Habitability

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Why this lecture

- Habitability is a widely used word in the geoscience, planetary science, and astrobiology literature, but what does it mean?
- Defining habitability sets the stage for the search of life outside the Earth.

Goals for today

- Define habitability.
- Describe conditions that influence habitability on Earth and on other planets.

Definition of habitability

- The ability of an environment to support the activity of at least one known organism.
- Environments such as entire planets might be capable of supporting more or less species diversity or biomass compared with that of Earth
- Instantaneous habitability: the conditions at any given time in a given environment required to sustain the activity of at least one known organism
- Continuous planetary habitability: the capacity of a planetary body to sustain habitable conditions on some areas of its surface or within its interior over geological timescales

Understanding habitability

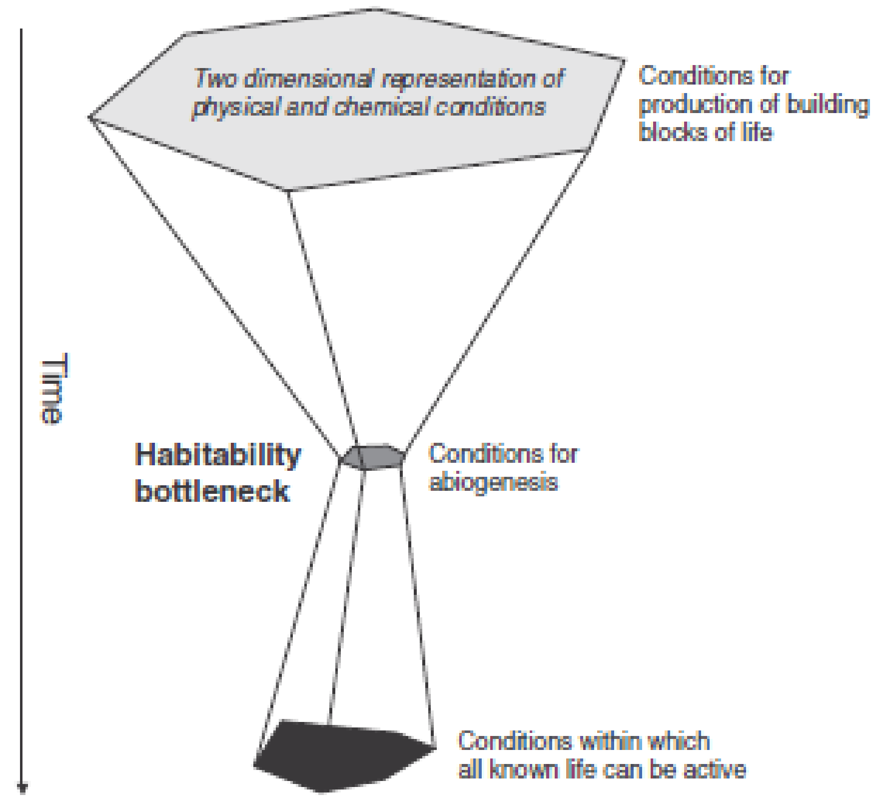
- Define the basic requirements for life to be metabolically active or to reproduce in planetary environments
- Describe processes that might be required for these conditions to be sustained over geological periods within the lifetimes of planetary bodies
- Habitable environments do not need to contain life
- Decoupling of habitability and the presence of life may be rare on Earth, but it may be important for understanding the habitability of other planetary bodies

What is a habitat?

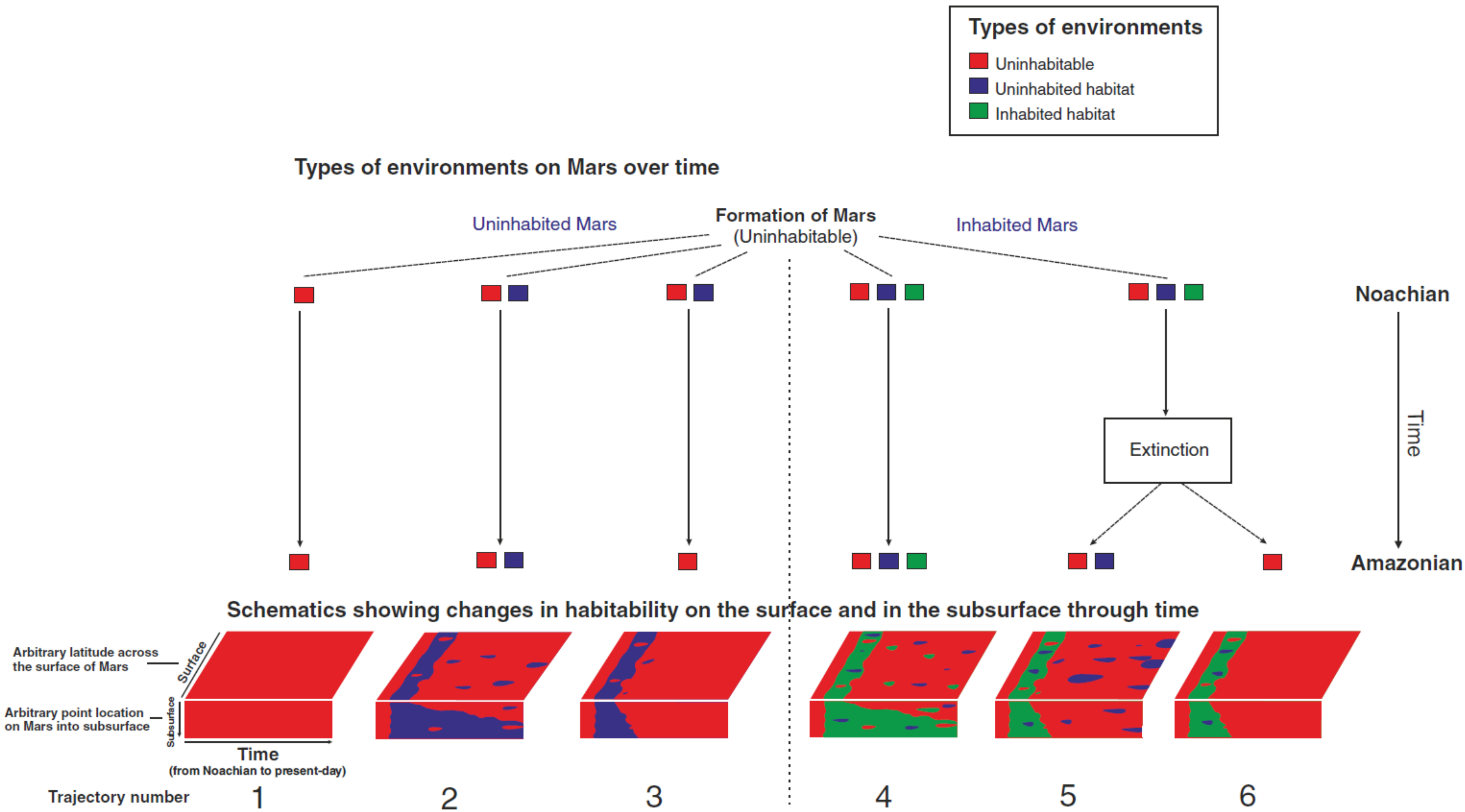
- "A habitat is the physical location of an organism" (Odum, 1971)
- "A habitat is the range of environments or communities over which a species occurs" (Whittaker et al., 1973)
- "A habitat is the subset of physical environmental factors that a species requires for its survival and reproduction" (Block and Brennan, 1993)
- "A habitat is the resources and conditions present in an area that produce occupancy - including survival and reproduction - by a given organism" (Hall et al., 1997)
- Life can change the habitable space for other life-forms (example: large-scale oxygenation of a planetary atmosphere)

