Ancient life as a guide for Alien Earths

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THE KAÇAR LAB
M.U.S.E. METAL UTILIZATION & SELECTION ACROSS EONS
NASA
LIFE FROM EARLY CELLS TO MULTICELLULARITY

their existence. The first widely accepted discovery of an extrasolar planet came in the year 1993, when Dr. Alexander Wolszczan, a radio astronomer at Pennsylvania State University, reported what he called "unambiguous proof" of extrasolar planetary systems. Wolszczan had discovered two or three planet-sized objects orbiting a pulsar, a superdense, rapidly spinning remnant of a star gone supernova. Wolszczan made his discovery by observing regular variations in the pulsar's rapidly pulsing radio signal, indicating the planets' complex gravitational effects on the dead star. The first discovery of a planet orbiting a medium-sized star similar to the sun came in 1995. The Swiss team of Michel Mayor and Didier Queloz announced a discovery of a hot world located close to the star 51 Pegasi. The planet was at least half the mass of Jupiter and no more than twice its mass. It was observed indirectly, using the radial velocity method. By the end of the 20th century, several dozen other exoplanets had been discovered, many the result of years of observation of nearby stars. Significant improvements in spectrometers, telescope sensors and software discerning the fluctuations in starlight and the stellar wobbling motion caused by nearby orbiting planets have enabled an abrupt surge of exoplanet discoveries in the recent years. The French CoRoT mission, launched in 2006, was the first space mission dedicated solely to exoplanets, searching for planets that passed in front of their host stars. It has contributed dozens of confirmed exoplanets to those already discovered, including some of the most well-studied planets outside our solar system. First NASA exoplanet mission, Kepler Space Telescope, launched in 2009 and quickly became the most succesful exoplanet-focused mission in history. Among its many discoveries, Kepler has found several hundred terrestrial planets, some of them in the habitable zones of their stars, many multi-planet solar systems and also numerous hot jupiters of incredibly low density. As it continues its mission, it's likely that Kepler will find even more fascinating exoplanets, some of them possibly harboring life.

Being by far the easiest to discover, gas giant class planets form a large portion of known exoplanets. PSR B1620-26 b, the first exoplanet to be discovered also belongs into this class.

Although both gas planets in the solar system (Saturn and Jupiter) are located in the remote and cold regions, with cloud layers mostly composed of ammonia, most known gas planets belong to the class of "Hot Jupiters". Many of them orbit much closer to their parent stars than the planet Mercury is to the Sun, and their median temperature can reach thousands of kelvins, causing them to have cloud layers composed of alkali metals, silicon or even iron. Such hot gas giants are often also known as "puffy planets", as the intense heat from the star can inflate their atmosphere and decrease their density far below that of Saturn.

For gas giants with atmospheric temperatures similar to those of Jupiter there exists a maximum radius that those planets can attain, slightly larger than that of Jupiter, which occurs when their mass reaches a few Jupiter-masses. Adding any further mass beyond this point causes their radius to shrink and their density to sharply increase. Giant gas giants with over ±10 Jupiter masses are often no longer considered to be planets, but belong to a distinct class of brown dwarfs, also known as "failed stars".

Not all gaseous planets are giants, however, there also exists a class of smaller gaseous planets, called "gas dwarfs". These planets are usually smaller than Neptune, sometimes even smaller than the Earth, and are composed mostly of gaseous matter. Such planets are thought to be quite rare in the universe, occurring only in very distant orbits and in very low-mass stars.

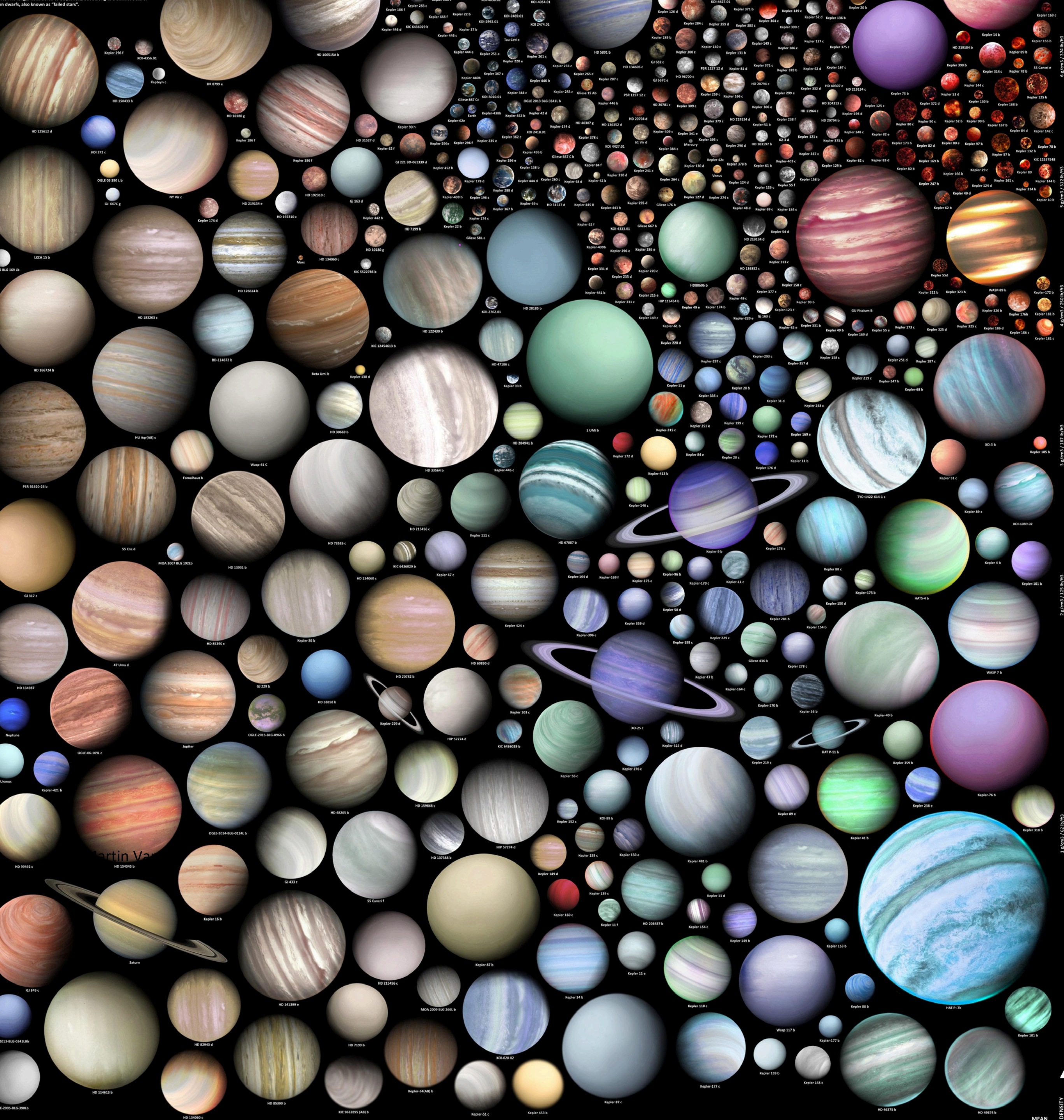
Closest equivalent to a gas dwarf in the solar system would be Saturn's moon Titan, with atmosphere much thicker and heavier than that of Earth. Hypothetical ninth planet of the Solar System that could be located at the edge of the Kuiper Belt might also belong into this class.

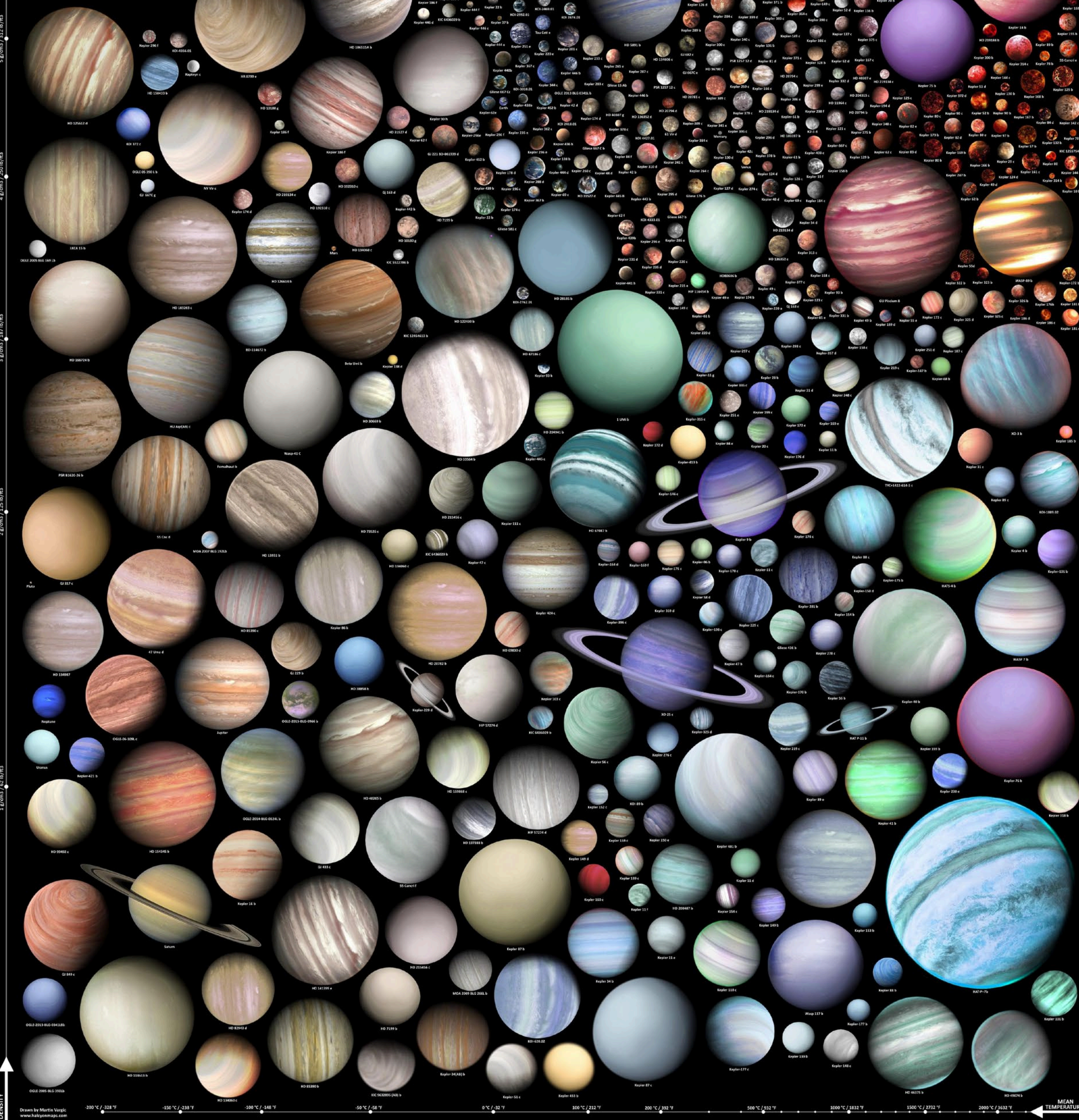
Ice giants are similar to gas giants in that they don't have any solid surface, and are mostly composed of liquids. However, they are not composed mostly of hydrogen and helium, as it is the case with gas giants, but instead of heavier elements, such as oxygen, nitrogen or carbon. Though their upper atmosphere is usually composed of hydrogen and helium, their lower layers are composed mostly of exotic forms of water, ammonia, carbohydrates, carbon dioxide and nitrogen oxides. Similar to gas giants, most ice giants are also presumed to have a large solid core composed of ices and rock.

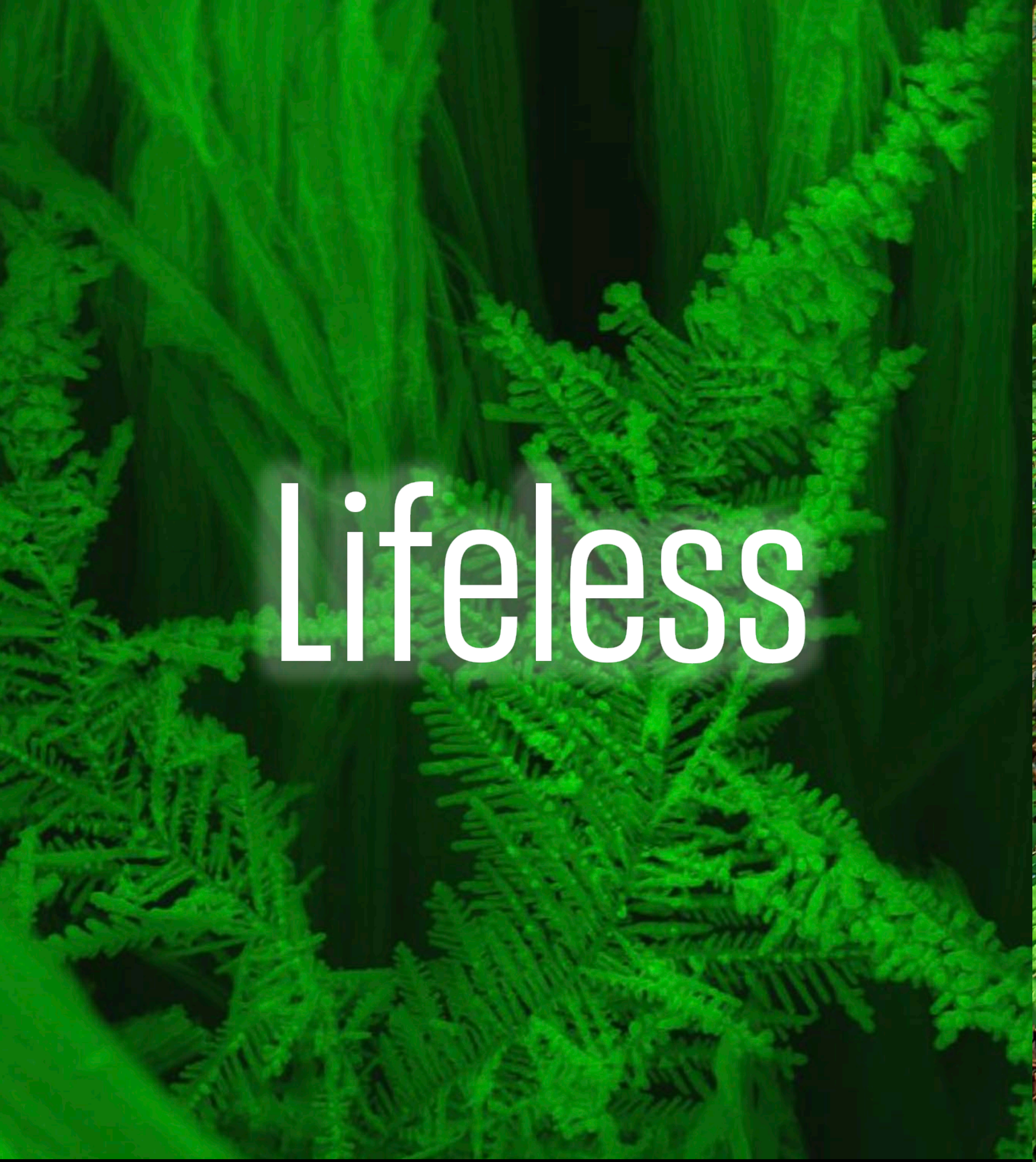
There are two ice giants in the solar system, Uranus and Neptune, however there are probably a lot more orbiting other stars. Most known ice giant exoplanets belong to the class of "hot neptunes", orbiting very close to their parent stars, and their temperature often reaches thousands of kelvins.

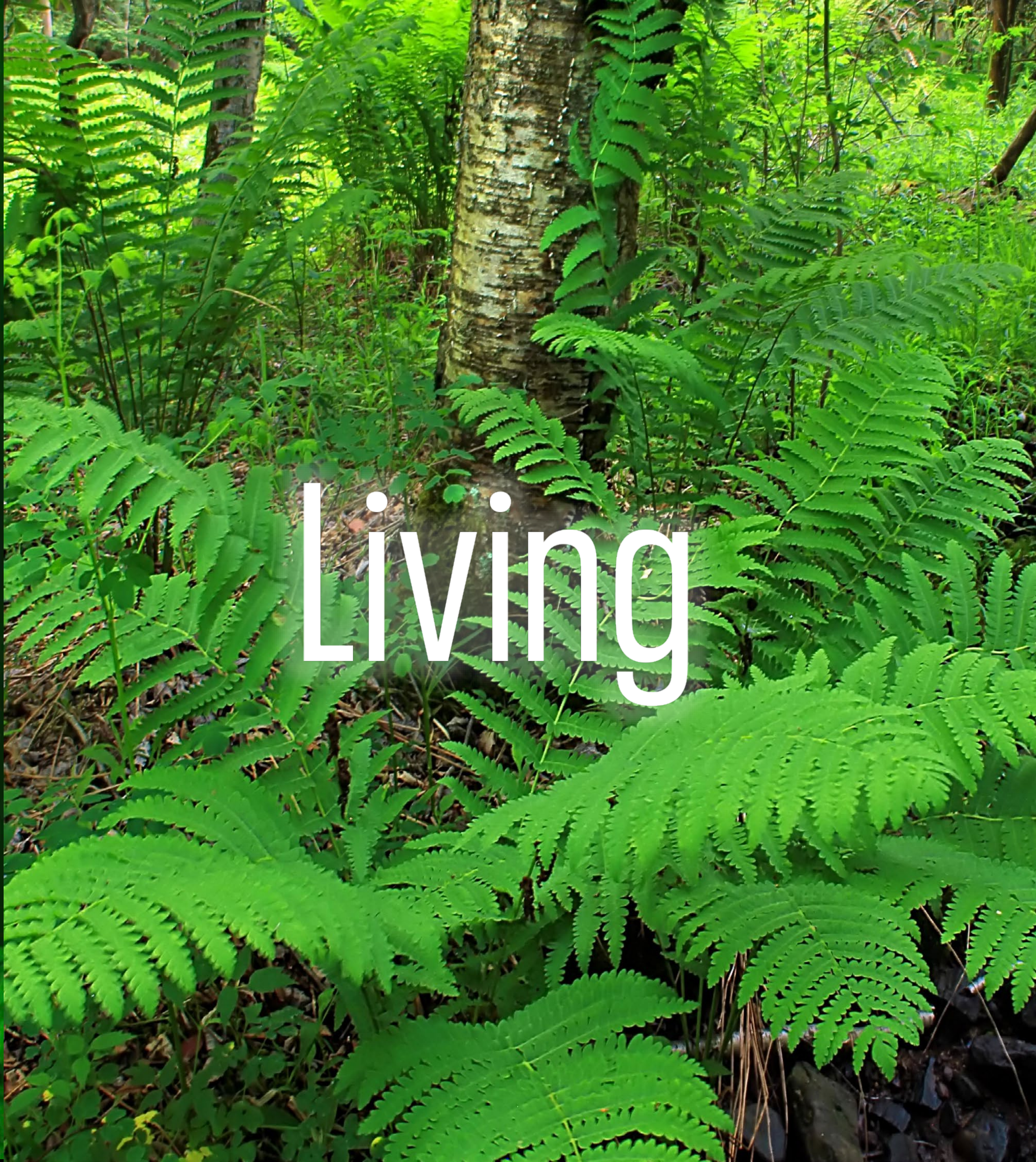
Many of the newly discovered exoplanets belong to othe class of terrestrial (rocky) planets, and are likely composed mostly of silicates and heavy metals. These are the planets most similar to Earth, and many of them are very likely to have oceans of liquid water, enabling the possibility that they bear life.

