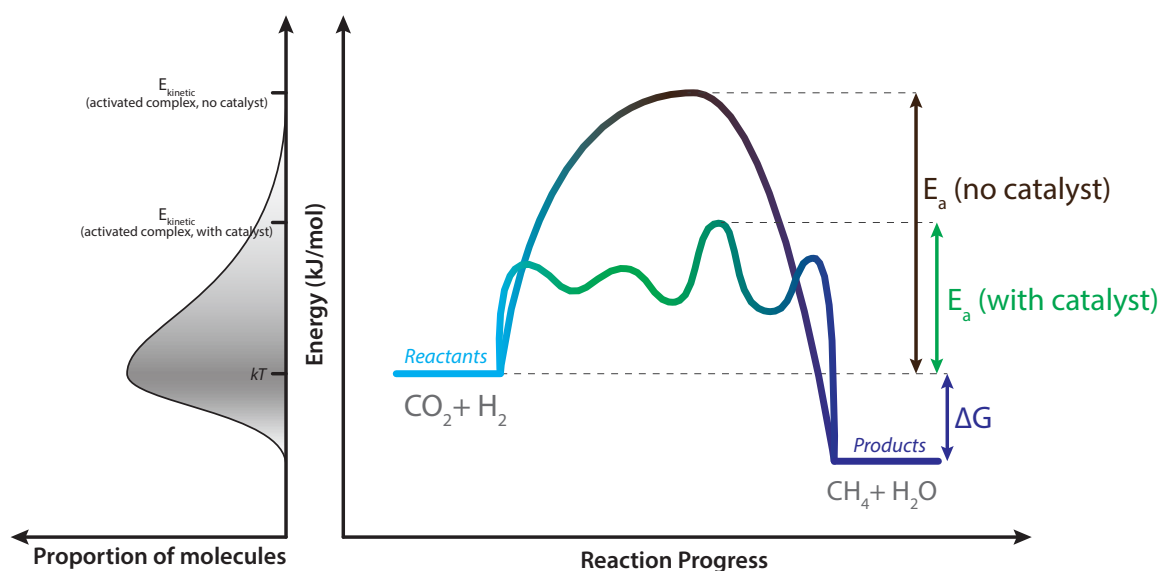


Figure 1.8: The relationship between environmental kinetic energy kT (represented by the Maxwell-Boltzmann distribution on the left), and energies associated with chemical reactions (on the right). Any metabolic reaction used by life must have activation energies higher than kT (the average energy of reactant molecules and the environment) otherwise the reaction would proceed to equilibrium without being mediated by the bio-catalysts of life Shock and Holland (2007). Life makes a living by developing bio-catalysts to lower the activation energy of the reactions of available redox pairs. Metabolism is based on the ability to control the presence of these bio-catalysts Nealson and Conrad (1999). Life elsewhere could extract energy from a variety of abiotically produced chemical disequilibria since both the ingredients and the free energy sources (redox or photon based) should be available at the atmosphere:rock-surface or the ocean:rock-surface interfaces on Mars, Titan, Europa and other exoplanetary systems.

If solvents are required for biochemistry, then the temperature at which the solvent remains a liquid, will set the energies of the reactions that biological catalysts can control (Figure 1.8). Typically in terrestrial biochemistry, $E_a(\text{no catalyst}) / E_a(\text{with catalyst})$ is greater than 10, so the choice of catalyst provides a strong control of the reaction rate (Alberly, 2005; Quinn and Sikorski, 2014). When life was first emerging on Earth and the first catalysts were evolving, this ratio must have been ~ 1 , and then gradually evolved to the much larger values (10–30) that are typical of catalysts used by biota today.

Energy sources based on redox gradients should be plentiful on rocky planets in circumstellar habitable zones because of the ubiquity of differentially oxidised minerals in the presence of water heated by radiogenic or convective sources in the first approximately 0.5 to 1 billion years of an active wet rocky planet. Over time, life would evolve new catalysts that give access to a wider range of redox pairs and photons, plausibly resulting in a remotely detectable atmospheric biosignature.

If the conditions that permitted terrestrial abiogenesis based on energy-yielding metabolic reactions, such as those plotted in Figure 1.7, are not available on other planets, then the search for life elsewhere in the universe may yield the discovery of numerous habitable planets that have remained uninhabited. This is one possible outcome of Mars exploration. The search for life elsewhere in our Solar System has focused on Mars because it is relatively close and because Mars probably contains a lot of subsurface water (Jones, Lineweaver and Clarke, 2011; Michalski et al., 2013). In Figure 1.5, the substantial overlap of the green and red areas represents extensive water at habitable temperatures on Mars. This, combined with much other evidence for water on Mars, suggests that we will find liquid water in the Martian subsurface at temperatures compatible with terrestrial life. If appropriate redox pairs exist, psychrophilic terrestrial life should be able to live between tens of centimeters and ten kilometers beneath the Martian surface (Jones, Lineweaver and Clarke, 2011). However, Mars exploration has not yet found any life. In 1976, two Viking spacecraft landed on Mars with life-detection instruments, which returned ambiguous results that have been interpreted as offering no evidence for life (Klein, 1979, 1999; Navarro-González et al., 2010) (see, however, Levin, 1981). Although the Viking mission only attempted to search for active life on the surface (and not in the region below 10 cm where liquid water might be present), there are other potential biosignatures of subsurface life that may be detectable on the surface. One such potential biosignature was recently detected as transitory faint traces of methane (Formisano et al., 2004; Krasnopolsky et al., 2004; Lefèvre and Forget, 2009; Mumma et al., 2009). The debate about whether this methane could be biotic or abiotic seems to be leaning toward an abiotic explanation: Hot olivine exposed to water and CO_2 undergoes serpentinization and produces methane (Kasting, 2012; Webster and Mahaffy, 2011).

NASA's Mars Science Laboratory (MSL), launched on November 26, 2011, has 10 instruments to help determine if life did, or does, exist on Mars. The ongoing exploration of the Martian subsurface is one of the most promising fields where progress in our understanding of habitability can be made. For example, MSL recently detected trace amounts of methane in the Martian atmosphere (in the parts per billion by volume range). The transient spikes in methane abundance suggest episodic production of methane possibly from extant methanogenesis or released from past reservoirs, or both (Webster, Mahaffy et al. (2015)). Other promising destinations include Jupiter's moons Europa, Ganymede, and Callisto and Saturn's moons Titan and Enceladus. These large moons may have provided wet incubators where life could have emerged (and might still exist). Evidence from the Galileo mission (Spohn and Schubert, 2003) suggests that Europa, Ganymede, and Callisto contain a combined volume of liquid water 30–35 times that of Earth's oceans. For reviews of the habitability of our Solar System, see Shapiro and Schulze-Makuch (2009) and McKay (2011). There are also specific papers on the habitability of Europa (Chyba and Phillips, 2001; Hand et al., 2007), Enceladus (McKay, Porco et al., 2008), Titan (Benner et al., 2004; McKay and Smith, 2005; Raulin, 2008), and Venus (Grinspoon, 1998; Svedhem et al., 2007).

Since stars appear to be suns, and suns, according to the common opinion, are bodies that serve to enlighten, warm, and sustain a system of planets, we may have an idea of the numberless globes that serve for the habitation of living creatures.
— William Herschel

1.2 What fraction of stars have terrestrial planets

Outside our own Solar System, terrestrial planets or large rocky moons in the circumstellar HZs around other stars are the most likely habitable places. Since 1995, when the first exoplanet was detected around a Sun-like star (Mayor and Queloz, 1995), the fraction of stars with planets has been periodically reported. These are listed in Table 1.2 and plotted in Figure 1.9. The values depend on what fraction of the mass-period parameter space of Figure 1.10 has been sampled or extrapolated over. Because no technique can sample the entire space, coverage is always incomplete and any reported value such as “10% of stars have planets” is a lower limit—the actual value is larger. Because of this incompleteness, the data are, and always have been, consistent with 100% of stars having planets. This is represented in Figure 1.9 by the blue arrows extending from the reported lower limits to 100%. See Cassan et al. (2012) for supporting evidence from microlensing observations.

Reference	%	Mass Range		Orbital limits a < (AU)	Detection Technique
		M_{min}	M_{max}		
Mayor and Butler (1998)	6	0.5	7	2	RV
Cumming and Marcy (1999)	8	0.57	11	5	RV
Mayor and Butler (2000)	5	0.5	8	3	RV
Tabachnik and Tremaine (2002)	4	1	10	4.6	RV
Lineweaver and Grether (2003)	25	0.04	13	6.1	RV
Mayor, Butler et al. (2005)	12	0.02	13	20	RV
Cumming, Butler et al. (2008)	19	0.02	13	20	RV
Lovis et al. (2009)	30	0.015	0.1	P < 50 days	RV
Howard, Marcy, Johnson et al. (2010)	23	0.0015	0.0063	P < 50 days	RV
Howard, Marcy, Bryson et al. (2012)	48	0.003	13	0.26	Transits
Mayor, Marmier et al. (2011)	75	0.003	13	P < 10 yrs	RV + Transits

Table 1.2: Fraction of stars with planets

Figure 1.9 refers to reported values from surveys of Sun-like stars of spectral type FGK. All are radial velocity (RV) surveys with the exception of Howard, Marcy, Bryson et al. (2012), which is based on Kepler transits. Planets orbiting substantially smaller M stars probably have smaller masses (Johnson, Aller et al., 2010) and smaller semi-major axes. (See Gould et al. (2010) and Cassan et al. (2012) for microlensing results with predominantly M star hosts. For disk imaging results from A stars, see Bowler et al. (2010).)

Planet detections have technique-dependent limits (Cumming, 2010). Figure 1.10 shows how the eight planets of our Solar System (dashed purple line) compare to the ~1,870 exoplanets compiled from six detection techniques listed in the lower right. The estimated masses of the planets are plotted as a function of their orbital periods.

The most important take-home message is: Yes, there are planets around other stars. The second message is that most of the patterns in the data tell us more about instrument sensitivity and survey durations than about the underlying real distribution of planets. Thus, the relatively empty region in

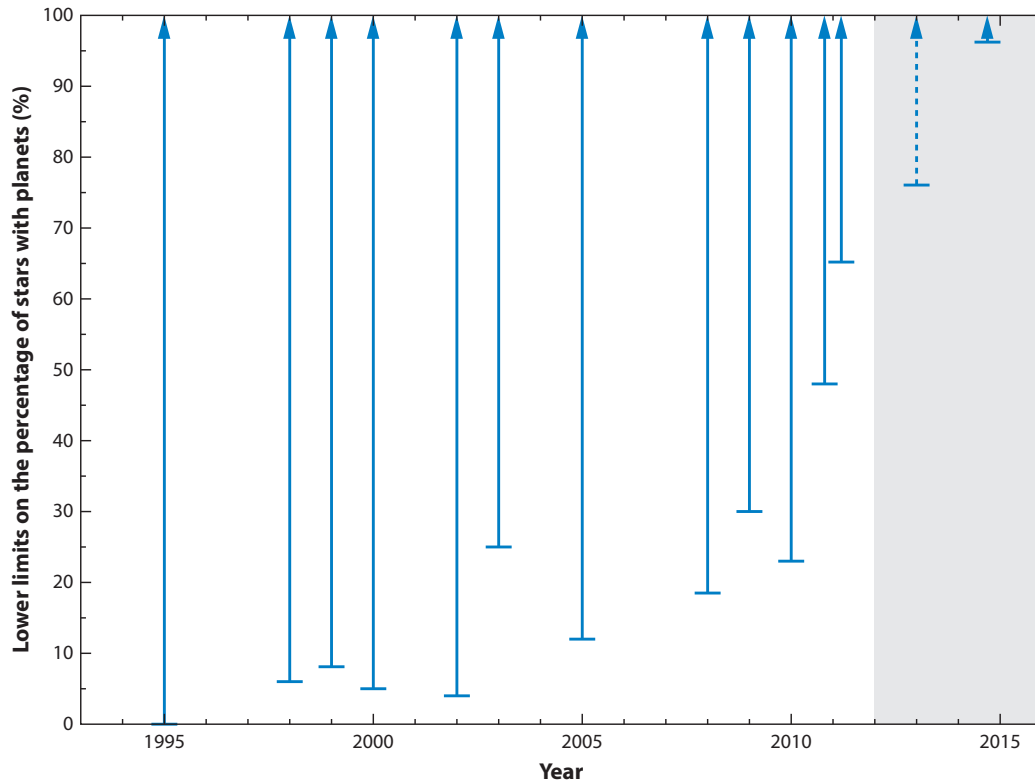


Figure 1.9: Lower limits to the fraction of stars with planets as a function of time. Because published values are based on limited ranges in mass or period (i. e. , small areas in the parameter space of Figure 1.10), they are not estimates of the real fraction of stars with planets but are lower limits. These lower limits have been rising as the durations of surveys increase and detection sensitivity improves. The predicted lower limits at 2013 and 2015, suggesting that 100% of stars have planets, are based on the trends seen in the past three years and the plausible range over which these trends can be extrapolated

the lower right (low mass, long period) appears empty because it has not been well explored. And the blob of dark gray points in the upper left, from ground-based transit searches, is concentrated at high mass and short period because that is where this technique has the highest sensitivity, not because there is a natural concentration of planets there.

The left edge of the red cloud of Kepler points is a real edge due to the underlying distribution of planets and tells us that planets with orbital periods less than a couple of days are rare. The lower right edge of the red cloud (indicated by the red curve) is a result of instrument sensitivity and the duration of observations (only 90 days). At the end of the nominal Kepler mission in 2014, Kepler's region of sensitivity will have extended to the dashed red curve, much closer to the region of Venus- and Earth-like planets.

The background of Figure 1.10 is color-coded to show the sensitivity of the RV technique to planets orbiting solar-mass stars. The ability of the RV technique to detect planets is 100% in the white region in the upper left, decreases across the "RV being detected" region, and sinks to near 0% in the "RV not detected" region. Thus, in the white "RV detected" region, any observed pattern of RV planets (blue dots) is a real pattern and is not due to instrument sensitivity or survey duration. The most obvious pattern is that in the high-mass region ($1\text{--}10 M_{\text{Jupiter}}$), as periods increase (approaching Jupiter's 12-year period), the number of planets increases dramatically. Thus, Jupiter-mass planets become more numerous as we look in more Jupiter-like orbits.

