Review Article

Habitability Models for Astrobiology

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Abstract

Habitability has been generally defined as the capability of an environment to support life. Ecologists have been using Habitat Suitability Models (HSMs) for more than four decades to study the habitability of Earth from local to global scales. Astrobiologists have been proposing different habitability models for some time, with little integration and consistency among them, being different in function to those used by ecologists. Habitability models are not only used to determine whether environments are habitable, but they also are used to characterize what key factors are responsible for the gradual transition from low to high habitability states. Here we review and compare some of the different models used by ecologists and astrobiologists and suggest how they could be integrated into new habitability standards. Such standards will help improve the comparison and characterization of potentially habitable environments, prioritize target selections, and study correlations between habitability and biosignatures. Habitability models are the foundation of planetary habitability science, and the synergy between ecologists and astrobiologists is necessary to expand our understanding of the habitability of Earth, the Solar System, and extrasolar planets. Key Words: Habitability—Habitat Suitability Models—Planetary habitability—Biosignatures—Exoplanets—Astrobiology. Astrobiology 21, xxx–xxx.

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1. Introduction

L IFE ON EARTH is not equally distributed. There is a mea-
surable gradient in the abundance and diversity of life,
both spatially (*e.g.,* from deserts to rain forests) and tem-
porally (*e.g.,* from seasonal to geological timescales). Our
planet has also experienced global environmental changes
from the Archean to the Anthropocene, which further con-
ditioned life to a broad range of conditions. In general, *a
habitable environment is a spatial region that might support
some form of life* (Farmer, 2018), *albeit not necessarily one
with life* (Cockell *et al.,* 2012). One of the biggest problems
in astrobiology is how to define and measure the habitability
not only of terrestrial environments but also of planetary en-
vironments, from the Solar System to extrasolar planets (also
known as *exoplanets*). The word *habitability* literally means
the *quality of habitat* (the suffix *-ity* denotes a quality, state, or
condition). Astrobiologists have been constructing different
general definitions of habitability, not necessarily consistent
with one another (*e.g.,* Hoehler, 2007; Shock and Holland,
2007; Cárdenas *et al.,* 2014, 2019; Cockell *et al.,* 2016;
Heller, 2020). Other more specific habitability definitions,
such as the canonical Habitable Zone (*i.e.,* the orbital region
in which liquid water could exist on the surface of a planet),
are used in exoplanet science (Kasting *et al.,* 1993). Ecolo-
gists developed a standardized system for defining and mea-
suring habitability in the early 1980s; however, this is seldom
utilized in the astrobiology community (USFWS, 1980).

The popular term *habitability* is formally known as
habitat suitability in biology. Ecologists before the 1980s
were using different and conflicting measures of habitability,
a situation not much different from today for astrobiologists.
The U.S. Fish and Wildlife Service (USFWS) decided to
solve this problem with the development of the Habitat
Evaluation Procedures standards in 1974 for use in impact
assessment and project planning (USFWS, 1980). These pro-
cedures include the development and application of Habitat
Suitability Models (HSMs) (Hirzel and Lay, 2008). Other
names for these models are Ecological Niche Models,
Species Distribution Models, Habitat Distribution Models,
Climate Envelope Models, Resource Selection Functions, and
many other minor variants (Guisan *et al.,* 2017). These mul-
tivariate statistical models are widely used by ecologists to-
day to quantify species-environment relationships with data
obtained from both ground and satellite observations. HSMs
integrate concepts as needed from ecophysiology, niche
theory, population dynamics, macroecology, biogeography,
and the metabolic theory of ecology.

Astrobiologists have largely not utilized HSMs for at least
three reasons. First is the naming: *habitability* is a common
word in the earth and planetary sciences, but it is not gener-
ally used by biologists. Thus, a quick review of the scientific
literature shows no definition of this concept in biological
terms. The second reason is the specialization: HSMs are a
specialized topic of theoretical ecology, which is not highly
represented in the astrobiology community. The third is ap-
plicability: HSMs are mostly used to study the distribution
of specific wild animals and plants, not microbial communi-
ties or ecosystems in general (generally the focus of astro-
biological studies), so it may not seem readily applicable to
the field of astrobiology, but this is changing (*e.g.,* Treseder
et al., 2012). Yet microorganisms (bacteria, fungi, and other

unicellular life) exhibit endosymbiotic relationships with
animals and plants and also play a key role in their survi-
val. Thus, anything that can be said about habitability at the
macroscopic level is tightly coupled to habitability at the
microscopic level. Indeed, potential methods for incorporat-
ing microbial ecology into ecosystem models are discussed
in the work of Treseder *et al.* (2012). In one way, the mathe-
matical framework behind HSMs is easier to apply to micro-
bial communities than animals because the spatial interactions
of animals (*e.g.,* predation) tend to be much more complex.
However, microbial life is not easy to quantify in free-living
populations, and it is thus harder to validate the HSMs
with them, although molecular methods are changing this
(Douglas, 2018).

