Social and Conceptual Issues in Astrobiology

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KELLY C. SMITH AND CARLOS MARISCAL

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C10

10
What Are Extremophiles?
A Philosophical Perspective

Carlos Mariscal and Tyler Brunet

C10.S1

Introduction

C10.P1 In the 1970s, R. D. MacElroy coined the term "extremophile" to describe microorganisms that thrive under extreme conditions (MacElroy, 1974). This hybrid word transliterates to "love of extremes" and has been studied as a straightforward concept ever since. In this chapter, we discuss several ways the term has been understood in the scientific literature, each of which has different consequences for the distribution and importance of extremophiles. They are, briefly, *human-centric*, at *the edge of* life's habitation of *morphospace*, by appeal to *statistical rarity*, described by *objective limits*, and at the *limits of impossibility* for metabolic processes. Importantly, these concepts have coexisted, unacknowledged and conflated, for decades. Confusion threatens to follow from the wildly varied inclusion or exclusion of organisms as extremophiles depending on the concept used. Under some conceptions, entire kinds of extremophiles become meaningless. Since our understanding of how life works is shaped by what we take to be its extremes, clarifying extremophily is key for many large-scale projects in biology, biotechnology and astrobiology.

C10.P2 In what follows, we proceed as if a noncontroversial account of life is possible and that it is possible to find complex chemistry in the universe that is similar enough to life on Earth such that both may be considered instances of "life" (but see Mariscal & Doolittle, 2018). We raise, but do not address, the questions of whether the distribution of life on Earth is representative of what we may find elsewhere in the universe, whether the same kinds of extremophiles would exist given a replay of the tape of life. Additionally, each of these concepts assumes life based on some sort of biochemistry in this universe, effectively ruling out claims made by some artificial life proponents that their digital organisms are genuine examples of life (Langton, 1989; Ray, 1995). On the distinction between extremophilic and extremotolerant, we note that all accounts will accept the latter as a broader category than the former, since tolerance of extreme conditions is a prerequisite for extremophily under any conception. Indeed, there will be

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many extreme environments where tolerance is the only option (e.g., *Bacillus marismortui* was extracted and grown from 250-million-year-old salt crystals in the Permian Salado Formation in an inactive yet persistent state; Vreeland et al., 2000). The nature of the environment precluded any organisms *thriving*.

C10.P3 We also note that extremophily, as a functional category, is potentially applicable at many levels of the biological hierarchy. Extremophily at one level does not necessarily extend to higher and lower levels. For instance, a microorganism in isolation might be quite intolerant to certain environmental conditions yet flourish when subjected to the same conditions in the presence of a natural biofilm. Alternatively, a protein molecule might be quite active under certain conditions even if the optimal environment for the organism containing it is far more mesophilic. There is an industry of artificially selecting organisms and proteins to adapt to extreme environments (see van den Burg & Eijsink, 2002), providing some justification to consider "functioning at extremes" as a worthwhile category of investigation.

C10.P4 Finally, we also note certain physico-chemical ranges are rarely considered with respect to extremophily (e.g., time span, size, nutrient availability; Hoehler & Jørgensen 2013), as well as some *biological* parameters (abundance, isolation, competition, etc.). Perhaps scientific interest must also come into play as to the reason these criteria are not considered relevant. We return to this and other issues later.

C10.P5 In the next section, we give five definitions of extremophily and show their benefits, drawbacks, and unintended consequences. These arguments are summarized in Table 10.1 and represented visually in the three figures. Given research on polyextremophiles, it seems Figure 10.2 is a more plausible representation of the state of current knowledge than the idyllic Figure 10.1 (Harrison et al., 2013). Apparently, life is patchily distributed across various dimensions, which may reflect its contingent history, poor sampling, fundamental limits, or something else. Figure 10.3 shows the conceptual flowchart for all of these views. In the following section, we take a step back to ask whether we should choose between these definitions and how such a judgment could be made. We argue for a limited pluralism, in which some, but not all, of the concepts are acceptable relative to certain practical and theoretical aims.

C10.S2

Extremophile Concepts

AQ: Please move note superscript to text (cannot appear in heading).

