Conjectures on Photosynthesis and Evolution in the TRAPPIST-1 System

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INTRODUCTION

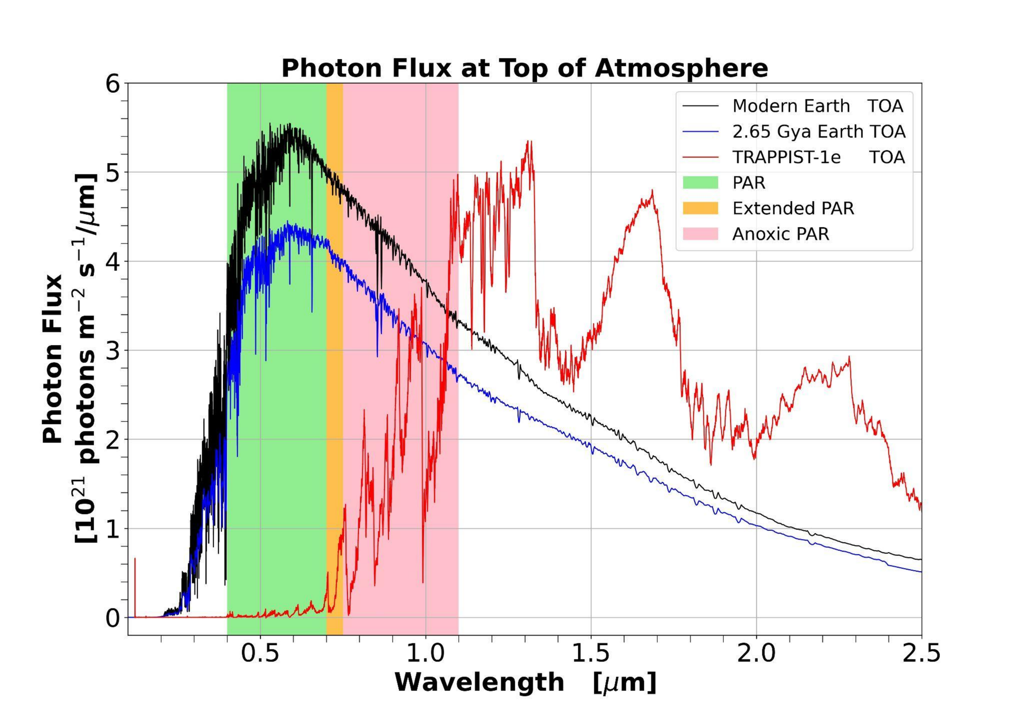
The emergence of oxygenic photosynthesis is arguably the most significant event in the history of life on Earth after the genesis of life itself [1,2,3]. Oxygenic photosynthesis allows life to tap into a virtually limitless supply of energy (sunlight) to enable the synthesis of organic molecules from carbon dioxide. Light in the 400-700 nm range is **known as "*PAR*": Photosynthetically Active Radiation** [3], and is required for oxygenic photosynthesis. Roughly 23% of the Sun's photons are in this range. Longer wavelength photons do not carry enough energy to enable the splitting of water molecules (the source of the oxygen). This will have a profound influence for life on a planet orbiting a late M-dwarf where the spectral energy distribution peaks at much lower energies [1,4,5,6].

A realistic investigation of life on such a planet is not currently possible given the large number of unknowns. However, we can explore a closely related question: *"What If The Earth Orbited TRAPPIST-1 Instead of the Sun?"*. Using such an analogy, we can gain insight into a problem that would otherwise be mired in specific assumptions.

TRAPPIST-1

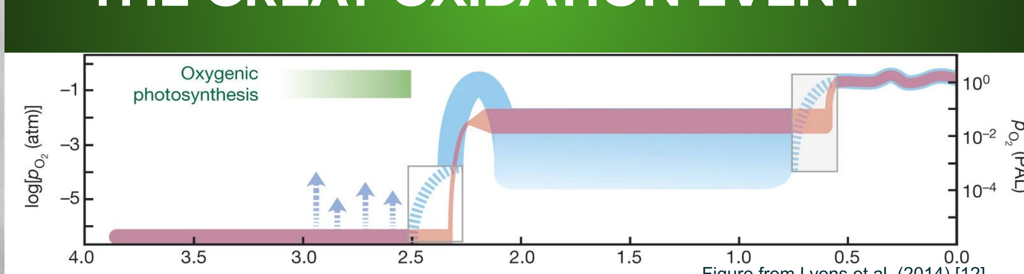
TRAPPIST-1 is a fascinating system with 7 Earth-size planets, three of which are in the habitable zone [7]. The TRAPPIST-1 star is an ultra-cool M dwarf with T_{eff} ~ 2560 K [8,9], and so only 0.2% of its photons fall in the PAR range: 10x less than the Sun.

