

**EVOLUTION OF TERRESTRIAL HABITABILITY.** Nicole J. Torres<sup>1</sup> and Abel Méndez<sup>2</sup>, <sup>1</sup>Department of Biology, University of Puerto Rico at Arecibo (nicole.torres22@upr.edu), <sup>2</sup>Planetary Habitability Laboratory, University of Puerto Rico at Arecibo (abel.mendez@upr.edu).

Habitability is generally defined as the suitability of environments for life. Photosynthetic primary productivity on Earth is the main supporter of terrestrial life and one of the main indicators of terrestrial habitability (Geider et al., 2001; Milesi et al., 2005; Méndez, 2009). In this study we will use the mass and energy habitability model of Méndez et al., (2018) to trace the evolution of terrestrial habitability from early Earth to climate change. Here we are exploring the main environmental factors to include in our model, including applications to exoplanets.

The use of primary productivity as a measure of habitability is not new. For example, estimates of potential photosynthetic habitable zones (pHZ) on exoplanets have been used to assess the number of habitable planets in the galaxy (von Bloh et al., 2010). Planets around long-lived stars, like M dwarfs, have more time for life to develop, but they also receive less light in the visible range, which might be necessary for photosynthetic life. Certainly, evolution could make exolife better adapted to these conditions, but those cases are harder to compare with geolife because there are many more assumptions to make. As a first approach, it is necessary to establish a terrestrial life baseline for comparison purposes.

Net primary productivity (NPP) is a measure of the organic matter produced by photosynthetic life per unit time and area in land or ocean surfaces. Almost all life, from herbivores to carnivores, depend of this organic matter for survival. For practical reasons, this organic matter is usually measure in grams of carbon, although units of biomass and energy are also used. The mean global NPP of Earth today is about 206 g C m<sup>-2</sup> year<sup>-1</sup> (105 Pg C year<sup>-1</sup>), coincidentally, almost half divided between land and the ocean (Geider et al., 2001).

NPP is determined by many environmental abiotic and biotic factors. Land and ocean NPP is mainly controlled by temperature, light, and atmospheric carbon dioxide. The effect of temperature on NPP is very important at seasonal, and longer scales. Atmospheric opacity, clouds and water turbidity affect light but the solar output is only important at very large time scales in the orders of million years. Carbon dioxide is relevant from centennial and longer time scales. On land, water availability is also a limiting factor and nutrients on the ocean (especially iron and Sulphur). Even biotic interactions with microbial life controls NPP (Van Der Heijden et al., 2008).

One of the main factor affection terrestrial NPP is temperature. Most terrestrial vegetation are only able to photosynthesize between 0°C to 50°C, with a mean optimum near 25°C for both C3 and C4 plants (higher for C4 plants). This is also true for different biomes where optimum growth temperatures are between 17°C to 29°C (Woodward and Smith, 1994). This is higher than Earth's mean global temperature of 15°C, which forced vegetation closer to the equator and produced clear latitudinal gradients. Consequently, the low latitudes have a higher productivity and support a larger biodiversity, among other explanations (Willig et al., 2003).

Carbon constitutes about 40% of cells dry mass. Primary producers incorporate carbon to their metabolism from atmospheric carbon dioxide. Most of it is extracted during photosynthesis and some is returned back to the atmosphere through respiration. The net effect is some standing biomass with losses due to decomposition and herbivores. The dependence of photosynthesis on carbon follows a Michaelis–Menten model. The minimum CO<sub>2</sub> partial pressures needed for any photosynthesis (C4) is estimated at near 0.01 mbars (10 ppmv) (Percy and Ehleringer, 1984). Growth response at elevated CO<sub>2</sub> quickly saturates beyond 0.45 mbars (450 ppmv) for most plants, with C3 plants being more sensitive than C4 plants (Poorter and Navas, 2003).

Light is the essential ingredient for photosynthesis. Earth's primary producers experience a photon flux density of 1.8 mmol of photons m<sup>-2</sup> s<sup>-1</sup> at the surface (Kiang et al., 2007a). Theoretical unicellular light lower limits have been estimated to near 0.1 μmol of photons m<sup>-2</sup> s<sup>-1</sup> (Raven, 1984). However, brown sulfur bacteria, living at near 80 m depth in the Black Sea, is adapted to even lower values of 0.003–0.01 μmol of photons m<sup>-2</sup> s<sup>-1</sup> (Overmann et al., 1992). The upper limit has been estimated close to 6–9 mmol of photons m<sup>-2</sup> s<sup>-1</sup> before photo damage (Wolstencroft and Raven, 2002). Photosynthesis over this saturation conditions is still possible under the protection of haze, cloud cover, water, or ice.

Primary productivity on land and ocean surfaces by plants and phytoplankton, respectively, is not the only system supporting complex life on Earth, and certainly not the only scenario expected on habitable exoplanets. For example, chemosynthetic bacteria from hydrothermal vents are also known to sustain ecosystems using reduced Sulphur (Cavanaugh et al.,

1981; Felbeck, 1981), methane (Childress et al., 1986; Cavanaugh et al., 1987), and more recently hydrogen (Petersen et al., 2011). Also, other more exotic forms of photosynthesis might be possible (Haas, 2010).

Earth's evolutionary history is also an example on how habitable exoplanets could be observed in any stage. The discovery of bacteria fossils from 3,500 Ma (millions of years ago) rocks suggests the presence of Sulphur-metabolizing cells in anoxic environments in the early Earth. Photosynthesis probably started during this time but was only dominant after 2,500 Ma (Anbar et al., 2007). However, it was not after 542 Ma, when oxygen levels were higher and Earth escaped from the last global glaciation, that primary productivity in the surface supported a large and complex diversity on both land and ocean environments. Exoplanets with detectable atmospheric biosignatures but without a discernable biological surface features are possible (Cockell et al., 2009).

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