C10.S3

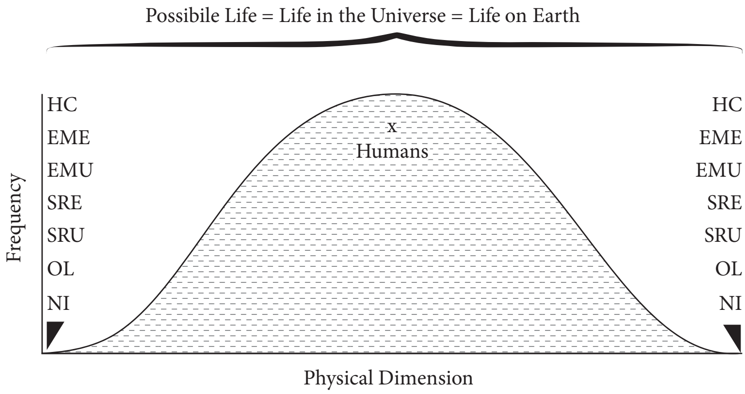
Humanc-Centric

C10.P6 **Explanation:** As a first attempt, we might view something as an extremophile if it thrives in the kinds of environments that would be considered extreme for

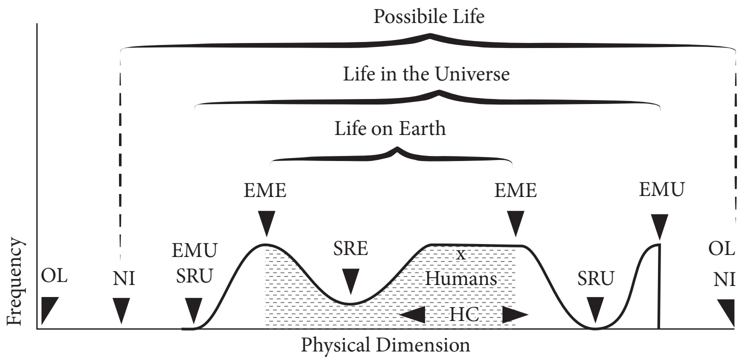
C10.T1

Table 10.1. Summary of the Extremophile Concepts Discussed in the Text, Including Benefits and Drawbacks

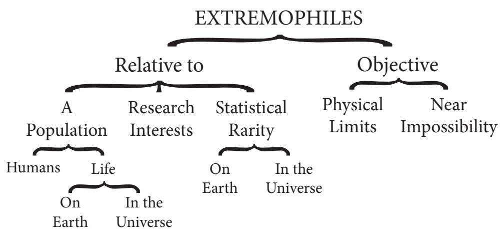
Definitions	Description	Benefits	Drawbacks
Human-Centric	As extremophile is an organism that thrives in environments which would be hazardous to humans or human cells.	Clear, operational, relatively constant	Instrumental, seemingly arbitrary, excludes humans as extreme by definition
Edge of Morphospace (Earth)	Extremophiles are known organisms that inhabit the limits of some physical or chemical continuum relative to life as we know it.	Operational, does not require extremophiles to be rare	As research advances, those extremophiles once thought to be at the edge no longer count as such, contingent on the course of evolution on Earth
Edge of Morphospace (Universe)	Extremophiles are those organisms in the universe that inhabit the limits of some physical or chemical continuum relative to all other life.	Clear, universal	Empirically intractable
Statistical Rarity (Earth)	An extremophile is a known organism that thrives in conditions under which most other organisms do not.	Empirically tractable	Contingent on the course of evolution on Earth, extremophiles can exist by chance, extremophiles may be possible in otherwise average environments
Statistical Rarity (Universe)	An extremophile is an organism that exists somewhere in the universe and thrives in conditions under which most other organisms do not.	Clear, universal	Empirically intractable, may imply everything is an extremophile
Objective Limits	An extreme is the limit(s) of some physical or chemical phenomenon. Extremophiles are organisms that do well in these environments.	Objective, determinable independent of any examples of life	Appropriate to physics or chemistry, problematic for life. If research thresholds are overly broad, it is unclear what this definition adds that is not better captured by other accounts
Near Impossibility	Extremophiles, when they exist, are at the limits of what life's mechanisms can possibly handle.	Useful for very different research questions	Potentially theory-laden, may require an uncontroversial definition of life, may be scientifically impracticable
Research Interest	Extremophiles are any organisms, parts, or behaviors of organisms that meet certain research interests much more so than other organisms, parts, or behaviors.	Pragmatic, flexible, compatible with other definitions	Difficult to pin down, potentially unsatisfying



C10.F1 **Figure 10.1.** The easy case of extremophily is when life on Earth is representative of what we will find in the universe. In this case, all our definitions collapse and "extremophile" can proceed as an unanalyzed concept.