Habitability and life

- We do not know whether terrestrial life represents a universal norm
- Constraining habitability to known life, we avoid the term becoming inextricably linked to the problem of defining life
- The physical and chemical conditions required to produce the building blocks of life are broader than the conditions for abiogenesis, which are presumed to be narrower than the total physical and chemical space that can be occupied by all life



Habitability without life?

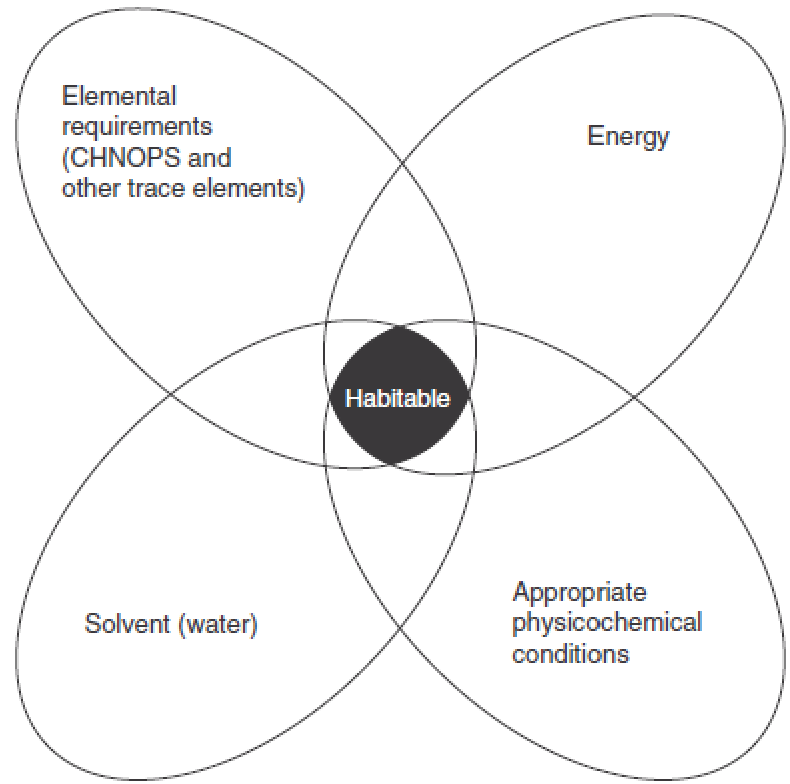


Instantaneous habitability

- At an instant in time in a particular location, a set of requirements for all known organisms to be active can be identified:

1. A solvent.
2. Appropriate temperature conditions and other physicochemical conditions (such as water activity).
3. Available energy.
4. Major elements required by all known life (CHNOPS).
5. Other elements required by a specific organism.

- These requirements can be assessed for any given environment or planetary body
- For an environment to be habitable, they must be present and co-located at the scale of the organism



1. A solvent

- Liquid water is the solvent required for biochemical reactions to occur.
- At the current time it is the only compound known to be used by life as the primary biochemical solvent.
- There have been speculations about the use of liquid ammonia, organic solvents (such as methane and ethane), formamide, and even sulfuric acid.
- For liquid water to be present in any location at a given time, there must be environmental conditions of temperature, pressure, and chemical impurities that allow water to fall within the liquid phase space determined by the equation of state.

2. Appropriate temperature conditions and other physicochemical conditions

- The lower limit for metabolic activity in microbes is thought to be -25°C
- No convincing evidence for reproduction has been demonstrated below -15°C
- Eutectic solutions of perchlorates have theoretical freezing points down to -65°C
- The current upper limit for microbial growth is 122°C
- Chemical reaction rates (including destructive processes) increase exponentially with temperature according to the Arrhenius equation
- A point will reached when destruction of cellular structures and noncovalent interactions caused by thermal energy exceeds the energy that can be used by an organism to repair damage
- This limit may be something on the order of 140-150°C
- Liquid water can exist at greater than 300°C at pressures exceeding 10 MPa
- Life has been found growing in extremes of different physical and chemical stressors, such as ionizing and UV radiation, pressure, pH, salinity, aridity, and toxic metals.
- The absolute limits for many of these stressors are not fully known.