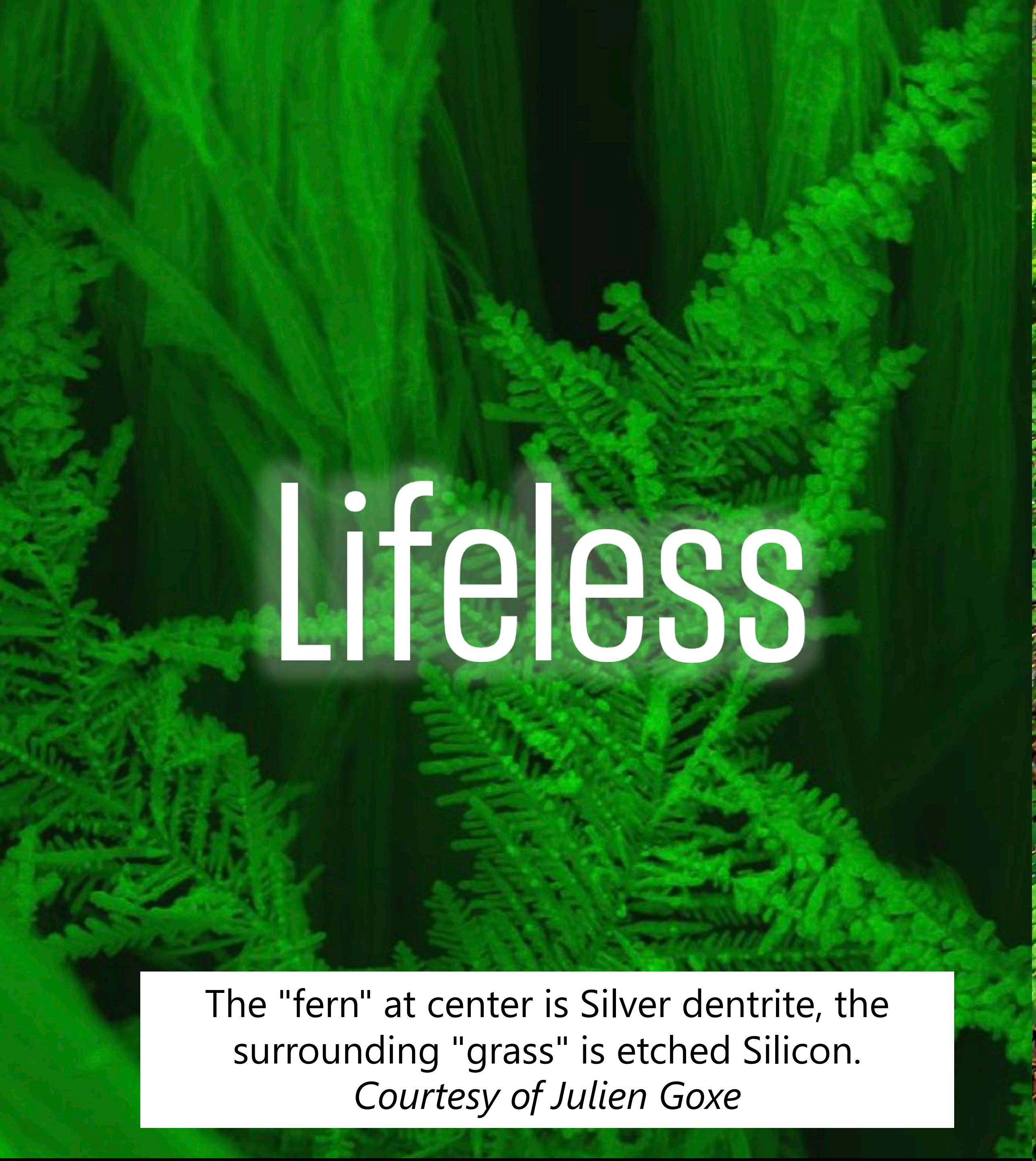
Most of the known rocky planets belong to the class of "super-earths", many times heavier than the Earth and other rocky planets in the Solar System. Various other classes of rocky planets exist, based chiefly on their composition and temperature, such as lava planets - molten planets that often orbit their parent star in less than a week, water worlds - planets completely covered by an ocean of liquid water, carbon planets - planets made chiefly out of carbon, with carbohydrate oceans, graphite mountains and diamond cores or cannonball planets - planets made almost entirely out of iron and other metals.



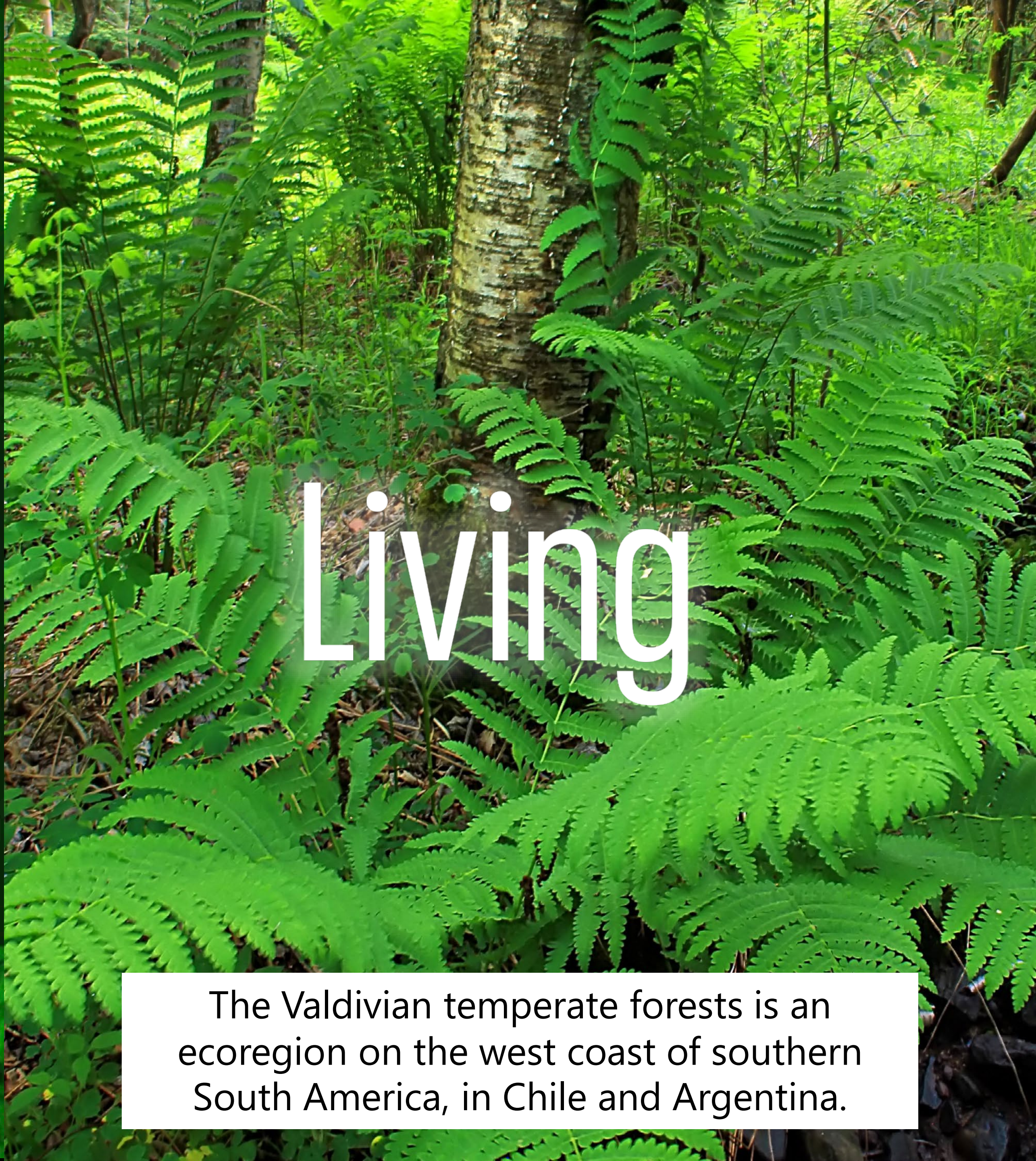




Lifeless


Living

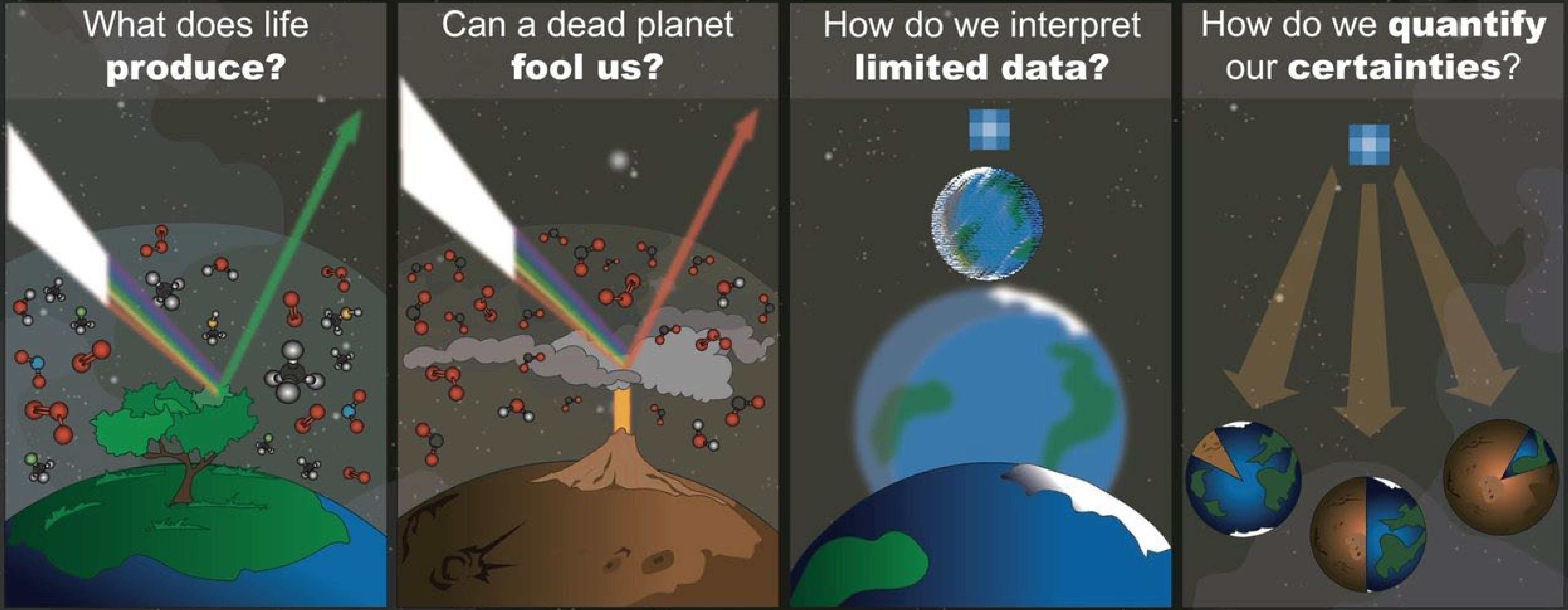


The "fern" at center is Silver dentrite, the surrounding "grass" is etched Silicon.
Courtesy of Julien Goxe



The Valdivian temperate forests is an ecoregion on the west coast of southern South America, in Chile and Argentina.

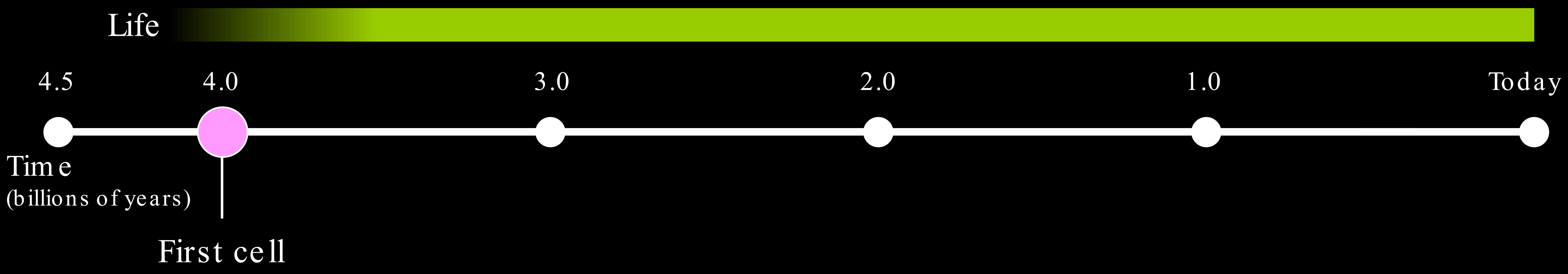
To become a **biosignature**, a phenomenon must be reliably produced by life.



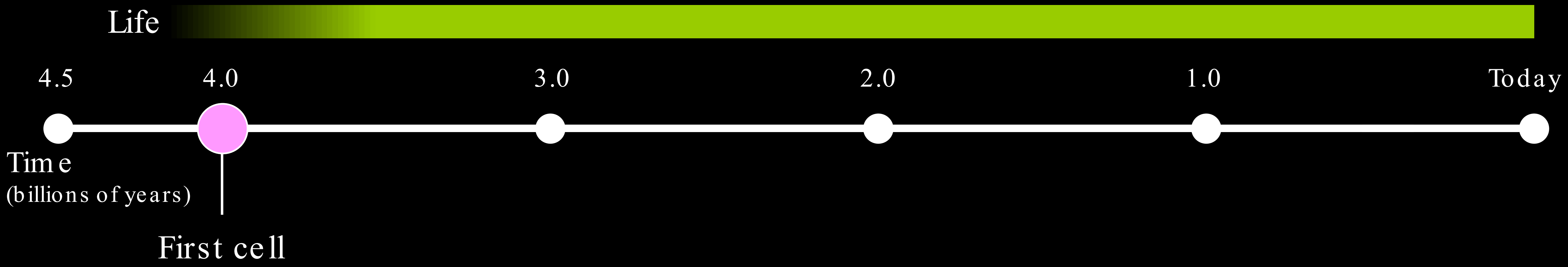
Source: NASA Astrobiology

We are largely unaware of how environmental and evolutionary changes impacted our planet

Nor the circumstances and timing of events that made the early Earth a much different place


Life
4.5
4.0
3.0
2.0
1.0
Today
Time
(billions of years)
First cell

Life has been imprinted by very extreme planetary conditions



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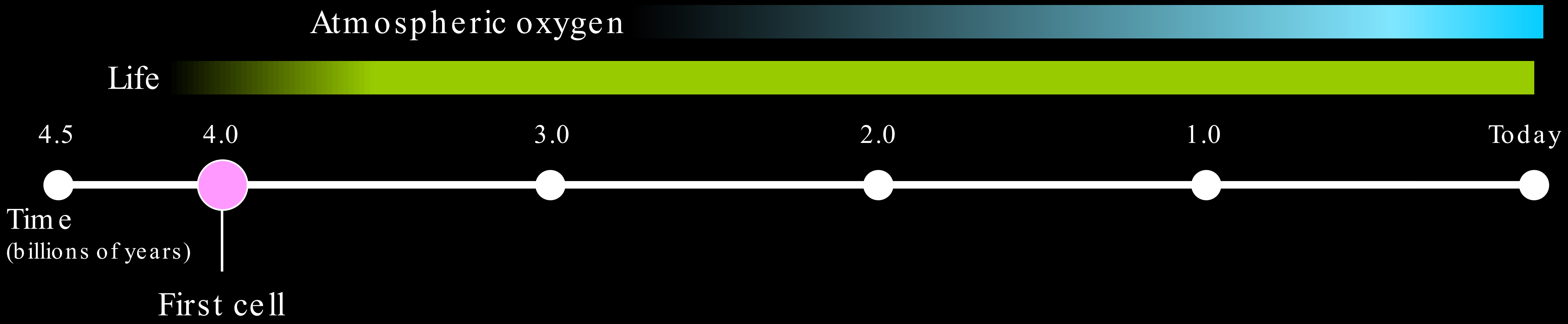