C10.F2 **Figure 10.2.** A situation in which each of the definitions comes apart from each of the others. *Objective limits* (OL) picks out the edges of the physical dimension. Extremophiles under the *near impossibility* (NI) concept may reach the limits of a physical dimension (right dashed line) or fall short (left dashed line). The least populated area in the dimension is picked under one *statistical rarity* (SRU), which may coincide with the actual limits occupied by life in the universe (EMU on left) or not (EMU on right). A similar distinction could be made with respect to life on Earth (SRE and EME in the shaded area). Humans appear somewhere on this space, and extremes may be defined relative to them (HC).



C10.F3 **Figure 10.3.** Extremophile concepts can either be objective or relative. Of the three relative concepts, *population relative, research interest relative*, and *statistical rarity*, the latter seems unmotivated. Abundance itself is neither necessary for being an extremophile, nor sufficient. The *humancentric* approach is likely to only be interesting to a subset of cases. Relative to the edges of what is inhabited by life on Earth or in the universe (*edge of morphospace*; see the text) is particularly interesting for many uses, although the latter less so than the former. *Research interest* definitions of extremophiles are pragmatic in nature and thus not subject to the same theoretical concerns as other approaches. Of two absolute concepts, *objective limits of physical dimensions* and *near the limits of possibility for life*, only the latter is scientifically interesting, although it raises a number of conceptual issues.

humans. This definition[1] is yoked to contemporary current human habitability, which allows it to be used for even the study of ancient, distant, or hypothetical samples. We take this definition to be the driving idea behind such claims as:

C10.P7 Extremophiles are organisms which permanently experience environmental conditions which may be considered as extreme in comparison to the physico-chemical characteristics of the normal environment of human cells: the latter belonging to the mesophile or temperate world. (Gerday, 2002, p. 1)

C10.P8 Extremophiles survive in environments that would be lethal to humans. (Cohen & Steward, 2001)

C10.P9 **Benefits:** There is a benefit in such a straightforward, instrumental approach: we are well aware of our tolerance for temperature, pressure, salinity, and so on. Under this definition, we would draw clear boundaries around mesophiles as "organisms that like what we like" and extremophiles as everything else. So this definition is explicit, clear, and relatively constant. Given its clear methodological advantage, it may make sense for many practicing scientists to use this as an operational definition, regardless of whether they ultimately define extremophiles using other criteria in more rigorous settings (see Bich & Green [2018] and chapter 5 in this volume for similar issues with respect to "life").

C10.P10 **Drawbacks:** The most immediate problem for this definition is its arbitrariness. It may strike some as unscientific to have a definition so closely linked to the human condition. It would be akin to using the criterion of "most impressive mountain" to identify Everest rather than "Earth's tallest mountain." Additionally, there are many environments in which humans could not survive, which nevertheless do not seem to be physically, chemically, or biologically extreme. For example, humans could not survive for long at 1 meter under the ocean surface or in the Paleozoic. A variant of the human-centric concept would appeal to the range of survivability conditions of human cells, as in some of the previous quotes. Unfortunately, there are just as many intuitively benign environments that are inhospitable to human cells (e.g., outside of a human body).

C10.P11 **Implications:** One unintended consequence of this definition is that it rules humans as mesophiles by definition. This renders some uses of extremophily as nonsensical. For example, some astrobiologists have claimed "we are extremophiles" to describe the rarity of breathing oxygen (Rothschild & Mancinelli, 2001). According to the human-centric account, humans can never be extremophiles regardless of how rare or unusual they may be, *even* if humans would be considered extreme according to every other definition. Perhaps these implications are unimportant for most purposes. Focusing on humans is, fundamentally, a pragmatic move to highlight important differences. It seems unlikely scientists will think keep to this definition if it is inconsistent with the questions they hope to answer.

C10.P12 **Verdict:** The human-centric approach may be useful for many practical purposes, even if it is not the full account of "extremophiles" that any scientist would accept.