Because the RV technique is most sensitive in the upper left of Figure 1.10, Figure 1.9 is predominantly telling us about the fraction of stars with massive Jupiter-, Saturn-, Uranus-, and Neptune-sized planets that have been scattered or have migrated from their region of formation (farther from the host star) into a region closer to their host star where they could be detected with the RV technique. However, we are more interested in exoplanets that are more similar to Earth in both mass and period.

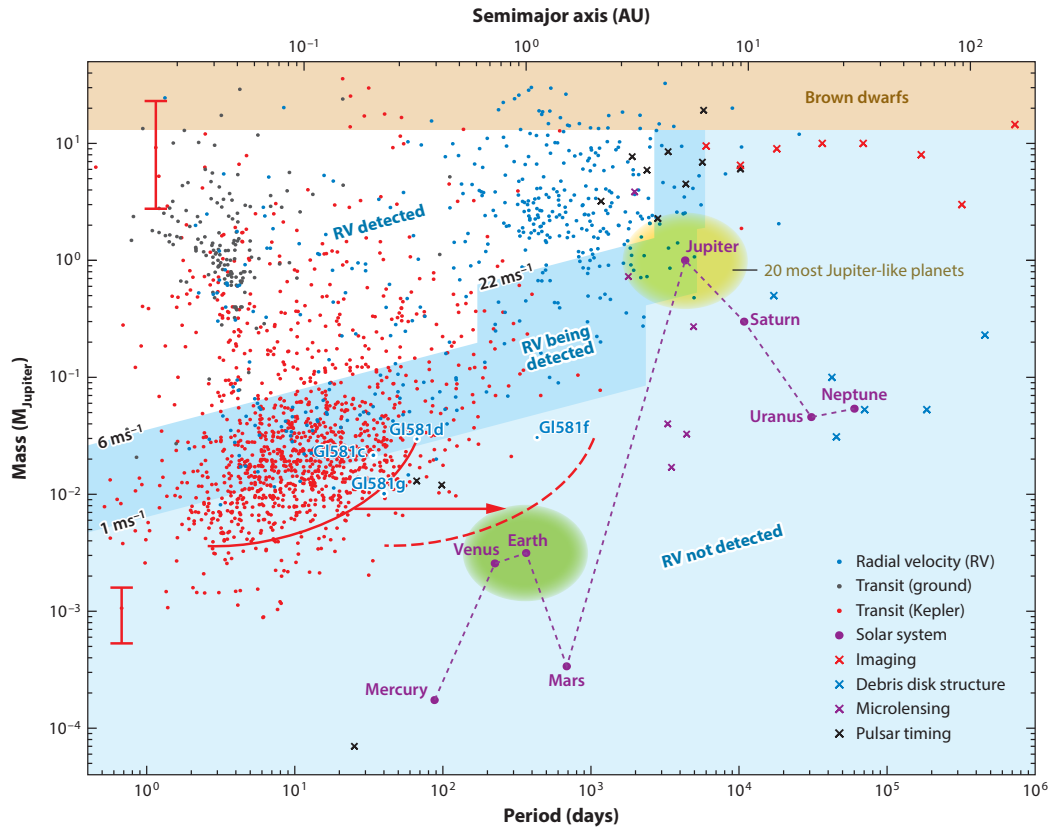


Figure 1.10: Our Solar System compared to $\sim 1,870$ exoplanets detected using various techniques. The region around our planetary system and to the lower right has not been well explored. The red cloud of points in the lower left represents the $\sim 1,200$ Kepler planet candidates from [Borucki et al. \(2011\)](#). The other ~ 670 exoplanets were detected by other instruments. After the nominal approximately four-year Kepler mission, the red curve, approximating the limit of the Kepler cloud, will have moved to the dashed red curve. At least a few Earth-mass planets in Earth-like periods around Sun-like stars are expected within the green oval surrounding Earth. If the Sun were removed to some typical distance (~ 30 light years) and were on the target list of our planet-hunters, it would probably still be listed as having no planets. The yellow oval contains the 20 most Jupiter-like planets, which are plotted separately in Figure 1.12. Timothy Bovaird was instrumental in helping to make this figure.

In Figure 1.10, planets indicated by the red Kepler dots are the most similar to Earth in mass. If the fraction of stars with large planets is $\sim 100\%$, what about the fraction of stars with low-mass rocky planets like Earth? Based on extrapolation of RV data, [Howard, Marcy, Johnson et al. \(2010\)](#) report “23% of stars harbor a close-in Earth-mass planet (ranging from 0.5 to 2.0 Earth masses).” [Wittenmyer et al. \(2011\)](#) report 17% for planets with mass less than $\sim 13 M_{\text{Earth}}$.

Catalogs of exoplanet detections can be found in [Schneider \(2011\)](#) and [Wright et al. \(2010\)](#). The Kepler planet candidates are from [Borucki et al. \(2011\)](#). The radii of Kepler candidates have been converted to masses using the average radius-dependent density of the dozen or so least massive exoplanets detected by the transit and radial velocity techniques. Representative uncertainties on this conversion are given in Figure 1.10 by the size of the vertical error bars on two red points on the far left.

The radii of planets can be extracted from small dips in Kepler’s precision photometry of $\sim 150,000$ stars. Figure 1.11 is a recent result ([Howard, Marcy, Bryson et al., 2012](#)). As the fraction of stars with planets approaches its maximum value of 100% (Figure 1.9), this fraction becomes uninformative about the average number of planets per star, which is the y-axis in Figure 1.11. The two bins in the region to the left of the dashed gray line ($1 < R < 2 R_{\text{Earth}}$) are incomplete because planets that small are harder to detect and need to transit more times for their signal to emerge out of the noise. These incomplete bins were not used to produce the red dashed fit.

On the left side of Figure 1.11 notice that the dashed red line crosses $R = R_{\text{Earth}}$ at 0.4 planets per star. Because there are many more single-planet stars than multiple-planet systems in the Kepler database,

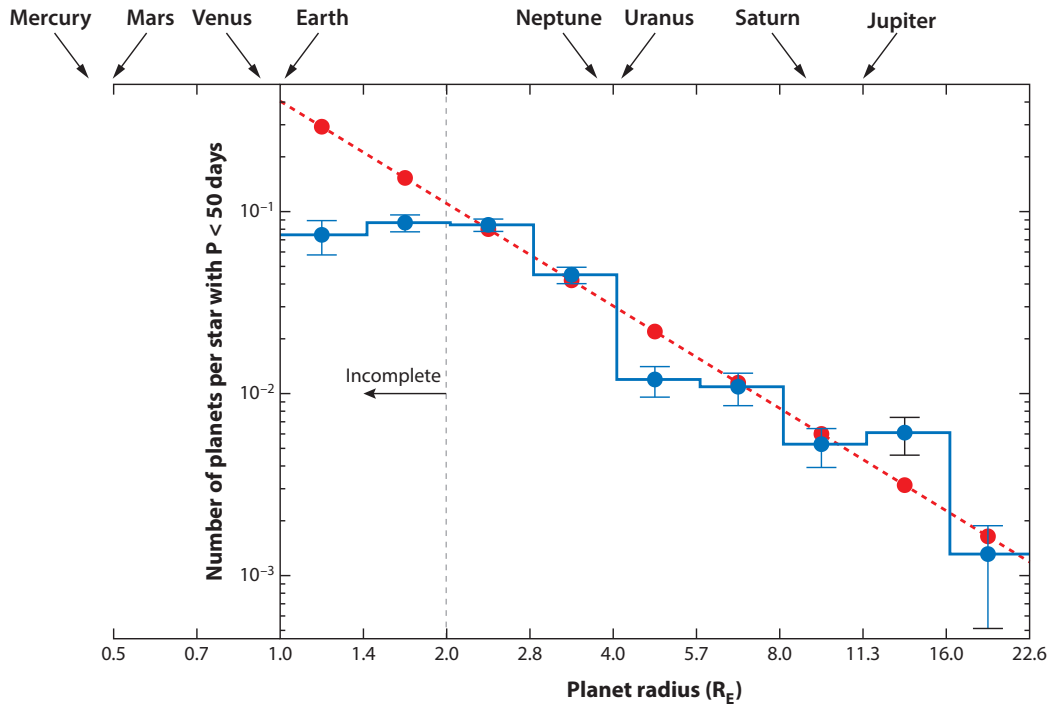


Figure 1.11: Kepler results (as per 2012). The amplitude of the red line tells us that there are many planets close to stars ($P < 50$ days; for comparison, $P_{\text{Mercury}} = 88$ days). The slope of the red line tells us that there are approximately ten times as many Earth/Venus-sized planets as there are Uranus/Neptune-sized planets and approximately ten times as many Uranus/Neptune-sized planets as there are Jupiter-sized planets. Figure modified from the top panel of Figure 1.6 in Howard, Marcy, Bryson et al. (2012).

this 0.4 means that $\sim 35\%$ of stars are expected to have planets with radii $0.8 < R < 1.2 R_{\text{Earth}}$ and with orbital periods $P < 50$ days. That is a large fraction for such a small range of radii and periods. Adding up the values of the red points for the entire range of radii yields the average number of planets (with radii $1 < R < 23 R_{\text{Earth}}$ and $P < 50$ days) per star: 0.6. When converted to the fraction of stars with a planet, this becomes the 48% plotted in Figure 1.9. Adding up only the values for rocky planets (the three bins with radii $1 < R < 2.8$) yields more than 0.5 rocky planets per star. This high frequency within such a small region close to the star (< 0.25 AU) indicates that rocky planets are extremely common.

After Kepler detects more planets with $R \approx R_{\text{Earth}}$, if the trend of the red line accurately describes the next smaller bin, the vast majority (perhaps 90%) of planetary systems may be found to have an Earth-size planet with an orbital period $P < 200$ days. With Venus's 224-day orbital period and radius $R = 0.95 R_{\text{Earth}}$, and Mercury's $P = 88$ days and $R = 0.38 R_{\text{Earth}}$ (too small to detect), such a high observed frequency of close-in exoplanets would make our planetary system unusual for having relatively fewer Earth-sized planets, or having them unusually distant from the host star, or both.

The data collected in Figures 1.9 and 1.10 illustrate that as stars are monitored for longer periods of time, and as we extend our detection sensitivity to Jupiter-like periods, we detect more planets and require less extrapolation to reach the conclusion that $\sim 100\%$ of stars have massive planets. In addition, as we extend our observations to smaller planets (left side of Figure 1.11, $0.5 < R < 2 R_{\text{Earth}}$) the numbers increase and again suggest that $\sim 100\%$ of stars have at least one Earth-sized planet.

Other evidence that the fraction of stars with planets is $\sim 100\%$ is that protoplanetary accretion disks are ubiquitous in young star clusters. The observed fraction of young stars with protoplanetary disks approaches 100% for star-forming regions less than ~ 0.5 million years old (Fedele et al., 2010; Mamajek, 2009). Also, there are no large planets without a retinue of rocky/icy moons. Many of the moons of Jupiter, Saturn, Uranus, and Neptune are part of miniature planetary systems formed from their planet's miniature accretion disk. "Planets around every star. Moons around every large planet" is probably the most reasonable position from which to ponder habitability. Soon we will have

detected so many Earth-like planets that our efforts will have to be focused on determining which ones are the most habitable ([Horner and Jones, 2010](#)).

*If they be inhabited, what a scope for folly;
if they not be inhabited, what a waste of space.*
— Thomas Carlyle

1.3 Circumstellar Habitable Zones

Exoplanet research is moving beyond counting planets and plotting their masses and orbital periods. We are beginning to study their temperatures, densities, compositions, tectonic regimes, atmospheric chemistries, and albedos—all factors that can influence habitability. Figure 1.12 shows that there are several dozen known planets in circumstellar HZs. The least massive are three to five times the mass of Earth. Because the mass of moons seems to scale with the mass of the host planet, the most massive planets in the HZ could harbor habitable moons.

For each planet in our Solar System (Figure 1.12), notice the difference between the computed effective temperature ($T_{\text{effective}}$, small light purple dots) and the actual surface temperatures T_{surface} (larger purple dots). We have plotted error bars around T_{surface} , indicating the range of surface temperatures on Mercury, Venus, Earth, and Mars. Because $\Delta T = T_{\text{surface}} - T_{\text{effective}} > 0$ for all eight planets of our Solar System, all experience some kind of warming.

For Earth we have $\Delta T_{\text{Earth}} = 33^\circ$, but the thick 90 bar Venutian CO_2 atmosphere produces $\Delta T_{\text{Venus}} = 440^\circ$. The variation of ΔT values within our Solar System is large: $15^\circ < \Delta T < 440^\circ$, due to differences in albedos and greenhouse gas (CO_2 , H_2O) column densities. This range gives us an idea of the expected range of exoplanet ΔT s that will shift exoplanets to the left in Figure 1.12. Thicker atmospheres provide more greenhouse warming and larger ΔT s (Marcus et al., 2010). Because we expect $\Delta T_{\text{super-Earths}} > \Delta T_{\text{Earth}}$, the shift of the HZ to be centered on the $T_{\text{effective}}$ of Earth represents a minimal correction. Thus super-Earths, such as Gl581d just to the right of the HZ, should be considered the best candidates for habitable planets.

A reasonable assumption is that super-Earths ($3 < M < 10 M_{\text{Earth}}$) are probably endowed with a mass of greenhouse gases, M_g , proportional to the mass of the planet, M : $M_g \sim M$. Thus, the column density Σ responsible for greenhouse warming would be $\Sigma \sim M_g / \text{surface area} \sim M / R^2 \sim R \sim M^{1/3}$. With this plausible scaling we would expect the ΔT s of super-Earths to be, very roughly, twice as large as the ΔT s of our Solar System's planets. Thus, it may be that the half-dozen planets in the middle and left side of the most habitable exoplanets region of the HZ of Figure 1.12 are greenhouse heated too far to the left to support life.