The definition and core framework of HSMs can be ex-
tended from Earth to other planetary environments. How-
ever, the astrobiology field does not have the luxury of
validating HSMs with the presence of life unless when ap-
plied to environments on Earth (*e.g.,* extreme environments).
Thus, known ecophysiology models are used instead to pre-
dict the occurrence, distribution, and abundance of putative
life in any planetary environment. Attempting to measure
the habitability of a system without knowing all the envi-
ronmental factors controlling it may seem like an impossible
task. However, even on Earth this problem can be appro-
ached by selecting a minimum set of relevant factors to
simplify the characterization of the systems. While the ob-
jective can be to establish whether a system is habitable, it
can also be simply to explore how the selected environ-
mental variables contribute to the habitability of the system.
Usually, a library of habitability metrics is created for each
environment or life-form under consideration, with each
metric dependent on the species, scales, or environmental fac-
tors under consideration. In a fundamental sense, the only
way to really know whether a place is habitable is to find (or
put) life on it (Zuluaga *et al.,* 2014; Chopra and Lineweaver,
2016). It is nearly impossible, nor is it desirable, to include
all factors affecting habitability in a model, even for environ-
ments on Earth. Thus, the objective of habitability models is
to understand the contributions of a *finite* set of variables
toward the *potential* to support a specific species or com-
munity (*e.g.,* primary producers, organisms that use abiotic
sources of energy) (Guisan *et al.,* 2017). So even if we do
not know or do not include all the relevant factors, we can
consider the effects of those we do know.

Here, we recommend adapting and expanding the ecolo-
gists' nearly four decades of experience in modeling hab-
itability on Earth to astrobiological studies. These models
can be used to characterize the spatial and temporal distri-
bution of habitable environments, identify regions of inter-
est in the search for life, and eventually explore correlations
between habitability and biosignatures. For example, such
models would help test the hypothesis that biosignatures
(or *biomarkers*) are positively correlated with proxy indi-
cators of geologically habitable environments (or *geo-
markers*); *that is,* there is life whenever there are habitable
environments on Earth (Martinez-Frias *et al.,* 2007). We
also note that the concept of biosignatures encompasses
any detectable signature of life or its by-products on a
planet's atmosphere, which includes possible signatures
of planetary-scale technology, known as *technosignatures*
(Wright and Gelino, 2018). Measurements by past and

future astrobiology-related observations (*e.g.,* from ground, telescopes, or planetary missions) can be combined into a standard library of habitability models. Results from different observations can then be compared, even when using different measurements, since, through the use of HSMs, their results can be mapped to the same standard scale (*e.g.,* zero for worst and one for best regions). A Habitability Readiness Analysis could be developed for any observation campaign to determine how its current instruments could be used, or what new instruments should be added, for habitability measurements in the spatial and temporal habitability scales of interest. Furthermore, it might also be possible to develop new instruments for direct habitability measurements.

This review addresses many of the misconceptions about habitability and stresses the need for better integration between the habitability models used by ecologists and astrobiologists. This is not a review of those factors affecting habitability, which are discussed elsewhere (*e.g.,* National Research Council, 2007; Des Marais *et al.,* 2008; McKay, 2014; Hendrix *et al.,* 2018), but about the multivariate models that integrate these factors. Section 2 presents an overview of current ecology models with an emphasis on the HSM. Section 3 discusses some examples of how habitability is currently implemented in the astrobiology field. Section 4 describes our recommendations on how to adapt and expand the ecology models to the astrobiology field. Section 5 presents important science questions that could be answered from habitability models. Finally, Section 6 presents our concluding remarks.

2. Habitability in Ecology

Habitat Suitability Models (HSMs) are widely used in ecology to study the habitability of environments, many times under different definitions: Species Distribution Models or Ecological Niche Models (Kuhn *et al.,* 2016; Guisan *et al.,* 2017). An important step in the construction of HSMs is the selection of spatially explicit environmental variables at the right resolution to determine a species' preferred environment (*i.e.,* its niche) as close to its ecophysiological requirements as possible. Environmental variables (such as edaphic, from the Greek noun ''edaphos'' meaning ground factors—defined as any chemical, physical and biological properties of the soil) can exert complex direct or indirect effects on species (*e.g.,* Oren, 1999, 2001; Fierer *et al.,* 2007; Allison and Martiny, 2008; Lauber *et al.,* 2008; Rajakaruna and Boyd, 2008; Fierer *et al.,* 2012). These variables are ideally chosen to reflect the three main types of influence on a species: (1) regulators or limiting factors, defined as factors controlling a species' metabolism (*e.g.,* physical-chemical conditions such as temperature and salinity); (2) disturbances, defined as any perturbations affecting environmental systems; and (3) resources, defined as all compounds that can be consumed by organisms (*e.g.,* nutrients). There are many other variables that exert an indirect, rather than a direct, effect on species distribution. The construction of HSMs follows five general steps: (1) conceptualization; (2) data preparation; (3) model calibration; (4) model evaluation; and (5) spatial predictions (Guisan *et al.,* 2017).