Breaking news

nature ecology & evolution

Article | Published: 28 October 2019

Hyperdiverse archaea near life limits at the polyextreme geothermal Dallol area

Jodie Belilla, David Moreira, Ludwig Jardillier, Guillaume Reboul, Karim Benzerara, José M. López-García, Paola Bertolino, Ana I. López-Archilla & Purificación López-García

Nature Ecology & Evolution **3**, 1552–1561(2019) | Cite this article

Abstract

Microbial life has adapted to various individual extreme conditions; yet, organisms simultaneously adapted to very low pH, high salt and high temperature are unknown. We combined environmental 16S/18S ribosomal RNA gene metabarcoding, cultural approaches, fluorescence-activated cell sorting, scanning electron microscopy and chemical analyses to study samples along such unique polyextreme gradients in the Dallol–Danakil area in Ethiopia. We identified two physicochemical barriers to life in the presence of surface liquid water defined by (1) high chaotropicity–low water activity in Mg^{2+}/Ca^{2+}-dominated brines and (2) hyperacidity–salt combinations (pH ~0/NaCl-dominated salt saturation). When detected, life was dominated by highly diverse ultrasmall archaea that were widely distributed across phyla with and without previously known halophilic members. We hypothesize that a

3. Available energy

- The process of using chemical energy from redox processes is named chemotrophy
- If the energy is obtained by using inorganic electron donors, it is designated chemolithotrophy.
- If the energy is obtained from organic compounds as the electron donor, it is designated chemoorganotrophy (chemoheterotrophy)
- If the organisms use sunlight as energy source, it is designated phototrophy.
- The energy-yielding process in life involves the formation of a proton gradient across a membrane, which in turn is generated by electron transport.
- An electron is transferred from a donor element or molecule to an acceptor element or molecule with or without the help of energy available in light.
- The movement of an electron through the electron transport chain drives the pumping of protons across a cell membrane, thus producing a proton gradient, or proton motive force, which can be used to do work.
- For an environment to have sufficient energy to make it habitable, there must be sufficient electron donors and acceptors thermodynamically favorable to the organism, or sufficient light (the energy supply), to generate sufficient energy for the organism to carry out the activities it requires (maintenance, growth, or survival).
- The energy supply available from a given redox couple can be calculated as a Gibbs free energy based on chemical considerations, although in reality this calculation may be difficult.

4. Major and trace elements

- Of all the elements in the Periodic Table, six are ubiquitous in the macromolecules of known life: C, H, N, O, P, and S.
- Carbon is required as the core element in a vast variety of macromolecules.
- Hydrogen is covalently linked to carbon and other atoms in macromolecules.
- Nitrogen is similarly to be found, particularly in the linkages of long-chained molecules such as proteins and in the base pairs of DNA.
- Oxygen is used in alcohols, sugars, and a variety of molecules.
- Phosphorus forms part of the backbone of DNA and is used in energy-rich molecules such as ATP.
- Sulfur is used in protein bridges and a variety of iron-sulfur clusters in molecules involved in energy acquisition.
- A variety of other elements, such as magnesium and even tungsten (in anaerobic taxa), are used by different organisms for different functions.
- Their concentrations are determined by planetary conditions.
- The forms in which some of these elements are available are also forms that can be used as electron donors or acceptors in energy acquisition.
- Therefore, there is a tight coupling, particularly in the microbial domains of life, between habitability with respect to the availability of CHNOPS and redox couples for energy acquisition.
- The detection of diverse chemical compounds and elements on other planetary bodies allows for the link between CHNOPS elements and energy availability to be used in an assessment of the habitability of other planetary bodies.

A Planetary Habitability Table for Earth

Requirement		*Comments and references*
Liquid water	Oceans, seas, and bays: 1,338,000,000 km^3 (96.54%) Groundwater (fresh): 10,530,000 km^3 (0.76%) Groundwater (saline): 12,870,000 km^3 (0.93%) Lakes (fresh): 91,000 km^3 (0.007%) Lakes (saline): 85,400 km^3 (0.007%) Swamp water: 11,470 km^3 (0.0008%) Rivers: 1,120 km^3 (0.0001%)	Source: Shiklomanov, 1993
Main elements		Plate tectonics and atmospheric photochemical processes continuously supply substrates and remove products (Falkowski *et al.*, 2008)
C	CO_2, CO, bicarbonates, organic compounds	
H	H_2O, H_2, organic compounds	
N	NH_3, NO_3^-, N_2, NO_2^-, NO, organic N-species	
O	O_2, H_2O, H_2O_2, oxides, organic compounds	
P	PO_4^{3-}, ATP, phosphite, phosphides, organic P-species	
S	S, $S_2O_3^{2-}$, S_3O_6, H_2S, SO_4^{2-}, organic S-species, metal sulfides (FeS, CuS, ZnS, NiS, etc.)	
Other elements	Igneous, metamorphic, and sedimentary rocks. These rocks provide all stable elements in the periodic table.	

Energy—full redox couples[a]	*Electron donor*	*Electron acceptor*	Kim and Gadd, 2008
Chemolithotrophy			
Methanogenesis, acetogenesis	H_2	CO_2	
H_2 oxidation	H_2	O_2, SO_4^{2-}, Fe^{3+}	Sulfate and iron reduction, other variable valence-state metals
Phosphite oxidation	HPO_3^{2-}	SO_4^{2-}	Oxidation of phosphite is coupled with reduction of sulfate
Oxidation of reduced S-species	H_2S, S, $S_2O_3^{2-}$	O_2, nitrate, Fe^{3+}	
Ammonia oxidation	NH_3	O_2	
Nitrite oxidation	NO_2^-	O_2	
Anoxic ammonium oxidation (AAM)	NH_4^+	NO_2^-	
Fe oxidation	Fe^{2+}	O_2, nitrate, perchlorate	
Mn oxidation	Mn^{2+}	O_2	
Methylotrophy	Methane, CO, C1 compounds	O_2	
Trace metal and metalloid oxidations	Various valence states of metals and metalloid, *e.g.*, U, Se, Cr, Co, As, Tc, V	O_2	
Chemoorganotrophy			
Aerobic respiration	Organics	O_2	
Fe and sulfate reduction	Organics	SO_4^{2-}, Fe^{3+}	
Nitrate reduction	Organics	NO_3^-	
Trace metal and metalloid reductions	Organics	Various valence states of metals and metalloid, *e.g.*, U, Se, Cr, Co, As, Tc, V	
Perchlorate reduction	Organics	ClO_4^-	
Methanogenesis	Formate, methanol, acetate, methylamines, carbon monoxide, ethanol, 2-propanol, 2-butanol, ketones, dimethyl sulfide	CO_2	Anaerobic respiration; methylotrophic methanogens use compounds such as methanol and methylamines, aceticlastic methanogens use acetate.