Gliese 581 is an M star approximately 20 light years away, with a mass $M = 0.31 M_{\text{Sun}}$ and $\sim 1\%$ of the Sun's luminosity. Gliese 581's planetary system contains several rocky planets whose habitabilities are being debated (Bloh, Bounama, Cuntz et al., 2007; Mayor, Bonfils et al., 2009; Selsis et al., 2007; Udry et al., 2007; Wordsworth et al., 2011). The system contains four confirmed planets (Gl581b, -c, -d, -e) and possibly two more unconfirmed planets (Gl581f, -g) (Vogt et al., 2010). With poor signal to noise at the edge of RV sensitivity, the fitted eccentricities can vary between 0 and as much as 0.4. Of the four confirmed planets, Gl581d looks like the best current candidate for being a rocky habitable planet (see also (Kaltenegger et al., 2011)). Its mass is $10^{+4}_{-3} M_{\text{Earth}}$. It receives 35% less stellar energy than Mars, and its orbital eccentricity is ~ 0 . Its period is ~ 66 days and it is tidally locked. It has a radius of $\sim 2 R_{\text{Earth}}$, and its surface gravity is approximately twice that of Earth's. Using a global climate model designed for exoplanets, with CO_2 and H_2O as greenhouse gases, Wordsworth et al. (2011) find that the range of possible atmospheric pressure is 5-30 bars.

The importance of Gl581 is based on the proximity of its planets to its circumstellar HZ. Kasting (2012, ch 10) gives an informed review of the history of the circumstellar HZ and discusses the details of the most cited HZ paper, Kasting (1993). For details of how the inner and outer limits of the circumstellar HZ are computed, see Forget and Pierrehumbert (1997) and Abe, Abe-Ouchi et al. (2011). The idea of a circumstellar HZ is based on the scenario of surface life kept warm and powered by stellar photons. In the context of the present Earth, this is a reasonable scenario because solar photons control the temperature of the ocean and the top few meters of the continental crust and power most of current life (Figure 1.4). But Earth's AHZ may not have been powered by the Sun. If life emerged from a dark hydrothermal vent, vent redox chemistry and the plate tectonic regime that drives it may have more to do with whether life can emerge on a planet than whether the planet is in the circumstellar HZ and

has liquid water on its surface. Moving beyond the circumstellar HZ, planets not bound to any star, drifting around between the stars, seem to be the abundant remnants of the gravitational free-for-all in the earliest stages of planet formation in dense star clusters. Using microlensing observations [Sumi et al. \(2011\)](#) report nearly twice as many unbound Jupiters as there are main sequence stars in the galaxy. If there are super-Earths among them with enough hydrogen in their atmospheres ([Pierrehumbert and Abbot, 2011](#)), and if life can emerge and persist without photons from a star, then there may be no outer limit to the circumstellar HZ. There may be life-sustaining planets in interstellar space ([Stevenson, 1999](#)).

1.4 Water and Temperature

Because life as we know it is water-based carbon chemistry, the processes that control the supply of water and carbon to a planet control its habitability. Water is also essential to aid the continual tectonic reworking and erosion that supply key redox gradients and biochemical substrates to sustain habitability (Table 1.1; [Nisbet, Zahnle et al., 2007](#)). ([Morbidelli, Chambers et al., 2000](#)) and [Mottl et al. \(2007\)](#) summarize our understanding of the origin of water on Earth. D/H ratios ([Robert, 2001](#)) and much other evidence suggest that the sources of terrestrial water were hydrous bodies such as carbonaceous chondrites (5%–20% water) from the outer part of the main asteroid belt. An alternative wet accretion model has between one and three oceans of water accreting with the planetary embryos that formed the bulk Earth ([Drake, 2005; Drake and Richter, 2002](#)). A third possibility discussed by [Mottl et al. \(2007\)](#) is the acquisition of hydrogen and water directly from the solar nebula by adsorption onto accreting material and dissolution into a magma ocean.

Because variations in temperature and water content are the two most important variables in delimiting the habitability of Earth, they should be the basis of any classification scheme for the habitability of planets. The green circumstellar HZ in Figure 1.12 is based on effective temperature computed from stellar type and semimajor axis. To obtain more accurate surface temperatures, we need to know more about planetary greenhouse gas content and albedos. The amount of water on a rocky planet can depend on the C/O ratio of the star (because C/O controls the amount of water in the protoplanetary disk), but like T_{surf} , water content depends on many variables. Numerical simulations that take into account the notionally most important parameters indicate that water content on a terrestrial planet can vary typically by factors of a few ([Raymond, Quinn et al., 2007](#)) and probably much more (perhaps an order of magnitude) when more parameters are allowed to vary. Variations in water supply are caused by variations in the number of impacts with water-rich planetesimals. The number of impacts is a function of planetary position (proximity to the snowline) and planetary mass (to gravitationally focus the impactors). Impacts also depend on the mass, eccentricity, and orbital evolution of the Jupiter analog in the system (if there is one) ([Levison and Agnor, 2003; O'Brien et al., 2006](#)).

Table 1.3: Planet classification according to water content

Name	% surface liquid water	Features
Ocean planet	~ 100%	Hydrothermal vents, little erosion (Kuchner, 2003; Léger, Selsis et al., 2004)
Earth-like planet	1%-99%	Continental and oceanic crust, surface erosion, fresh water
Desert planet	~ 0%	Wider habitable zones ? (Abe, Abe-Ouchi et al., 2011)

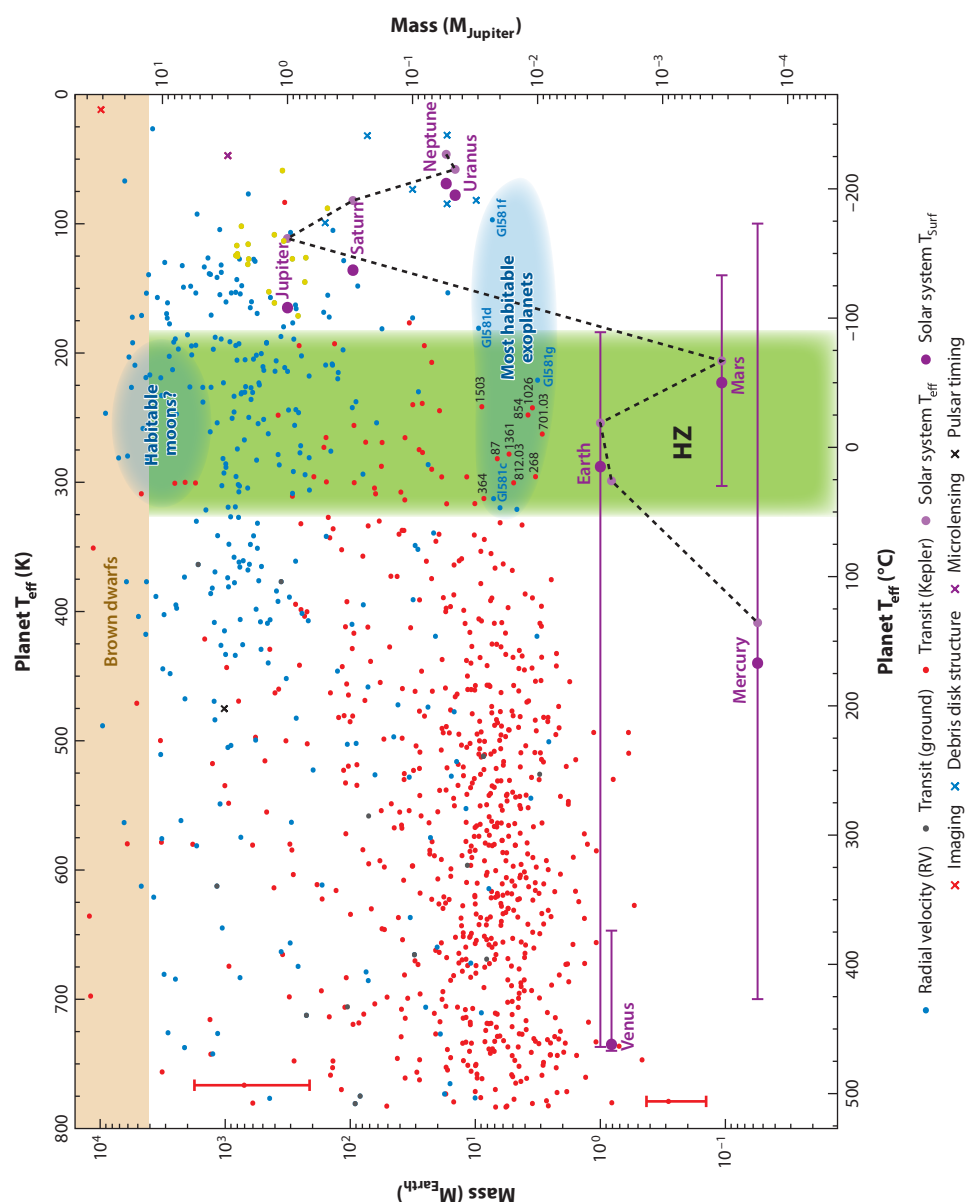
Another complication is that Earth may have acquired far more water during its formation than exists in its ocean and mantle today ([Abe, Ohtani et al., 2000](#)). Variations in the ability of a planet to hold onto the supplied water depend on planetary mass, temperature (through thermally induced hydrodynamic escape), atmosphere, the amount of collisional erosion ([Genda and Abe, 2005; O'Neill and Palme, 2008](#)), and the degree of differentiation of the impacting planetesimals. In the first few million years, ^{26}Al (half-life 0.7 million years) provides much of the radiogenic heat (in addition to the heat of accretion) responsible for the density segregation of planetesimals, exposing water on the outside while sequestering iron on the inside ([Grimm and McSween, 1993; Hester and Desch, 2005](#)). Importantly, the ^{26}Al content of a protoplanetary disk can vary by several orders of magnitude since

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it depends on how close the disk is to the closest supernovae produced by the largest stars in the birth cluster ([Adams, 2010](#); [Bizzarro et al., 2004](#); [Gaidos, Krot et al., 2009](#); [Gilmour and Middleton, 2009](#)). Because of the large variation possible in the water content of rocky planets, it makes sense to classify them by water content and by the phase of that water (solid, liquid, or gas) (see Table 1.3).

Ocean, Earth-like, and desert planets will each have low-, moderate-, and high-temperature versions. For example, a low-temperature ocean planet will be covered with ice (Europa-like), possibly because it is too small to maintain ongoing volcanism, or too poor in the four long-lived radiogenic isotopes to recover from episodes analogous to snowball Earth ([Hoffman, 2002](#)). A high-temperature version of an ocean planet would be a steam planet. Desert planets, low in H₂O owing to a small amount of radial mixing of material beyond the snowline, would also be low in carbon. Low carbon could also be a factor limiting the habitability of planets orbiting stars with low C/O ratios. See [Bond et al. \(2010\)](#) and [Delgado-Mena et al. \(2010\)](#) for a discussion of how stellar variation in C/O and Mg/Si can affect the mineralogy and habitability of rocky planets. For example, they find that stars with C/O > 0.8 will host reduced carbide planets with little water.



1.5 The Galactic Habitable Zone

Life is embedded in a hierarchy of supporting environments that provide the requirements for habitability. Estimation of a circumstellar HZ assumes the presence of a star and a planet and addresses the question, Where can the planet be located such that its surface is at the right temperature for life? The galactic HZ is a similar idea but on a much larger scale: Given an 11-billion-year-old galaxy, where can you find a star, a rocky planet, and clement conditions that last long enough to maintain life? The idea of a galactic HZ was intimated by [Lem \(1986\)](#), clearly articulated by [Gonzalez et al. \(2001\)](#), extended and more carefully quantified by [Lineweaver, Fenner et al. \(2004\)](#) (Figure 1.13), and refined spatially to individual stars in a Monte Carlo simulation by [Gowanlock and Patton \(2011\)](#) (see however, [Prantzos, 2008](#)). Stars in our galaxy are not distributed uniformly in either space or time, nor do they all have enough metallicity (elements excluding H, He) to accrete rocky planets. And some are dangerously close to supernovae that disrupt habitability. [Lineweaver, Fenner et al. \(2004\)](#) mapped the distribution in space and time of four prerequisites for complex life: the presence of a host star, enough heavy elements to form terrestrial planets, sufficient time for biological evolution (~ 4 billion years), and an environment free of life-extinguishing supernovae. We identified the galactic HZ as an annular region between seven and nine kiloparsecs from the galactic center that widens with time and is composed of stars that formed between eight and four billion years ago. Similar to the boundaries of the circumstellar HZ, these limits are not sharp, but do indicate where the potential for complex (= 4 billion years old) life may be the highest. This galactic HZ yields an age distribution for the complex life that may inhabit our galaxy: 75% of the stars in the galactic HZ are older than the Sun.