One of the main HSM tools is the *Habitat Suitability Index* (HSI), which provides one way of quantifying the capacity of a given habitat to support a selected species. An index is the ratio of a value of interest divided by a standard of comparison. The value of interest is an estimate or measure of the quality of habitat conditions for a species in the studied environment, and the standard of comparison is the corresponding value for the optimum habitat conditions for the same evaluated species. An HSI of zero (minimum value) represents a totally unsuitable habitat, and a maximum value of one represents an optimum habitat. In developing an HSI, we should obtain a direct and linear relationship between the HSI value and the carrying capacity of the environment for the species under consideration (USFWS, 1980). The functions describing the species distribution or abundance along each environmental variable in an HSM are called *species response curves* (Austin and Gaywood, 1994). These curves, when plotted, can vary from simple boxlike envelopes resulting in binary indices to more gradual and complex responses resulting in continuous indices (Fig. 1). ◀F1

Carrying capacity is generally defined as the maximum supported population density in equilibrium. More precisely, carrying capacity is the user-specified quality biomass of a particular species for which a particular area will supply all energetic and physiological requirements over a long, but specified, period (Giles, 1978). Since habitability could be taken as proportional to carrying capacity, as defined by the HSI, it is then related to the fraction of mass (*e.g.,* nutrients) and energy (*e.g.,* light) available or usable by a particular species or community from the environment. A common and difficult problem for HSIs is how to combine the effect of many environmental variables into a single index. In theoretical ecology, the solutions are known as aggregation methods. These methods can combine the variables by using arithmetic, geometric, or harmonic means, among others. The general rule is to keep the index proportional to carrying capacity and correlated with the presence and absence of the species of interest in the environment. Occurrences or presence probabilities are generally simpler to combine as products. Ecophysiological response curves often involve the fitting of standard statistical models to ecological data by using simple (multiple) regression, Generalized Linear Models, Generalized Least Squares, or Generalized Additive Models, among others.

The usual approach is to create a library of HSI models for all species (or communities) and environments under consideration, each with its own particular limitations (Brooks, 1997; Roloff and Kernohan, 1999). These models are easy to compare and combine since they use the same uniform scale (*e.g.,* a value between zero and one, proportional to the carrying capacity). Thus, each HSI is only applicable to a specific type of life and habitat as a function of a finite set of environmental variables within selected spatial and temporal scales. There are many other tools of the HSM that can be used to characterize species or their environment. For example, *similarity indices* are usually simpler to construct than an HSI and can be used for quick comparisons between a set of biological or physical properties (*e.g.,* diversity) (Boyle *et al.,* 1990). Similarity indices are also used in many other applications such as pattern recognition and machine learning (*e.g.,* Cheng *et al.,* 2011).

3. Habitability in Astrobiology

Astrobiologists have proposed many habitability models or indices for Earth, the Solar System, and extrasolar bodies
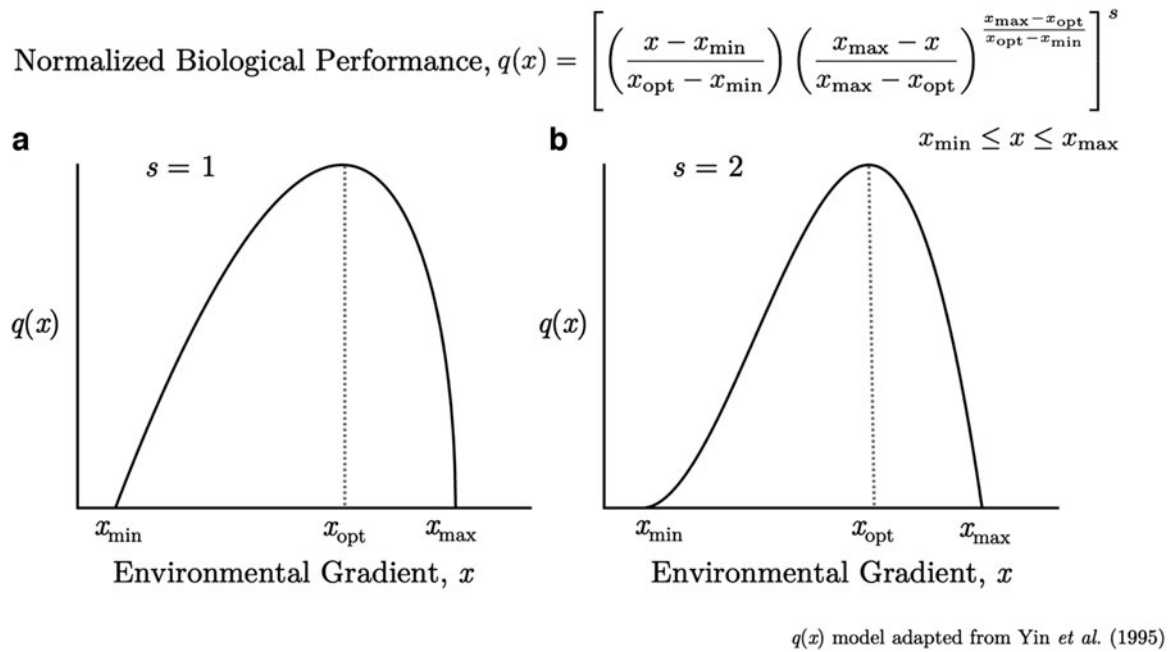
$$\text{Normalized Biological Performance, } q(x) = \left[\left(\frac{x - x_{\min}}{x_{opt} - x_{\min}} \right) \left(\frac{x_{\max} - x}{x_{\max} - x_{opt}} \right)^{\frac{x_{\max} - x_{opt}}{x_{opt} - x_{\min}}} \right]^s$$