C10.S4

Edge of Morphospace

C10.P13 **Explanation:** Biological organisms exist across several physical dimensions, like temperature, pressure, salinity, and so on. Scientists can (and have) mapped those dimensions to multidimensional spaces to show the ranges occupied by life. Such spaces may be called "morphospace," a concept often used in biology to visualize evolution across physical dimensions (Raup, 1966). Similar concepts exist, such as "design space" (Dennett, 1995), "phase space" (Berne & Straub, 1997), and "habitable space" (Harrison et al., 2013). Life has explored a number of physical and chemical limits, although as we will see later, it has reached objective limits only in some of these cases. So perhaps the most natural way to define extremophiles may be with respect to the physical extremes life *has* explored. An extremophile, in this definition, is simply an organism that exists at the edge of the area of morphospace occupied by life on Earth (EME) or in the Universe in general (EMU). The edge, importantly, need not be near an objective limit nor sparsely populated. It may be most common, in fact, to be an extremophile with respect to some dimensions. Unlike the human-centric view, this approach would be consistent with humans occupying extremes, or even not existing. Additionally, this concept is not explicitly instrumental. Although this definition is n-dimensional, it may help to picture a three-dimensional space with respect to some variable or another (Harrison et al., 2013). We take such a definition to be the motivation behind such claims:

C10.P14 Life on Earth is limited by physical and chemical extremes that define the "habitable space" within which it operates. (Harrison et al., 2013, p. 204)

C10.P16 So the study of terrestrial organisms that can survive on the extreme boundary of these conditions, the so-called extremophiles, greatly informs astrobiology and the search for life beyond Earth. (Dartnell, 2011) AQ: Please include pages for all quotes throughout the chapter

C10.P18 Our two formulations, EME and EMU, would be equivalent if life on Earth was the only life in the Universe. EME has the benefit of being empirically tractable, and we might describe some research into extremophily as *extending* the boundaries of morphospace. EMU will never be empirically tractable, but it may be a good conceptual goal of research into extremophily. For EMU, research into extremophily merely *discovers* the boundaries of morphospace.

C10.P19 **Benefits:** EME is empirically tractable and visualizable. Unlike statistical rarity, it is not important for extremophiles to be rare, which is a potentially counterintuitive result. While in many cases, they will be equivalent, edge of morphospace accepts instances in which extreme life is common. In other words, that in which the frequency of life does not decrease as certain dimensions are reached or in which morphospace is occupied evenly across a dimension. Suppose life was evenly distributed across the pH continuum. The edge of morphospace concept would still consider organisms living at pH 0 and pH 14 as acidophiles and alkaliphiles, respectively. Although it is possible for there to be a number of internal boundaries of morphospace in any dimension, we suspect that is rare (see Figure 10.2). For EME or EMU, some examples of life will be extremophilic for every physical and chemical dimension, even if they are not impressive from objectively physical standards. For example, *Deinococcus radiodurans* is an EME extremophile with respect to cold, dehydration, vacuums, and acid, even though it never approaches the objective physical limits of many of these variables.

C10.P20 **Drawbacks:** The edge of morphospace concept has drawbacks, however. First, EME is contingent within the course of evolution (on Earth) and with respect to current scientific sampling. EMU avoids the latter problem at the cost of scientific intractability. Theoretically, EMU may still be contingent within the span of life in the universe if there are possible configurations life may hold but never approximates. This situation may arise, for example, if "islands of stability" exist with respect to evolution. That is, there may be biologically possible life forms that can never arise naturally because the evolutionary path to them is implausible, but that could occur if intelligently designed (i.e., zebras with machine guns).

C10.P21 **Implications:** This concept seems to underlie two research programs with respect to extremophiles: the synthesis or evolution of extremophily and the seeking out of extreme environments to discover new extreme organisms. Both of these approaches expand the "envelope" of where life is possible. Like several other approaches, his approach requires consideration of life as it actually exists and cannot be determined a priori.

C10.P22 **Verdict:** EME is a very useful concept and likely what many researchers intend by the term "extremophile." EMU is less obviously useful, and its theoretical benefits are unclear. We will consider EMU again in the discussion of near impossibility.