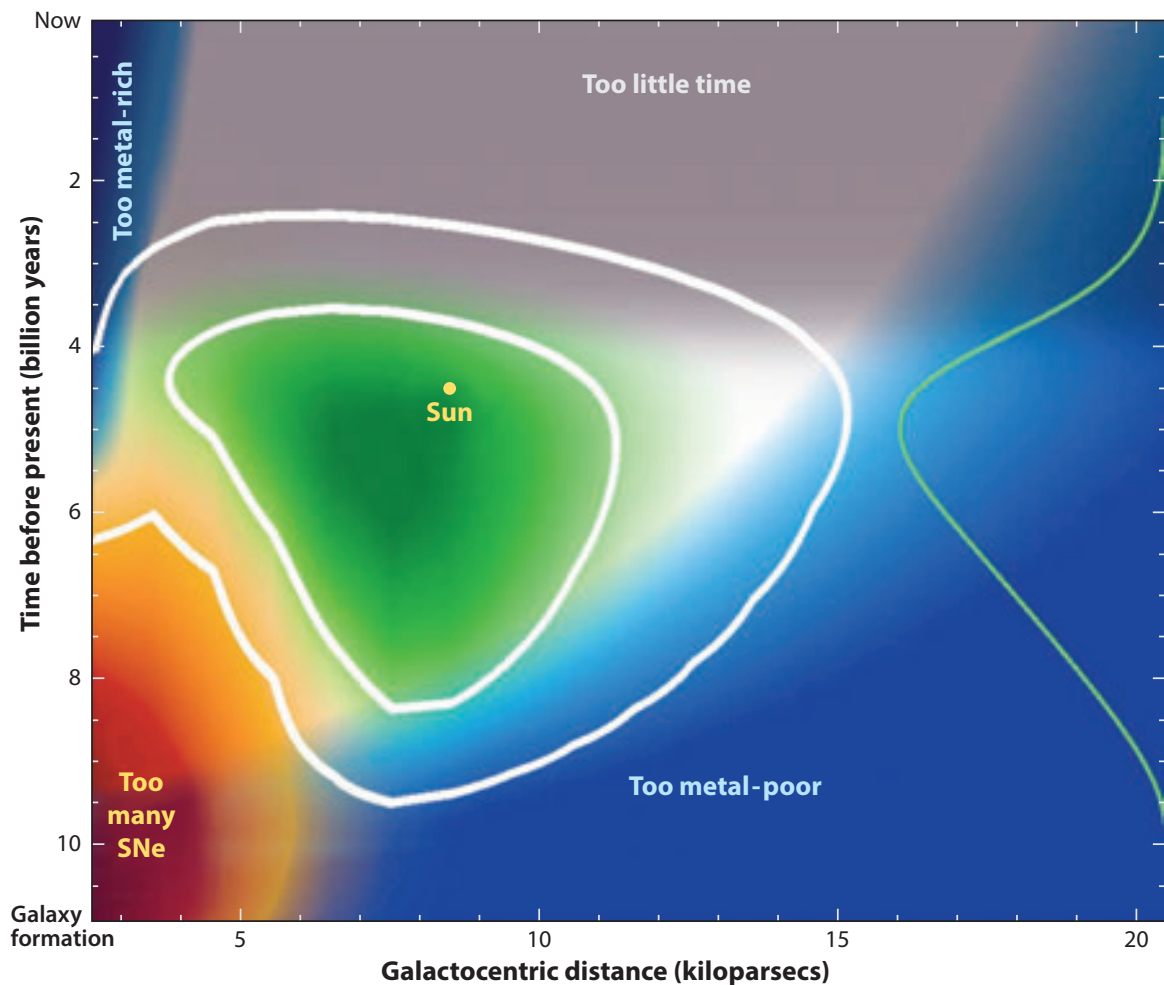


Figure 1.13: Galactic habitable zone (HZ) of our Milky Way Galaxy from [Lineweaver, Fenner et al. \(2004\)](#). “Too many SNe” indicates the region where the supernovae (SNe) rate is probably too high to be compatible with the evolution of life.

Stars in our galaxy are not distributed uniformly in either space or time, nor do they all have enough metallicity (elements excluding H, He) to accrete rocky planets. And some are dangerously close to supernovae that disrupt habitability. [Lineweaver, Fenner et al. \(2004\)](#) mapped the distribution in space and time of four prerequisites for complex life: the presence of a host star, enough heavy elements to form terrestrial planets, sufficient time for biological evolution (~ 4 billion years), and an environment free of life-extinguishing supernovae. We identified the galactic HZ as an annular region between seven and nine kiloparsecs from the galactic center that widens with time and is composed of stars that formed between eight and four billion years ago. Similar to the boundaries of the circumstellar HZ, these limits are not sharp, but do indicate where the potential for complex (= 4 billion years old) life may be the highest. This galactic HZ yields an age distribution for the complex life that may inhabit our galaxy: 75% of the stars in the galactic HZ are older than the Sun.

One can extend the concept of HZ beyond the galaxy to the universe. For example, a cosmic temporal HZ can be constructed from the age distribution of terrestrial planets in the universe ([Lineweaver, 2001](#)). There are times that are habitable and times that are not. In the first two to three billion years after the big bang, there were no terrestrial planets because there was not enough condensable material to make them. There are also many other features of our universe that play a role in its habitability. These are discussed insightfully elsewhere ([Barrow, Morris et al., 2006](#); [Barrow and Tipler, 1988](#); [Bostrom, 2002](#); [Carroll, 2006](#); [Carter, 1974](#); [Dicke, 1961](#)).

Following Lovelock's 1965 idea that the simultaneous presence of oxygen and reduced gases (e. g. CH_4 , H_2) is unlikely without life, [Sagan, Thompson et al. \(1993\)](#) analyzed a spectrum of Earth taken by the Galileo probe, searching for signatures of life. They concluded that the large amount of O_2 and the simultaneous trace amounts of CH_4 are strongly suggestive of biology. This has been a model of how we might be able to remotely detect life elsewhere ([Léger, Ollivier et al., 1999](#)). However, oxygen can be produced abiotically by photolysis of water with subsequent hydrogen escape and photolysis of CO_2 with subsequent burial of carbon. The future search for extraterrestrial life will rely on our improved ability to understand and spectrally characterize the abiotic and potentially biotic contributions to atmospheric chemical disequilibria ([Kaltenegger et al., 2011](#); [Kasting, Traub et al., 2009](#); [Krissansen-Totton et al., 2016](#); [Seager and Deming, 2010](#); [Vázquez et al., 2010](#)).

The study of habitability, *habitology*, is a new, cross-disciplinary synthesis of facts and theory from Earth and planetary sciences, biology, and astronomy. As new data come streaming in from these disparate disciplines, the preliminary steps of their integration is exhilarating and confusing. We can only find out who we are and how we fit into the universe by studying and interpreting these data with the goal of finding other life-forms. Our search for extraterrestrial life is a search for ourselves and our place in the universe. If we cannot find extraterrestrial life-forms that fit our definition of life, perhaps we will have to broaden our definition until we do. Even if we fail to find life elsewhere, we will soon find the closest uninhabited habitable planet. That will be crucial, sooner or later, for our survival as a species.

Chapter 2

The Biology of Habitability

This chapter was published as

A. Chopra and C. H. Lineweaver (2016). 'The Case for a Gaian Bottleneck: the Biology of Habitability'. *Astrobiology*, 16(1), pp. 7–22. DOI: [10.1089/ast.2015.1387](https://doi.org/10.1089/ast.2015.1387)

Abstract

The prerequisites and ingredients for life seem to be abundantly available in the universe. However, the universe does not seem to be teeming with life. The most common explanation for this is a low probability for the emergence of life (an emergence bottleneck), notionally due to the intricacies of the molecular recipe. Here, we present an alternative Gaian bottleneck explanation where the emergence of life could be much more common than its long term persistence. If life emerges on a planet, it only rarely evolves quickly enough to regulate greenhouse gases and albedo, thereby maintaining surface temperatures compatible with liquid water and habitability. Such a Gaian bottleneck suggests that (i) extinction is the cosmic default for most life that has ever emerged on the surfaces of wet rocky planets in the universe and (ii) rocky planets need to be inhabited to remain habitable. In the Gaian bottleneck model, the maintenance of planetary habitability is a property more associated with an unusually rapid evolution of biological regulation of surface volatiles, than with the luminosity and distance to the host star. Liquid water on the surface of a planet (particularly old planets) would then not just be a prerequisite for life, but a plausible biosignature.

2.1 Where is everybody?

We see no evidence that our galaxy has been colonized by an advanced technological civilization. Archaeological excavations have not unearthed alien spaceships, and the optical and radio searches for extraterrestrial intelligence have not been successful (Tarter, 2001). If one assumes that, once life emerges it evolves towards intelligence and technological civilizations, we are faced with Fermi's paradox: Where is everybody? (Ćirković (2009); Webb (2002); but also see Gray (2015) and Ward and Brownlee (2000)). To put this information in context, Hanson (1998) introduced the concept of a Great Filter, describing the possible bottlenecks in the assumed progression from molecular chemistry to life, from life to intelligence, and from intelligence to galactic colonization. If the emergence of life is a rare and difficult process, then an emergence bottleneck could resolve Fermi's paradox. However, if technological civilizations inevitably destroy themselves, this self-destruction bottleneck could also resolve Fermi's paradox.

Bostrom (2008) argued that the Great Filter is a valuable tool for assessing existential risks to humanity. If the biggest barrier in the Great Filter is the emergence bottleneck, then we will find no independently evolved life on Mars, and the apparent absence of advanced technological civilizations in our galaxy is because life's emergence is difficult and rare. In this case, humanity has already survived the biggest threat to its continued existence; the biggest bottleneck is behind us and we can relax. However, if we find life on Mars that has evolved independently of life on Earth, this would be strong evidence that there is no emergence bottleneck. If we find such life, Bostrom argues that the biggest bottleneck – the self-destruction bottleneck – would then be in front of us. This would be “by far the worst news ever printed on a newspaper cover.” As a plausible alternative to such catastrophic logic, we introduce the concept of a Gaian bottleneck, a bottleneck that life on Earth has already passed through. If such a bottleneck exists, the discovery of *extant*, independently evolved martian life might be bad news, but the discovery of *extinct* independently evolved martian life, would not be.

In the standard view, the decrease in bombardment rate from ~ 4.5 to ~ 3.8 Gya is associated with making Earth more clement and thus enabling life to emerge and persist (Maher and Stevenson, 1988). In contrast to this view, we postulate a Gaian bottleneck model in which early life (on Earth and elsewhere) is not just a passive passenger, but comes under strong selection pressure to actively modify and regulate its environment. The emergence of life's abilities to modify its environment and regulate initially abiotic feedback mechanisms (what we call Gaian regulation) could be the most significant factor responsible for life's persistence on Earth.

This highlights an important difference between physics-based estimates of habitability and the more unpredictable patterns of biological evolution on the highly unstable surface environments of young terrestrial planets. For example, bombardment rates inevitably decrease in the circumstellar habitable zones (CHZ) of stars, but the time scales for the evolution of Gaian regulation is probably unpredictable and would not inevitably evolve rapidly (or at all). Thus, if there is anything special about what happened on Earth to allow life to persist here, it might have less to do with the decreasing bombardment rate in the Hadean, or special chemical ingredients, or sources of free energy, or even a rare recipe for the emergence of life. The existence of life on Earth today might have more to do with the unusually rapid biological evolution of effective niche construction and Gaian regulation in the first billion years. Habitability and habitable zones would then not only be a passive abiotic property of stellar and planetary physics and chemistry (such as stellar luminosity, initial water content, and decreasing bombardment rate) but would also be a result of early life's ability to influence initially abiotic geochemical cycles and turn them into the life-mediated biogeochemical cycles that we are familiar with on the current Earth (Falkowski, Fenchel et al., 2008; Kump et al., 2009; Lenton, 1998; Lenton, Schellnhuber et al., 2004; Schneider, 2004). Without rapid evolution of Gaian regulation, early extinction would be the most common fate of planetary life. Even if the emergence of life is a common feature of wet rocky planets throughout the universe, the Gaian bottleneck model suggests that inhabited Earth-like planets would be rare.

2.2 Is abiogenesis rare?

2.2.1 Possible physics and chemistry based bottlenecks

No stellar bottleneck. No wet-rocky-planet bottleneck. Sun-like stars and Earth-like planets are common.

If our Sun were the most uranium-rich star in the galaxy, and if life on Earth were uranium-based (instead of carbon-based), then we would have good reason to believe that life (either its emergence, persistence, or both) requires a rare kind of uranium-rich host star. However, we have been unable to identify any significant differences between the Sun and other stars that could plausibly be connected with an increased probability of abiogenesis. Sun-like stars are common in the universe (Robles et al., 2008). Thus, there seems to be no stellar bottleneck responsible for reducing the probability for the emergence of life.

Over the past decade, estimates for the frequency of rocky planets in, or near, the CHZ have increased (Bovaird and Lineweaver, 2013; Bovaird, Lineweaver and Jacobsen, 2015; Burke et al., 2015; Fressin et al., 2013; Howard, Marcy, Bryson et al., 2012; Lineweaver and Chopra, 2012a; Marcy, Weiss et al., 2014; Petigura et al., 2013). Rocky planets in the CHZ are likely to be a common outcome of planetary formation. This result is supported by observational, theoretical, and computational models of rocky planet formation in which gas-rich protoplanetary disks evolve into dust disks in which planetesimals form and undergo oligarchic growth into planetary embryos as they differentiate into iron-nickel-rich cores, silicate mantles, and crusts dominated by incompatible lithophiles (Chambers, 2014; Elkins-Tanton, 2012; Hardy et al., 2015; Morbidelli, Lunine et al., 2012). Models and observations suggest that this sequence – the formation of terrestrial planets – is not a rare occurrence that needs special initial conditions. There seems to be no rocky-planet-in-the-CHZ bottleneck responsible for reducing the probability for the emergence of life.

No elemental or molecular ingredient bottleneck.

Life on Earth is made of hydrogen, oxygen, carbon, nitrogen, sulfur, and phosphorus: “HOCNSP” (Chopra, Lineweaver et al., 2010). HOCNPS are among the most abundant atoms in the universe (Lineweaver and Chopra, 2012b; Lodders et al., 2009; Pace, 2001). Since the elemental ingredients for life are the most common elements in the universe, it is not surprising that the molecular ingredients of life are also common.

Of the elements in the universe that form molecules, water (H₂O) is the combination of the first and second most abundant elements. Water should be a common feature of rocky planets (Elkins-Tanton, 2012; Raymond, Quinn et al., 2004, 2007). Radial mixing during the epoch of oligarchic growth ensures that some water-rich materials from beyond the snowline are injected into the more water-poor material of the feeding zones of rocky planets in the CHZ. Thus, it is likely that Mars and Venus both started out, like Earth, hot from accretional energy and impacts, and wet from impacts of large hydrous (5% - 20% water) asteroids from the outer asteroid belt (Morbidelli, Chambers et al., 2000; Morbidelli, Lunine et al., 2012) and other “wet” accretionary material (Drake, 2005; Drake and Righter, 2002). Terrestrial planets in other planetary systems are also likely to start with variable, non-negligible amounts of water.