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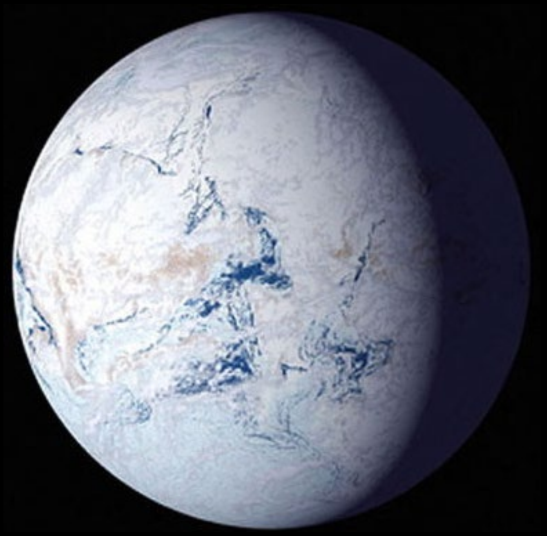
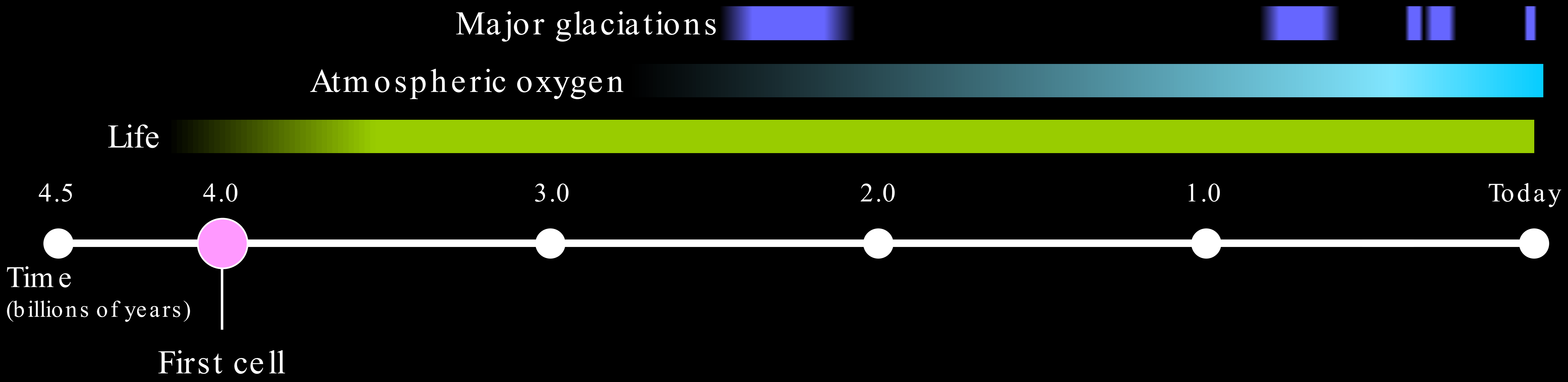
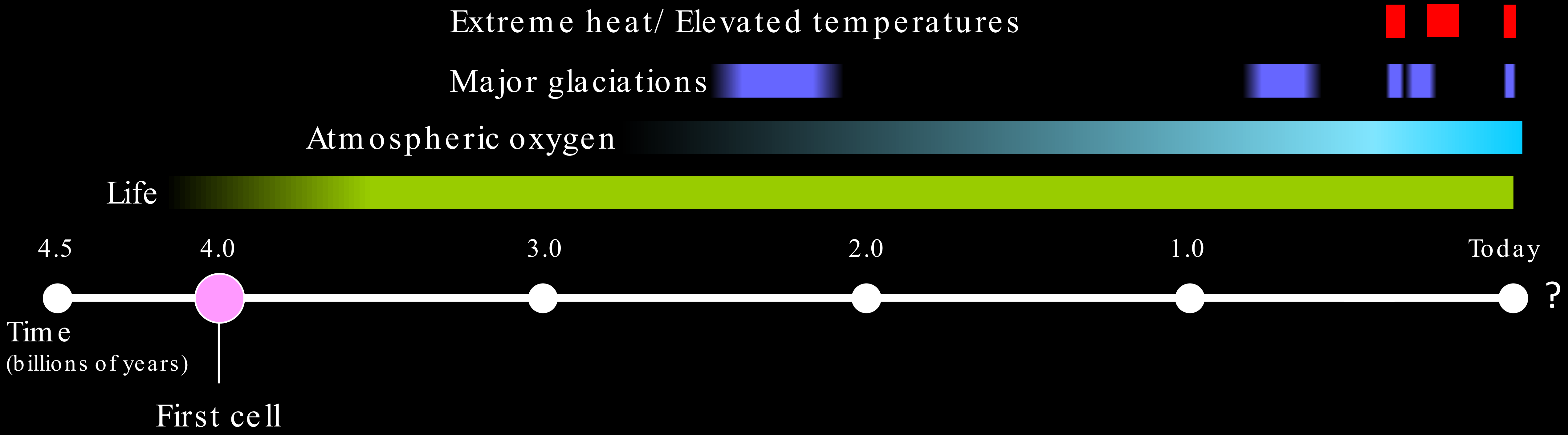
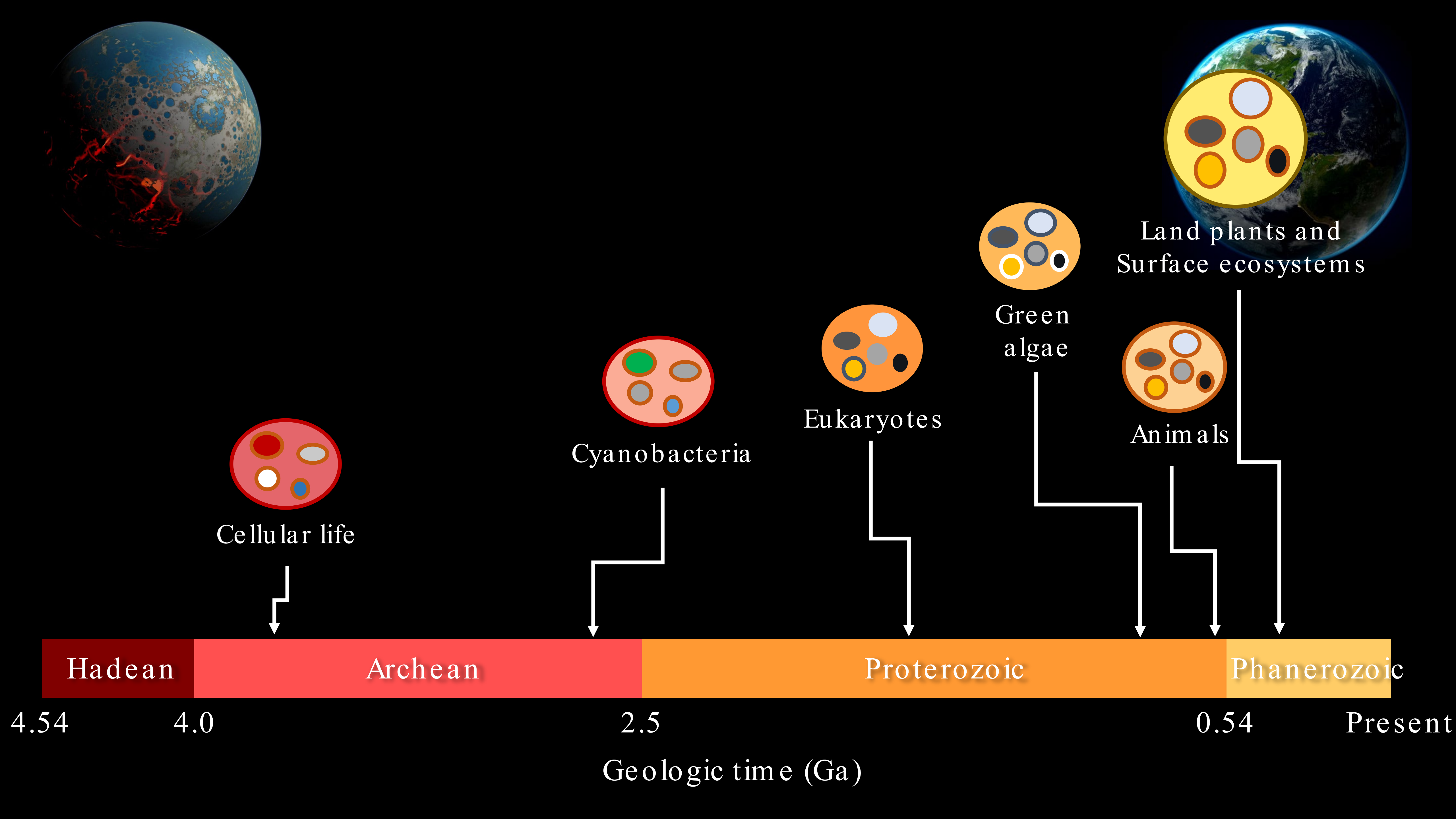




Life has been imprinted by very extreme planetary conditions

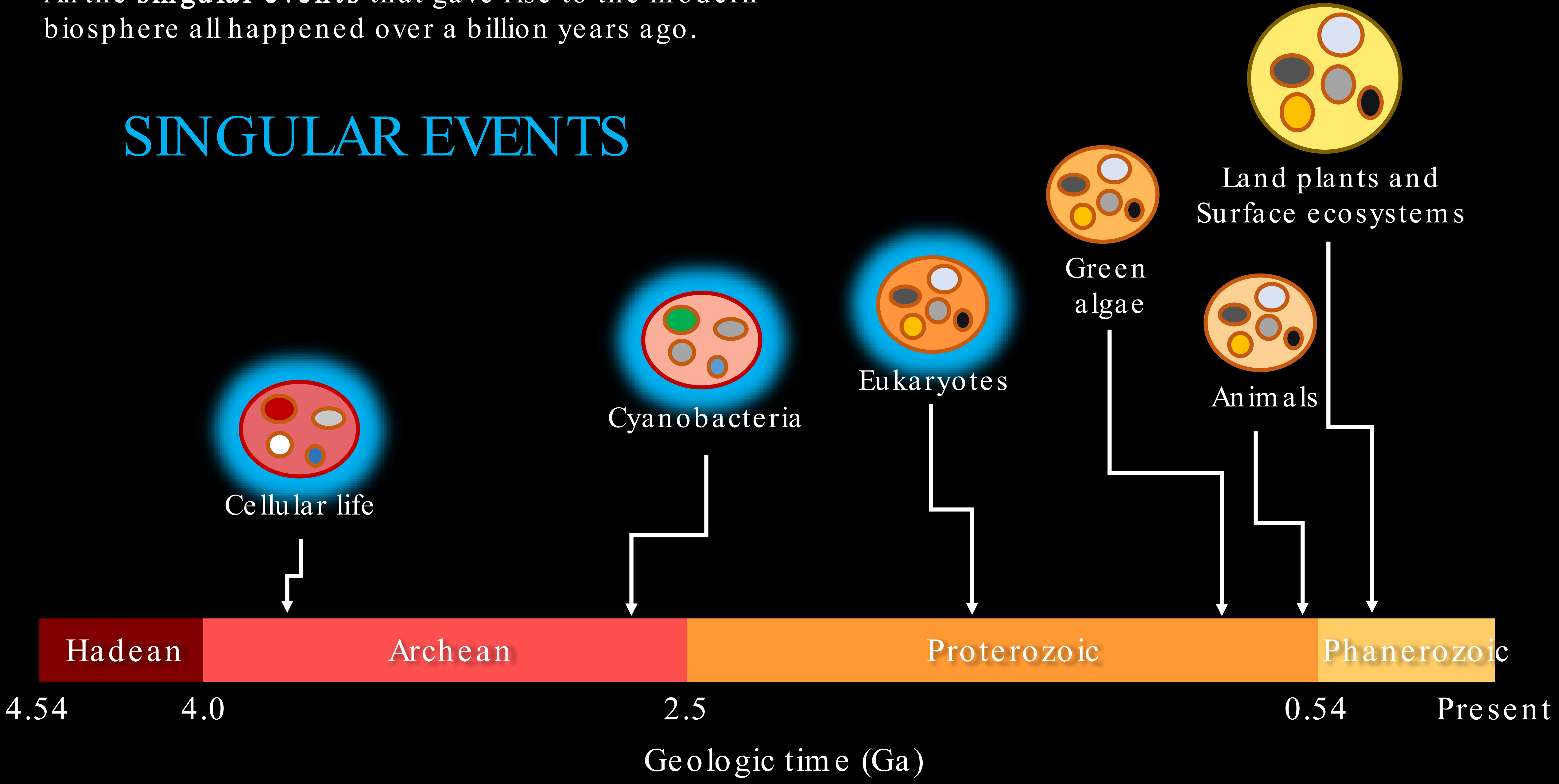




Land plants and
Surface ecosystems
Green
algae
Cyanobacteria
Eukaryotes
Animals
Cellular life
Hadean
Archean
Proterozoic
Phanerozoic
4.54
4.0
2.5
0.54
Present
Geologic time (Ga)

All the **singular events** that gave rise to the modern biosphere all happened over a billion years ago.

SINGULAR EVENTS



Early life.. It's complicated.

Adding to the challenge

Major problems piecing together Earth's biosignature history.

Early life.. It's complicated.

Adding to the challenge

Major problems piecing together Earth's biosignature history.

Example: Dominant drivers of biogeochemistry are poorly constrained

- Microbes are everywhere, but eukaryotes dominate land biomass
- O_2 is current major atmospheric component
- O_2 undoubtedly shifted ecosystem complexity AND enzymatic functions AND mineral weathering

There is no substitute for biology in the assessment of planetary-scale life in the universe.

There are almost no direct remains of life from the Earth’s earliest history.

We need another way to look at ancient life on Earth

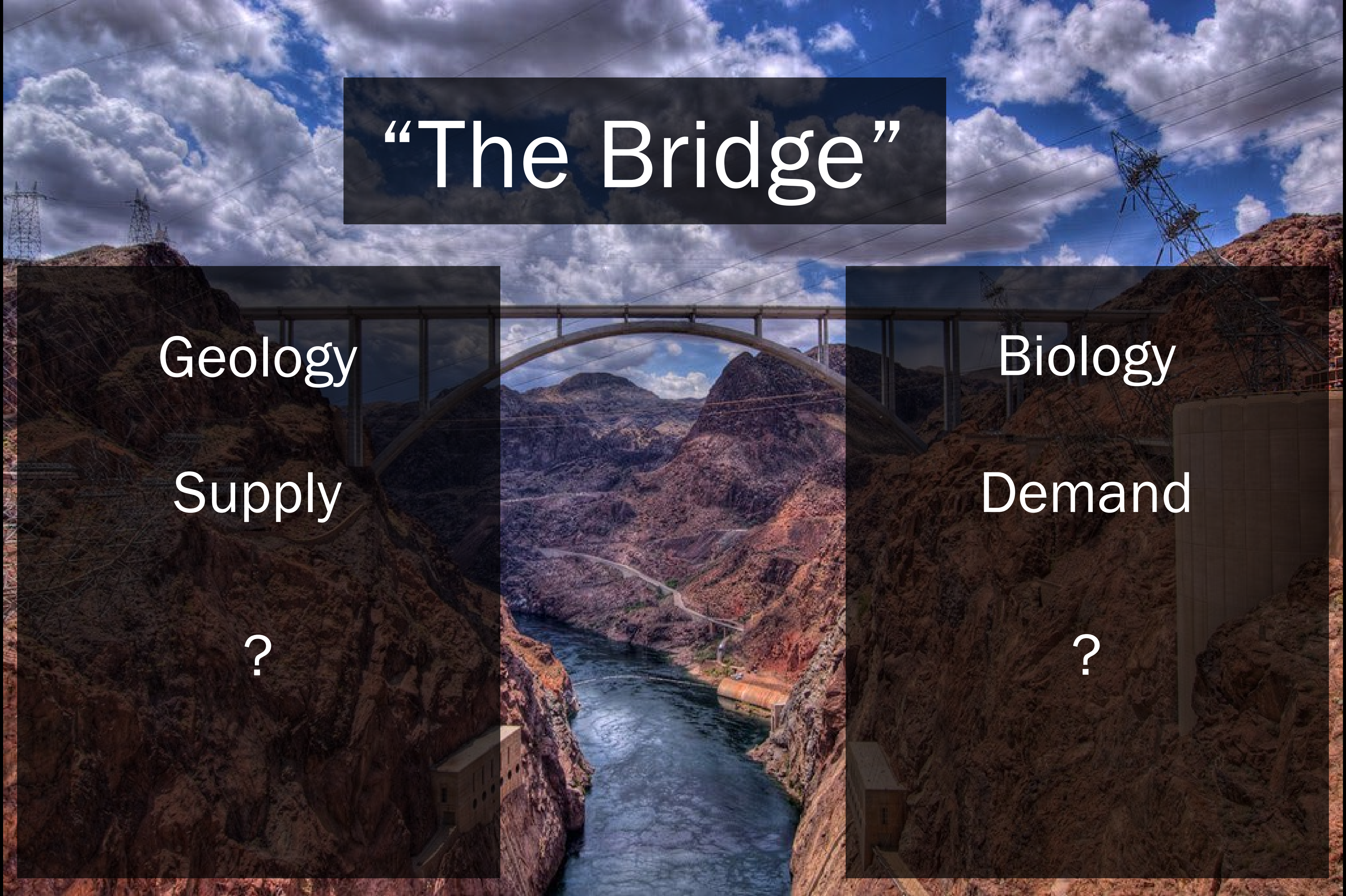
- Without the benefit (and the limitation) of comparing these events to any other in evolutionary history.

But how do we do this?

Building "The Bridge"


“The Bridge”
Geology
Biology


"The Bridge"
Geology
Supply
Biology
Demand


"The Bridge"
Geology
Supply
?
Biology
Demand
?