$$x_{\min} \leq x \leq x_{\max}$$

a $s = 1$

$q(x)$

$x_{\min}$ x_{opt} $x_{\max}$

Environmental Gradient, x

b $s = 2$

$q(x)$

$x_{\min}$ x_{opt} $x_{\max}$

Environmental Gradient, x

$q(x)$ model adapted from Yin *et al.* (1995)

FIG. 1. Typical shapes of ecophysiological or species response curves along an environmental gradient (*e.g.,* temperature) for the biological performance (*e.g.,* relative growth rate) of plants (**a**) and microbial life (**b**) modeled after Yin *et al.* (1995). Species perform best near a physiological optimum and decrease asymmetrically near the extremes. The response curves of different species vary in shape and amplitude and are subject to biological evolution (Lenton and Lovelock, 2000). Responses of multiple variables or species could be combined with different aggregations statistics (*e.g.,* arithmetic or geometric means).

in the last decade (*e.g.,* Stoker *et al.,* 2010; Schulze-Makuch *et al.,* 2011; Armstrong *et al.,* 2014; Irwin *et al.,* 2014; Barnes *et al.,* 2015; Silva *et al.,* 2017; Kashyap Jagadeesh *et al.,* 2017; Rodríguez-López *et al.,* 2019, Seales and Lenardic, 2020). There are some specific universal biological quantities that can be used as proxies for habitability such as carrying capacity, growth rate, metabolic rate, productivity, or the presence of some requirements of life, or even genetic diversity (Heller, 2020). There is also an ongoing debate as to whether any concept of habitability needs to be binary (yes/no) in nature (Cockell *et al.,* 2019), continuous (Heller, 2020), or probabilistic (Catling *et al.,* 2018). While a binary interpretation of habitability only allows a given planet to be habitable (for a given species) or not, a continuous model also allows for the possibility of a world (planet or moon) to be even more habitable than Earth, that is, to be superhabitable (Heller and Armstrong, 2014; Schulze-Makuch *et al.,* 2020). Constructing a direct measure of habitability requires knowing how the environment affects one of the biological quantities for some species or community. We do not need to specifically estimate these quantities, but only to know how the environment proportionally affects them. For example, we know how temperature affects the productivity of primary producers such as plants and phytoplankton. Most require temperatures between 0°C and 50°C, but such producers do better (*i.e.,* have the highest productivity) near 25°C (Silva *et al.,* 2017). Their "thermal habitability function" looks like a bell-shaped curve centered at their optimum productivity temperature. Direct measures of habitability are also better represented as a fraction from zero to one.

Biological productivity (the dry or carbon biomass produced over space and time) is one of the best habitability proxies for astrobiology since it is easy to estimate for many ecosystems, via ground or satellite observations. The *Miami Model* was the first global-scale empirical model to give fair estimates of terrestrial net primary productivity (NPP, the rate of fixed photosynthetic carbon minus the carbon used by autotrophic respiration) (Zaks *et al.,* 2007). This simple model only uses two measurements, annual mean surface temperature and precipitation, to successfully infer the global distribution of vegetation (Adams *et al.,* 2004). One important limitation of this type of model is that climate variables such as precipitation not only affect but also are affected by vegetation. There is increasing evidence, for example, that tropical forests have strong impacts on cloud base heights (Van Beusekom *et al.,* 2017) and precipitation patterns on Earth (Molina *et al.,* 2019). Today, many complex biogeochemical models and satellite observations (*e.g.,* NASA's TERRA, AQUA, and Soumi NPP models) are combined to estimate local to global NPPs (Cramer *et al.,* 1999; Ito, 2011). These satellite products are being used to create habitability indices to monitor terrestrial biodiversity now and through climate change (*e.g.,* Pan *et al.,* 2010; Radeloff *et al.,* 2019). Therefore, the NPP is also a measure of global terrestrial health or habitability since primary producers are the basis of the food chain.