Requirement			*Comments and references*
Homoacetogenesis	Methanol, 2,3-butanediol, ethylene glycol, phenylmethylether, sugars, lactate, methodylated aromatics, butanol ethanol, glycerol, betaine, trihydroxybenzenes, trimethoxybenzoate, pyruvate, malonate, vanillate	CO_2	Anaerobic respiration
Dehalorespiration[b]	H_2, formate, pyruvate, lactate, acetate	SO_4^{2-}, NO_4^{3-}, chloroethene, 2,4,6-TCP, PCE, PCP, TCE, 3-CB, 2-CP, 2,6-DCP, DCE	Anaerobic respiration
Other forms of energy			
Microbial fermentations	Alcoholic, homolactic, heterolactic, propionic acid, mixed acid, butyric, butanol, caproic acid, homoacetogenic, methanogenic; acetylene, glycerine, resorcinol, phloroglucinol, putrescine, citric acid, aconitate, glyoxylate, succinic acid, oxalic acid, malonic acid, benzoic acid		
Anoxygenic photosynthesis	H_2O, Fe^{3+}, S, H_2, H_2S, organics		Photosynthesis is divided into anoxygenic and oxygenic photosynthesis. During the latter O_2 is generated

Continuous Planetary Habitability

What conditions are required for at least part of a planetary body to have instantaneous habitability over geological timescales?

- Water: surface liquid water worlds and interior liquid water worlds
- Available energy
- Major elements
- Other elements

Surface liquid water worlds and interior liquid water worlds

- The distribution of liquid water can be used to recognize two types of planetary bodies
- The first type is a planet with liquid water on its surface as well as in its interior
- The liquid is sustained from a combination of internal heating and stellar energy
- The latter in most cases will be the dominant form of energy for keeping water on the surface in a liquid state
- These are "surface liquid water worlds", Earth is an example
- The second type of planetary body is one where stellar radiation is not sufficient to maintain surface liquid water but where liquid water exists in the interior. These are "interior liquid water worlds"
- This type of planetary body includes icy moons with subsurface oceans (Enceladus, Europa, and Ganymede) and some terrestrial-type rocky planets where stellar flux alone is not sufficient to maintain liquid water (on the surface), but internal sources of energy maintain liquid water
- Isolated lone planets in interstellar space have also been suggested as locations for liquid water

Surface liquid water worlds vs. interior liquid water worlds

- In the case of surface liquid water worlds, the presence of liquid water may occur spatially co-located with the presence of light, thus allowing for photosynthesis.
- If the emergence of multicellularity and intelligence is linked to the presence of high concentrations of oxygen from oxygen photosynthesis that allows for aerobic respiration, then these worlds may be the only type capable of producing the conditions for instantaneous and continuous planetary habitability required by intelligent organisms.
- By contrast, interior liquid water worlds may have habitable conditions for a range of metabolisms but not conditions for photosynthesis.
- Some calculations, however, suggest that production of surface oxidants, if cycled into the interior, could lead to sub-oceanic oxygen concentrations as high as terrestrial surface waters.
- It is unknown whether such a scenario could support multicellular life, let alone intelligence.

Appropriate temperature conditions for surface liquid water worlds

- Maintaining temperatures within the range required for biological activity on the surface of a planet depends on a sufficiently powerful greenhouse forcing.
- If the effective temperature of a planetary surface exceeds certain values, set by the energy received from its star and the greenhouse effect caused by the gases present in its atmosphere, then the water on the planet will evaporate at sufficient levels to supply the upper atmosphere with a moist greenhouse effect.
- As the moist greenhouse becomes more effective at raising the temperature, a positive feedback may develop between the increasing levels of atmospheric humidity, the surface temperature, and rates of evapotranspiration.
- The moist greenhouse may eventually result in a runaway greenhouse effect.
- As observed on Venus, a runaway greenhouse will cause all loss of water from the planet, making it uninhabitable.
- The moist and runaway greenhouse effects therefore define an orbit that is too close to the star for liquid water to be sustained on the surface of a planet.

Appropriate temperature conditions for surface liquid water worlds (2)

- A planet too far from a star will suffer the effects that the carbon dioxide in the atmosphere can condense onto the surface, reducing the concentration of this greenhouse gas and contributing to low temperatures, resulting in a frozen surface.

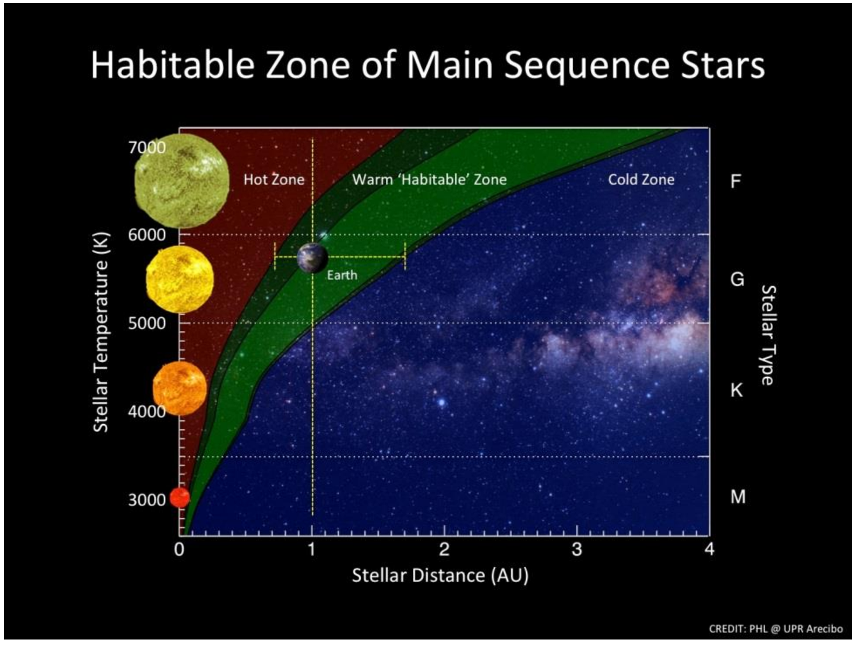
- If CO_2 is abundant enough, scattering can contribute to ineffective heating of the surface.