"The Bridge"

Natural Phenomena

- "bioinorganic bridge" (Anbar & Knoll 2002)

The Science

- New tools!
- Us!

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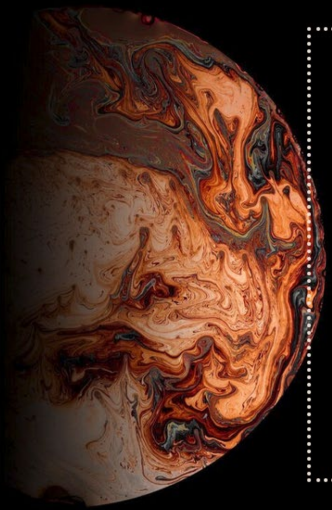
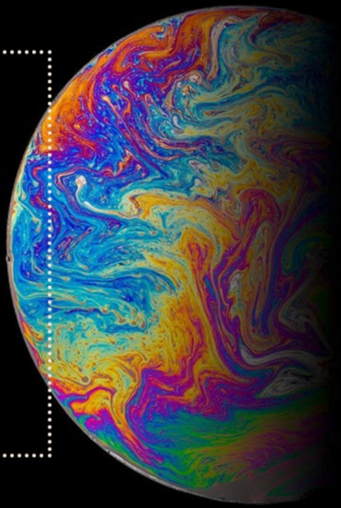
METAL UTILIZATION & SELECTION ACROSS EONS

Studying biological innovations across eons



Biology & geochemistry of Earth's history

Life's metal requirements



Life as we don't know it

M·U·S·E

METAL UTILIZATION & SELECTION ACROSS EONS

Meet the **MUSE** team

WISCONSIN
UNIVERSITY OF WISCONSIN–MADISON

Arizona State University

UNIVERSITY OF ALBERTA

UNIVERSITY OF MINNESOTA

IOWA STATE UNIVERSITY

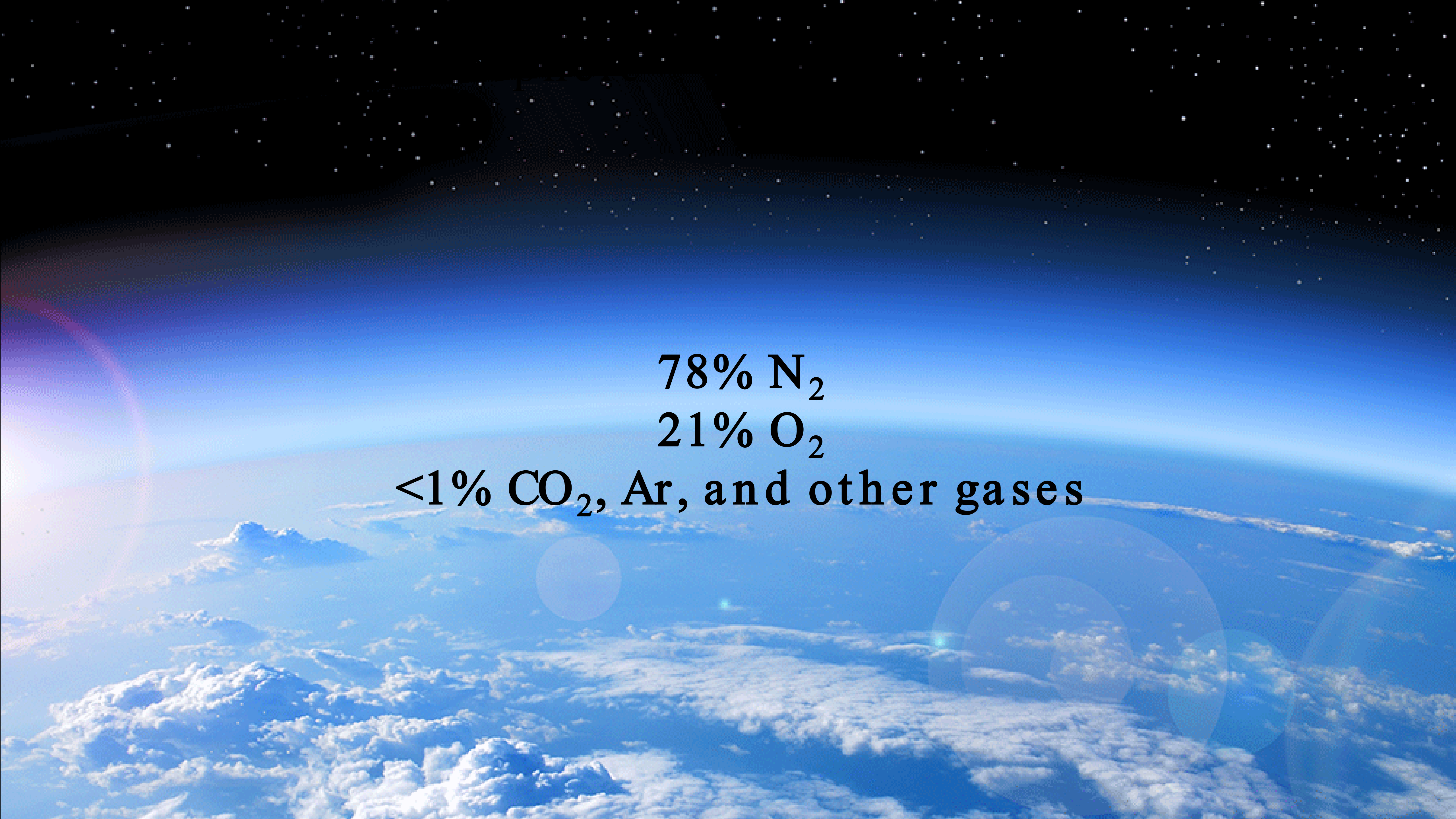
THE UNIVERSITY OF CHICAGO

HARVARD UNIVERSITY

Stanford University

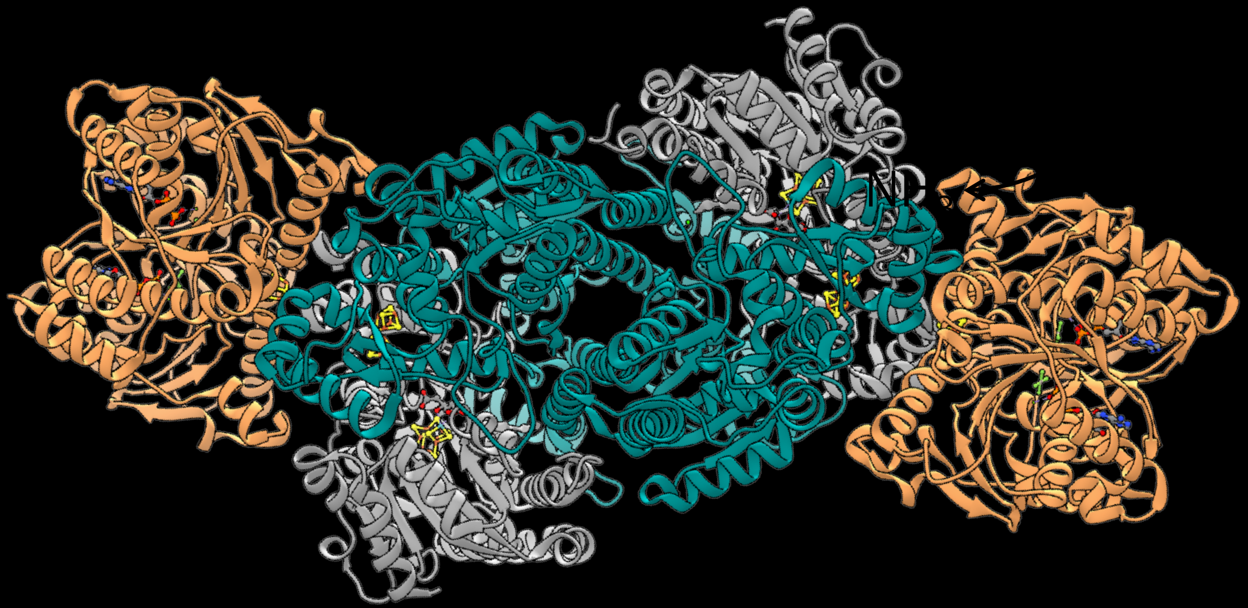
UtahState University

M·U·S·E
METAL UTILIZATION & SELECTION ACROSS EONS


78% N_2
21% O_2
<1% CO_2, Ar, and other gases

Nitrogenase

Life's **<u>only</u>** trick to convert atmospheric nitrogen to bioavailable ammonia



Life depends on nitrogen, nitrogenase has been a core feature of the Earth biosphere for billions of years.

$$N_2 + 8\ H^+ + 8\ e^- + 16ATP \rightarrow 2\ NH_3 + H_2 + 16ADP + 16P_i$$

Nitrogenase

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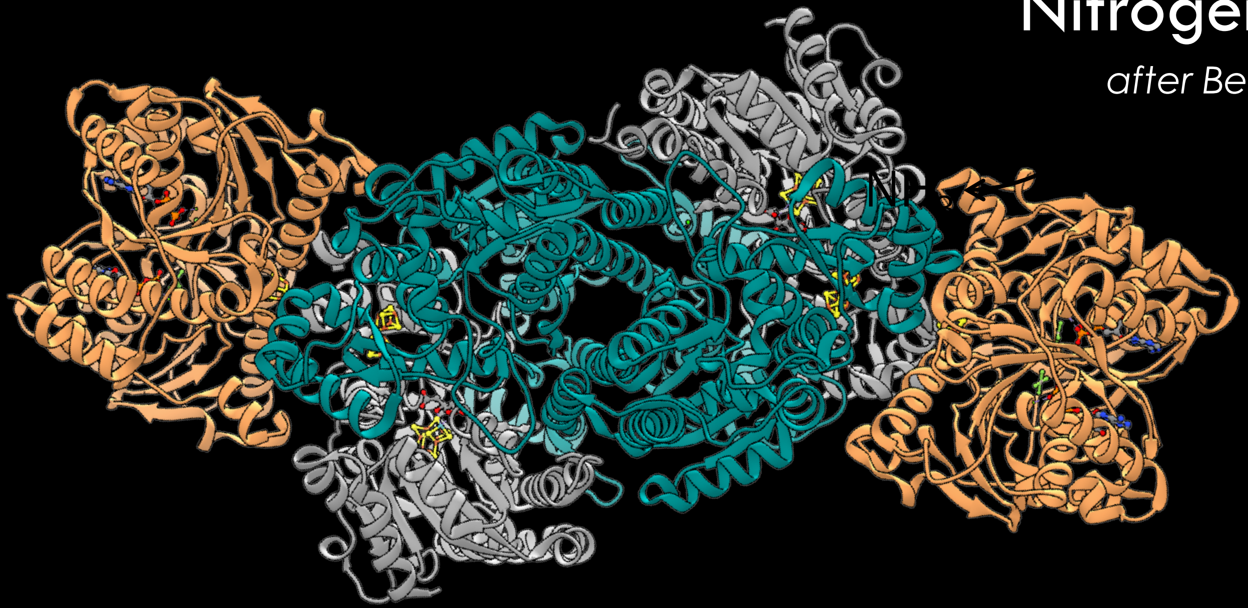
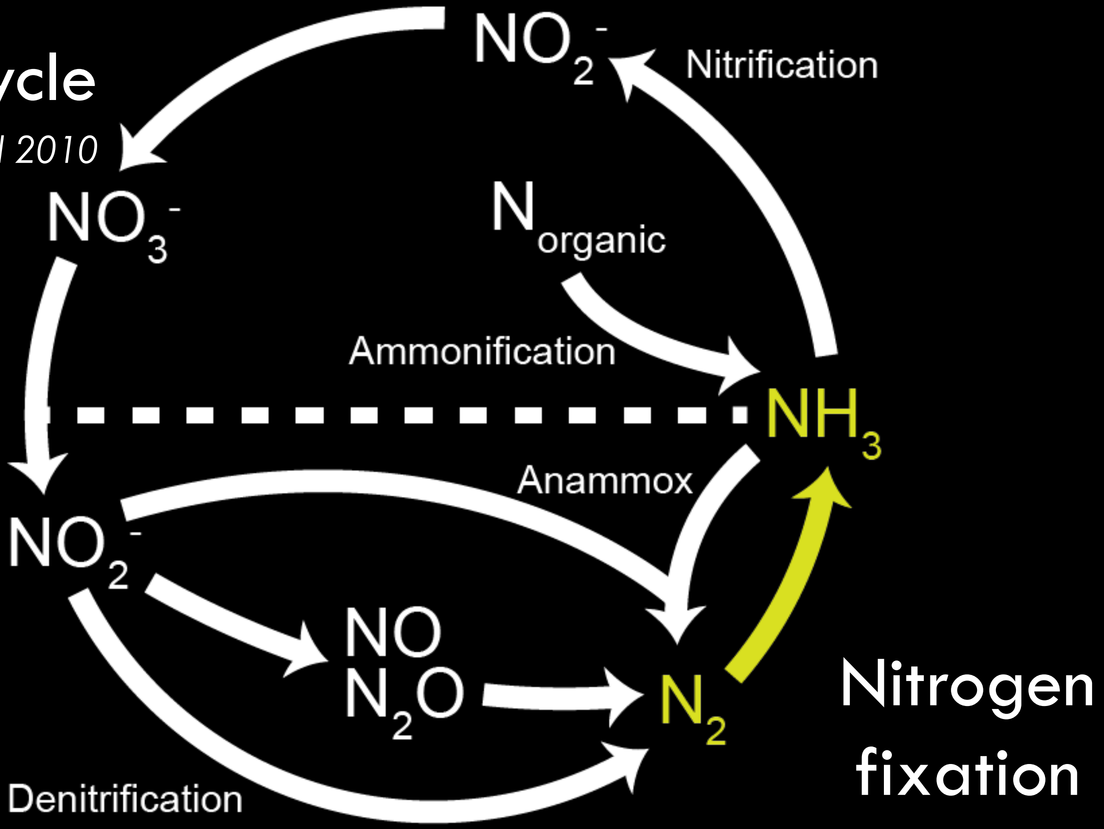
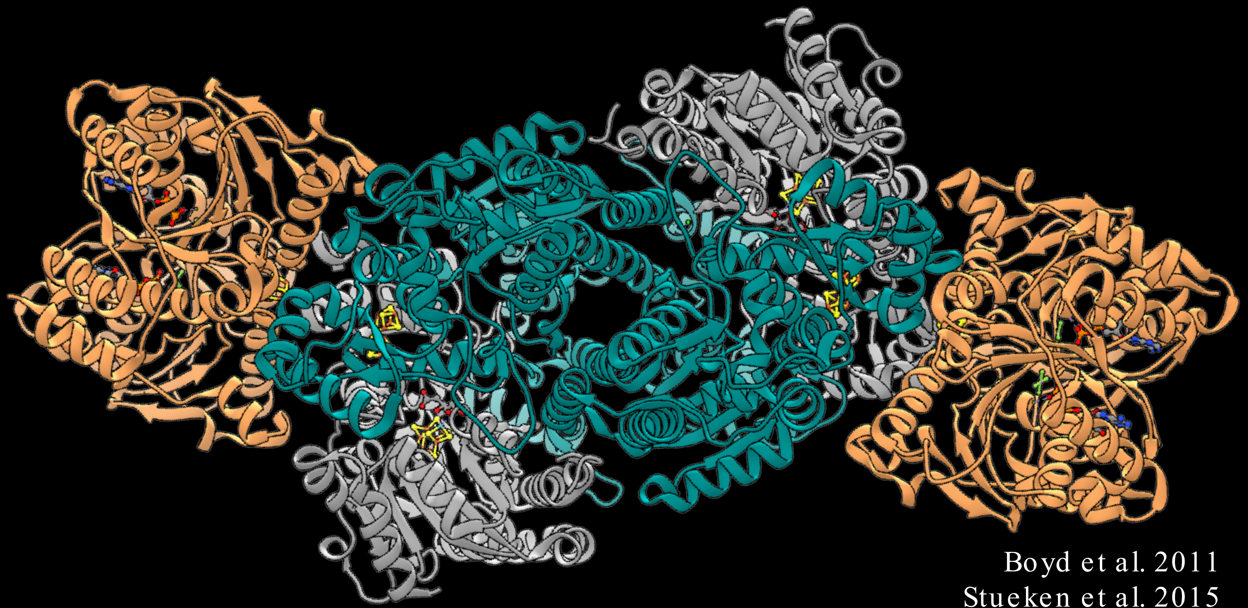


Nitrogen Cycle

after Bernhard 2010



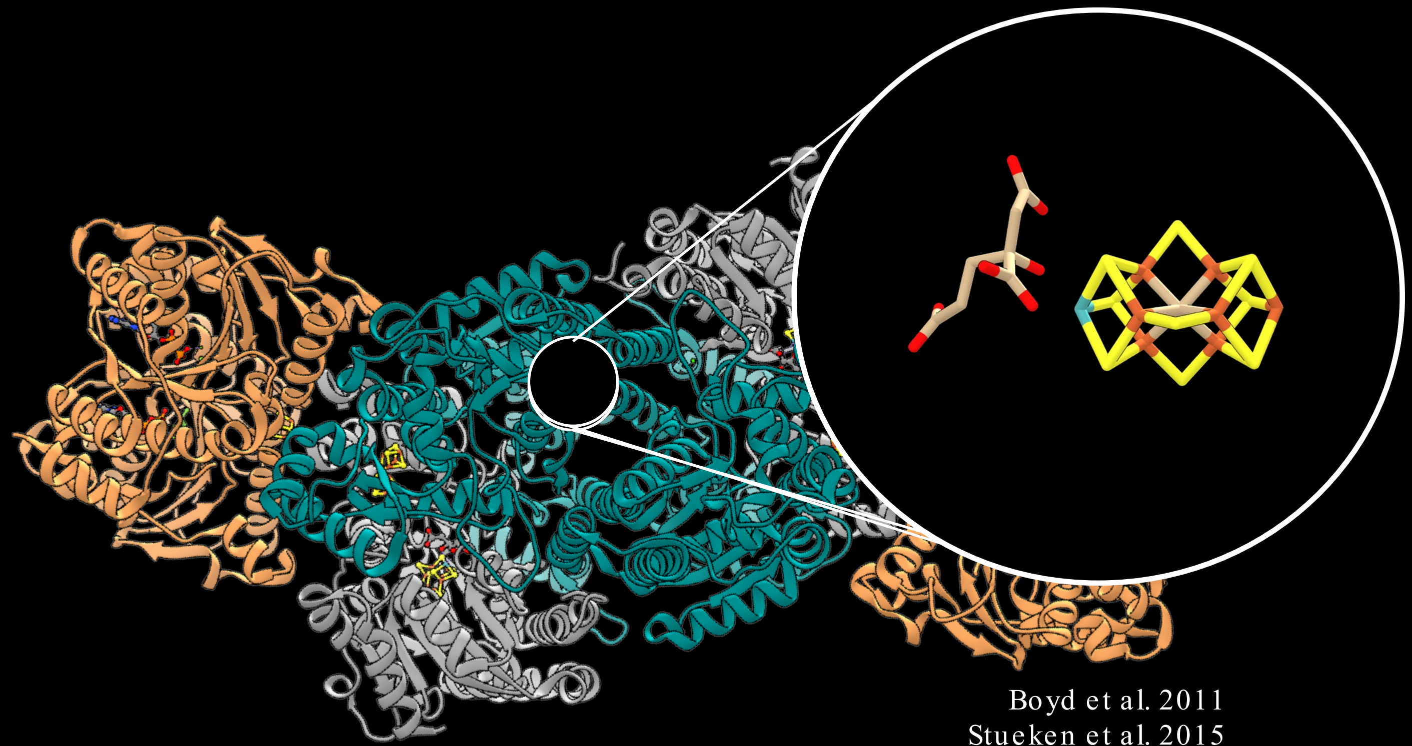


Boyd et al. 2011
Stueken et al. 2015
Garcia et al. 2020

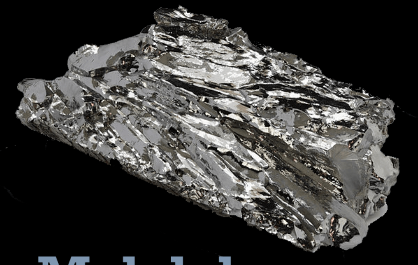
4.5 4.0 3.0 2.0 1.0 Today

Time
(billions of years)

Origin of nitrogenase



Life depends on nitrogenase, nitrogenase depends on **Molybdenum**!