Most habitability models are limited to indirect measures of habitability due to a lack of information. This is especially true for exoplanets. For example, the occurrence of Earth-sized planets in the Habitable Zone of stars (termed the *Eta-Earth* value) can be considered a continuous indirect

measure of stellar habitability (*i.e.,* the suitability of stars for habitable planets). The Habitable Zone, the region around a star where an Earth-like planet could maintain surface liquid water, is generally considered to be a binary indirect measure of planetary habitability (Kasting *et al.,* 1993), although others have argued that it should be regarded as a probability density function (Zsom, 2015; Catling *et al.,* 2018). While the location of the Habitable Zone depends on stellar type, its extension also greatly depends on the assumed atmospheric composition (*e.g.,* Heng, 2016). Furthermore, atmospheric dynamics effectively work to homogenize differential heating of the surface, creating a short-term response on the planet's global temperature. This differential heating is a result of the planet's obliquity, which governs the latitudinal distribution of incoming stellar radiation (Spiegel *et al.,* 2009; Nowajewski *et al.,* 2018). The Habitable Zone boundaries themselves also evolve over time. This has major implications for water delivery, water retention, and oxygen build-up on potentially habitable planets (*e.g.,* Ramirez and Kaltenegger, 2014; Luger and Barnes, 2015).

The Habitable Zone can be defined in terms of either the planet's distance from the star, its incoming stellar flux, or its global equilibrium temperature. When using the equilibrium temperature definition, the extension of the Habitable Zone depends on the planet's orbital forcings, particularly eccentricity and obliquity. For example, when orbital eccentricity increases, the average equilibrium temperature decreases, thus extending the size of the Habitable Zone (Méndez and Rivera-Valentín, 2017). Similarly, higher fixed obliquity and/or rapid changes in obliquity values result in higher average equilibrium temperatures, which also result in extending the outer edge of the Habitable Zone (Armstrong *et al.,* 2014). Furthermore, when using the equilibrium temperature definition, the extension of the Habitable Zone depends ultimately on the planet's energy balance. On Earth, the global energy balance is a result of the complex interaction between physical and biological processes. Biota affect the global energy balance in manifold ways including direct effects on surface albedo and latent heat fluxes (*e.g.,* transpiration) (Jasechko *et al.,* 2013; Duveiller *et al.,* 2018). Tidal heating from the newly formed and nearby Moon might have played a role early in Earth's history (Heller *et al.,* 2020) but is irrelevant today. On Earth-sized planets in the Habitable Zones around M dwarf stars, tidal heating can have a strong effect on the planetary energy budget, potentially making some parts of the Habitable Zone uninhabitable (Barnes *et al.,* 2009).

The Earth Similarity Index, inspired by the diversity similarity indices used in ecology to compare populations (Boyle *et al.,* 1990), is a measure of Earth-likeness for a selected set of planetary parameters (Schulze-Makuch *et al.,* 2011). Future observational constraints of Earth-similar atmospheric constituents (*i.e.,* N_2, CO_2, H_2O) could improve our handle on this and similar metrics. For instance, 3D global climate models indicate that spectral features of water vapor on close-in terrestrial exoplanetary atmospheres may be detectable by the James Webb Space Telescope (Kopparapu *et al.,* 2017; Chen *et al.,* 2019), depending on the presence of clouds (Komacek *et al.,* 2020). Even though the presence of water vapor in the atmospheres of terrestrial exoplanets can indicate habitability, it is necessary to perform exhaustive work to determine which species could survive under conditions of extreme humidity. For example, mammals are not capable of surviving hyperthermia produced under high air temperatures and high humidity conditions, so planets with extreme differential heating between latitudes may be uninhabitable for them, despite having liquid water on their surface (Nowajewski *et al.,* 2018). Furthermore, many animals (including all mammals) may not survive in atmospheres with CO_2 (N_2) pressures exceeding ◄AU1 ~ 0.1 (2) bar (Ramirez, 2020).