C10.S5 Statistical Rarity

C10.P23 **Explanation:** A broader approach to defining extremophiles might appeal to their abundance. Under this definition, an extremophile would be one that exists in conditions where life is quite rare, either (a) on Earth (SRE) or (b) in general across the universe (SRU). This rarity could be with respect to external, physicochemical properties, such as pressure or temperature ranges, or relational properties, such as isolation or extreme competition. Like the prior approaches, this approach is relative, though it is relative to the broader category of life rather than humans. Something akin to this definition seems to be behind such claims as:

> C10.P24 An extremophile (from Latin extremus meaning "extreme" and Greek philiā (φιλία) meaning "love") is an organism that thrives in and may even require physically or geochemically extreme conditions that are detrimental to the majority of life on Earth. (Gupta et al., 2014, p. 1)

> C10.P26 several organisms are able to thrive in these hostile locations where most life would perish. (Reed et al., 2013, p. 2)

C10.P28 There are two interesting interpretations of the statistical rarity. We call it SRE when we refer to rare organisms which thrive in conditions hostile to the majority of *life as we know it on Earth.* We call it SRU when these rare organisms thrive in conditions hostile to the majority of *all life in the Universe*. SRU includes all life that ever will exist, but not life that is possible but never comes into existence. Since our only examples of life are those based on Earth, SRE and SRU are equivalent, for practical purposes. But they would also be equivalent in theory if it turned out Earth held the only example of life in the universe. Until a second "example" of life is discovered, SRU is merely a theoretical ideal, albeit one with curious consequences. For example, if life on Earth is significantly different from other life elsewhere (as could happen if Earth is a peculiarly inhospitable environment in the universe), it could be that SRE and SRU pick out entirely different kinds of organisms (i.e., Earth life could be a biased sample of life's extremes; see Figure 10.2).

C10.P29 **Benefits:** In terms of benefits, it makes sense that extremophiles would be relatively rare organisms. So defining extremophiles based on their rarity is intuitive. With respect to most parameters, it is plausible that life forms a normal distribution. In this normal case, the rarity of organisms will correlate with the extremity of the environment. Additionally, SRE is empirically tractable, although it is subject to changing over time as new organisms are discovered. SRU, while not empirically tractable, is appealing in theory. Given many potential instances of life in the universe, the most rare kinds of organisms are also likely to be the most extreme in any number of measures.

AQ: Please check and correct as necessary.

C10.P30 **Drawbacks:** Statistical rarity definitions has unintuitive consequences, however. Consider Figure 10.2, which belies our musings that life on Earth fit a normal distribution across many (or any) physical parameters. There are likely many combinations of pressure, temperature, and so on in which no organisms exist even though they do in nearly identical situations. Statistical rarity is also grounded on contingent natural history. So even if life would thrive in a certain environment, it may never be exposed to such scenarios. If we ran the tape of life again, perhaps the extremes of various metrics might be more inhabited than the more moderate middles (Gould, 1989). Although it is presumably uncommon, it is certainly possible that life might not occupy some environmental variable by chance. For example, the metal iridium is rare on Earth but common in igneous deposits and asteroids (Alvarez et al., 1980). Since iridium is a very rare element, areas once struck by asteroids may have orders of magnitude more iridium than other areas. If areas with moderate amounts of iridium are quite rare, the few organisms that live in these areas would be SRE extremophiles with respect to iridium *even if they have no other extreme properties*. Though critiques from contingency and chance are less effective against SRU, that view carries other, unintuitive consequences. Suppose the vast majority of life worlds in the universe required liquid ammonia. Under SRU, in such a situation, unbeknownst to us, all of life as we know it would be extremophilic with respect to the solvent it uses. Earth might be populated by extremophiles.

C10.P31 **Implications:** Perhaps extremophily must always be relative. With such a perspective, it would never make sense to describe an organism as simply an extremophile. Instead, extremophiles must always be defined *with respect to* a range of entities. As a result, any time scientists describe a microbe as "an extremophile," they must either be speaking incorrectly or implicitly reference a class of other organisms (e.g., SRE). Consider *Chlamydomonas nivalis,* alternatively described as "cold-tolerant microbes growing on . . . snow fields and glaciers from *many parts of the world*" (Takeuchi et al., 2006; emphasis added), "cryophilic," and "a remarkable extremophile, able to survive and thrive *in an environment that would be fatal to most plants*" (Gorton et al., 2001; emphasis added). If we take relativism seriously, *C. nivalis* might be considered an extremophile with respect to the habitats of most terrestrial plants (SRE), just extremotolerant with respect to snow and glacial environments, and perhaps again extreme with respect to all of the universe (SRU).

C10.P32 **Verdict:** Given the availability of other concepts, we view these critiques as devastating to any formulation of *statistical rarity*.