Molybdenum

Boyd et al. 2011
Stueken et al. 2015
Garcia et al. 2020

4.5 4.0 3.0 2.0 1.0 Today

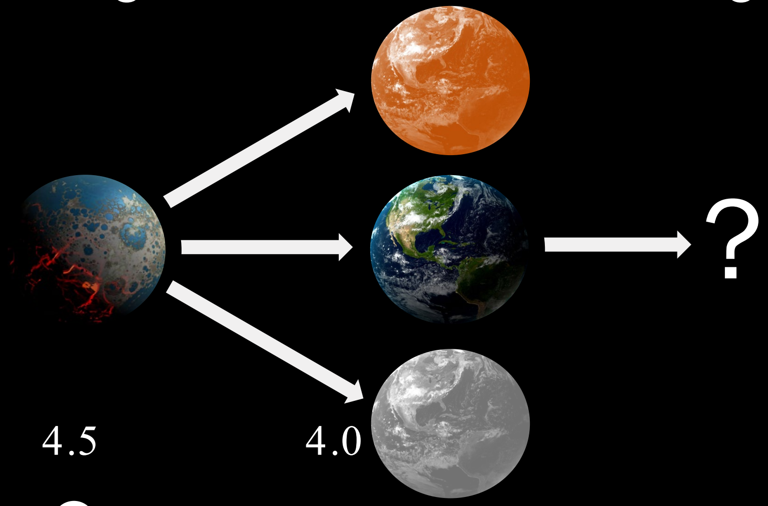
Time
(billions of years)

Origin of nitrogenase

Life as we know it requires nitrogen, but how does our understanding of the N cycle inform our search for life in the universe?

In order to understand the evolution of the nitrogen cycle, we need to understand the planetary conditions that gave rise to biological nitrogen fixation.

Nitrogenase evolution: Seeking guidance from Earth history



A case for "planetary microbiology"

4.5 | 4.0 | 3.0 | 2.0 | 1.0 | Today

Time
(billions of years)

Mo-dependence likely evolved under a low Mo but high Fe ocean.
Why?

Anbar and Knoll

Questions for biological N-cycle evolution:

- How have changes in abiotic/biotic nutrient cycling influenced the evolution of these enzymes?

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  - i.e., metal abundances, nutrient limitation/minimums, environmental conditions, ecological processes, etc.

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  - Ex. Isotope fractionation data from non-model organisms, undiscovered N-cycle pathways/enzymes, etc.

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- What are the observable signatures of this phenomenon?

Earth's past biology offers a unique opportunity. The early Earth is a natural laboratory to identify potential biosignatures in the context of their environment.

Run the 'what if' experiment

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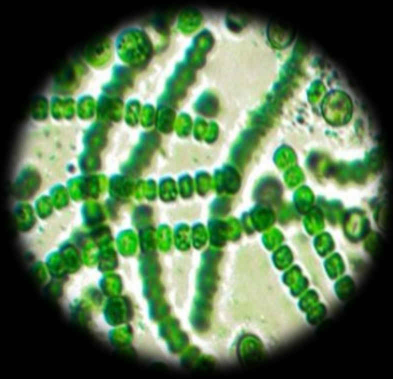
“Planetary Microbiology”

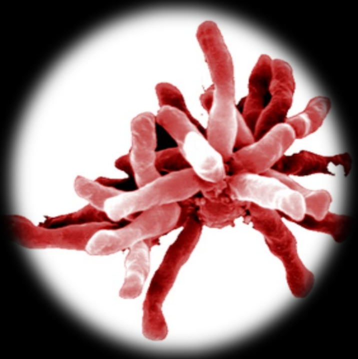
Microbes

E. coli

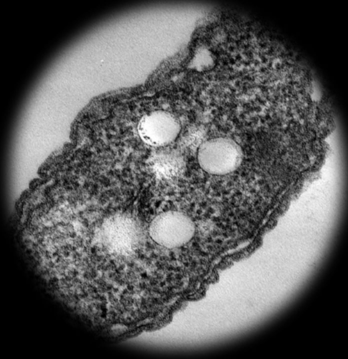


S. elongatus

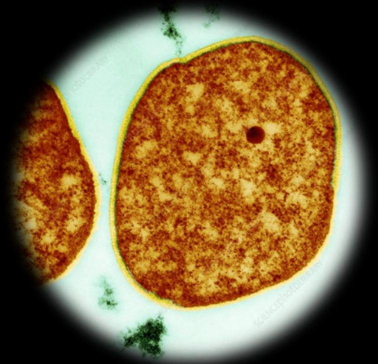
A. vinelandii



R. palustris



K. variicola



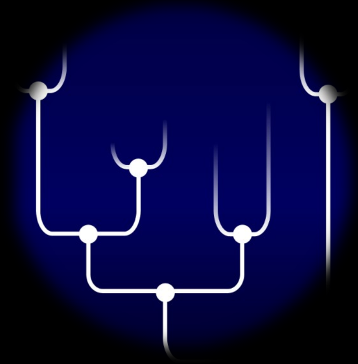
Sulfolobus archaea

THE KAÇAR LAB “Planetary Microbiology”

We have several questions that we can answer with modern tools in biology

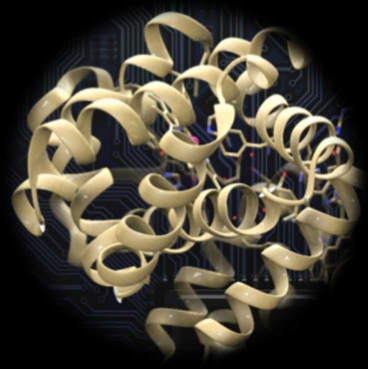
Such as CRISPR, computational biology, AI predictions, laboratory evolution, etc.

First question: How did nitrogenase evolve?



Ancestral reconstruction

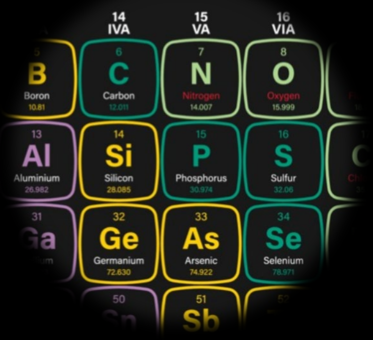
Synthetic biology



Protein biochemistry

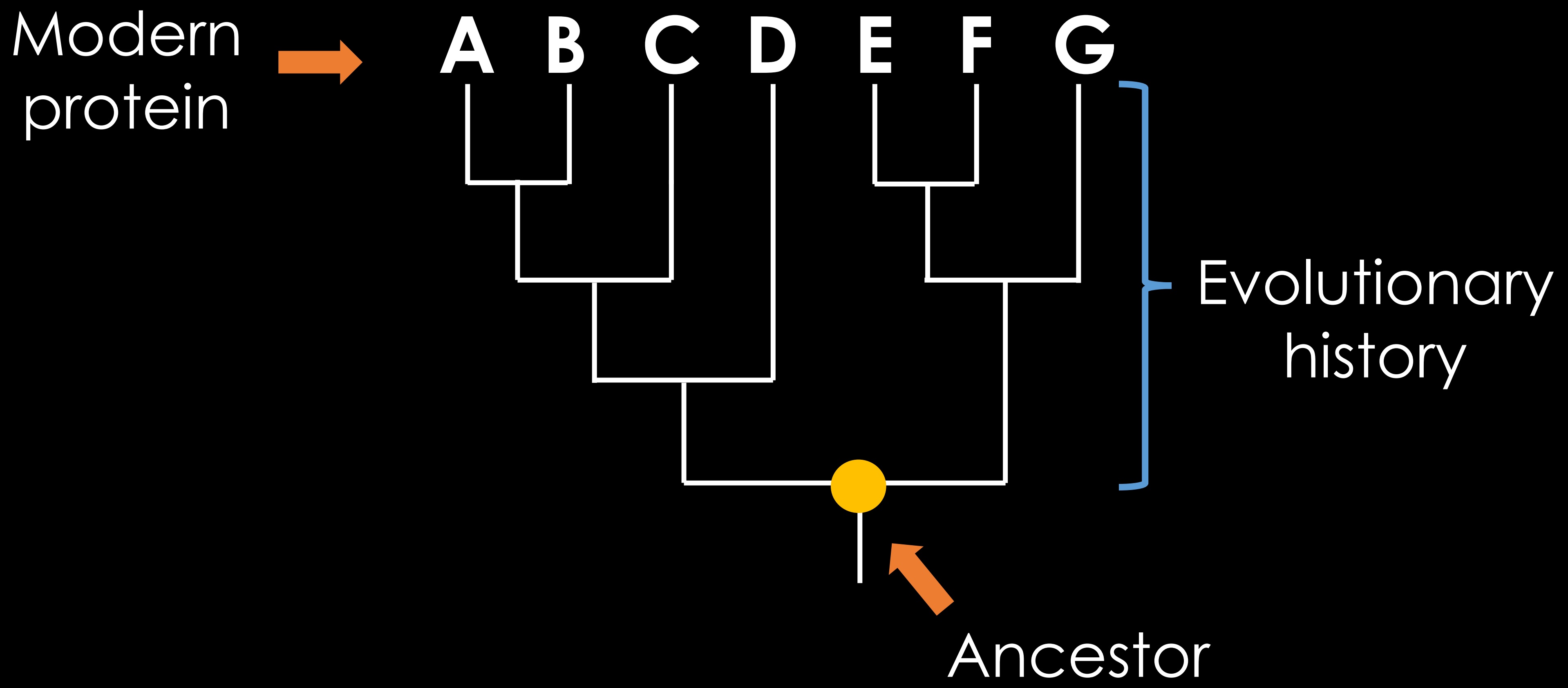
Experimental evolution

Machine learning



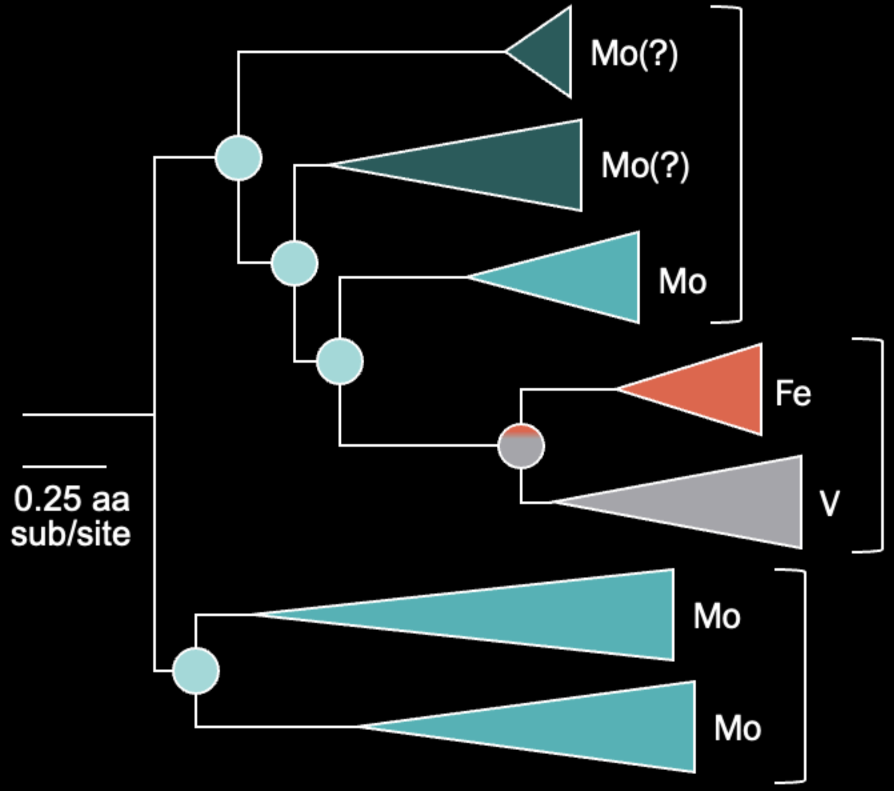
Isotope geochemistry

Ancient DNA reconstruction



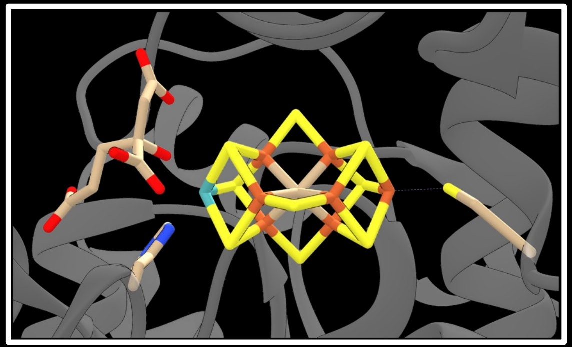
Reprogram cells to generate extinct biosignatures

Nitrogenase protein phylogeny



*colored by experimentally determined or computationally inferred metal dependence

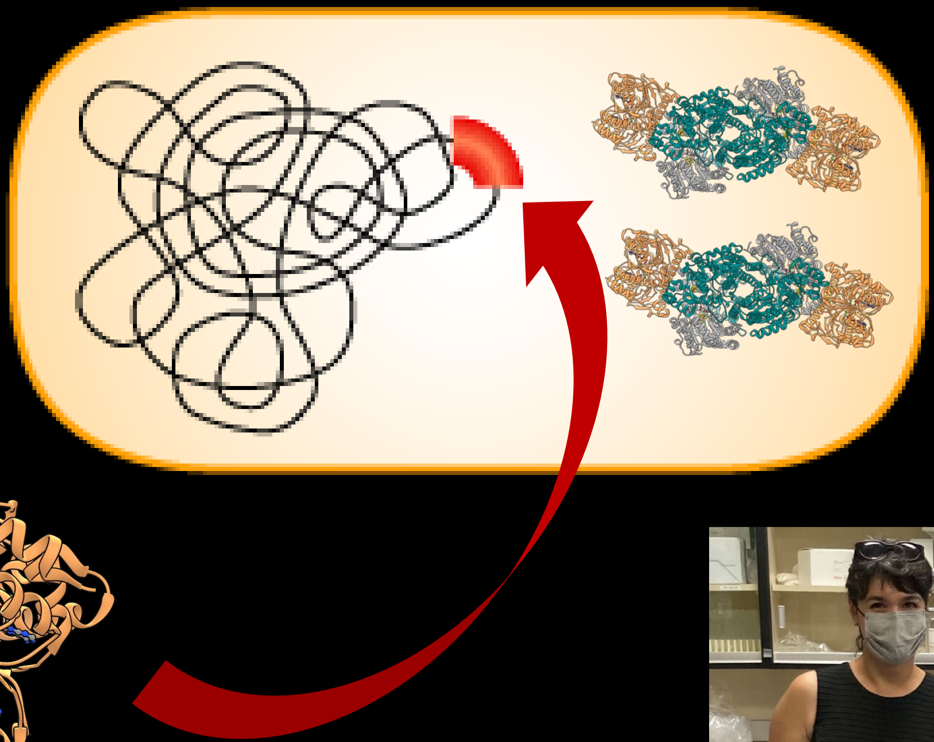
- Built machine learning models to infer ancient protein and metabolism & properties