Current terrestrial life is built of monomers such as amino acids, fatty acids, sugars, and nitrogenous bases. Amino acids link together to form proteins; fatty acids link to form lipids; sugars link to form carbohydrates; and nitrogenous bases combine with sugar and phosphate to make nucleotide monomers, which link to form RNA/DNA (Lineweaver and Chopra, 2012b). Thus, life on Earth emerged when available monomers linked together to make polymers. Amino acids and other organic monomers fall from the skies in carbonaceous chondrites. We have no reason to believe that the availability of these monomers is somehow unique to Earth or the Solar System. The flux of such organics was particularly high during the first billion years of the formation of Earth, and we have no reason to believe that this will not be the case during the formation of terrestrial planets in other planetary systems. The assortment of organic compounds found in carbonaceous chondrites and the probable universality of early heavy meteoritic bombardments indicate that new planetary systems should also be supplied with organic ingredients and be conducive to the synthesis of prebiotic molecules (Ehrenfreund and Charnley, 2000; Herbst and Dishoeck, 2009; Tielens, 2013). We expect

all the ingredients of life as we know it (HOCNPS, water, amino acids, sugars, nucleic acids, HCN, and other organics) to be present and available on wet rocky planets throughout the universe. An ingredient bottleneck seems implausible.

No free energy bottleneck since photon and chemical redox based energy sources are common.

Life (here and elsewhere) needs to do something for a living (Conrad and Nealson, 2001; Nealson and Rye, 2013). This living depends on extracting free energy from an environment out of thermodynamic equilibrium (Branscomb and Russell, 2013). This extraction is based on catalyzing redox reactions or absorbing photons (Kleidon, 2012). The interiors of rocky planets throughout the universe are denser and hotter than their surfaces. Thus, thermal gradients, density gradients, and the fluid flows they drive, set up redox potentials that can be exploited (Nisbet and Fowler, 2014). The environmental factors that enabled abiogenesis on Earth, such as the geochemical disequilibria between rocks, minerals, aqueous species, and gases, are likely to be ubiquitous on wet rocky planets throughout the universe. In addition, for planets in the CHZ, fusion in a nearby star shines ~6000 K photons onto ~300 K surfaces and enables metabolisms based on photon capture (Annala and Annala, 2008; Lineweaver and Egan, 2008).

Recipe bottleneck ? How ubiquitous are Abiogenesis Habitable Zones?

With the absence of bottlenecks associated with stars, planets, ingredients, and sources of free energy, the only other factor that could produce an emergence bottleneck would be “recipe.” While we do not know the specifics of the prebiotic chemistry and geochemical environments necessary for life to emerge (e. g. , Orgel, 1998; Stüeken et al., 2013), the view that life will emerge with high probability on Earth-like planets is shared by many scientists. Darwin (1871) speculated that the environment, ingredients, and energy sources needed for the origin of life could be common, when he wrote about life emerging in...

...some warm little pond with all sort of ammonia and phosphoric salts, light, heat, electricity present, that a protein compound was chemically formed, ready to undergo still more complex changes.

De Duve (1995) has been a more recent proponent of the view that the emergence of life is a cosmic imperative:

Life is either a reproducible, almost commonplace manifestation of matter, given certain conditions, or a miracle. Too many steps are involved to allow for something in between.

Discarding miracles, de Duve leaves us with life as an “almost commonplace manifestation of matter.” As far as we know, Darwin’s warm little pond, or deDuve’s “certain conditions” are common on Earth-like planets and may be sufficient for the emergence of life. Biota throughout the universe would emerge from chemistry through proto-biotic molecular evolution (e. g. , Eigen and Winkler, 1992; Eschenmoser and Volkan Kiskurek, 1996; Martin and Russell, 2007; Orgel, 1998; Russell et al., 2013; Ward and Brownlee, 2000).

There is some tension between this conclusion and the inability of synthetic biologists to produce life, despite having access to a wide variety of ingredients, environmental set ups, and energy sources. Plausible explanations for this tension include: (1) there is an emergence bottleneck due to a convoluted recipe whose requirements only rarely occur naturally. Or (2) there is no emergence bottleneck – the recipe for life is simple – but we are not as imaginative or as resourceful as nature, so we have not replicated the recipe in the relatively short time we have been investigating the origin of life.

We conclude that the idea of an emergence bottleneck is still plausible. However, the evidence for it is getting weaker as we find out more about the proto-biotic molecular evolution that led to the emergence of life on Earth (e. g. , Benner, 2013; England, 2013; Nisbet and Fowler, 2014; Sousa and Martin, 2014). This weakness provides motivation for alternative explanations for the apparent paucity of life in the universe. The Gaian bottleneck hypothesis is one such alternative.

As we learn more about the origin of life, we can begin to define an abiogenesis habitable zone (AHZ) where the requirements for life’s emergence are met. Many initially wet rocky planets in the CHZ may possess the necessary and sufficient conditions to get life started (“AHZ” in Figure 2.1). The habitability requirements for the origin of life may be substantially different from, and more specific

than, the requirements to maintain life on a planet (as in the difference between the need to have a spark plug to start an engine and a radiator to keep it from overheating). In Figure 2.1, we have assumed that the AHZ is not necessarily a subset of currently inhabited planetary environments.

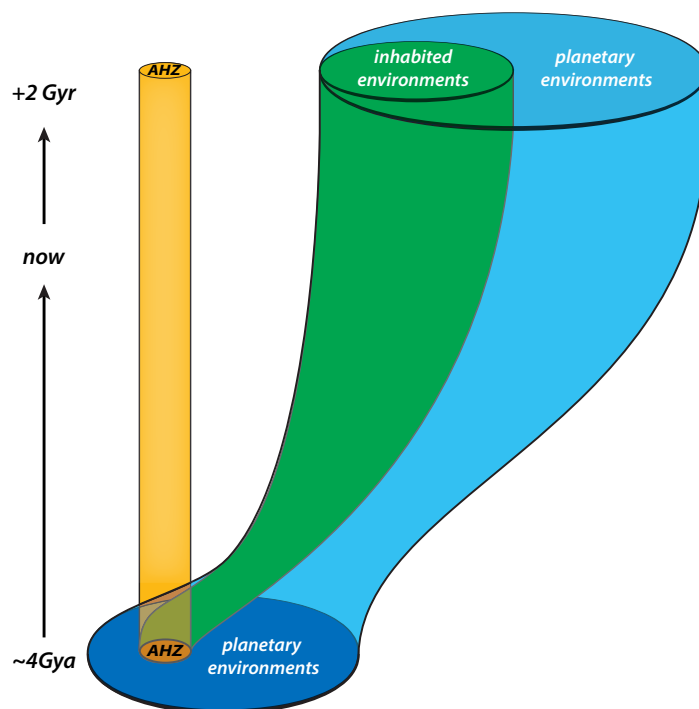


Figure 2.1: The conditions needed for the origin of life are in the Abiogenesis Habitable Zone or “AHZ.” Inhabited environments (green) are a subset of planetary environments (blue). Both of these can change with time. The AHZ conditions are probably narrower than the broader conditions to which life can now adapt (“inhabited environments”). Through its management of the greenhouse and its partitioning of reductants and oxidants, the activity of life increases the range of inhabited environments (Nisbet, Zahnle et al., 2007). Hence, the green cylinder emerges out of the AHZ and gets broader with time. More specific reasons for this broadening include (1) the evolution of increasingly efficient catalytic enzymes offering tighter control over reaction rates, (2) the ability of new enzymes to access the energy from different redox pairs providing larger $|\Delta G|$ values (Nealson and Conrad, 1999), and (3) the evolution of ecosystems (Smith and Morowitz, 2015), global level niche construction, and global biogeochemical feedback cycles (see Section 2.4) which we refer to as the “evolution of Gaian regulation of the biosphere.”

2.2.2 Emergence Bottlenecks vs Gaian Bottlenecks

An emergence bottleneck is illustrated in Figure 2.2. The left panel shows a hypothetical planet with non-evolving planetary conditions. The right panel shows a more plausible planet which initially had some habitable regions but, through volatile evolution or other transient factors, lost its surface water and evolved away from habitable conditions (e. g. , a runaway greenhouse or runaway glaciated planet). Without significant abiotic negative feedback mechanisms, the surface environments of initially wet rocky planets are volatile and change rapidly without any tendency to maintain the habitability that they may have temporarily possessed as their early unstable surface temperatures transited through habitable conditions (Figure 2.6 C). If there is no emergence bottleneck (Figure 2.3), typical wet rocky planets have initial conditions compatible with the emergence of life (AHZ). We postulate that almost all initially wet rocky planets on which life emerges (left panel of Figure 2.3) quickly evolve like the abiotic planets represented in the right panel of Figure 2.2. This unregulated evolution of planetary environments away from habitable conditions constrains the duration of life’s existence on the planet. We call this early extinction of almost all life that ever emerges the *Gaian bottleneck*. In rare cases (for example on Earth), life will be able to evolve quickly enough to begin to regulate surface volatiles through the modification of abiotic feedbacks (right panel of Figure 2.3). The potentially relevant feedbacks involved in such early Gaian regulation are illustrated in Figure 2.5 and discussed in Table 2.1 and Section 2.4.

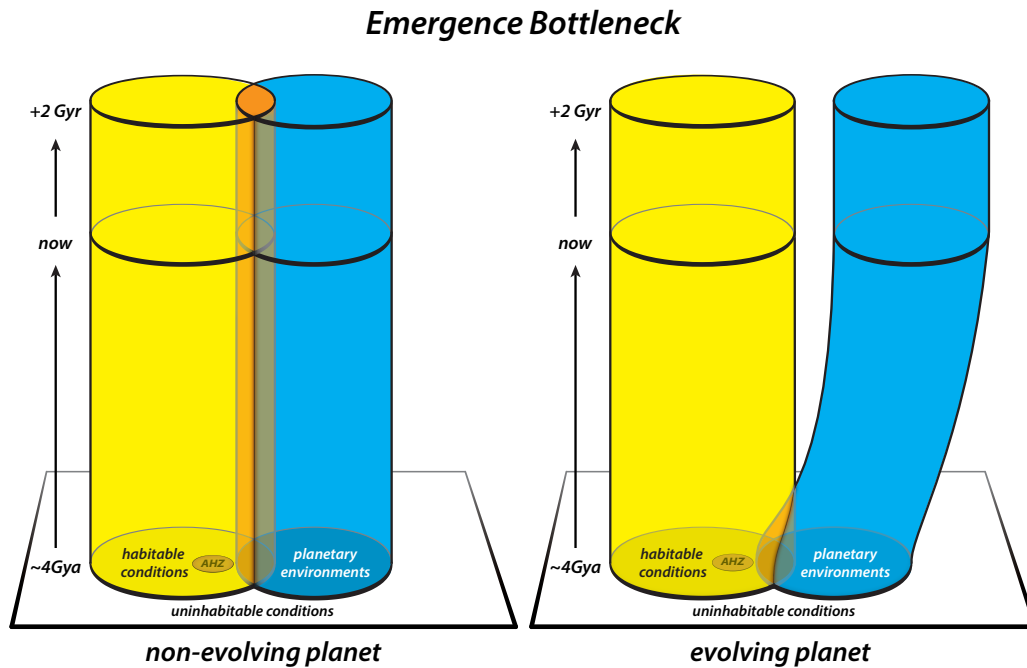


Figure 2.2: Emergence Bottleneck: planets on which life does not get started. Here, we show habitable conditions (yellow) and planetary environments (blue), from the time of planet formation at the bottom to ~6 billion years later at the top. Life will not emerge on either of these planets since their initial planetary environments do not overlap with the Abiogenesis Habitable Zone (AHZ) where life could get started. Both of these planets are initially habitable since their environments overlap with habitable conditions. *Left panel:* In this unrealistic, non-evolving model, planetary environments do not change with time. Habitable regions remain uninhabited because life does not get started. Such planets are uninhabited but remain habitable. *Right panel:* Parts of this evolving planet were habitable, but life does not emerge. The planet undergoes abiotic evolution and moves quickly away from habitability. We argue (Section 2.3.2) that evolution away from habitability is probably the default for initially wet rocky planets. We would find such planets to be uninhabited (and if older than ~1 Gyr, uninhabitable) – consistent with the idea that a planet has to be inhabited to remain habitable.

2.3 Early extinction in the first billion years

2.3.1 Bombardment and impact frustration

During the late phases of Earth's accretion (~4.5 to ~4.0 Gya), episodes of cold "Norse ice-hell" were punctuated by brief periods of hot inferno with magma oceans (Elkins-Tanton, 2008; Nisbet, 2002). Frequent, large, random impacts produced wide-ranging, unstable temperatures. The largest impacts were so large that any life that did emerge during the transitory habitable periods was probably bombarded into extinction. These early bombardment-induced extinctions have been called the impact frustration of life (Davies and Lineweaver, 2005; Maher and Stevenson, 1988; Marchi et al., 2014; Sleep, Zahnle, Kasting et al., 1989; Sleep, Zahnle and Lupu, 2014). The early heavy bombardment of Earth decreased by more than ~13 orders of magnitude during this period (Bland (2005); Köberl (2006) Figure 2.6 A). As the rate of planetary accretion slowed, the impact rate and the size of the largest impactors decreased. Habitable conditions became, at least fleetingly, more available for life (Abramov, Kring et al., 2013; Abramov and Mojzsis, 2009). Impact heating may have provided strong selection pressure on early life to evolve into deep environments to survive thermal perturbations (Mat et al., 2008; Nisbet and Sleep, 2001; Sleep, Zahnle, Kasting et al., 1989).