The current Habitable Zone paradigm is misunderstood by many people—the public, the press, as well as other scientists—but as with all habitability models, it has a specific application and is neither incorrect nor useless for neglecting the subsurface oceans in the outer Solar System, venusian clouds, or other environments far from Earth-like conditions. The Habitable Zone does not tell us whether planets are habitable (or even if there are planets there), but it shows the impact of a few important variables on planetary habitability. The concept of a Habitable Zone was developed to identify terrestrial exoplanet targets that could potentially host life. It was first proposed by Edward Maunder in 1913 (Maunder, 1913; Lorenz, 2020) in his book *Life on Other Planets,* with refining definitions later on (Huang, 1959; Hart, 1978; Kasting *et al.,* 1993; Underwood *et al.,* 2003; Selsis *et al.,* 2007; Kaltenegger and Sasselov, 2011; Kopparapu *et al.,* 2013, 2014; Ramirez and Kaltenegger 2017, 2018; Ramirez, 2018). The Habitable Zone can be defined as *the circumstellar region where standing bodies of liquid water could be stable on the surface of a terrestrial planet.* Here, the insistence on the presence of liquid surface water is based on the fact that all known examples of life on Earth require liquid water to exist. However, this definition is suitable *only* for remote observations of planets and does not consider any life which might exist within the subsurface. There is a reason for this: the search for life on exoplanets will rely on remote observations of atmospheres for the foreseeable future, lacking the luxury of *in situ* measurements used in solar system planetary science. Therefore, identifying water in the atmosphere of planets (in addition to other biosignature-relevant gases) is the only way to narrow down potential life-hosting targets, since subsurface life deep in the interior may not be able to modify the atmospheres of planets enough to be detectable remotely.

Abundance of liquid water in a planetary environment may be inherently unstable (Gorshkov *et al.,* 2004), which leads to questions about the role of life in the definition of habitability itself (Zuluaga *et al.,* 2014). Thermodynamic disequilibrium may be one the most conspicuous signatures of a habitable and inhabited planet (Lovelock, 1965, 1975; Kleidon, 2012; Krissansen-Totton *et al.,* 2016); consider, for example, the composition of Earth's atmosphere (Lenton, 1998). One common problem with some, if not all, biological models is that they assume that the full set of physical characteristics of the environment, including climate, is *a boundary condition* for life, *that is,* that biological systems depend on climate but not the other way around. This premise is challenged by the fact that the observed state of the Earth system is the result of a complex and dynamic interaction between biological (*e.g.,* ecosystems) and physical (*e.g.,* climate) systems (Budyko, 1974; Gorshkov *et al.,* 2000; Kleidon, 2012; Zuluaga *et al.,* 2014). A critical question is how such a thermodynamically unstable state can be

maintained during eons (*e.g.,* the span of Earth's life) despite variable (*e.g.,* solar luminosity) and sudden large (*e.g.,* asteroid impact) external forcings . The answer depends on the interactions between biological and physical systems on Earth. A planet might enter a habitable state (*i.e.,* allow for the presence of liquid water at its surface) at any given point in time simply through *chance occurrence*—a random change in planetary energy balance, for example. However, *long-term persistence* of a habitable state (*e.g.,* the persistent habitable state of Earth over the last 4 billion years, approximately) indicates the existence of natural regulation mechanisms (Walker *et al.,* 1981; Lenton, 1998; Gorshkov *et al.,* 2000; Kleidon and Lorenz, 2004, Salazar and Poveda, 2009).

4. Recommendations for Astrobiology

The astrobiology field is playing a critical role in our understanding of planetary habitability. The habitability of Earth, the Solar System, and exoplanets can be studied thanks to measurements taken with multiple ground, orbital, or remote sensors. At the same time, astrobiology-related missions can synergistically take advantage of the predictions of habitability models in their selection of potential exploration strategies, mission priorities, instrument design, and observations and experiments. Here we list four recommendations for the astrobiology community:

(1) **Increase and widen the participation of more experts on HSMs.** Ecologists are the experts in the ground-truth proven measurement of terrestrial habitability, yet they are seldom represented in the planetary and astrobiology community. New synergies between NASA and the national and international ecological societies, for example, the Ecological Society of America, Soil Ecology Society, and the International Society for Microbial Ecology, should be established via, for example, a joint conference session at the Lunar and Planetary Science Conference, the Astrobiology Science Conference, or the European Astrobiology Network Association. There should be worldwide participation to guarantee global standardization, which will stimulate exploration of the Solar System, promote use of the Solar System as a laboratory for expanding our current understanding of the habitability of Earth, and deepen our understanding of potentially habitable conditions elsewhere.