Active-site amino acids tuned to cofactor metal composition

Garcia et al., Geobiology, 2020

Generate new experimental system



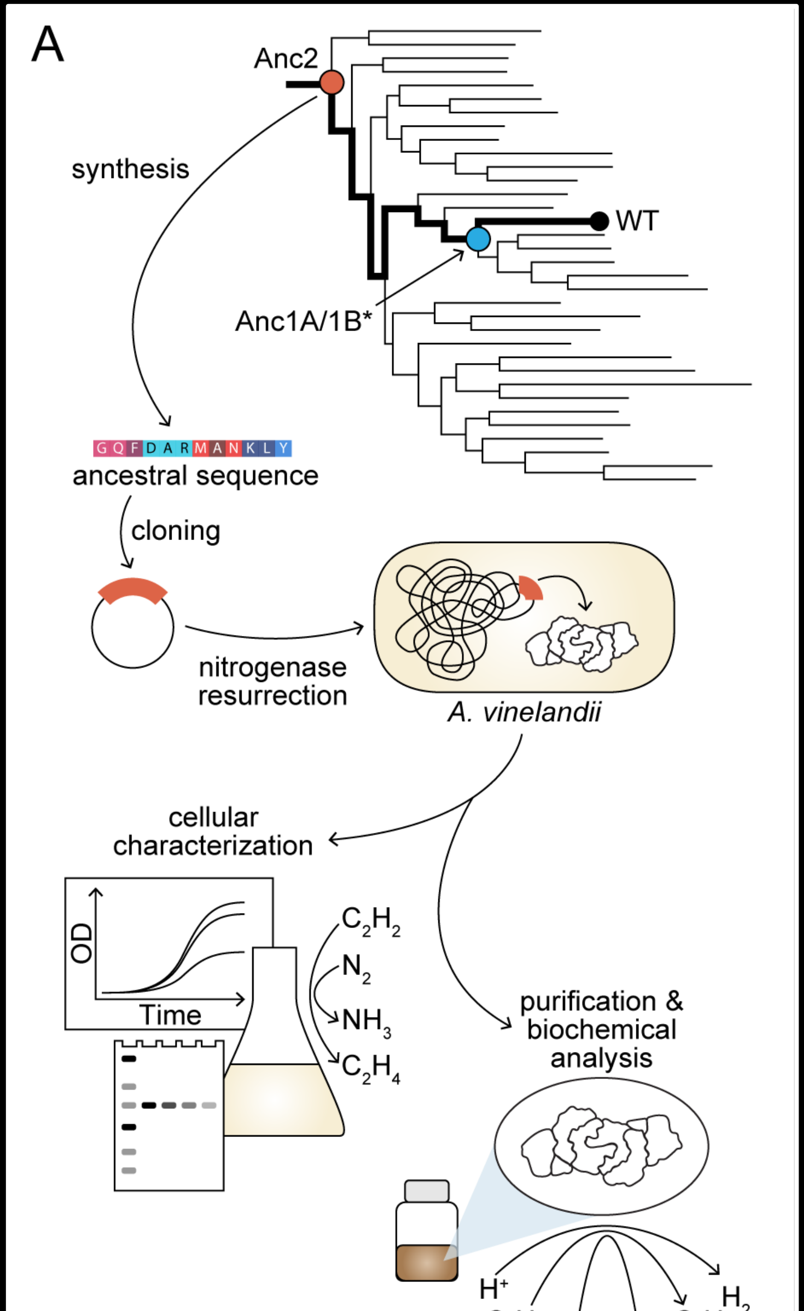
A vinelandii

Engineer ancient DNA in microbes

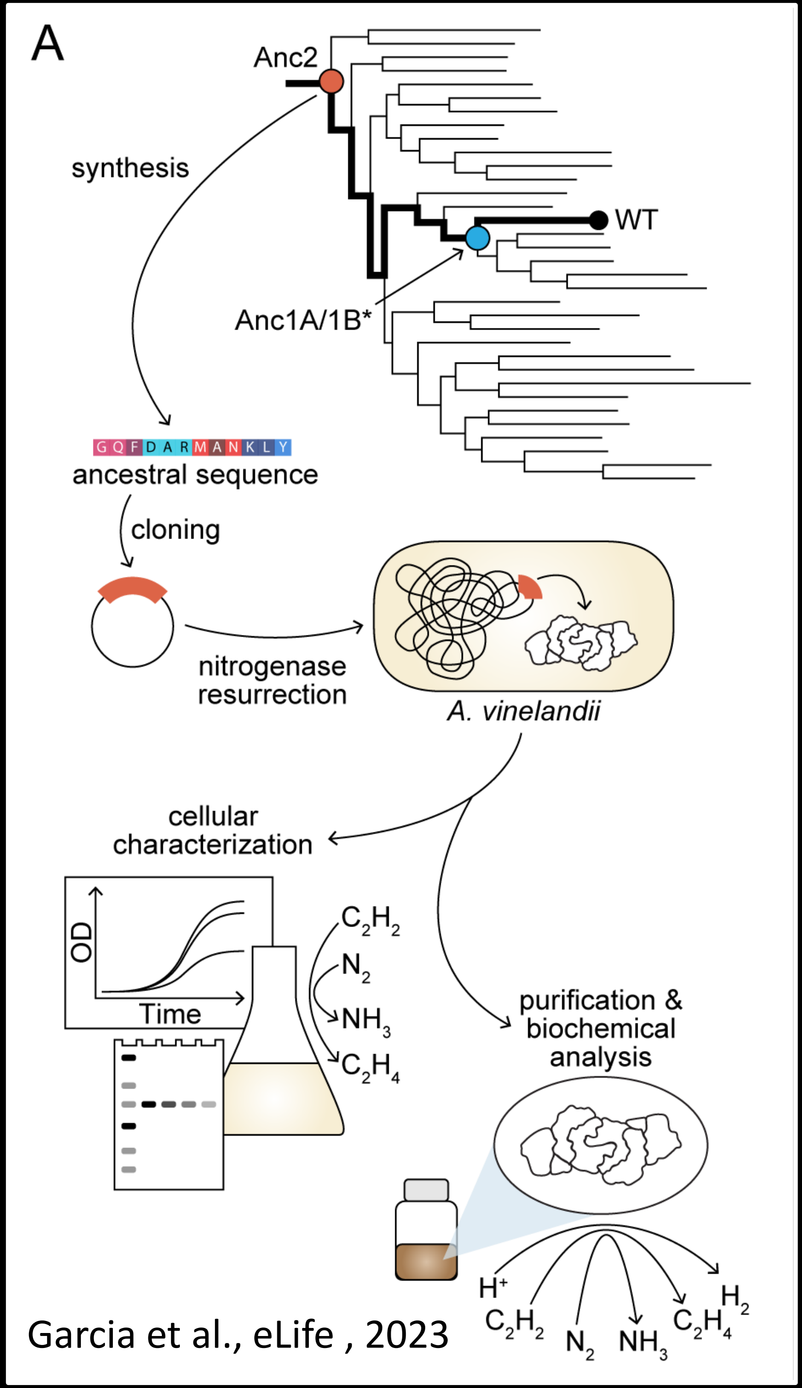
Amanda Garcia (NPP)

Kacar et al., mBio, 2017
Venkataram et al., PNAS, 2020
Garcia et al., eLife , 2023

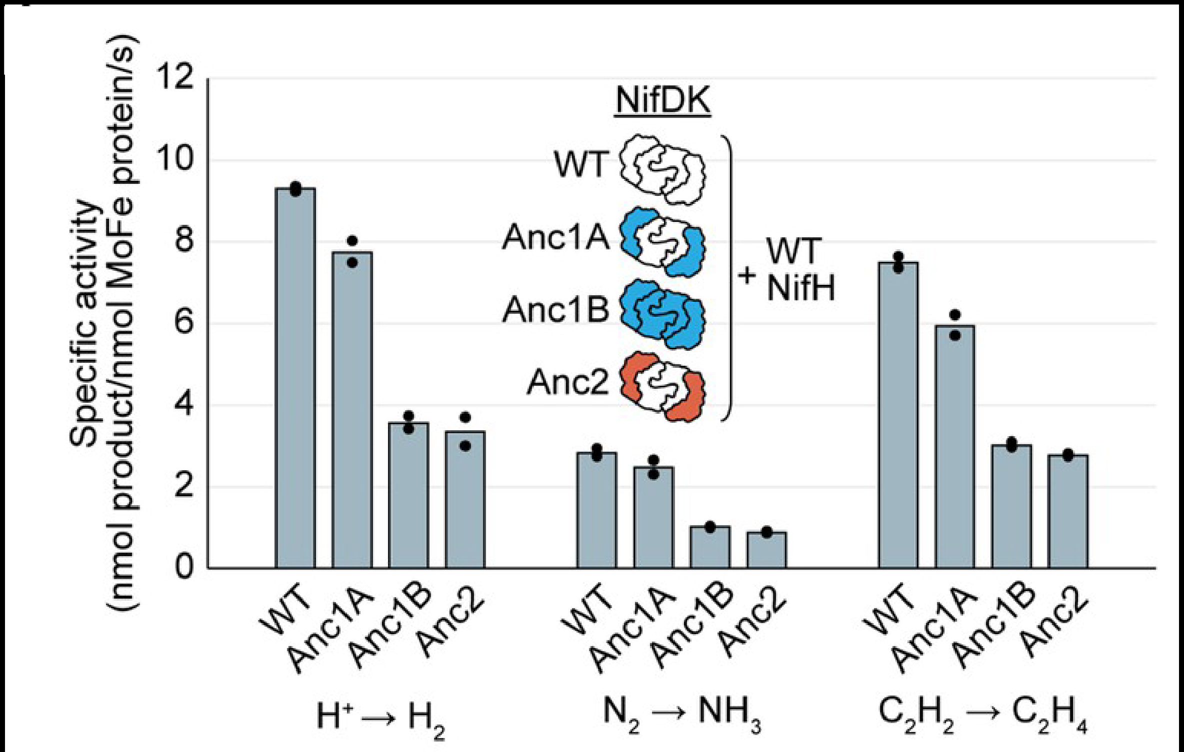
Environmental pressures 🤝 Evolutionary opportunities
Bridging enzymes to ecosystems & observables



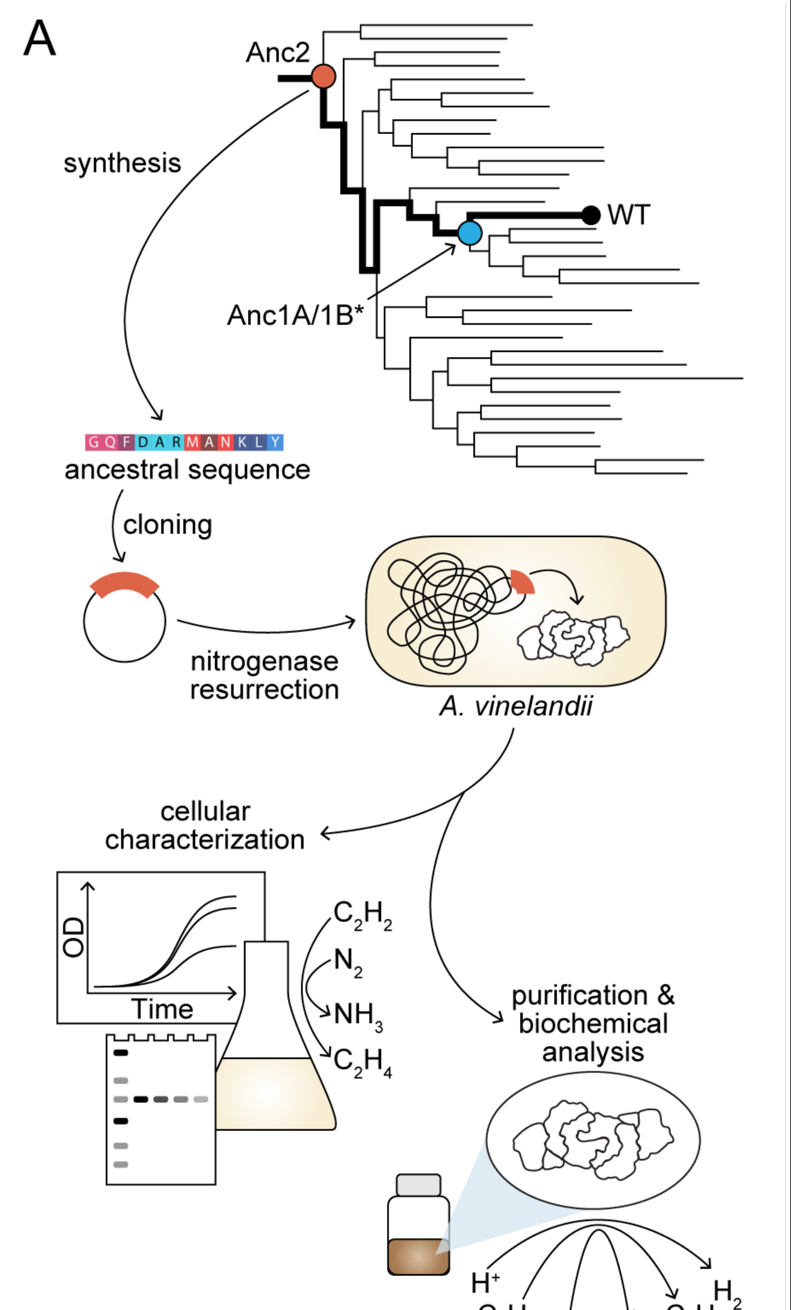
Garcia et al., eLife , 2023



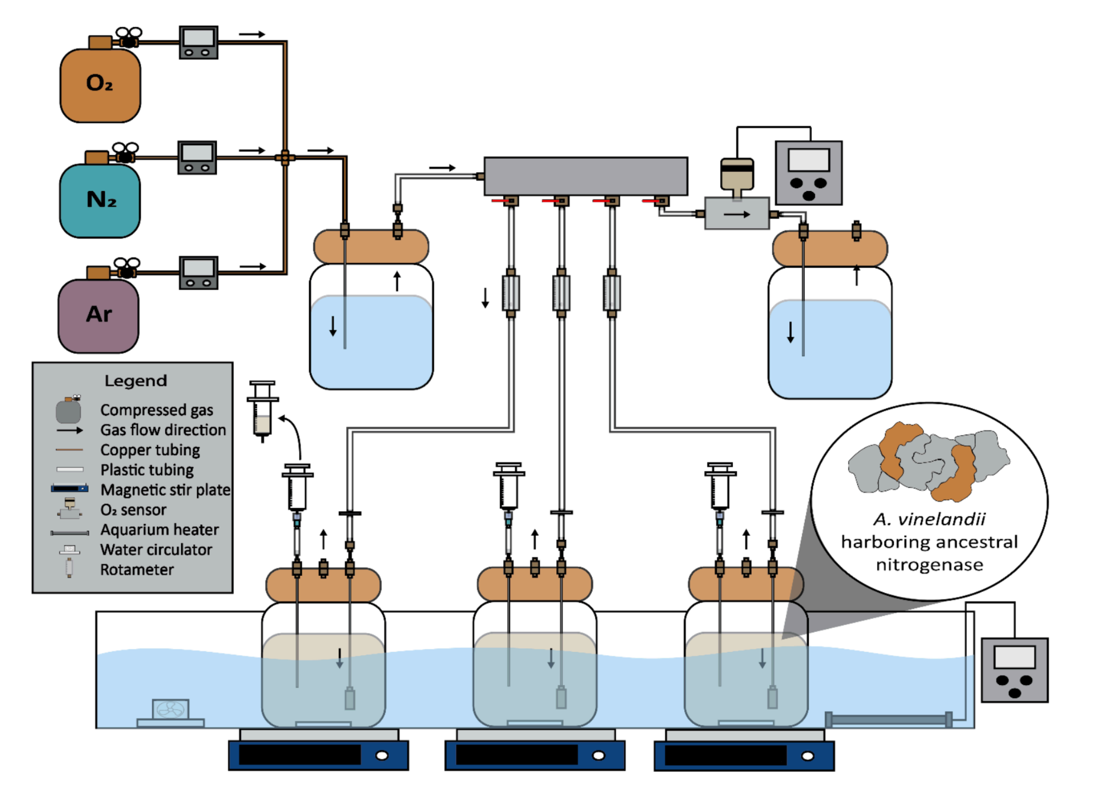
Garcia et al., eLife , 2023



- Generate ancient metabolisms in the lab:
  - Despite scarcity, early nitrogenases preferred Mo
  - Study and evolve them under ancient Earth conditions
  - Laboratory resurrection of ancient isotope signatures



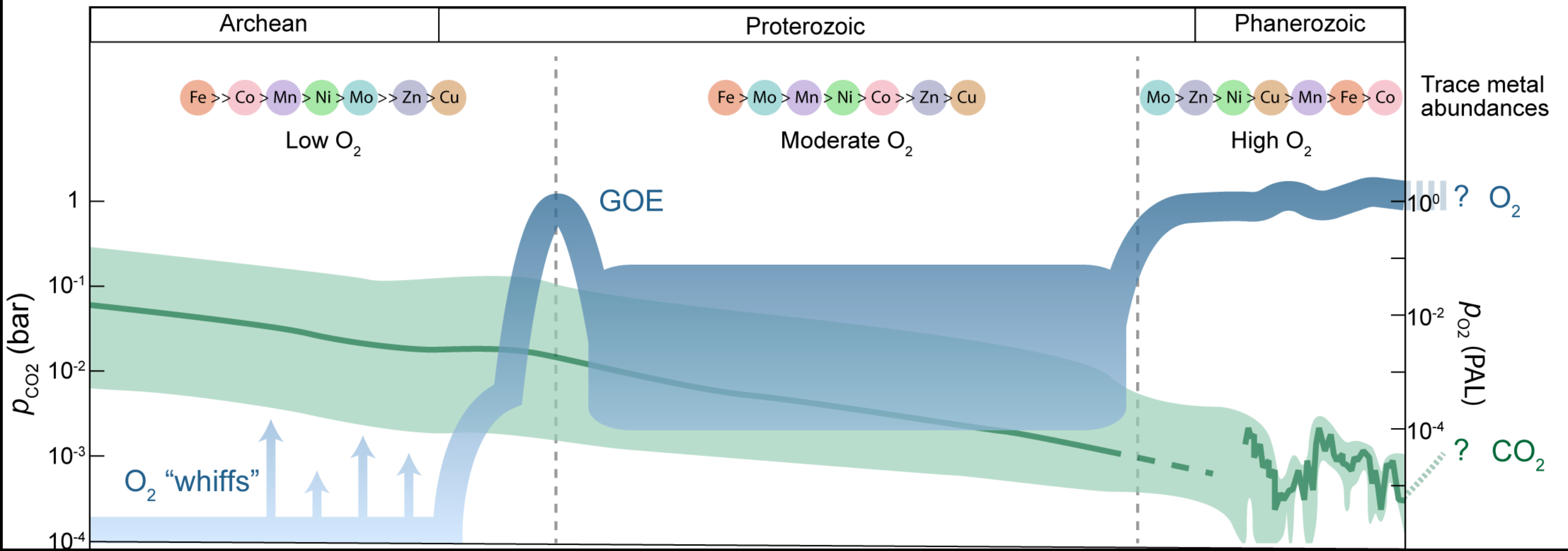
Garcia et al., eLife , 2023



Rivier et al., Spectrum, 2023
Rucker et al., Trends in Micro, 2023

- We simulate ancient & alien Earth conditions in the laboratory to generate a high-throughput biosignature library