We place our hypothetical Earth in orbit around TRAPPIST-1 at the same distance as TRAPPIST-1 e (0.02925 au [9]). This fictitious planet will be in the HZ with an equilibrium temperature similar to the true Earth, but **the number of PAR photons is only 0.9% of what is the incident on Earth from the Sun.** This immediately tells us that there may be a problem for oxygenic photosynthesis, and the subsequent evolution of life on such a planet.



The spectra above show the incident photon flux at the top of the atmosphere for Earth and TRAPPIST-1e [8]. The modern Sun (black [10]) and the Archean Sun (blue [11]) are shown. The green shaded area denotes the PAR range (400-700 nm). The orange marks the extended PAR (out to 750 nm). The pink region marks the extra wavelength range (out to 1100 nm) accessible to bacteria engaged in non-oxygenic photosynthesis.

THE GREAT OXIDATION EVENT



Oxygenic photosynthesis first arose in cyanobacteria, roughly 3 billion years ago (Gya) [13]. At that time, the Earth's atmosphere contained only trace amounts of oxygen. Due to a large number of oxygen sinks, it took ~700 million years before oxygen began to accumulate. **The sudden rise in the level of oxygen at 2.3 Gya** [14] **is known as the "Great Oxidation Event" (GOE).** It then took an **additional 1.76 billion years before the Cambrian explosion occured (the "big bang of biology")**, which marks a **burst of diversity and the onset of complex animal life** at 0.54 Gya.

If we assume the rate of oxygen production on our hypothetical Earth is linearly proportional to the number of PAR photons, the time it would take for a GOE-like event to occur is 77 Gyr – much older than the universe! A Cambrian explosion event would take a staggering 270 Gyrs. However, in biology rarely does the spherical cow approximation provide sufficiently accurate insight. In particular, the linear assumption is poor, and we must take into account the actual behavior of cyanobacteria under low-light levels.