- This in itself will depend on the quantity of CO_2 outgassed by the planet, linking habitability to planetary interior structure.

- These conditions define an outer limit for habitability, with the boundary conditions for life additionally depending on the star type.

The circumstellar habitable zone

- Hot stars, such as F stars, have boundary conditions for surface liquid water farther from the star compared to our own Sun (a G star). Cooler low-mass stars, such as K and M stars, have boundary conditions closer in.
- The outer limit of the habitable zone may be considerably extended on planets with strong greenhouse gases such as hydrogen, which theoretically could expand the outer limit to 10 AU.
- In extreme cases, free-floating planets not gravitationally bound to a star may even harbor surface habitable conditions.
- In binary star systems, the presence of a second star can influence the habitable zone boundaries.
- Depending on the dynamics of the system, the boundaries can vary over time as a result of the gravitational interactions of the two stars, or a bright second star can cause the boundaries to be further out than they would in a single star system.



Habitable lifetime

- As a star’s luminosity changes over time, generally increasing (a consequence of hydrogen burning on the main sequence), the habitable zone will move outward.
- Integrated over time, there is therefore a narrower band, the continuously habitable zone, within which conditions for surface liquid water are met.
- As the boundaries of the habitable zone move outward, a planet can eventually cross the inner boundary, and surface temperatures will become too great to sustain liquid water.
- Therefore, a planet remains in the habitable zone for a given length of time, known as its "habitable lifetime".
- This lifetime largely depends on stellar mass (but the physical properties of a planet and its atmosphere play a role).
- The more massive a main sequence star, the faster it burns through its hydrogen fuel supply, causing a more rapid increase in its luminosity.
- This pushes the habitable zone boundaries outward at a greater rate.

Appropriate temperature conditions for interior liquid water worlds

- There could be planets with insufficient atmospheric conditions (or no appreciable atmosphere) to sustain surface liquid water but a sufficient internal source of energy to generate liquid water within the interior.
- This source of energy raises the possibility of planets outside the habitable zone with habitable conditions.
- In the case of icy moons, if a body has an eccentricity, obliquity, and/or nonsynchronous rotation state, then tidal effects can heat the interior. These conditions can melt internal ice over geological time periods.
- This phenomenon is inferred from the observations of water plumes emanating from Enceladus and inferred for the three Galilean moons Europa, Ganymede, and Callisto based on induced magnetic fields and thermodynamic calculations
- Tidal interactions enable liquid water to exist, but it remains unknown whether the other factors required for instantaneous habitability to exist and for these requirements to persist are met in these subsurface water bodies.
- What is crucial is whether the body of water is in contact with the surface or a subsurface core.
- From the surface, meteoritic matter, such as organics and various cations and anions, or other matter, such as radiation-produced oxygen and other oxidants, has a chance of being entrained within the ocean.
- In the subsurface, contact with a rocky core could provide cations and anions, which, as for the surface, may include not only required elements for growth but diverse half reactions required for energetic redox reactions such as iron and sulfate reduction and methanogenesis.

Major elements

- Carbon may always be available as CO_2 in an atmosphere throughout most of the lifetime of a terrestrial-type planet.
- The long-term presence of hydrogen depends on its source. Serpentinization reactions (e.g., the reaction of the mineral fayalite with water) producing H_2 cannot be sustained over geological time periods unless there is geological activity to sustain water flow through the crust.
- Hydrogen can be obtained from organic molecules which could be endogenously produced by Urey-Miller-type reactions.
- Hydrogen could also be obtained from diverse carbon compounds in meteoritic material.
- Hydrogen is also pervasively present in water, the latter being required for habitable conditions to exist in the first place.
- Nitrogen is present in the atmospheres of Venus (3.5%), Earth (78.1%), and Mars (1.9%).
- An environment can be habitable if it contains N_2 at a partial pressure suitable for biological nitrogen fixation.
- In the absence of biological nitrogen fixation, fixed nitrogen compounds such as ammonia, nitrite, and nitrate must be available.
- Abiotic processes such as impact events, hydrothermal activity, and lightning discharge can generate these compounds.
- On planets with reducing conditions in their interior, nitrogen is expected to be predominantly in the form of ammonia, which is sequestered within silicates.
- In more oxidizing conditions, such as Earth's mantle, the element is in the form of nitrogen gas, which is more readily degassed.