(2) **Further terrestrial exploration.** Many Earth habitats (*e.g.* the cloud layer, stratosphere, deep ocean, deep ice, deep earth, or the mantle) are vastly underexplored biologically (*e.g.,* Lollar *et al.,* 2019; DasSarma *et al.,* 2020). Astrobiologists should create stronger connections with the researchers working in these under-studied environments (*e.g.,* The Deep Carbon Observatory[1]) to ensure that there is a cohesive understanding of the state-of-the-art science being learned and that continuing efforts to study these environments are supported. These field studies should provide new data to test the applicability of current habitability models with extreme environments and

thus identify a more diverse range of planetary and exoplanetary conditions. At the same time, unicellular life continually surprises us with new ways to survive and obtain energy from its environment (rock-eaters, electric currents, and even radioactivity), which shows us we need to be flexible in considering energy sources for habitability.

(3) **Improve habitability models.** New habitability models should be developed and validated with field and laboratory experiments, including simulated extreme and planetary analog environments (*e.g.,* Taubner *et al.,* 2020). The main goal is to identify knowledge gaps. For example, new ecophysiological response curves for some organisms are necessary (*e.g.,* growth rate as a function of water activity—a measure of water available for biological reactions), especially in dynamic environments such as gradient-rich biotopes and higher-complexity extreme environments (*i.e.,* those with multiple extremes, such as deep-sea brines). Also, there are insufficient models on microbial growth in near-surface dynamic environments (*e.g.,* as applicable to martian diurnal cycles). There is a growing body of literature about the manifold mechanisms through which life affects Earth's climate system, including the global energy balance and atmospheric composition and dynamics. Advances in the understanding of climate-life interactions (*e.g.,* Bonan and Doney, 2018) as well as climate-technology interactions (*e.g.,* Frank *et al.,* 2017) in the Earth system can provide new insights for habitability models.

(4) **Develop a habitability standard.** Existing and future studies should specify how they assess habitability for each of their observations according to a shared habitability standard. For example, measurements of surface temperature and water vapor from landers or orbital missions could be converted into a simple habitability model. The advantage of a standard is that past and future missions could be compared to each other and their habitability assessments refined, while new habitability knowledge gaps could be identified. This dynamic standard should be evaluated and updated regularly by a diverse and multidisciplinary committee, for example during a Decadal Survey and/or mid-decade review. Currently, the closest concept to an NHS is specific language included in, for ex- ◄AU2 ample, the NASA Astrobiology (Des Marais *et al.,* 2008) and Ocean Worlds (Hendrix *et al.,* 2018) roadmaps. These documents stress the need for habitability evaluations and missions (*e.g.,* Europa Clipper and Titan Dragonfly) yet only focus on the individual habitability requirements and not how to combine the net contribution of these factors. Furthermore, the NHS might eventually become the standard of other ◄AU2 disciplines.

5. Science Questions

Each astrobiology-related project, mission, or instrument should anticipate and answer a series of basic scientific questions about the environment or environments to be studied as a core part of the planning process. The answers to these

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[1]https://deepcarbon.net

questions should be updated based on the results. To do so, it is important to define an environment of interest, both in space and time (termed a *quadrat* in ecology), and answer the following science questions as part of the initial analysis:

(1) **What are the limiting factors?** Usually, there is a small set of main factors (*e.g.,* edaphic factors) that influence living organisms (*e.g.,* water, nutrients). These will be the first set of variables to be used for the construction of a habitability model, which will later be refined with more variables. For example, primary productivity is mainly driven by temperature, precipitation, and nutrients on land, and by temperature, and oxygen and nutrient concentrations in the oceans, among other factors. In general, these factors should be directly or indirectly related to the mass and energy of the environment (*e.g.,* Martiny *et al.,* 2006; Pikuta *et al.,* 2007; Williams and Hallsworth, 2009; Harrison *et al.,* 2013; McKay, 2014; Lynch and Neufeld, 2015; Tecon and Or, 2017). Another important factor is whether the organisms are able to come into contact with the limiting factors.

(2) **What are the terrestrial and planetary analogs?** Identify at least one analog on Earth and one close planetary analog as the comparison standards (*i.e.,* model normalizations). For example, if studying a particular martian environment, select hyperarid terrestrial deserts and a martian analog based on the variables of interest. The cross-comparison of variants of similar types of environment (*e.g.,* salterns), as well as slightly different settings (*e.g.,* high-salinity biotopes with different pH, temperature, or chemical conditions), could also prove useful. The subsurface oceans of Europa or Enceladus could be compared with deep seawater, hydrothermal systems, or deep-sea brines (Antunes *et al.,* 2020). Planetary atmospheres could be compared with high altitude or near-space regions. An analysis of similarities (*e.g.,* ANOSIM[2]) could be used to formally select and compare these regions (Clarke, 1993).