C10.S6 Objective Limits

C10.P33 **Explanation:** An alternative to instrumental, relativistic, or contingent criteria may be a mere assessment of objective physical or chemical limits. Certainly, there are some extremes that can be defined in this way: temperature in this universe can range from -273.15°C to at least 200,000°C (Werner et al., 2008). Chemical concentrations (e.g., salinity, oxygen, water) can range from 0% to 100% saturation. Objective limits, then, takes any of these limits and sets some threshold whereby if an organism approaches the threshold, then it may be considered an extremophile with respect to that boundary condition. In this definition, extreme environments are identified first, and extremophiles are defined as creatures that happen to live in those environments. Unlike the previous two definitions, the objective limits account is applicable even if humans, or indeed all life, never existed. We take something like the objective limits view to motivate such claims as:

C10.P34

> Numerous microorganisms are extremophiles, which means they can metabolize and reproduce in extreme conditions of heat, cold, acidity, salinity and other seemingly inhospitable environments. (O'Malley, 2014, p. 5)

C10.P35

> Extremophilesare defined by the environmental conditions in which they grow optimally. (Gupta et al., 2014)

C10.P38 > An organism that thrives in an extreme environment is an extremophile . . . "Extremes" include physical extremes (for example, temperature, radiation or pressure) and geochemical extremes (for example, desiccation, salinity, pH, oxygen species or redox potential) (Table 1). It could be argued that extremophiles should include organisms thriving in biological extremes (for example, nutritional extremes, and extremes of population density, parasites, prey, and so on). (Rothschild & Mancinelli, 2001)

C10.P39 **Benefits:** The benefits of setting objective limits is that they can be clearly defined independent of any examples of life. These criteria could be used for as-yet-unknown life and apply universally. To fully flesh out a definition based on objective limits, we would need to specify some threshold or degree of extremophily (i.e. "anything within 10% of the extreme is an extremophile," or "organism X is an extremophile to degree Y"). Some may worry about the arbitrariness and vagueness of a threshold, though in fact these concerns are common in biology.

C10.P40 **Drawbacks:** Problematically, there are certain physical ranges of which life only ever explores a small sampling. For example, although some organisms are intuitively "cryophilic" and "thermophilic," most of these do not come close to the limits of temperature in the universe. Indeed, the closest example at present is perhaps the only extremo*tolerant* tardigrades, or tardigrade eggs, that can be subjected to vacuum and extreme cold conditions without significant damage (Jönsson et al., 2008; Persson et al., 2011). Nor does life thrive at objective extremes of size, pressure, or radiation, among many other parameters. There are no angstrom-sized organisms, no black hole populations, and no species that only thrive in super novae.

C10.P41 **Implications:** There is no guarantee that objective limits be relevant to scientific interests. Life on Earth thrives in the absence of Einsteinium, for example. We are all extremophilic with respect to the absence of Einsteinium. Huzzah. Unless scientific utility comes into play, the objective limits concept would rule every example of life as extremophilic in *some* respect. Admitting scientific utility comes into play with respect to the limits we count as important, interesting, or explanatory, but admitting such pragmatism undercuts the objectivity of the definition, which is its primary benefit.

C10.P42 **Verdict:** While objective limits are desirable in the abstract, they are less useful for scientific purposes than the near impossibility concept, discussed next.

C10.S7

Near Impossibility

C10.P43 **Explanation:** Extremophiles with respect to near impossibility exhibit adaptations to extreme environments that are at the very limit of what is even *possible* for life to tolerate. Most of the preceding definitions dealt with organisms in the real world. In some definitions, notably statistical rarity and edge of morphospace, this led to the unfortunate consequence of extremophily being a contingent concept. Certain versions of these (SRE and EME) also suffered from sampling biases, though this may not concern researchers who are only interested in known extant organisms. One appeal of objective limits was that it avoided both the worries of contingency and sampling biases. Objective limits exist, after all, independent of the existence of life. Problematically, objective limits ruled out many of the paradigmatic examples of extremophily, such as piezophiles, thermophiles, and radioresistant organisms, as the objective limits of those physical dimensions was well beyond what life could tolerate. Unlike objective limits, near impossibility takes living processes into account. Recall that the unabashedly anthropocentric human-centric concept appealed to where humans (or human cells) *could* live. One way to avoid the charge of anthropocentrism would be to take the humans out of the definition and abstract away to the limits of the processes fundamental to life, such as metabolism or evolution. Such an exploration of life's possibilities requires thorough biophysical and biochemical analyses in addition to (or instead of) ecological surveys.