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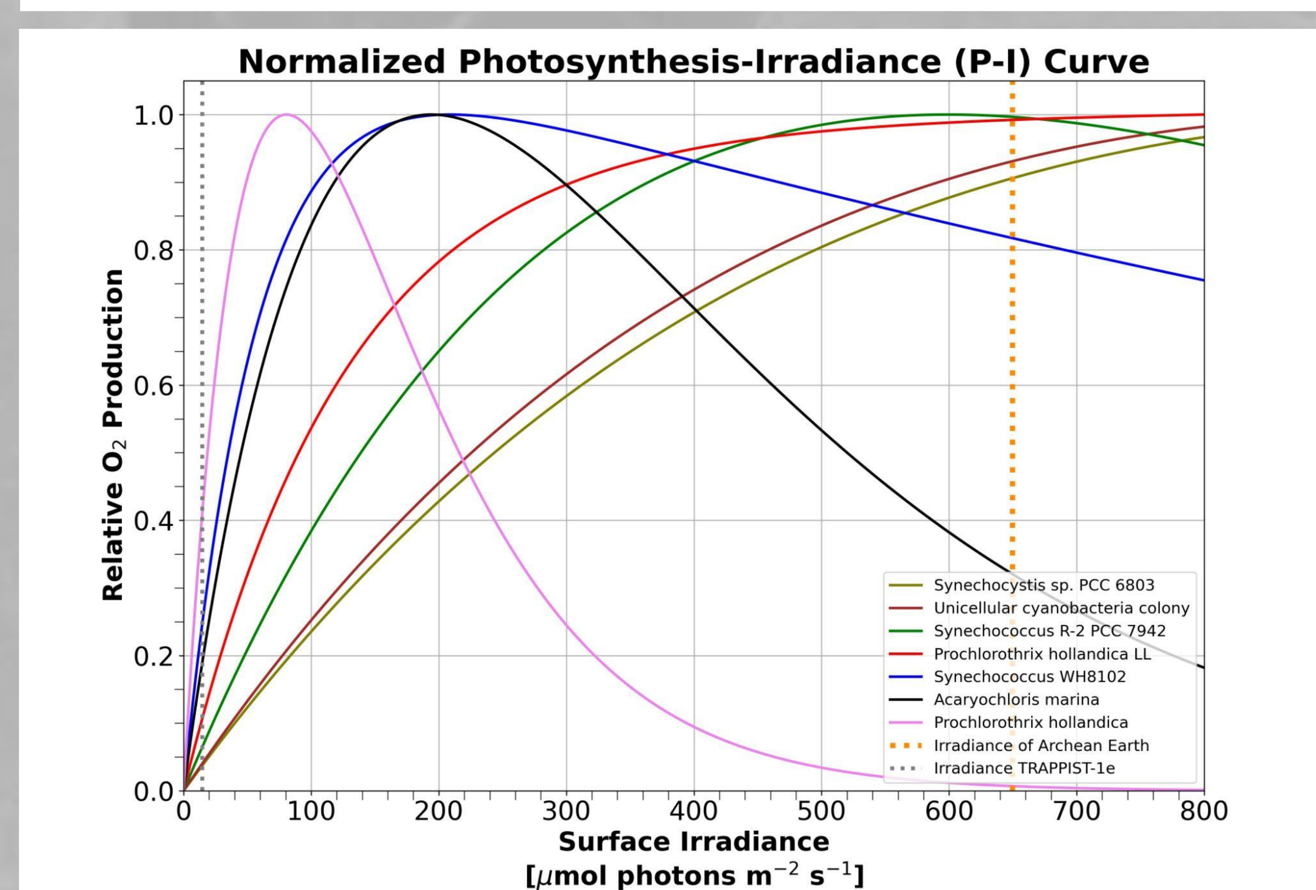
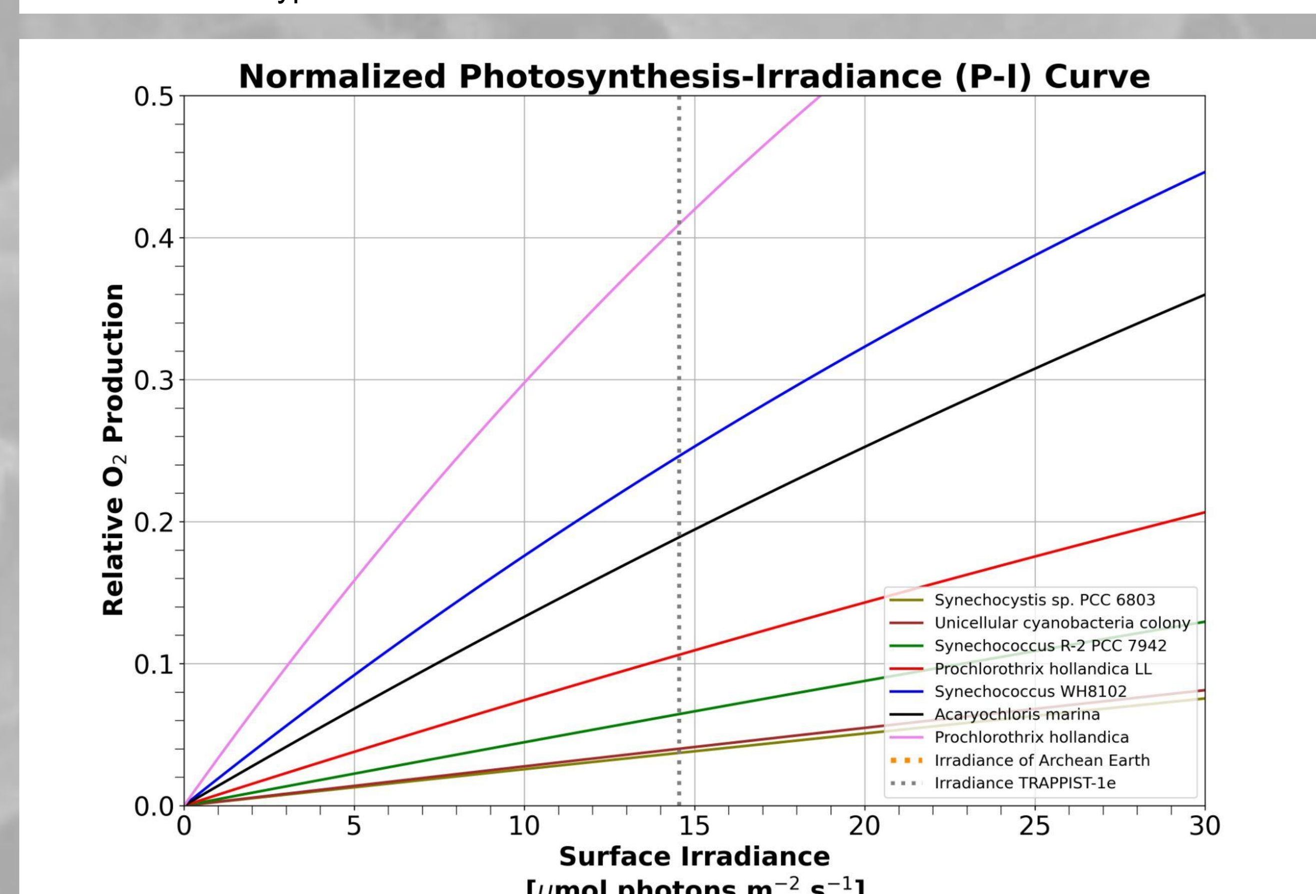
PHOTOINHIBITION