(3) **What is the habitability assessment?** The habitability of the region of interest is evaluated based on the selected environmental factors and then compared with the selected Earth and planetary analogs, using a normalized scale from zero to one for simplicity. A library of habitability measures is usually constructed (*i.e.,* a habitability matrix), each for different considerations (*e.g.,* species). These inputs are then used to construct multivariate habitability maps (also known as *niche quantification* in ecology) for site selections. A common assumption is that habitability models are only used to determine whether environments are habitable. Instead, they are used to characterize what key factors are responsible for the gradual transition from low to high habitability states. Therefore, a habitability threshold should also be defined to differentiate between habitable and nonhabitable conditions.

(4) **What is the potential biomass?** The upper limits of biomass can be predicted based on the fluxes of mass

and energy available for life, and usually a very small fraction of the total mass and energy. For example, biomass could be estimated from the available metabolic energy using the Metabolic Theory of Ecology (van der Meer, 2006; Schramski *et al.,* 2015; Clarke, 2017). These upper limits are used in the sensitivity designs of life-detection experiments. Available free energy from known disequilibria has been used to estimate an upper limit on the biomass in the subsurface of Mars, and its value depends on uncertainties of the abundances of metabolic reactants and the assumed microbial basal power requirement (Sholes *et al.,* 2019).

(5) **What is the expected correlation between habitability and biosignatures?** The potential upper values of biomass can be converted to estimates of observable biosignatures or disequilibrium chemistry (Catling *et al.,* 2018). Habitability and biosignatures are positively correlated on Earth, but this might not necessarily be true for other planets. A zero or negative correlation could indicate an incorrect habitability model, or biological or technological processes unlike Earth (in other words, *life as we don't know it*). The habitability-biosignatures correlation is a fundamental problem of astrobiology, but nondetections are also important. For example, it will be profound to detect planetary regions determined to be habitable by Earth standards yet devoid of any life. Such discoveries would place bounds on abiogenesis. Alternatively, if biosignatures are widespread in habitable regions but lack any plausible technosignatures, then this would suggest that the development of planetary-scale technology is a rare occurrence, even if life is common (Haqq-Misra *et al.,* 2020).

6. Conclusion

Habitability models are successful analysis tools for characterizing habitable environments on Earth. In this review, we compared some of the different models used by ecologists and astrobiologists and suggested how to integrate them into new habitability standards. These standards are relevant for any astrobiology-related observations, including the study of extreme environments on Earth, planetary missions, or exoplanets. Ecologists have been using these models for more than four decades to understand the distribution of terrestrial life at local to global scales (Section 2). Astrobiologists have been proposing different models for some time, with little integration and consistency between them and different in function to those used by biologists (Section 3). The astrobiology community should create habitability standards for observations and missions with astrobiology objectives, as the USFWS successfully did long ago for ecologists (Section 4). These standards are necessary to make sense of data from multiple observations, develop predictions for environmental niches that can be tested, and understand the extraterrestrial correlations between habitability and biosignatures (Section 5).

There is no need for the astrobiology community to reinvent the methods and tools used by ecologists. It is true that ecology methods are more capable than our limited planetary and astronomical data allow, but they also provide the basic language and framework to connect Earth and

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[2]https://www.rdocumentation.org/packages/vegan/versions/2.3-5/topics/anosim

astrobiology science for decades to come. For example, there are many theoretical and computational tools used in ecology to quantify environments and their habitability, mostly known as Habitat Suitability Models. See the work of Guisan *et al.* (2017) for an extensive review of these models and the work of Lortie *et al.* (2020) for a current review of the computational tools. Most of these tools are available as packages in the R Computing Language[3] in the Comprehensive R Archive Network (CRAN)[4] and GitHub (*e.g.,* Environmetrics[5], HSDM[6]). New, higher-resolution remote sensing instruments and exploration technologies will create better habitability maps from rover, lander, and orbiter data. Habitability models will eventually lead us to a better understanding of the potential for life in the Solar System and beyond, and perhaps even the factors that influence the development of life itself. *Habitability models are the foundation of planetary habitability science*. After all our scientific and technological advances, we still need a stronger integration between biology, planetary sciences, and astronomy (Cockell, 2020).

Acknowledgments

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[3]https://www.r-project.org
[4]https://cran.r-project.org
[5]https://cran.r-project.org/web/views/Environmetrics.html
[6]https://github.com/vdicolab/hsdm

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Abbreviations Used

HSI = Habitat Suitability Index
HSMs = Habitat Suitability Models
NPP = net primary productivity
USFWS = U.S. Fish and Wildlife Service

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AU1: Is ''pressures exceeding ~ 0.1 (2) bar'' correct as written?

AU2: Please spell out NHS.

AU3: The following are not found in the text: Atri (2017), Belilla et al. (2019), Dohm and Maruyama (2015), Kane (2013), Macalady et al. (2013), McEldowney and Fletcher (1988), Méndez et al. (2018, 2020), Rivera-Valentín et al. (2018, 2020), Spitoni et al. (2017), Wierzchos et al. (2013). Please reconcile.