C10.P44 The near impossibility concept, we believe, is a guiding thought in each of the following quotes:

C10.P45
> The limiting temperature above which life cannot flourish is of theoretical and practical importance to many biological and geochemical studies. (Bains et al., 2015)

C10.P46
> Microbial life exists in all the locations where microbes can survive. (Gold, 1992)

C10.P47 Many readers may assume that life exists everywhere it possibly can, and so near impossibility may collapse into either statistical rarity or edge of morphospace. But in fact, this is an open question, and there are reasons to assume it is false (Bains, 2004; Schulze-Makuch & Irwin, 2012).

C10.P48 **Benefits:** Some research in synthetic biology and controlled evolution only makes sense within the context of this definition. Under other approaches, the controlled evolution of radiotolerant bacteria, for example, would be merely the creation of new extremophiles. To make sense of such projects, we must understand them as exploring the theoretical limits of life. Analyses of the possibility conditions for life are important in biology. For example, in 1983, Baross and Deming argued some bacteria grew at temperature ranges of >250°C and 265 atm (Baross & Deming, 1983). In response, many scientists failed to replicate their results, and some argued properties of biomolecules suggested such growth it was "impossible in theory" (Trent et al., 1984; White, 1984).

C10.P49 **Drawbacks:** Although some work has been done to assess the limits of the mechanisms of life (Bains, 2015), these analyses have an inestimable margin of error. It may be the case that life *as we know it* cannot survive above 150°C, for example, but such a claim is dependent on Earth's life resembling all other possible life. We would only expect these analyses to be justified in the cases where we expect all possible examples of life would break down, which is problematic because various definitions of life might set this boundary differently. This analysis could be too narrow ,not considering the many ways life could be realized, or it could be too broad, assuming a broader range for living mechanisms than is actually tolerable based on unknown variables. Narrow definitions can be challenged empirically, by attempting to discover or evolve more extreme lineages, but too-broad definitions may be untestable. Because this definition focuses on life that may not exist, it is more subject to theory-laden assumptions than other definitions. One need only take a brief look through the history of biology to see the frequency with which such assumptions and conjectures are overturned by new empirical evidence or new theoretical understanding.

C10.P50 **Implications:** Note that this approach is tantamount to assuming or stipulating a definition of life. As such, near impossibility may come in as many variants as there are definitions of life. They will share each's problems to boot: Near impossible extremophiles will not settle questions about whether A-Life is alive, for example. Given these worries, near impossibility for life as we know it is not a good enough characterization for this concept. Work in this area ought to highlight the aspects of life in which organisms are bordering on impossibility and why: too hot for proteins, too much sodium for conventional cell membranes, and so on.

C10.P51 **Verdict:** Scientific work in synthetic biology and related areas may rely on a near impossibility characterization of extremophiles.

C10.S8 Monism, Pluralism, Pragmatism

C10.S9 Monism

C10.P52 Given the many distinct definitions presented, one might ask whether there is any justified way to decide between the various candidate definitions. Perhaps one could study these definitions, choose the one that most fits one's scientific aims, stamp one's foot, and declare the rest as instances of poor thinking. Alternatively, scientists might opt for a mixed strategy in which we take the best features of each definition and splice them together into an unholy amalgamation. A skeptical reader might conclude these definitions rarely come apart, and so they may insist a precise definition is unnecessary for most scientific use. Finally, we could stamp our other foot and declare, as in the famous declaration of judicial candor, "I know it when I see it" (Stewart, 1964). Each of these three strategies aims to justify a single definition at the expense of the rest—what philosophers call "monism."

C10.P53 A monist strategy is one that takes a stand on a single, proper understanding is a concept, especially in the face of many proposed alternatives. Monism is conceptually preferable in a scenario in which the object of study is naturally unified. There are also methodological advantages of monism: its delineations are explicit, meaning they can be questioned, tested, and negotiated. Monism is problematic in cases in which the subject matter is not conceptually unified. Biology is replete with such examples, and the desire for monism has arguably fueled the interminable debates over the nature of species, fitness, function, and so on.