Oxygen production is highly non-linear due to an effect called *photoinhibition* [3]. **At high, or even moderate, light levels, oxygen production saturates then declines**. Accounting for photoinhibition is challenging but it makes a very significant difference.

The rate of oxygen production versus incident photon flux is known as a "photosynthesis-irradiance (P-I) curve". Examples for various species of cyanobacteria are shown below [15-19]. For species accustomed to bright light, oxygen production often flattens and declines when light levels exceed the daily average incident photon flux level on Earth's surface: 800 μmol photons/m^2/s [20]. But at 2.65 Gya, the Archean Sun was 20% fainter [11], providing an average insolation of 650 μmol PAR photons/m^2/s. But this is still much brighter than many low-light environments on Earth (e.g. marine/aquatic habitats, shade, etc.). Cyanobacteria accustomed to low-light environments can have P-I curves that saturate at much lower irradiance. For such species, estimating the timescale to a GOE by using the average Earth irradiance is not valid. For these cases we make the assumption that the peak of the P-I curve corresponds to the irradiance level in the environments they are adapted to. The oxygen production at the peak is then compared to the oxygen production at the irradiance level TRAPPIST-1e receives. This ratio is then used to scale the 700 Myr timescale that occurred on Earth. Unfortunately, the large differences in the P-I curves results in a large range for the timescale for oxygenation on our hypothetical planet.



Normalized P-I curves show the rise and fall of the oxygen production rate as the incident light level increases for various species of cyanobacteria. The mean surface irradiance the Earth receives from the Sun is at the right-hand edge of the figure; the vertical orange line is the mean for the Archean Sun. By contrast, the vertical gray dotted line at the left edge shows what our hypothetical Earth would receive from its TRAPPIST-1 host star.

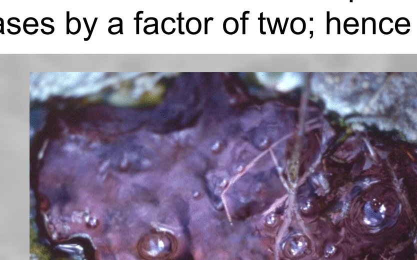


Shown above are normalized P-I curves for low-light irradiance levels similar to what TRAPPIST-1e receives (14.5 μmol photons/m^2/s in the PAR).

THE EXTENDED PAR AND TIDAL LOCKING

Oxygenic photosynthesis can use six types of chlorophyll [3]. Plants usually use chlorophyll a and b, and algae typically use chlorophyll c, but some cyanobacteria can also use chlorophyll d and f. These cyanobacteria can use light beyond the "red limit" of the standard PAR. In particular, **chlorophyll d & f can extend the PAR out to 750 nm** [1, 21]. On Earth, extending the PAR by 50 nm is not of great consequence: it adds ~17% more photons. But for TRAPPIST-1, whose spectrum peaks in the NIR, **this small extension *more than doubles* the number of photons available for oxygenic photosynthesis!** Chlorophyll d and f are not used by many species on Earth, but with such an abundance of extra photons available on a planet orbiting TRAPPIST-1, one would expect evolutionary pressures to push towards its use. This would reduce the timescale between the origin of oxygenic photosynthesis and the GOE by a factor of 2. This effect has been incorporated into the the estimated timescales for a GOE. Of the cyanobacteria examples considered, *Acaryochloris marina* lives in low-light level environments and uses chlorophyll d [1,19], and thus provides our "best estimate" value for the timescale for a GOE.

Note that TRAPPIST-1e's orbital period is 6.1 days so it is likely synchronously rotating. The day side will thus receive twice the incident number of photons, however, the planet's "daytime" surface area decreases by a factor of two; hence this will not alter the timescale.