Metal composition evolved across geologic time



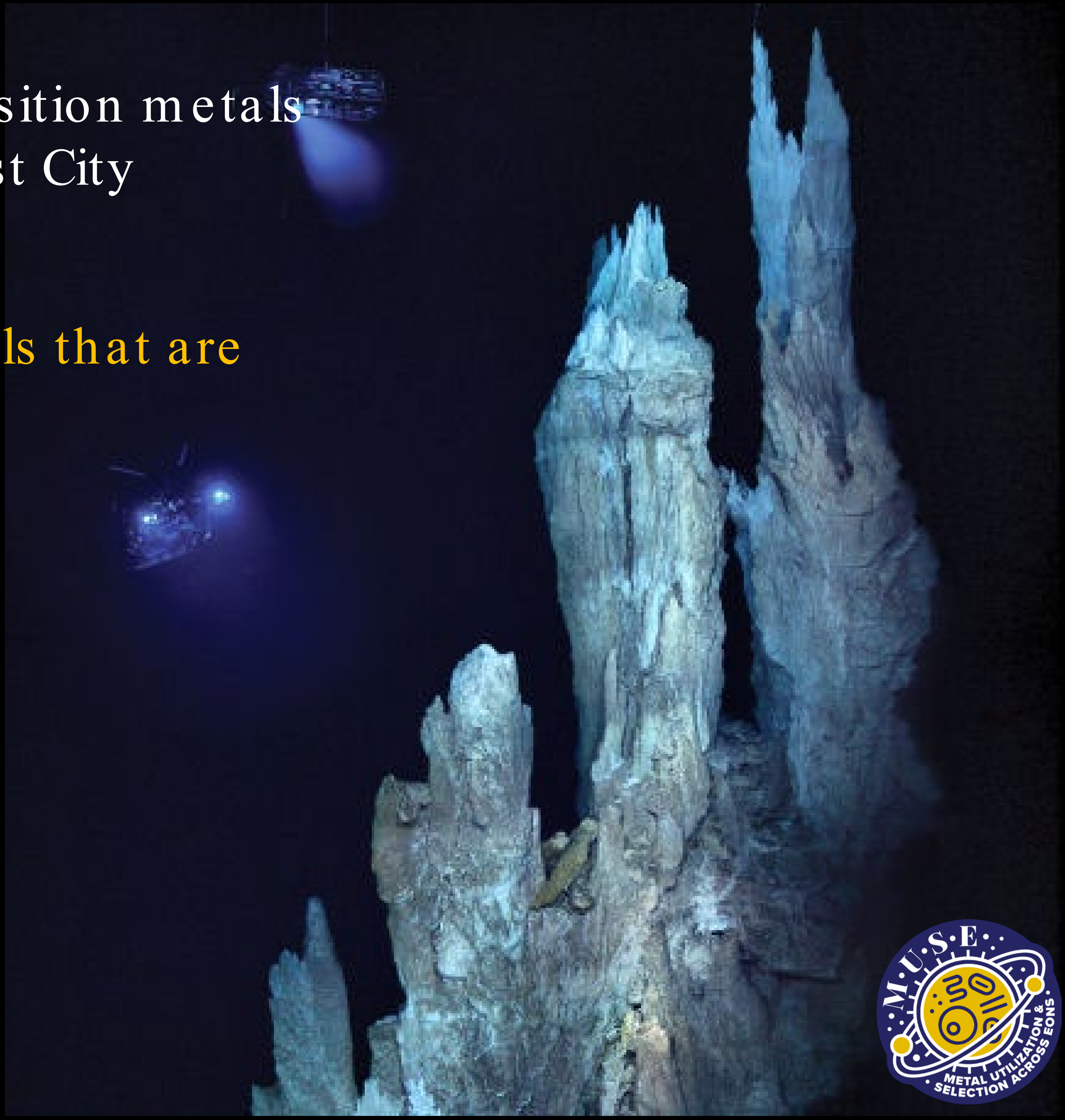
Rucker and Kaçar, *2023*

CellPress

Trends in Microbiology

Presenting new analyses of nutrient transition metals in seafloor vent fluids from the iconic Lost City Hydrothermal Field (LCHF)

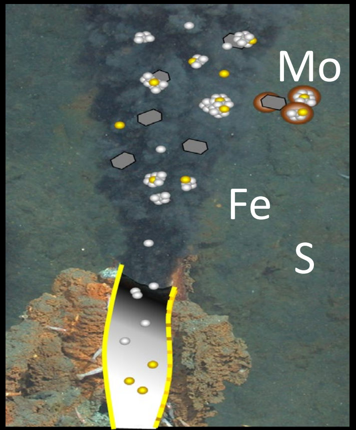
We have calculated the amounts of metals that are necessary to sustain life
(including Ni, Mo, Mn, Fe, Co, Cd, W)



Guy Evans et al.

Geochimica et Cosmochimica Acta

EARTH & PLANETARY SCIENCE LETTERS

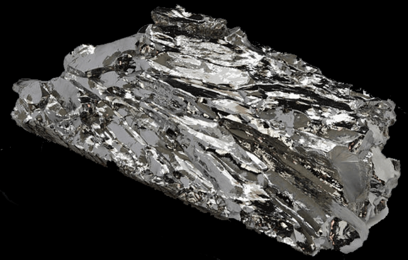


Recall…

Life as we know it requires nitrogen, but how does our understanding of the N cycle inform our search for life in the universe?

Looking for life in all the wrong (or right?) places?

We cannot put a lab on a spacecraft but we can distill that to a set of observables that can be measurable using a limited set of tools



Molybdenum

Iron

Vanadium

METAL UTILIZATION & SELECTION ACROSS EONS

Jet Propulsion Laboratory

UNIVERSITY OF WISCONSIN–MADISON

Looking for life in all the wrong (or right?) places?

We are recreating ancient Earth in the lab.
Can this tell us if Mars' past was alive or dead?

Goals:

- develop the techniques so that NASA astronauts can recognize the potential for past and present life elsewhere
- support planetary scientists in assessing potential for life on icy worlds
- help place exoplanets in context with ancient and present-day Earth

We study which elements may produce observable signatures under a variable conditions from Mars to icy-moons.

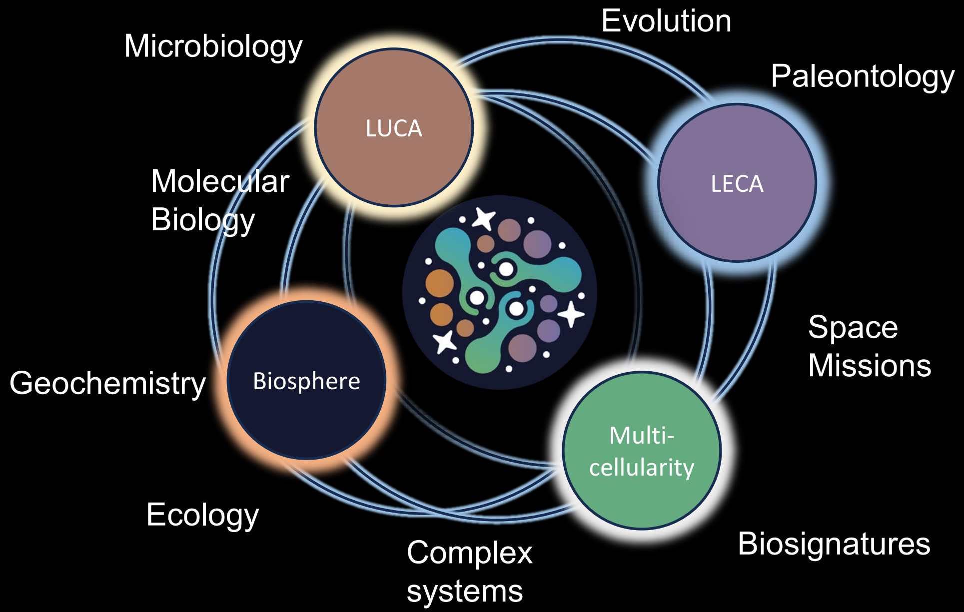
Our goal is to help people figure out what life looks life (or not!)

If we can tie *any* of the evolutionary singular events to the presence, absence, abundance or deficiency of elements, we might help to make this a problem that is more easily observable across interstellar distances.

Understanding life-planet co-evolution recorded in the rock record, in biodiversity, in genome databases, and modeled *in silico* or by lab proxy studies.

LIFE

FROM EARLY CELLS TO MULTICELLULARITY



A community dedicated to understanding life-planet co-evolution recorded in the rock record, in biodiversity, in genome databases, and modeled *in silico* or by lab proxy studies.

lifeRCN.org

FORBES > INNOVATION > SCIENCE

NASA Announces New Collaboration Probing How Life Evolved From Single-Cells On Earth

Allison Gasparini Contributor

I write about space.

Follow

May 17, 2022, 08:30am EDT

Forbes

LIFE joins four other research coordination networks currently in operation under NASA's Astrobiology Program. Researchers in the other coordination networks are currently investigating scientific questions pertaining to ocean worlds, planets with the potential to harbor life, prebiotic chemistry, and detecting signatures of life.

The coming decades will mark an increasingly dedicated search for habitable planets. The recently launched James Webb Space Telescope will be able to look for the chemicals that make up life in the atmospheres of planets that orbit in other star systems. A six-meter infrared optical and ultraviolet light telescope is on the top of the recommended projects for astronomers. Aimed for launch in the 2040s, the telescope would look for signs of life in faraway atmospheres in even more detail.

Kaçar hopes LIFE inspires early career researchers and students studying science to join in on the worldwide effort to understand life's evolution.

"There's a place for everybody here," she said. "As long as you're fascinated by life, there are many different ways to chase these questions and we want everyone to be excited and join us in this effort."

LIFE

FROM EARLY CELLS TO MULTICELLULARITY

There's a place for everybody here. As long as you're fascinated by life, there are many different ways to chase these questions and we want everyone to be excited and join us in this effort.

Co-Leads

- Mary Droser, UC-Riverside
- Betül Kaçar, UW-Madison,
- Frank Rosenzweig, GTech
- Ariel Anbar, ASU

Early Career Committee

- Christina Buffo, Georgia Institute of Technology
- Jaime Cordova, University of Wisconsin-Madison
- Bruno Cuevas-Zuviría, University of Wisconsin-Madison
- Ethan Edmans, Arizona State University
- Brandon Hasty, Arizona State University
- Adam Hoffman, University of California, Riverside
- Charles Ross Lindsey, Georgia Institute of Technology
- Kathryn Rico, Arizona State University
- Rachel Surprenant, University of California, Rivers

Steering Committee

- Tom Boothby, University of Wyoming
- Don Burke-Aguero, University of Missouri
- Shelley Copley, University of Colorado-Boulder
- Mark Ditzler, NASA Ames Research Center
- Ben Gill, University of Vermont
- Trinity Hamilton, University Minnesota
- Tim Lyons, University of California, Riverside
- Niki Parenteau, NASA Ames Research Center
- Daniel Stolper, University of California, Berkeley
- Cynthia Silviera, University of Miami
- Steve Vance, NASA Jet Propulsion Laboratory

NASA vpl NASA Goddard SPACE FLIGHT CENTER JPL Jet Propulsion Laboratory

Online community seminars and workshops

LIFE

FROM EARLY CELLS TO MULTICELLULARITY

LIFE is a network of astrobiologists focused on the coevolution of Earth and life. Together, we explore ways to advance this science, and its implications for the search for life on other worlds.

lifercn.org

@LIFE_RCN

youtube.com/@LIFE-RCN

LIFE
FROM EARLY CELLS TO MULTICELLULARITY

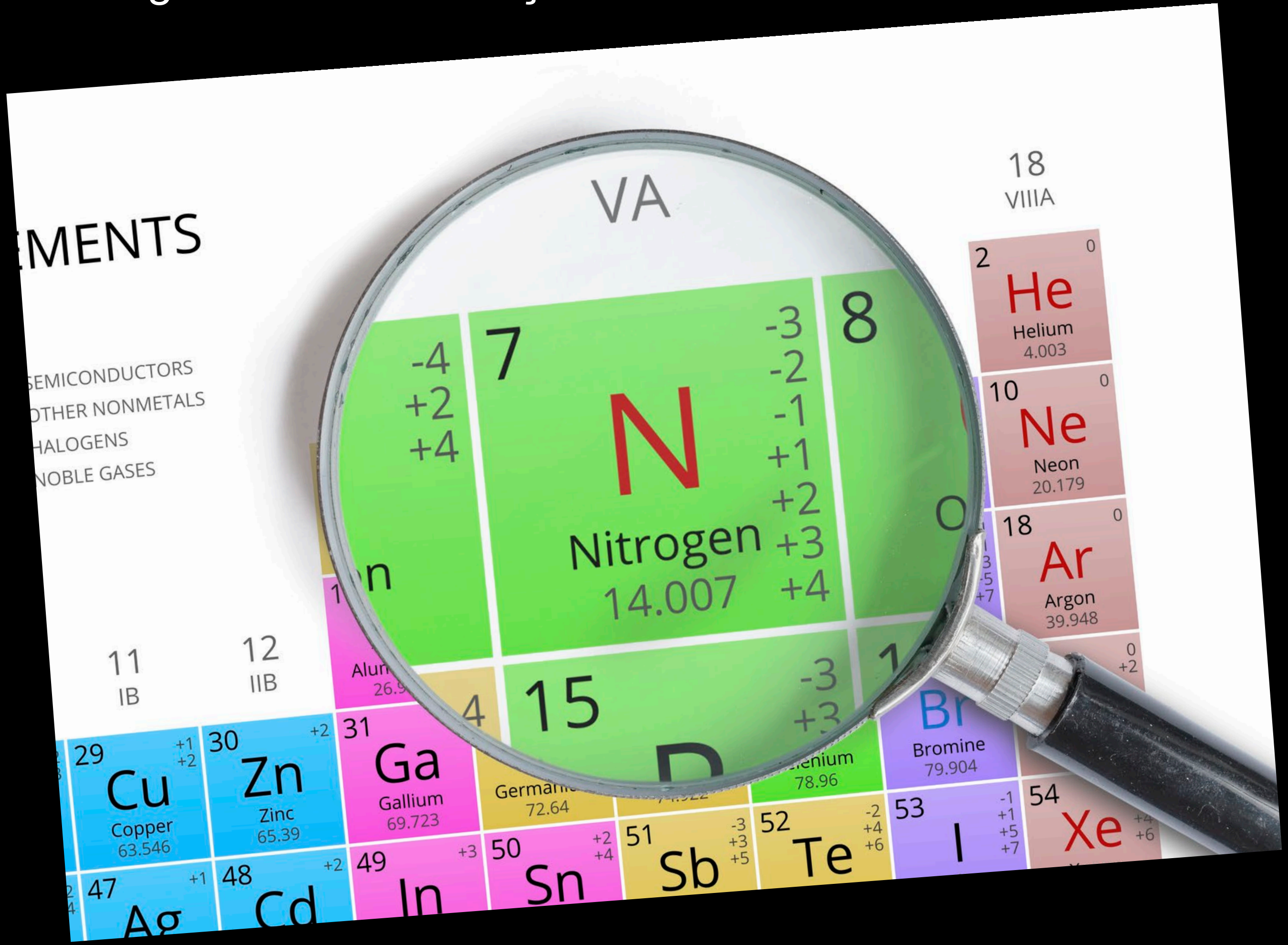
1st LIFE Workshop

Nitrogen Cycling Across Planetary Scales

October 18, 20, 2023

Lead Organizers: Eva Stueeken (St. Andrews Univ) & Ben Johnson (Iowa State)
LIFE organizers: Betül Kaçar and Ariel Anbar

