EVOLUTION OF TERRESTRIAL HABITABILITY. Nicole J. Torres-Santiago¹, Joemar Pérez¹, Karen Delgado¹, Eduardo Cruz², José Ramírez³, Natalia López⁴, Kevin Novoa⁴, Jadenys S. Díaz¹, Yovaniel Carrión¹, Eliud Rivas¹, Joshua Rivera¹ and Abel Méndez⁵, ¹Department of Biology, University of Puerto Rico at Arecibo (nicole.torres22@upr.edu), ²Department of Geology, University of Puerto Rico at Mayagüez, ³Department of Biology, University of Puerto Rico at Río Piedras, ⁴Department of Nursing, University of Puerto Rico at Arecibo, ⁵Planetary Habitability Laboratory, University of Puerto Rico at Arecibo.

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 on this organic matter for survival. For practical reasons, this organic matter is usually measured 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 m² year¹ (105 Pg C year¹), 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. 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 factors affecting 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.

Light is the essential ingredient for photosynthesis. Earth's primary producers experience a photon flux density of 1.8 mmol of photons m⁻² s⁻¹ at the surface (Kiang et al., 2007a). Theoretical unicellular light lower limits have been estimated to near 0.1 µmol of photons m-2 s-1 (Raven, 1984). Photosynthesis over 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. Having a clear understanding of how an earlier Earth might have looked and behaved can give us additional insight to studying exoplanets that are in stages similar to the early Earth. 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 on the surface supported a large and complex diversity on both land and ocean environments. Exoplanets with detectable atmospheric biosignatures but without a discernible biological surface features are possible (Cockell et. al., 2009).

Around 250 Ma, Pangaea started to break up in a prolonged disintegration that finished in the Cretaceous (Wignall, P.B. et al., 2005). The volcanic upheaval in Siberia in conjunction with hydrothermal processes (Benton, MJ. et al., 2018), continued for as long as one million years, releasing enormous amounts of greenhouse gases into the atmosphere, which produced intense global warming, massive disruption to the carbon cycle, ocean acidification, oxygen deficiency (superanoxia), and other environmental changes. These significant environmental changes in the onset of fragmentation of the supercontinent Pangaea (Button et al., 2017) impacted the evolution of life on Earth, leading it to collapse, as more than 90% of all marine species and 70 % of land animals became extinct. The Permian-Triassic mass extinction, or more commonly, the Great Dying, was the most severe extinction event in Phanerozoic.

According to the habitability model used, terrestrial habitability ranged from 0.92 to 1.06 in the last 650 million years. That is, it has changed around 5% in the time analyzed. There are two notable periods of greater habitability, one during the Cambrian and the other between the Permian and the Triassic. Our data indicates that in the Cambrian Period the habitability had the most drastic increase in the time studied. During this period, the Cambric Explosion occurred, in which most of the major groups of animals first appear in the fossil record. The peaks of habitability coincided with some known events that occurred on Planet Earth. A Pearson Correlations were made to correlate and associate possible events responsible of changes in habitability. The correlation between habitability and temperature is 0.38, with temperature being one of the parameters that have changed the most over time. The correlation between habitability and oxygen is 0.12, while with the diversity of land animal families it is 0.33, both positive.

We have used our habitability estimate to make several Pearson Correlations and estimate the association between paired samples. The habitability and number of insect families have a correlation of 0.28. Meanwhile, the habitability and diversity of marine animals is -0.20, which is interesting for the contrast with the families of terrestrial animals. According to the history of Planet Earth, we know that five major extinctions have occurred. We have observed that there is a relation between habitability and the Five Big Extinction with a correlation of 0.43.

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