We have no reason to believe that these processes are specific to Earth or to our Solar System. The surfaces of Earth-sized rocky planets will undergo an early heavy bombardment that produces severe intermittent temperature pulses. A decreasing bombardment rate is likely to be a generic process that controls the emergence and early persistence of life on wet rocky planets near the circumstellar habitable zones of host stars throughout the universe. As the bombardment rate decreases, these rocky planets cool down and can harbour, at least temporarily, habitable environments where life

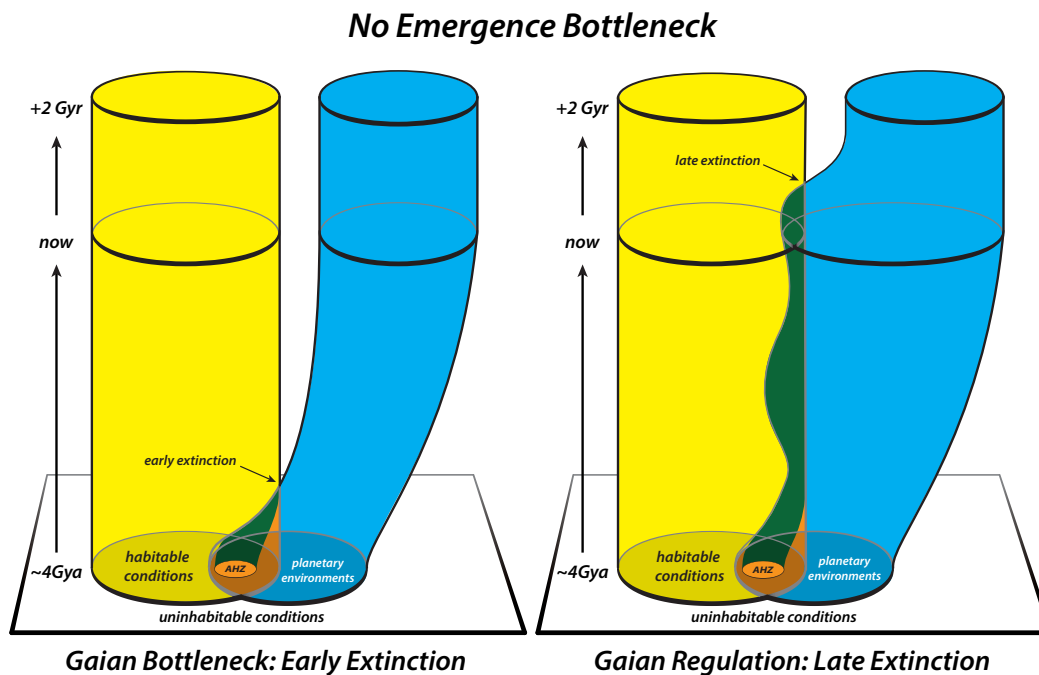


Figure 2.3: The Abiogenesis Habitable Zone may be a very common subset of the environments of rocky planets that are wet during their first billion years. As in the left panel of Figure 2.2, we assume that these planets are unregulated by any abiotic negative feedbacks and have no tendency to maintain habitability. We assume that life gets started on both these planets, so there is no “emergence bottleneck” (Section 2.2.1) as there was in Figure 2.2. *Left panel:* Life is unable to evolve rapidly enough to control runaway positive feedbacks. Gaian regulation does not emerge fast enough to maintain habitability. Thus, we have a “Gaian bottleneck.” We propose that most wet rocky planets are of this kind. *Right panel:* In rare cases (as on Earth), Gaian regulation evolves fast enough to make it through the Gaian bottleneck and keep at least part of the planet habitable for billions of years. Biospheric regulation maintains the habitability of the planet until ~5 Gyr after formation, at which time, increasing stellar luminosity and loss of water cause life to go extinct. Extinction happens in both panels but much later in the right panel. This figure illustrates our hypothesis that the emergence and rapid extinction of life may be quite common (left) but that the emergence of life, followed by the evolution of Gaian regulation and the long term persistence of life, could be quite rare (right).

can emerge from primordial soups, hydrothermal vents, or any other AHZ candidate. Whether life usually persists after this emergence is what we are calling into question.

We postulate that the combination of heavy bombardment, volatile evolution, and thermal instability almost always conspires to eliminate incipient life before it has a chance to evolve sufficiently to regulate initially abiotic global cycles. We also postulate that exceptionally, life on Earth was able to counter the effects of volatile evolution, thermal instability, and the general abiotic tendency to drift away from habitability. In other words, we argue that the same catastrophic events that life on Earth seems to have overcome, usually lead to extinction. In the first billion years on a wet rocky planet in the universe, impacts and an inability to control surface environments are usually not just frustrating, but fatal.

2.3.2 Devolatilization of habitable planets

Liquid water is not easy to maintain on a planetary surface. The initial inventory and the timescale with which water is lost to space due to a runaway greenhouse, or frozen due to ice-albedo positive feedback, are poorly quantified, but plausible estimates of future trajectories have been made. On Earth, dissociation of water vapor by ultraviolet radiation in the upper atmosphere is ongoing and will eventually (~1-2 billion years from now) lead to the loss of water from the bio-shell and the subsequent extinction of life on Earth (Bloh, Bounama and Franck, 2005; Caldeira and Kasting, 1992; Franck, 2000; Franck, Bloh et al., 2002; Lenton and Bloh, 2001).

In our Solar System, Venus, Earth, and Mars are usually assumed to have started out in similar conditions: hot from accretion and wet from the impacts of aqueous bodies from beyond the snow-line. However, atmospheric evolution of these planets diverged significantly (Driscoll and Berrovici, 2013; Kasting, 1988; Kulikov et al., 2007). The simplest interpretation of the D/H ratios of Venus:Mars:Earth:Sun (2000:70:10:1) is that (i) Venus has lost the vast majority of its H₂O, (ii) Mars lost about 85% of its initial water content and the rest froze into the polar ice-caps and subsurface permafrost (Kurokawa et al., 2014; Villanueva et al., 2015) and (iii) Earth was able to keep a larger fraction of its H₂O (Pope et al. (2012), Figure 2.4).

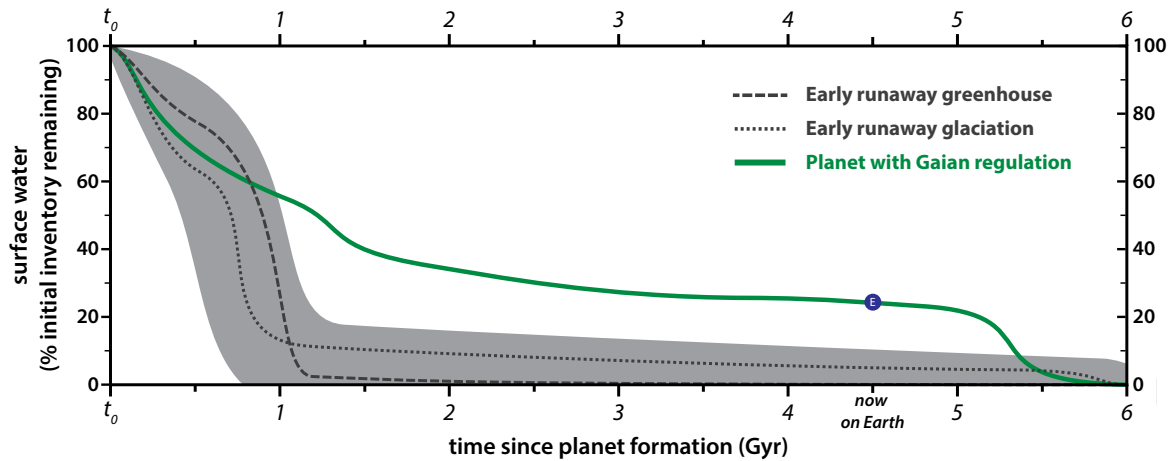


Figure 2.4: Schematic illustration of the water loss caused by impacts and hydrogen escape. Hydrogen escape may entirely desiccate a rocky planet within a few billion years (Lovelock, 2005). Desiccation is inevitable as the host star luminosity increases, a cold trap is lost and the stratosphere becomes moist (Lenton and Bloh, 2001; O'Malley-James et al., 2015).

However, the answer to the question “Why didn’t Earth undergo runaway greenhouse like Venus or a runaway glaciation like Mars?” may have as much, or more, to do with life on Earth than with Earth’s distance from the Sun. The biotic mechanisms of how this preservation has been achieved have been discussed in the context of the Gaia Hypothesis by Harding and Margulis (2010).

The early devolatilization of Earth-like planets around M-stars due to an extended pre-main sequence period of high extreme UV flux (above the dissociation energy of water, ~5 eV) could apply to some extent to Earth-like planets around more massive stars (Luger and Barnes, 2015; Tian, 2015).

The amount of water (and volatiles in general) deposited or devolatilized during the late accretion phase of rocky planet formation in the universe is highly variable (Raymond, O’Brien et al., 2009; Raymond, Quinn et al., 2004) and can produce desert worlds (Abe, Abe-Ouchi et al., 2011), ocean worlds (Léger, Selsis et al., 2004), and probably everything in between. Abiotic volatile evolution will be rapid, stochastic and hostage to the timing, mass, volatile content, and impact parameters of the largest impactors and the runaway feedbacks they could induce.

We argue that abiotic habitable zones are available initially and fleetingly to wet planets within a wide range of orbital radii (~0.5 to ~2 AU) because of the thermal instability of their surfaces. Wide-ranging unstable temperatures could provide transitory abiotic habitable zones during the first half billion years after formation (Nisbet (2002), Figure 2.6 B and 2.6 C).

There are two ways to influence the surface temperature of a planet (Figure 2.5): change the albedo (grey loops) or change the greenhouse gas content of the atmosphere (blue loops) (Kasting, 2012). The amount and the phases of the volatiles (H₂O, CO₂, CH₄) of rocky planetary atmospheres control both the albedo and greenhouse warming. Albedo and greenhouse warming, in turn, control the amount and phases of the volatiles. Strong positive feedback cycles (left side of Figure 2.5) may lead to both i) runaway greenhouse (temperatures too hot for life) with runaway loss of atmosphere (hydrogen loss and thus water loss) or ii) runaway glaciation (lowering the temperature and/or water activity to levels not conducive to life).

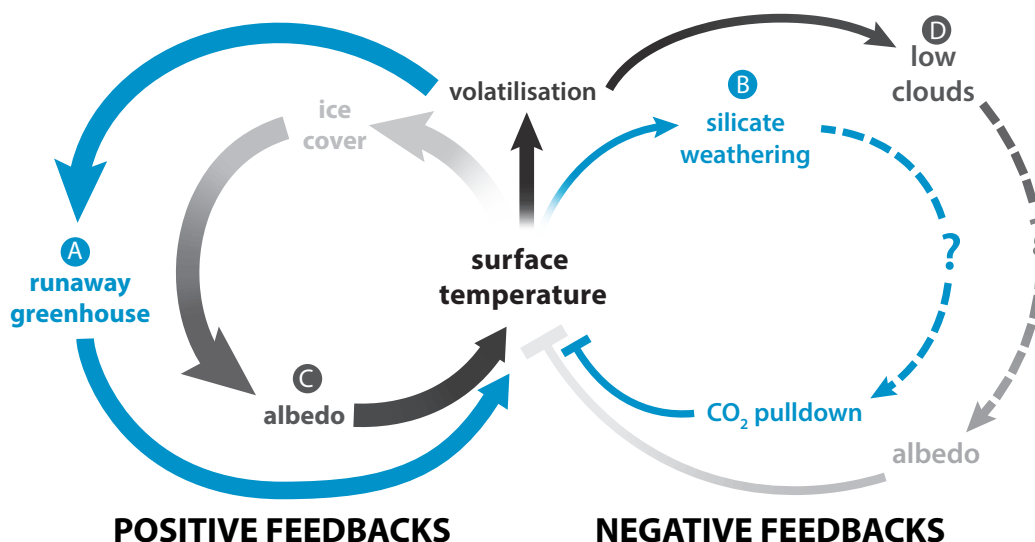


Figure 2.5: Early Abiotic Feedbacks. During the first billion years after the formation of Earth (or of Earth-like planets), abiotic positive feedbacks (left) can lead to runaway surface temperatures outside the habitable range (both too hot and too cold). These positive feedbacks lead to the loss of liquid water (either from hydrogen escape to space or condensation into ice (Figure 2.4)). Abiotic negative feedbacks (right) have been invoked to stabilize surface temperatures, but they may not be significant in the first billion years, hence the dashed lines and the question marks (Section 2.3.3). As life evolves, it can strengthen or weaken these initially abiotic geochemical feedback loops and turn them into biogeochemical cycles and feedback loops. Evolving life can insert itself into these feedbacks at the points labelled A, B, C and D. (Table 2.1 and Section 2.4).

2.3.3 Implausibility of early negative feedback cycles

In his original estimate of the continuous habitable zones, Hart (1979) considered runaway greenhouse and runaway glaciation feedback but did not account for the negative feedback of silicate weathering on his models. The resulting continuous habitable zone of 0.95-1.01 AU had such a narrow width that he wrote:

It appears, therefore, that there are probably fewer planets in our galaxy suitable for the evolution of advanced civilizations than has previously been thought.

Such a narrow CHZ could help solve the Fermi paradox (e.g., Webb, 2002, Solution 36, p.158). More recent work has taken into account a stabilizing negative feedback loop associated with the recycling of CO₂ by plate tectonics. Walker et al. (1981) proposed a greenhouse-gas-based negative feedback process employing the carbonate-silicate cycle through the mechanism of silicate weathering. Increasing surface temperatures increases the silicate weathering rate, freeing up more Ca²⁺ and other cations that combine with CO₂ (via aqueous bicarbonate HCO₃⁻) to produce insoluble carbonates. Thus, when the temperature rises, more atmospheric CO₂ is sequestered and temperature decreases (Walker 1985, and the blue negative feedback loop on the right side of Figure 2.5). This abiotic negative feedback is largely responsible for moving the outer edge of the CHZ from 1.01 AU, as estimated by Hart (1979), to the more modern, larger values of 1.5-1.7 AU (e.g., Kasting, Whitmire et al., 1993; Kopparapu et al., 2013).