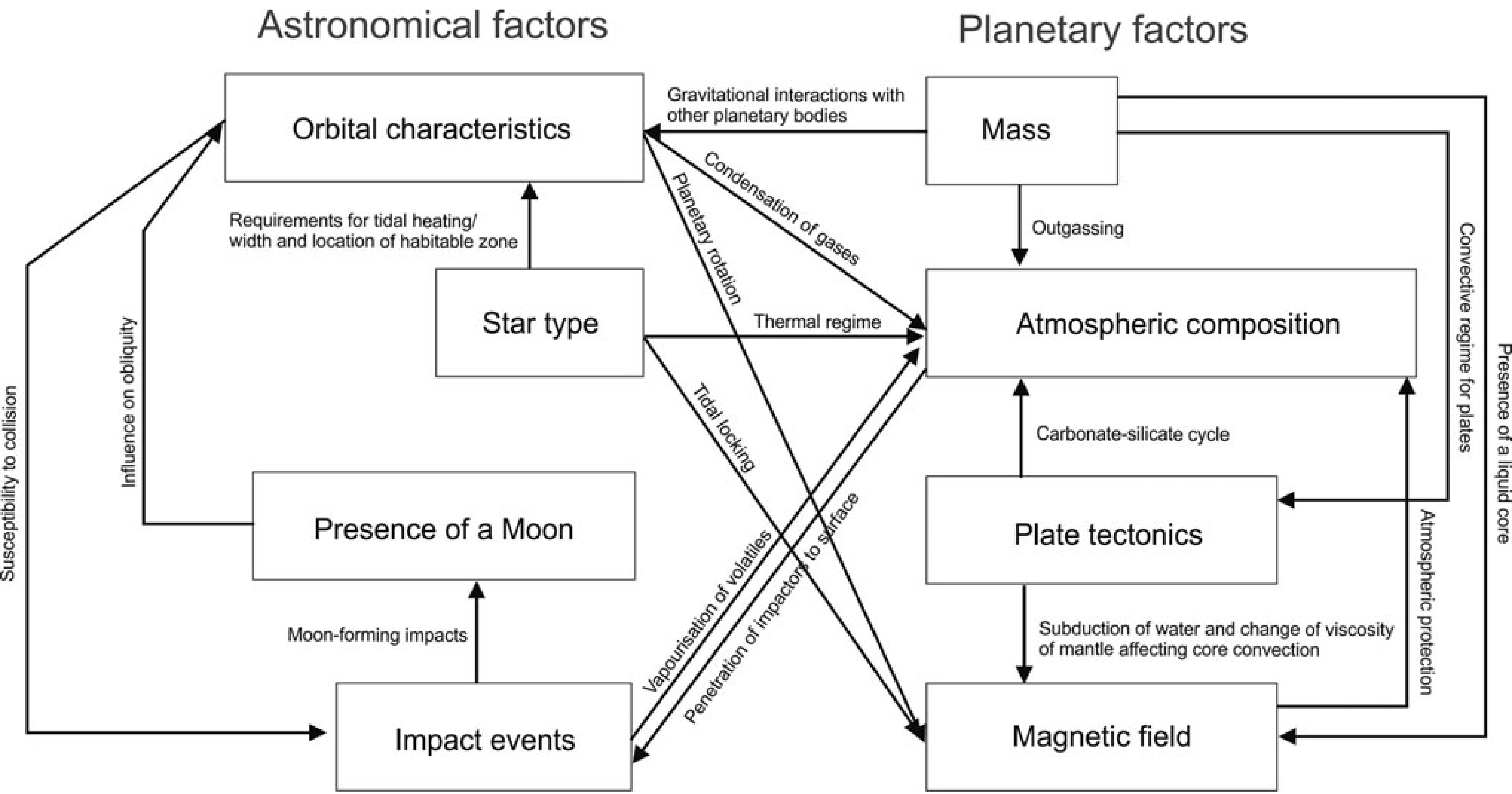
Major elements (2)

- Oxygen is present in a wide diversity of compounds, such as oxides.
- However, many of these atoms, such as oxygen atoms bound to silicon in silicates, are not directly accessible to life.
- Suitable sources of oxygen atoms include compounds such as sulfates and iron oxides found ubiquitously on Earth and on Mars.
- Oxygen exists in water, which is the source of this element for oxygen gas produced in oxygenic photosynthesis.
- Oxygen atoms also exist in organic molecules within, for example, alcohol and carboxylic acid groups.
- As for hydrogen, these organics can be produced endogenously or delivered exogenously.
- On Earth, phosphate is available in igneous rocks as apatite and merrillite and therefore available in other rock types as a consequence of the rock cycle.
- Its detection on Mars illustrates its potentially ubiquitous availability on terrestrial-type rocky planets.
- Phosphorus can also be delivered to the surface of planets in meteoritic material such as in schreibersite.
- Sulfur atoms are available in planetary bodies in diverse sources such as sulfides, sulfates, and compounds of intermediate oxidation state such as thiosulfate.
- The presence of water can enhance the diversity and abundance of these sources of sulfur.

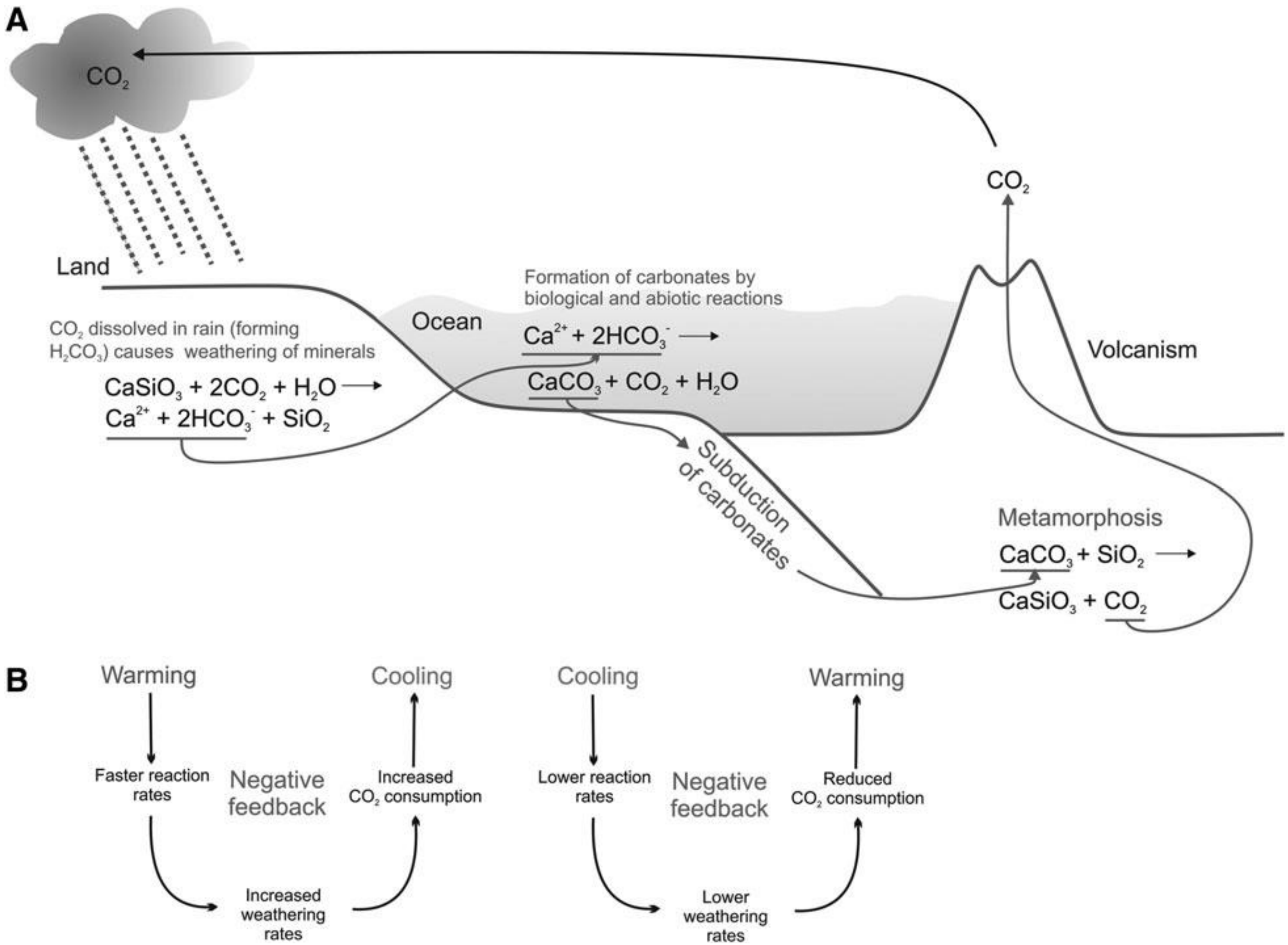
Factors for Continuous Planetary Habitability