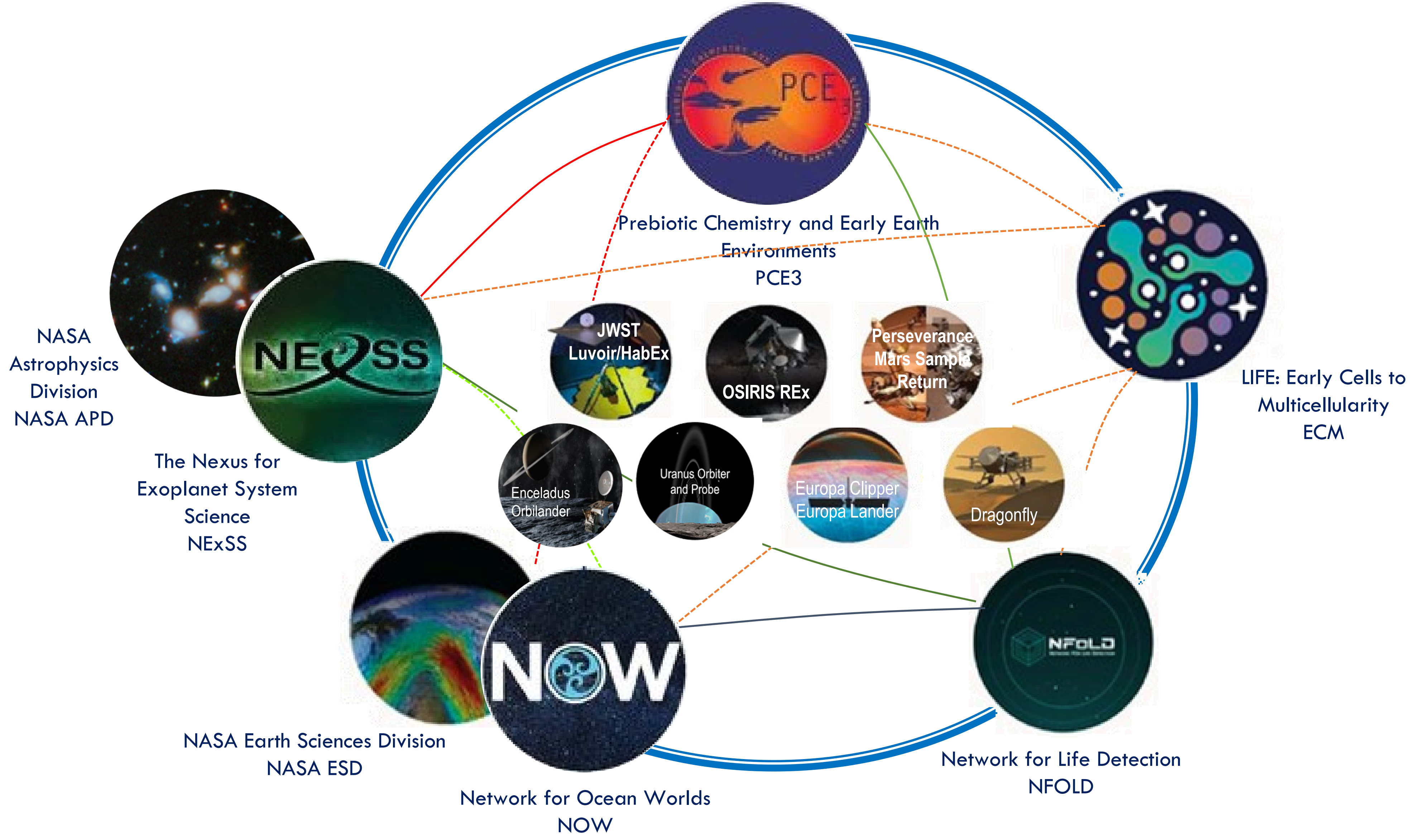
This workshop brought together a wide variety of scientists, including biologists, geologists, astronomers, and chemists to build connections and enhance understanding of the role of nitrogen in the search for life.



- 170 participants
- Over 8 countries
- 12 presenters, 4 panelists
- 1 white paper, 1 review paper

“The cosmic importance of nitrogen”

A connected network of networks – supporting current NASA Mission Science



Our goal is to help NASA and its missions to correctly assess the potential for past or present life

No single 'smoking gun' of biological presence

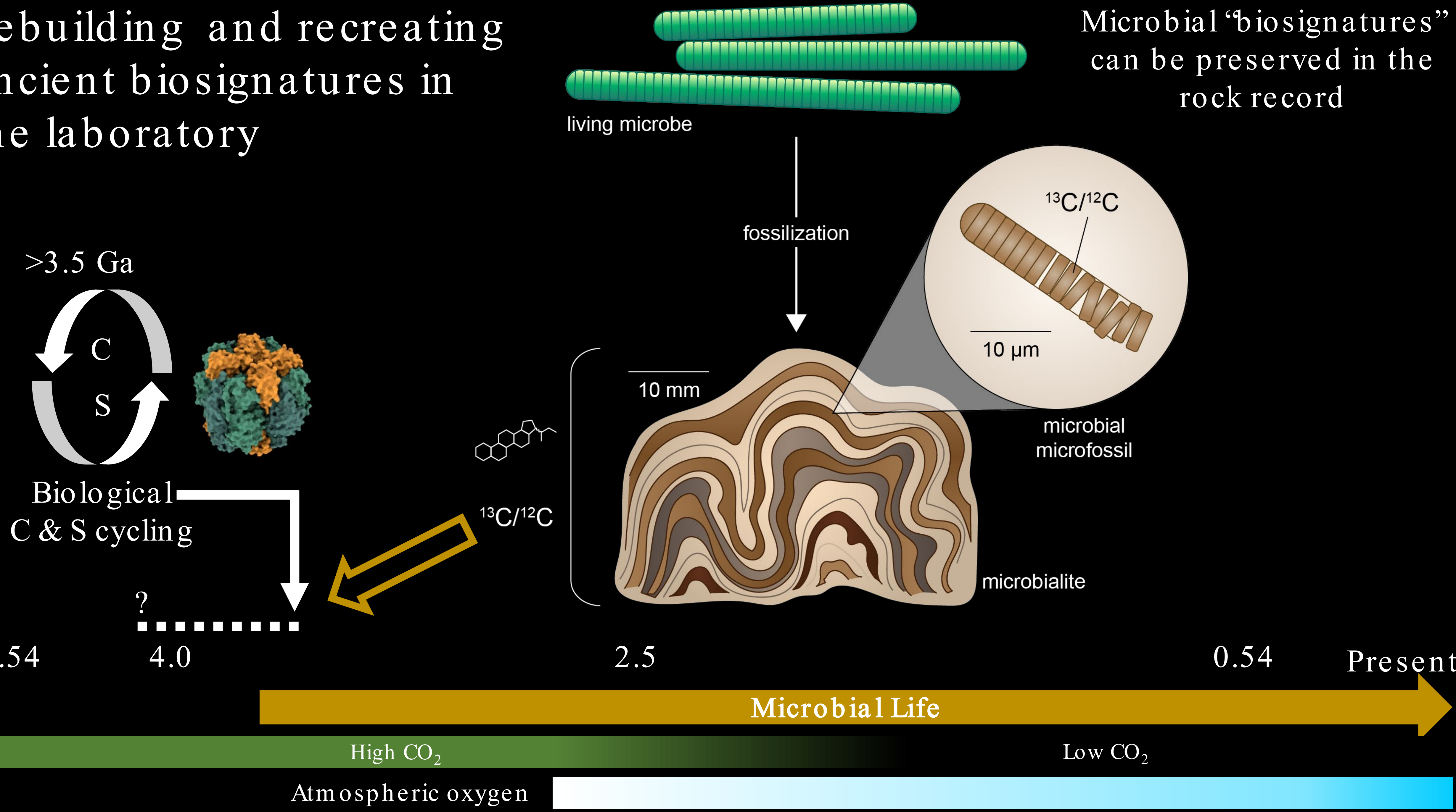
Strongest arguments will involve a mix of multiple, complementary biosignatures that reinforce a consistent view of biological impact.




Thank you!

Rebuilding and recreating ancient biosignatures in the laboratory

Microbial "biosignatures" can be preserved in the rock record



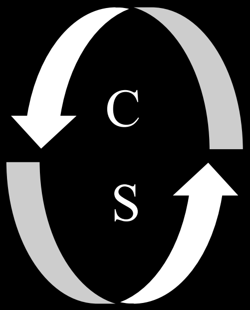
Rebuilding and recreating ancient biosignatures in the laboratory

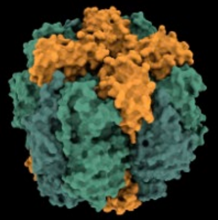
ORIGINAL ARTICLE | Open Access

Constraining the timing of the Great Oxidation Event within the Rubisco phylogenetic tree

Laboratory resurrection of ancient biosignatures (Kedzior, 2022)

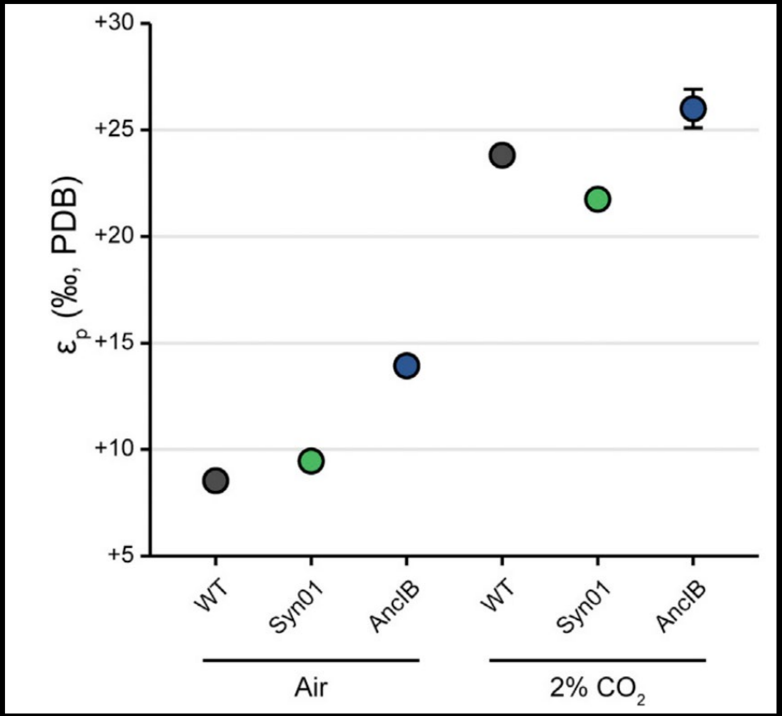
>3.5 Ga

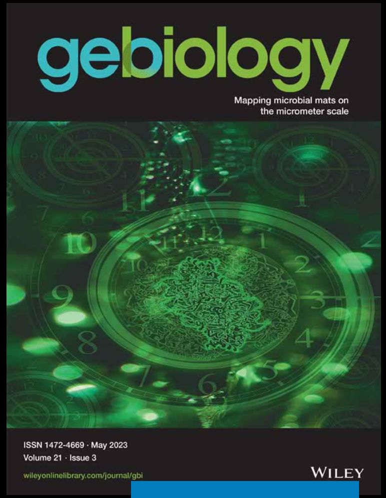




Biological C & S cycling

?





Cell Reports
A Cell Press journal

Kedzior et al., Cell Reports, 2022
Garcia et al., Geobiology, 2023
Kacar et al., ISME J, 2021

4.54 | 4.0 | 2.5 | 0.54 | Present

Microbial Life

High CO_2 | Low CO_2

Atmospheric oxygen

Reviewed 200-year-old literature. Reporting 270 combinations of molecules across the periodic table.

The data will be used in laboratory experiments simulating multiple planetary conditions, providing insight into <u>how</u> and <u>where</u> these ingredients could form complex cycles.

Supporting Information 4: Examples of Comproportionation-based Autocatalytic Cycles (interactive version)

Cmp.: Count of **Comp**ACs that are compatible with the common definition of comproportionation, corresponding to Table S1.

Brd. : Count of **Broad**-sense CompACs that affect the element and are only compatible with the rare definition of comproportionation, corresponding to Table S2; note that for a Broad-sense CompAC, any element that is involved in an autocatalyst is considered affected by this Broad-sense CompAC.

$_{1}$H Cmp.: 8 Brd.: 26																															$_{2}$He Cmp.: Brd.:
$_{3}$Li Cmp.: Brd.:	$_{4}$Be Cmp.: Brd.:																									$_{5}$B Cmp.: 7 Brd.: 4	$_{6}$C Cmp.: 9 Brd.: 10	$_{7}$N Cmp.: 8 Brd.: 3	$_{8}$O Cmp.: 7 Brd.: 31	$_{9}$F Cmp.: Brd.: 3	$_{10}$Ne Cmp.: Brd.:
$_{11}$Na Cmp.: Brd.: 6	$_{12}$Mg Cmp.: Brd.:																									$_{13}$Al Cmp.: 2 Brd.: 5	$_{14}$Si Cmp.: 5 Brd.: 1	$_{15}$P Cmp.: 9 Brd.: 3	$_{16}$S Cmp.: 11 Brd.: 12	$_{17}$Cl Cmp.: 7 Brd.: 5	$_{18}$Ar Cmp.: Brd.:
$_{19}$K Cmp.: Brd.:	$_{20}$Ca Cmp.: 1 Brd.: 8															$_{21}$Sc Cmp.: 1 Brd.:	$_{22}$Ti Cmp.: 2 Brd.:	$_{23}$V Cmp.: 9 Brd.:	$_{24}$Cr Cmp.: 5 Brd.: 1	$_{25}$Mn Cmp.: 15 Brd.:	$_{26}$Fe Cmp.: 5 Brd.: 1	$_{27}$Co Cmp.: 6 Brd.: 1	$_{28}$Ni Cmp.: 7 Brd.:	$_{29}$Cu Cmp.: 3 Brd.: 1	$_{30}$Zn Cmp.: Brd.: 4	$_{31}$Ga Cmp.: 5 Brd.:	$_{32}$Ge Cmp.: 2 Brd.:	$_{33}$As Cmp.: 8 Brd.: 2	$_{34}$Se Cmp.: 8 Brd.: 1	$_{35}$Br Cmp.: 6 Brd.: 1	$_{36}$Kr Cmp.: Brd.:
$_{37}$Rb Cmp.: Brd.:	$_{38}$Sr Cmp.: Brd.:															$_{39}$Y Cmp.: 1 Brd.:	$_{40}$Zr Cmp.: 2 Brd.:	$_{41}$Nb Cmp.: 7 Brd.:	$_{42}$Mo Cmp.: 3 Brd.:	$_{43}$Tc Cmp.: Brd.:	$_{44}$Ru Cmp.: Brd.:	$_{45}$Rh Cmp.: Brd.:	$_{46}$Pd Cmp.: Brd.:	$_{47}$Ag Cmp.: 4 Brd.:	$_{48}$Cd Cmp.: 1 Brd.:	$_{49}$In Cmp.: Brd.:	$_{50}$Sn Cmp.: 2 Brd.:	$_{51}$Sb Cmp.: Brd.:	$_{52}$Te Cmp.: 6 Brd.:	$_{53}$I Cmp.: 8 Brd.:	$_{54}$Xe Cmp.: 4 Brd.:
$_{55}$Cs Cmp.: Brd.:	$_{56}$Ba Cmp.: 1 Brd.:	$_{57}$La Cmp.: 1 Brd.:	$_{58}$Ce Cmp.: Brd.:	$_{59}$Pr Cmp.: Brd.:	$_{60}$Nd Cmp.: Brd.:	$_{61}$Pm Cmp.: Brd.:	$_{62}$Sm Cmp.: Brd.:	$_{63}$Eu Cmp.: 2 Brd.:	$_{64}$Gd Cmp.: Brd.:	$_{65}$Tb Cmp.: Brd.:	$_{66}$Dy Cmp.: Brd.:	$_{67}$Ho Cmp.: Brd.:	$_{68}$Er Cmp.: Brd.:	$_{69}$Tm Cmp.: Brd.:	$_{70}$Yb Cmp.: Brd.:	$_{71}$Lu Cmp.: Brd.:	$_{72}$Hf Cmp.: Brd.:	$_{73}$Ta Cmp.: 2 Brd.:	$_{74}$W Cmp.: 3 Brd.:	$_{75}$Re Cmp.: 6 Brd.:	$_{76}$Os Cmp.: Brd.:	$_{77}$Ir Cmp.: Brd.:	$_{78}$Pt Cmp.: Brd.:	$_{79}$Au Cmp.: 2 Brd.:	$_{80}$Hg Cmp.: 6 Brd.:	$_{81}$Tl Cmp.: Brd.:	$_{82}$Pb Cmp.: 4 Brd.: 6	$_{83}$Bi Cmp.: Brd.:	$_{84}$Po Cmp.: Brd.:	$_{85}$At Cmp.: Brd.:	$_{86}$Rn Cmp.: Brd.:
$_{87}$Fr Cmp.: Brd.:	$_{88}$Ra Cmp.: Brd.:	$_{89}$Ac Cmp.: Brd.:	$_{90}$Th Cmp.: 4 Brd.:	$_{91}$Pa Cmp.: Brd.:	$_{92}$U Cmp.: 1 Brd.:	$_{93}$Np Cmp.: Brd.:	$_{94}$Pu Cmp.: Brd.:	$_{95}$Am Cmp.: Brd.:	$_{96}$Cm Cmp.: Brd.:	$_{97}$Bk Cmp.: Brd.:	$_{98}$Cf Cmp.: Brd.:	$_{99}$Es Cmp.: Brd.:	$_{100}$Fm Cmp.: Brd.:	$_{101}$Md Cmp.: Brd.:	$_{102}$No Cmp.: Brd.:	$_{103}$Lr Cmp.: Brd.:	$_{104}$Rf Cmp.: Brd.:	$_{105}$Db Cmp.: Brd.:	$_{106}$Sg Cmp.: Brd.:	$_{107}$Bh Cmp.: Brd.:	$_{108}$Hs Cmp.: Brd.:	$_{109}$Mt Cmp.: Brd.:	$_{110}$Ds Cmp.: Brd.:	$_{111}$Rg Cmp.: Brd.:	$_{112}$Cn Cmp.: Brd.:	$_{113}$Nh Cmp.: Brd.:	$_{114}$Fl Cmp.: Brd.:	$_{115}$Mc Cmp.: Brd.:	$_{116}$Lv Cmp.: Brd.:	$_{117}$Ts Cmp.: Brd.:	$_{118}$Og Cmp.: Brd.:

(Peng et al. 2023)

MUSE "Encyclopedia Autocatalytica"
Peng et al., JACS, 2023

Other N-cycle metalloenzymes