Since the temperature-dependent carbonate-silicate cycle provides a negative feedback, it could have been responsible for the long term stabilization of Earth's surface temperature. With a sufficiently high silicate weathering rate, even a lifeless planet could remain habitable. However, since temperature-dependent silicate weathering requires sub-aerial weathering of silicate rocks (either granitic or basaltic), the magnitude of the negative feedback of silicate weathering is roughly proportional to the amount of sub-aerial continental crust. In the first billion years of Earth's history, the fraction of the surface of Earth where sub-aerial erosion would have been possible may have been extremely small (Abbot et al., 2012; Dhuime et al., 2015; Flament et al., 2008). Flament et al. (2008) modeled the sub-aerial weathering as a function of time and estimated that in the late-Archean (~2.5 Gya) 2-3% of the Earth's surface was sub-aerial continent. The little continental crust present was largely submerged.

Table 2.1: Abiotic feedback processes active during the first billion years of a wet rocky planet's history and potential biotic enhancements of the feedback cycle.

Feedback	Mechanism	Feedback Type	Potential Biological Mediation
greenhouse	greenhouse gases (Abe, Abe-Ouchi et al., 2011; Ingersoll, 1969)	positive	A (Catling et al., 2001; Goldblatt, Claire et al., 2009; Harding and Margulis, 2010; Kasting, 2012)
greenhouse	silicate weathering (Walker et al., 1981)	negative?	B (Catling et al., 2001; Höning et al., 2014; Lovelock and Whitfield, 1982; Rosing, Bird, Sleep, Glassley et al., 2006; Schwartzman and Volk, 1989)
albedo	ice albedo (Budyko, 1969; Hoffman, 1998; Kopp et al., 2005)	positive	C (Harding and Margulis, 2010; Watson and Lovelock, 1983)
albedo	low clouds (Abe, Abe-Ouchi et al., 2011)	negative?	D (Rosing, Bird, Sleep and Bjerrum, 2010)

Thus, it is likely that early in Earth's history, the negative feedback of the carbonate-silicate cycle may have been inoperative or at least significantly less effective than today. This undermines the main negative feedback mechanism proposed to stabilize surface temperature on wet rocky planets for the first billion years or so, when they are most likely to experience runaway greenhouse or runaway glaciation due to high inventories of primordial greenhouse gases, higher bombardment rates, and higher volcanism: hence, the “?” associated with this negative feedback loop in Figure 2.5 and Table 2.1. Without this abiotic feedback cycle to extend the outer edge of the CHZ, the much narrower Hart-like continuously habitable zone (Figure 2.6 B) becomes more plausible.

The other abiotic negative feedback on surface temperature shown in Figure 2.5 is associated with low clouds: higher temperatures → more volatilization → more low altitude clouds → higher albedo → lower temperatures. Low clouds increase albedo and decrease surface temperatures more than they contribute towards raising the surface temperature because of the greenhouse effect associated with clouds (Abe, Abe-Ouchi et al., 2011). This is problematic because increasing volatilization produces both i) more low altitude clouds (which could cool Earth due to their higher albedo), and more high altitude clouds, which could have a stronger greenhouse effect than albedo effect and thus increase surfaces temperatures (Goldblatt and Zahnle, 2011; Leconte et al., 2013). For this reason, the effects of clouds are often considered the biggest source of uncertainty in global climate models and thus the “?” associated with this cycle in Figure 2.5 and Table 2.1.

While it may be possible to vary albedo and greenhouse gases within some plausible range and construct a wide CHZ, without negative feedback, there is no justification for tuning these abiotic variables to maintain habitability. We postulate that the abiotic stabilizing feedbacks (two cycles on the right side of Figure 2.5) were probably negligible on early Earth. In their absence, it is hard to understand how habitability would have been maintained. Driver-less cars don't stay on roads. Without significant abiotic stabilization, we propose that the most plausible default becomes the abiotic tendency to evolve away from habitability shown in Figure 2.1 and Figure 2.6 C.

Just because Earth is at 1 AU and has been inhabited for ~4 billion years does not mean that there is a physics-based, biology-independent, computable continuous habitable zone. With thermal instability and increasing stellar luminosity, it is not clear that a physics-based continuously habitable zone even exists. There may be no range of orbital distances (or any region of multi-dimensional abiotic parameter space) for which the surface environments of initially wet rocky planets have sufficiently strong abiotic negative feedback to maintain habitability. If this is the case, purely abiotic computations of a continuously habitable zone may be misleading, and Gaian regulation becomes a plausible explanation for the continuously inhabited HZ in which we find ourselves.

2.4 The need for Gaia

It is usually assumed that the CHZ is determined by abiotic physical parameters: stellar mass and luminosity, planetary mass and atmospheric greenhouse gas composition, surface albedo, and sometimes clouds. More recently planetary spin, orbital eccentricity, obliquity, and initial water content have been added to the list of physical parameters (e. g. , Gaidos, Deschenes et al., 2005;

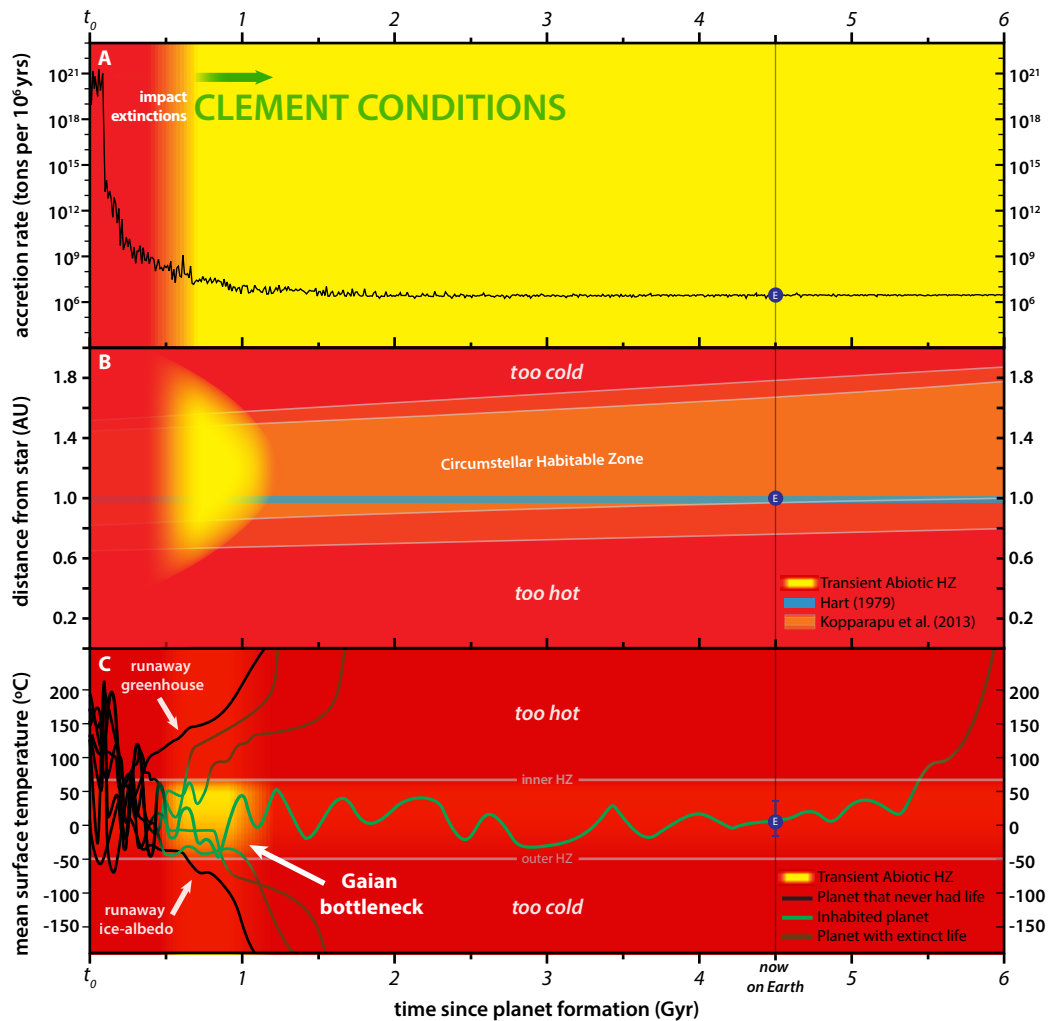


Figure 2.6: Bombardment, habitable zones, and the Gaian bottleneck. **A.** Early heavy bombardment precludes life for the first ~0.5 billion years, indicated by red in all three panels. These impacts produce heat pulses and both deliver and remove volatiles (Elkins-Tanton, 2011). Thus, the *amount* of H₂O at the surface is highly variable during this period. The *phase* of the H₂O at the surface is also highly variable during this period because of impact-induced alternation between greenhouse warming and ice-albedo runaway. **B.** The width of the circumstellar habitable zone (CHZ) is usually considered to be a function of physics and chemistry, but is often computed without the largely uncertain influence of clouds, and placed between Venus (0.7 AU) and Mars (1.5 AU). Here the blue region is from the work of Hart (1979), and the orange regions are based on estimates by Kopparapu et al. (2013) for the conservative (light orange) and optimistic (dark orange) limits. Life plays no role in these computations. The ~30% increase in the luminosity of the Sun since its formation is responsible for the outward migration of the traditional CHZ and some of the narrowness of Hart's continuously habitable zone. The yellow zone in B represents our speculative version of a short-lived abiotic habitable zone at the tail end of the impact-induced thermal instabilities shown in the first billion years of panel C. The width of the abiotic habitable zone begins with a fairly wide range of semi-major axes, but lasts only from ~0.5 to ~1 Gyr and then shrinks to zero. After ~1 Gyr, rapid impact-induced thermal excursions diminish and surface temperatures drift away and runaway from habitability. Planets become devolatilized because of the runaway greenhouse effect (top of panel C), and because liquid water condenses out into ice due to the runaway ice-albedo effect (bottom of panel C), with no abiotically stable zone between them. The early evolution of Gaian regulation may be the main feature responsible for maintaining the surface temperature of Earth within a habitable range for the past ~4 billion years (Lovelock, 2000).

Gonzalez, 2005; Güdel et al., 2014; Lammer et al., 2009; Shields et al., 2015). Here, we argue that these abiotic parameters can fleetingly enable the emergence of life but cannot maintain habitable surface conditions with liquid water. As the early heavy bombardment subsides, strong selection pressure on life begins to regulate, control, and even dominate the mechanisms that create or maintain the temperatures and pressures at the surface of a planet that allow liquid water. If so, then biology (rather than physics or chemistry) can play the most important role in maintaining habitability.

In addition to the abiotic environmental changes (due to bombardment and devolatilization), there could be a long struggle that starts early between life and an environment that does not, abiotically, stay habitable. Feedback between life and environment may play the dominant role in maintaining the habitability of the few rocky planets in which life has been able to evolve Gaian regulation quickly.

If life gets started on a planet, there are many potential ways in which life can regulate the mechanisms that create or maintain the temperatures and pressures needed for liquid water (Harding and Margulis, 2010; Schneider, 2004; Schneider and Boston, 1991). Gaia researchers propose that life on Earth evolved to become integrated into previously abiotic feedback systems that can modify or regulate surface temperature and the hydrological cycle (e.g., Lenton, 1998; Nisbet, Fowler and Nisbet, 2012). Life can evolve to enhance and regulate the feedback loops (biological mediation processes A-D in Figure 2.5 and Table 2.1). Biologically mediated feedback loops are stabilizing or Gaian (Ricklefs and Miller, 2000). For habitability to be maintained, life could down-regulate the positive runaway feedback loops and enhance the negative feedback loops. On Earth, life began to modulate the greenhouse gases composition of the atmosphere as soon as life became widespread (Johnson and Goldblatt, 2015; Nisbet, 2002; Nisbet and Fowler, 2014; Nisbet, Fowler and Nisbet, 2012).

The use of the Gaia hypothesis in ecology was reviewed by Free and Barton (2007). They argued (in agreement with Dawkins (1982)) that selection for global stability is implausible. However, they defined a Probable Homeostatic Gaia model: a planet “with appropriate starting conditions for life will probably generate a biosphere the lifespan of which will be extended, rather than reduced, by life-environment feedback.” In their Probable Homeostatic Gaia model, a “network of life-environment interactions, largely dependent on the by-product effects of evolved traits, leads to global stability.” This biology-based global stability is what we call Gaian regulation. We are invoking its rapid evolution to stabilize the early volatile and thermal instabilities of wet rocky planets.

If Gaian regulation plays the dominant role in maintaining liquid water at the surface (Harding and Margulis, 2010), then the width of the CHZ would depend more on the quirks of biological evolution than on the more deterministic physics and chemistry that can be more easily modeled. For most rocky planets in the CHZ to remain habitable, they may have to be inhabited: “habitability depends on inhabitation and the width of the habitable zone is difficult to characterize” (Goldblatt, 2015).

In Gaian literature, it is usually proposed that Earth became a Gaian planet in the Proterozoic (~2.5 Gya) and has been one ever since (Harding and Margulis, 2010, p.45). We are proposing that the onset of Gaian regulation could have occurred more than a billion years earlier, for example, through the production, consumption, and regulation of greenhouse active gases such as H₂, CO₂, and CH₄. If there is a biotic solution for the faint early Sun paradox (Feulner, 2012; Sagan and Chyba, 1997; Sagan and Mullen, 1972) based on higher concentrations of CO₂, on biotic methanogenesis, or on biotic albedo regulation, then this solution would necessarily have evolved quickly during the transient abiotic HZ (yellow regions in Figure 2.6 B and C) (Haqq-Misra et al., 2008; Pavlov et al., 2003; Rosing, Bird, Sleep and Bjerrum, 2010; Walker, 1985).

2.5 Evaluating the Gaian Bottleneck Hypothesis

After the early heavy bombardment, life emerges with some probability on initially wet rocky planets in the CHZ. However, due to large impacts and unstable abiotic volatile evolution with no tendency to maintain habitability, almost all life goes extinct early – with the rare exceptions of life that has undergone unusually rapid evolution and obtained some level of Gaian regulation. The most significant predictions of this Gaian bottleneck model can be seen in Figure 2.7 by comparing panels A and B, with C. In panels A and B, wherever life emerges, it persists for billions of years. Thus, it has time to evolve complex and perhaps multicellular forms. In panel C, which illustrates the Gaian bottleneck model, almost all emerging life goes extinct rapidly and therefore, does not have time to evolve into more complex forms. However, even planets with Gaian regulation will not be able to

counter indefinitely the increasing luminosity due to stellar evolution (Bloch, Bounama and Franck, 2005; Caldeira and Kasting, 1992; Franck, 2000; Franck, Bloh et al., 2002; Lenton and Bloh, 2001). Hence, the extinction at ~ 6 Gyr in all 3 panels.