Habitability factor	*Example of influence on habitability*
Planetary factors	
Mass	Insufficient mass to retain gases required for greenhouse warming and liquid water.
	Insufficient mass to generate heating for subsurface ocean. Influence on size of internal ocean and thus potential biomass.
Atmospheric composition	Insufficient greenhouse gases for surface liquid water. High concentrations of greenhouse gases lead to runaway greenhouse effect.
	Presence of oxygen for multicellular life.
	Production of reactants for energy and nutrients cycled into deep ocean (even in tenuous atmosphere).
Plate tectonics	Lack of plate tectonics shuts down carbonate-silicate cycle influencing surface temperature and presence of liquid water.
	Plate tectonics may enhance movement of surface material into a deep ocean.
Magnetic field	Insufficient field can result in early loss of atmosphere (*e.g.*, planets close to M stars).
	Strong magnetic field can enhance longevity of atmosphere and hence habitable conditions.
	May generate radicals and other species on the surface of an icy world with implications for energy/nutrients.
Astronomical factors	
Orbital characteristics	Obliquity may not critically determine habitability. Some combinations of orbital characteristics, such as high eccentricity and tidal locking can circularize orbit outside habitable zone.
	Extremity of climatic excursions caused by high eccentricity.
	Lack of tidal heating caused by tidal locking could prevent formation of habitable subsurface water bodies.
	Influences extent of tidal heating
Star type	Can influence early sputtering away of atmosphere.
	Influences longevity of habitable zone.
Presence of a moon	Lack or presence of a moon probably not critical for presence of habitable conditions on a planet but may influence extremity of climatic excursions caused by obliquity variations.
Impact events	Frequent large impacts that sterilize oceans could prevent life emerging. Frequent impacts create selection pressure for high-temperature tolerant/loving organisms or prevent atmospheric oxygen buildup from photosynthesis.
	Impacts may deliver material into subsurface ocean or enhance surface-subsurface exchange of material.

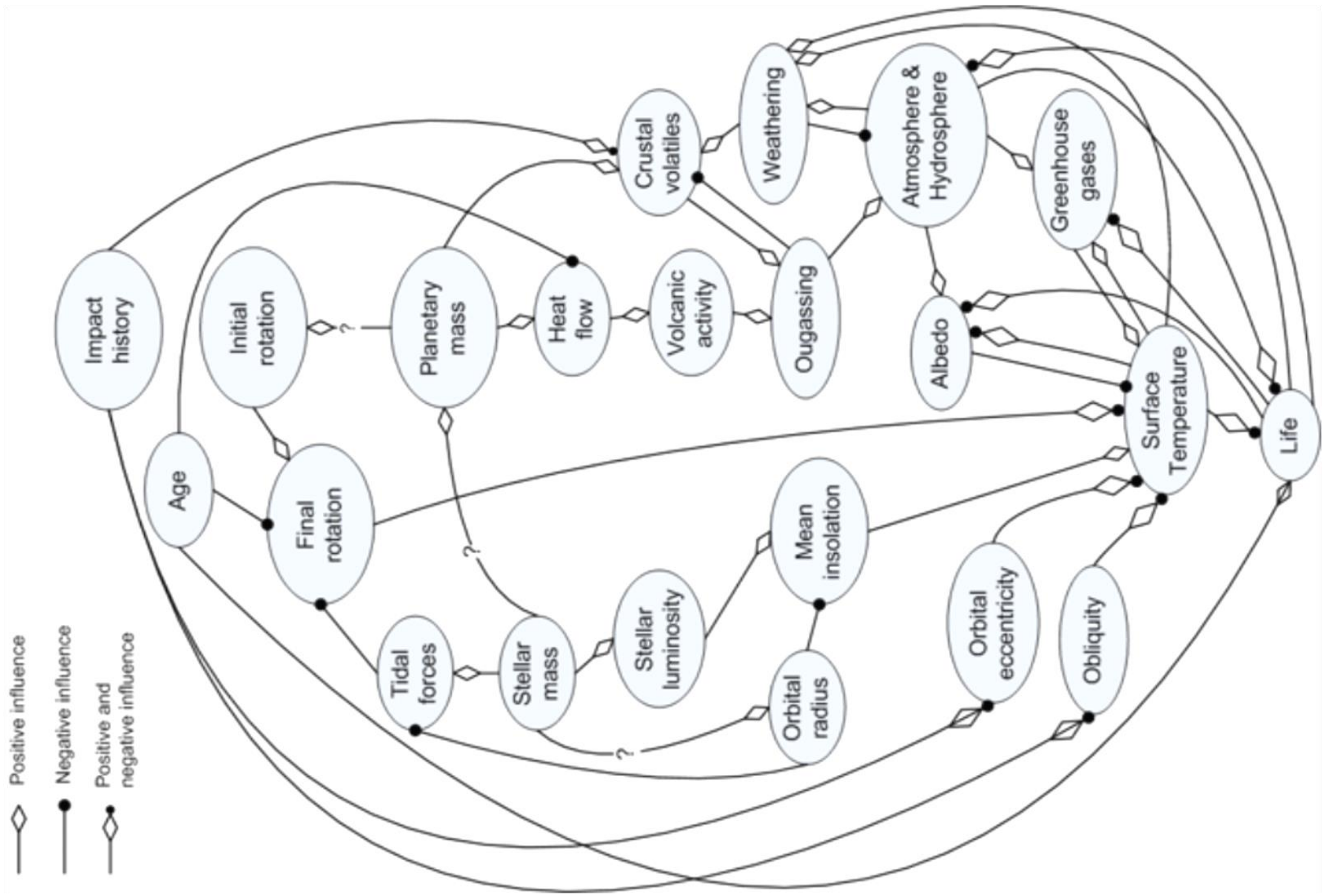
Astronomical and planetary factors and the presence of surface liquid water