Left: Photomicrograph of *Synechococcus* (rod-like cells, 1.2 μm wide); from Castenholz, R.W. 2015, Life, 5, 332
Middle: Mat of purple sulfur bacteria *Thermochromatium;* from Sattley, et al. 2022, Photosynth Research, 151, 12
Right: Macroscopic colony of *Gloeobacter*; from Montejano, G., et al. 2018, Plant Systematics & Evolution, 304, 1221
Poster background: Scanning electron micrograph of *Gloeobacter*; from Saw JHW, et al, 2013, PLoS ONE, 8, e76376

RESULTS

"What would happen if we replaced TRAPPIST-1e with the Archean Earth?" Because of TRAPPIST-1's very red spectrum, the planet would receive ~100x less photosynthetically active radiation than the Earth gets from the Sun. This would slow the oxygen production rate and a very naive calculation says that it would take ~77 Gyrs for oxygen to build up to even a few percent in the atmosphere.

A more realistic analysis that includes the effects of photoinhibition *for low-light species* and a more optimistic PAR wavelength range **results in a dramatic reduction in the timescale: as short as 1.8 Gyrs for a Great Oxidation Event.** This is less than the ~7.6 Gyr age of the TRAPPIST-1 system [22]. However, it would still take **over 6 Gyrs for a Cambrian explosion**-like event to occur.

In the table below, the shorter timescales are for the low-light level cyanobacteria, the longer are for the higher-irradiance species, and our best estimate comes from the species *Acaryochloris marina*.

	Origin of Oxygenic Photosynthesis to Great Oxygenation Event (GOE)	Origin of Oxygenic Photosynthesis to Cambrian Explosion
Modern Sun - No Photoinhibition	77 Gyr	270 Gyr
Archean Sun - No Photoinhibition	63 Gyr	235 Gyr
Archean Sun + Photoinhibition	3.4 - 38 Gyr	12 - 130 Gyr
Archean Sun + Photoinhibition + extended PAR	1.8 - 15 Gyr **[3.3 Gyr best]**	6.3 - 54 Gyr **[12 Gyr best]**

DISCUSSION AND CONJECTURES

Over the ~3.8 billion years life has existed on Earth, **only once has oxygenic photosynthesis evolved** [3]. Given numerous examples of convergent evolution we see in nature, this uniqueness suggests that the mechanism is particularly challenging to arise. **By contrast, *non-oxygenic* photosynthesis is present in many forms** and in a variety of life (e.g. green sulfur bacteria, purple sulfur bacteria, purple non-sulfur bacteria), *and evolved before oxygenic photosynthesis* [3]. Non-oxygenic photosynthesis does not split water molecules and thus **bacteriochlorophylls are able to use lower-energy photons, out to ~1100 nm** [6]. On a planet orbiting TRAPPIST-1, such **anoxic photosynthesis would have a *huge* advantage** because **22 times as many photons are available** (55 times as many in the standard PAR). **Anoxygenic photosynthetic bacteria would thus likely dominate** over oxygen-producing cyanobacteria. We speculate that **on such a hypothetical Earth, a GOE would never occur,** let alone a Cambrian explosion. **Complex animal life would not exist.**

While TRAPPIST-1 was chosen for this study because it is an extreme case of an ultracool M dwarf, the results are generalizable and any habitable zone planets orbiting late M-dwarf stars, such as LP 890-9 [23] or SPECULOOS-3 [24], may share this same fate.

FUTURE WORK

The results are very sensitive to the P-I curve employed. We used P-I curves for a variety of cyanobacteria, but the most **appropriate genus to use is *Goeobacter*, as this is a ancient lineage of cyanobacteria** [13]. We were unable to find such a P-I curve.

While the dates of the Great Oxidation Event at 2.3 Gya and the Cambrian Explosion at 0.54 Gya are fairly precisely known, the date of the origin of oxygenic photosynthesis is quite uncertain. It remains a very active research area. Using extremes ranges of what is plausible could result in a factor ~2 uncertainty in the timescales.

Red and NIR light is highly absorbed by water. Our scaling includes this to zeroth order, but for a very red incident stellar spectrum this would have the effect of lengthening the timescale to a GOE.

If future work shows we are incorrect, *i.e.,* abundant oxygen found in a late M-dwarf exoplanet's atmosphere, this would be extremely exciting and would suggest that life has found a way to carry out oxygenic photosynthesis with NIR photons.

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