If we are able to find well-preserved, ~ 3.8 to ~ 4.3 billion year old rocks on Venus or Mars, then we may be able to identify isotopic anomalies produced by biotic actions, in a way analogous to how $^{12}\text{C}/^{13}\text{C}$ ratios are used to infer the existence of the earliest life in Isua, Greenland (Ohtomo et al., 2014). Whether it evolved independently of life on Earth will be difficult to determine. If we find evidence of extant life on Mars or Venus that had an origin independent of Earth life, then this would be evidence against both the Gaian bottleneck hypothesis and the emergence bottleneck.

The surface temperature and existence of liquid water at, or near, the surface could be predominantly due to Gaian regulation rather than abiotic negative feedback. Liquid water on the surface of the planet (particularly old planets) would then not just be a prerequisite for life but a biosignature (Gorshkov et al., 2004). Existence of liquid water on the surface of a planet may be a better biosignature than oxygen (Luger and Barnes, 2015). Thus, the measurement of exoplanet surface temperatures compatible with liquid water could be an important part of future search for extra-terrestrial life. Remote detection of atmospheric chemical equilibrium may soon develop into a mature science of remote bio-detection (e.g., Krissansen-Totton et al., 2016; Lovelock and Kaplan, 1975). The Gaian bottleneck model predicts that the vast majority of the atmospheres of old terrestrial planets in the traditional abiotic CHZ of their host stars will be in chemical equilibrium because they are uninhabited. Hence, atmospheres in chemical disequilibrium will be rare except for young ($t \lesssim 2$ Gyr) terrestrial planets.

In a critique of Gaian logic, Dawkins (1982, p.236) wrote:

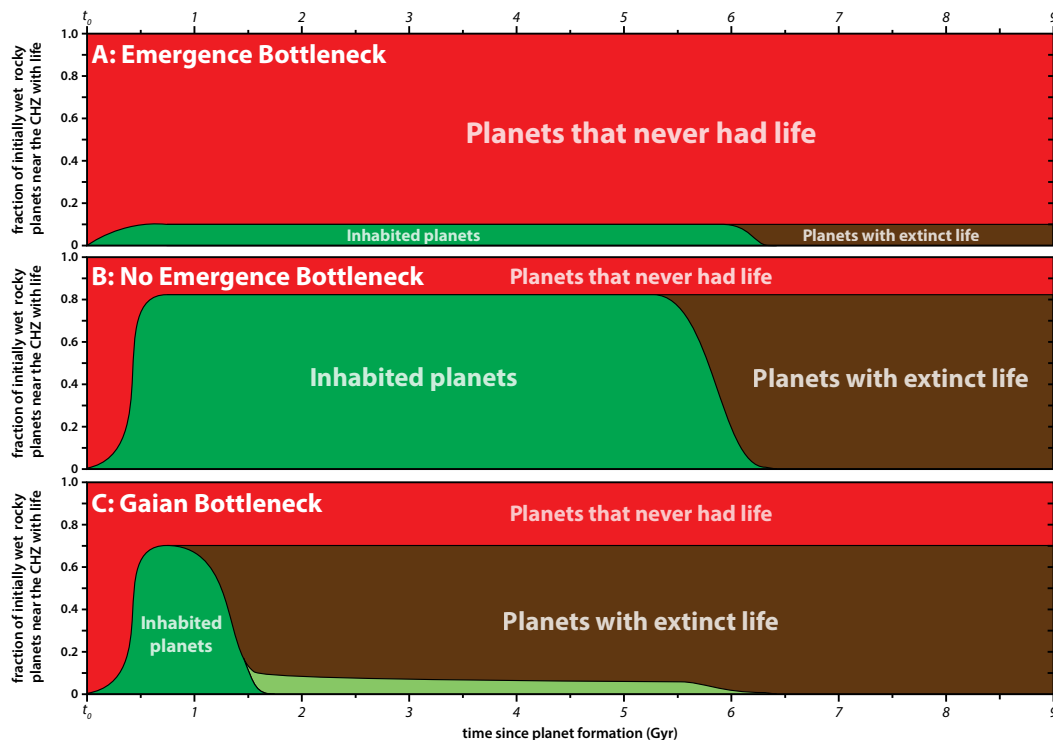


Figure 2.7: Different bottleneck scenarios and their fossil predictions. **A.** Emergence Bottleneck: Life rarely emerges even on wet rocky planets. Few planets will have life or even fossils of extinct life. On the few planets where life does emerge, it persists for billions of years. **B.** No Emergence Bottleneck. Life emerges with high probability and usually persists for billions of years. Thus, life will be abundant on planets throughout the universe. There will be many planets where life persisted for billions of years and then went extinct. On the oldest uninhabited planets, fossils of complex life will be abundant. **C.** Gaian Bottleneck. Life emerges with some probability (possibly quite high), but it goes extinct within a billion years (green). Alternatively, some small fraction of inhabited planets successfully pass through the Gaian bottleneck (light green). The Gaian bottleneck model predicts that the vast majority of the fossils in the universe will be from extinct microbial life.

For the analogy [of the Earth as an organism] to apply strictly, there would have to have been a set of rival Gaias, presumably on different planets. Biospheres which did not develop efficient homeostatic regulation of their planetary atmospheres tended to go extinct. The Universe would have to be full of dead planets whose homeostatic regulation systems had failed, with, dotted around, a handful of successful, well-regulated planets of which the Earth is one”.

What Dawkins describes here is also a prediction of the Gaian bottleneck hypothesis. The Gaian bottleneck model parallels evolution on Earth in that the vast majority (~99.9%) of species that have ever lived are now extinct; the vast majority of planetary life has gone extinct.

In the far future, we may be able to find evidence for biogenic isotopic anomalies on the initially wet rocky planets around most stars. Since life does not persist for long in the Gaian bottleneck model, it predicts a universe filled with isotopic or microscopic fossils from the kind of life that can evolve in ~1 Gyr, not the fossils of larger multicellular eukaryotes or anything else that would take several billion years to evolve.

Cockell (2014) divided all environments in the Universe into three types: (1) uninhabitable, (2) uninhabited habitats or (3) inhabited habitats (Cockell, 2011; Zuluaga et al., 2014). A prediction of the Gaian bottleneck (persistence-is-hard) model is that (2) and (3) will be rare. This is unfortunate for future colonization efforts since uninhabited, but habitable, planets are the most ethically appealing places – autochthonous life would not have to be displaced.

Our search for life beyond Earth may be thwarted by the short time-scales over which planets may remain inhabited. If it takes several billion years to develop radio telescopes, then the Gaian bottleneck ensures that the vast majority of life in the universe is either young and microbial, or extinct. Therefore, the Gaian bottleneck model is consistent with current SETI results and can help resolve the Fermi paradox, although it is not one of the solutions to the paradox listed by Webb (2002).

2.6 What could be wrong with our argument?

1. Gaian regulation is a controversial idea. It is usually invoked to explain the long-term stability of the surface temperature of Earth, starting in the Proterozoic (~ 2.5 Gya). So invoking early, pre-Proterozoic Gaia is even more controversial.
2. If estimates of sub-aerial continental crust (e. g. , by [Flament et al., 2008](#)) are significantly too low and there was abundant sub-aerial crust earlier than ~ 3.8 Gya (e. g. , [Van Kranendonk, 2010](#)), then abiotic negative feedback based on the carbonate-silicate cycle could have stabilized surface temperatures very early in Earth's history, without Gaian regulation. If early continent formation is a common feature of rocky planets, then invoking Gaian regulation may be unnecessary to explain Earth's early thermal stability.
3. We are arguing that:
 - (a) Gaian regulation evolved on Earth.
 - (b) The evolution of Gaian regulation is not common.

This could seem paradoxical, because to justify (a), we have presented arguments making the emergence of Gaian regulation plausible. These same arguments could suggest that Gaian regulation would be common. However, there is a large class of phenomena that did happen on Earth, that are uncommon or non-existent elsewhere. We can trace the evolution of these phenomena and explain how they evolved on Earth, but these explanations cannot be generalized. For example, the evolution of the English language can be traced and understood and made plausible, but this plausibility cannot be turned into a generic argument for the evolution of English on other planets. Human-like intelligence may be another member of this class ([Lineweaver, 2008](#)). We are suggesting that the evolution of a kind of life that can quickly and effectively regulate the volatiles on the surface of the planet on which it finds itself, may be a quirky product of the biological evolution of life on early Earth.

4. Why should Gaian regulation be rare? [Franck, Block et al. \(2001\)](#); [Franck, Bloh et al. \(2002\)](#) concluded that there are $\sim 500,000$ "sister Gaias" in the Milky Way galaxy but then listed a number of physical factors (e. g. , those discussed by [Ward and Brownlee, 2000](#)) that could reduce this estimate.
5. It could be that early heavy impacts almost always extinguish life and don't need any help from subsequent volatile evolution away from habitability. In which case, Gaian regulation would have nothing to do with life's early or late extinction. Evidence for this would be an anomalously low impact rate on Earth (compared to the early impact rates on other wet rocky planets). If this were the case, there would be no tendency for life to evolve and regulate its environment. In this context, [Tyrrell \(2013\)](#) suggested that "Lucky Gaia" as described by [Free and Barton \(2007\)](#), and the anthropic principle provide a better explanation for the continued habitability of Earth than "Probable Gaia," which we assume here.

If the probability of the emergence and persistence of life on wet rocky planets were infinitesimally small and there were only one life-harboring planet in the Universe, we would, of necessity, find ourselves on that planet. Therefore, our mere existence cannot be used to infer the probability of life elsewhere. Additionally, invoking a scenario in which persistent life on Earth is exceptional compared to other planets (as we do here) cannot be criticized with an argument such as: if Gaian regulation is rare, then we shouldn't be here. Self-selection overcomes this critique.

6. One argument against early Gaian regulation is that the unit of biological selection starts small and moves to larger groups as in the chronological sequence: genes, chromosomes, single cells, colonies of cells (bacterial mats), multicellular organisms, colonies of multicellular organisms (superorganisms), ecosystems of various sizes (which produce Gaian regulation only when they are widespread). In this sequence, the evolution of Gaian regulation happens last. However, among the earliest life forms we know of, stromatolites were already ecosystems of bacterial mats ([Walter et al., 1992](#)).
7. The universe does not seem to be teeming with life. This could be an observational selection effect: it is teeming with life but we just haven't been able to detect it yet. Even in the future

when the remote detection of biosignatures is possible, it will be difficult to detect subsurface life (Boston et al., 1992; Gaidos, Nealson et al., 1999; Jones, Lineweaver and Clarke, 2011; McMahon et al., 2013) that does not interact with the planet's atmosphere and is completely sustained by free energy based on geochemical disequilibrium. This would undermine some of the motivation for the Gaian bottleneck model but not the other arguments presented here.

2.7 Conclusion

We are proposing a potentially universal sequence of events on initially wet rocky planets that can be summarized thusly:

First ~0.5 Gyr: Hot, high bombardment, uninhabitable.

~0.5 to ~1.0 Gyr: Cooler, reduced bombardment, continuous volatile loss.

~0.5 to ~1.0 Gyr: Emergence of life in an environment with a tendency to evolve away from habitability

~1.0 to ~1.5 Gyr: Inability to maintain habitability, followed by extinction. As a rare alternative, this period would experience the rapid evolution of Gaian regulation and the maintenance of habitability, followed by the persistence of life for several billion more years.

Between the early heat pulses, freezing, volatile content variation, and runaway positive feedbacks, maintaining life on an initially wet rocky planet in the habitable zone may be like trying to ride a wild bull. Most life falls off. Life may be rare in the universe, not because it is difficult to get started, but because habitable environments are difficult to maintain during the first billion years.

In the book *Vital Dust*, De Duve (1995) presented the case that water and energy are common and abiogenesis may be a cosmic imperative. The most important constraint on the existence of life in the universe may be whether life, after emerging and evolving into a biosphere, can evolve global mechanisms rapidly enough to mediate the positive and negative feedbacks of abiotic atmospheric evolution. We hypothesize that the early evolution of biologically mediated negative feedback processes, or Gaian regulation as proposed by Lovelock and Margulis (1974), may be necessary to maintain habitability because of the strength, rapidity, and universality of abiotic positive feedbacks on the surfaces of rocky planets in traditional CHZs.

We argue that the habitable surface environments of rocky planets usually become uninhabitable due to abiotic runaway positive feedback mechanisms involving surface temperature, albedo, and the loss of atmospheric volatiles. Because of the strength, rapidity, and universality of abiotic positive feedbacks in the atmospheres of rocky planets in traditional CHZs, biotic negative feedback or Gaian regulation may be necessary to maintain habitability.

The evolution of biospheric regulation of surface volatiles, temperature, and albedo can become a Gaian bottleneck to the persistence of life. This Gaian bottleneck may be a better explanation for the non-prevalence of life than the traditional emergence bottleneck paradigm.

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Appendix A

Codes

A.1 Python models

Example to check whether an integer is a prime number or not using for loop and if...else statement.

A positive integer greater than 1 which has no other factors except 1 and the number itself is called a prime number. 2, 3, 5, 7 etc. are prime numbers as they do not have any other factors.

```
1  # To take input from the user
2  #num = int(input("Enter a number: "))
3
4  # define a flag variable
5  flag = False
6
7  # prime numbers are greater than 1
8  if num > 1:
9      # check for factors
10     for i in range(2, num):
11         if (num % i) == 0:
12             # if factor is found, set flag to True
13             flag = True
14             # break out of loop
15             break
16
17 # check if flag is True
18 if flag:
19     print(num, "is not a prime number")
20 else:
21     print(num, "is a prime number")
```

Model A.1.1: Python Program to Check Prime Number