The carbonate-silicate cycle

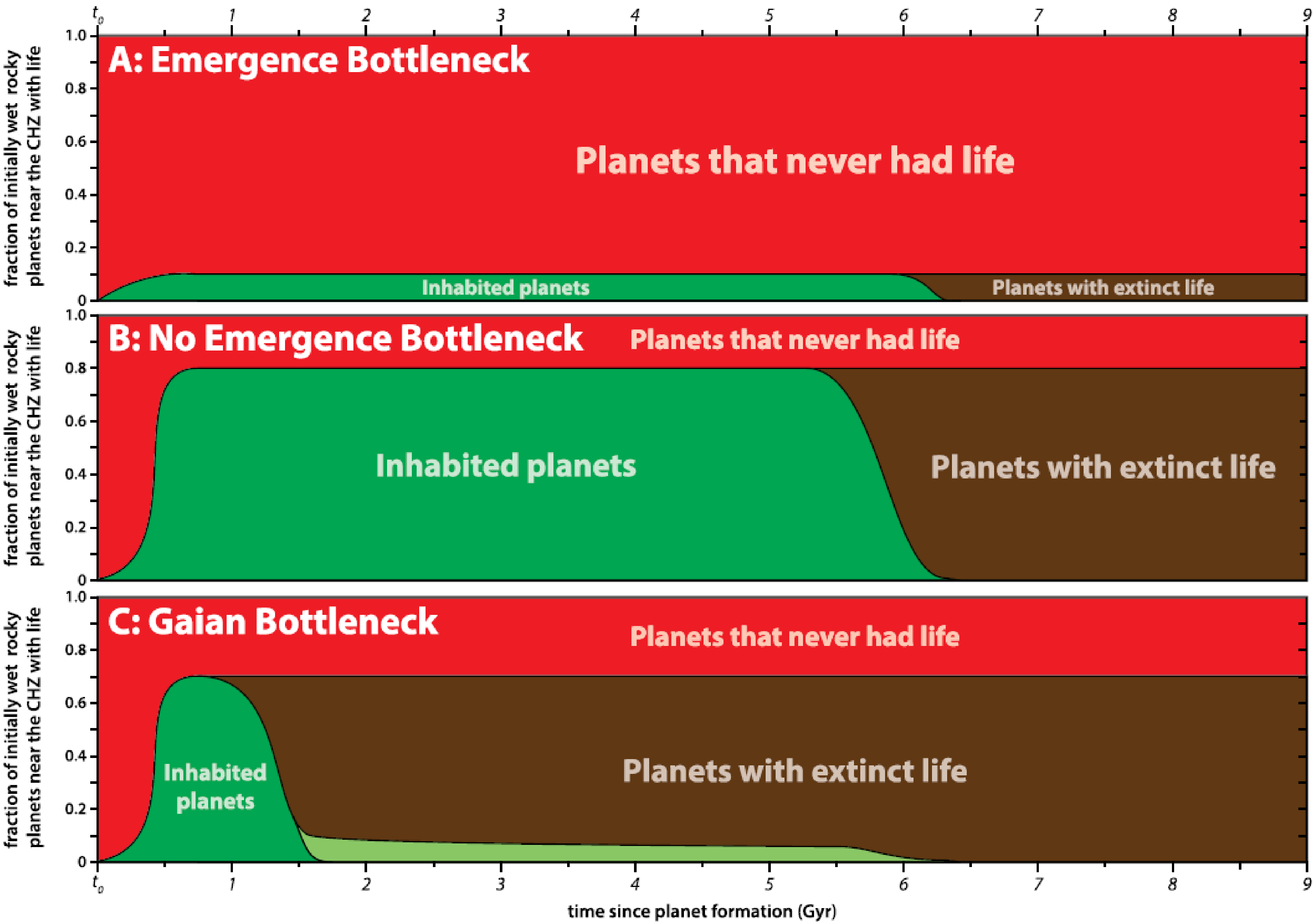


A complex picture



The Gaian bottleneck model

- 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.
- An alternative explanation: 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.



A: Emergence Bottleneck
Planets that never had life
Inhabited planets
Planets with extinct life
B: No Emergence Bottleneck
Planets that never had life
Inhabited planets
Planets with extinct life
C: Gaian Bottleneck
Planets that never had life
Inhabited planets
Planets with extinct life
fraction of initially wet rocky planets near the CHZ with life
time since planet formation (Gyr)
t_0
1
2
3
4
5
6
7
8
9
0
0.2
0.4
0.6
0.8
1.0

Technological Habitability

- Environments at local or planetary scale could be changed from uninhabitable to habitable by technological intervention.
- At the planetary scale, this process is sometimes called terraforming.
- A planet on which such schemes may be viable is Mars.
- There are a number of proposed means by which the surface of the planet could be made habitable.
- The introduction of chlorofluorocarbons (CFCs) or perfluorocarbons (PFCs) into the atmosphere could be used to terraform the planet.
- It would require 40 billion tonnes of CFCs to meet a required warming of 60°C.
- The release of CO_2 to create an atmosphere of 100 mb could make the surface suitable for plants.
- Over 100,000 years, plants would generate O_2, ultimately leading to a potentially human-breathable atmosphere.

Further reading

This presentation is based on the paper

- C.S. Cockell et al. Habitability: A Review. Astrobiology, Volume 16, Number 1, pp. 89-117, 2016.

with material taken from

- https://en.wikipedia.org/wiki/Planetary_habitability