C10.S10

Pluralism

C10.P54 Contrasted with monism is pluralism, an approach in which a number of definitions are all entertained simultaneously, sometimes with respect to a particular domain or explanatory issue. The pluralist position is often unappealing to people who desire a single account, for intellectual, personal, or aesthetic reasons. Some versions of pluralism have the methodological disadvantages of being hard to test or falsify, inviting equivocation, and relying on individual researchers to be clear. Nevertheless, extremophily faces similar empirical and theoretical challenges to those that have plagued analyses of other biological concepts (e.g., life, species, and genes). In each of those cases, it seems as if the plurality of natural processes and scientific aims has resisted a single, monist characterization. We hope to take lessons from those debates seriously. Our proposal is pluralist in nature. We conclude there are many aims for research into extremophily: from seeking extreme-tolerant biological products, assessing the abundance, variation, and efficacy of creatures in difficult environments, to inferring the limits of life in the universe.

C10.P55 Before looking into how one might decide on the most appropriate concept of extremophily within a particular research aim, there are overall distinctions to be made between the five concepts of extremophily. We feel the critiques facing the statistical rarity and the objective limits definitions are devastating, and nearly all scientific uses can proceed better with other definitions (see Figure 10.3). While much good science is done with a human-centric definition of extremophiles, it cannot be overlooked that this definition is fully anthropocentric. And epistemic limits preclude the scientific use of those definitions that quantify over undiscovered organisms (SRU and EMU). Thus, most (but not all) astrobiological research into extremophiles is best conducted within the bounds of near impossibility or EME. This timid form of pluralism, we maintain, is a conceptually sound groundwork on which we can vindicate the various roles extremophiles play in our understanding of life in the universe.

C10.S11

Pragmatism

C10.P56 While a broadly construed and conceptually sound pluralism is required for extremophile-based science in general, each discipline may differ in its preferred definition(s) of extemophily. The research aims of molecular ecologists, in search of extreme habitats, differ from those of biotechnologists seeking new sources of biochemical reagents (c.f. Lentzen & Schwarz, 2006). We might refer to a biotechnological utility (BU) concept to describe the norms of current biotech research. Part of the motivation for this chapter is that such norms are often unclear or inconsistent. The concepts used by most researchers are marshaled without considering other uses within the field, risking serious equivocation. Consider the aims of biotechnological research outlined here:

> C10.P57 As gene sequencing technology becomes more routine, researchers are *determining the sequences of more obscure microorganisms and delving into the diversity of the microbial world with the aim of discovering new products*. It is hoped that genome data on nonpathogenic bacteria will *lead to the discovery of biocatalysts resistant to extremes of pH*, temperature, or solvents; nutritionally beneficial bacteria for probiotics; new types of streptomycete antibiotics; and microorganisms with enhanced capabilities to degrade xenobiotic compounds. (Marshall, 2000; emphasis added)

> C10.P58 A novel application area for extremophiles is the use of "extremolytes," organic osmolytes from extremophilic microorganisms, to protect biological macromolecules and cells from damage by external stresses . . . A range of new applications, all based on the adaptation to stress conditions conferred by extremolytes, is in development. (Lentzen & Schwarz, 2006)

C10.P59 The act of investigating "obscure" organisms to the end of getting a better picture of the extremes is akin to what we have labeled as SRE, while extremes of pH, temperature, and solvents correspond to something closer to an EME. While we might expect that organisms inhabiting statistically rare environmental conditions would also be those with "biocatalysts resistant to extremes," this is far from certain. Moreover, there seems no a priori reason to suspect that the discovery of new products should be more likely in obscure organisms than in the mesophiles, unless, of course, we had already characterized the more common organisms. While SRE or EME alone are poor proxies for biotechnological applicability, other definitions might be better candidates. A few examples help illustrate this.

C10.P60 The *Taq* polymerase, extracted from the thermophilic archaeon *Thermus aquaticus* (Chien et al., 1976), has had a profound influence on biotechnology since its discovery and eventual use as a reagent in polymerase chain reaction (PCR; Saiki et al., 1988). The utility of *Taq* for PCR amplification derives from its stability at temperatures sufficiently high to denature, or separate, DNA strands in a mixture (Lawyer et al., 1993). At lower temperatures, the DNA strands are bound and thus not available for copying, while at higher temperatures other reaction components begin to degrade. *Taq* is not alone in this capacity, *Pfu* polymerase from *Pyrococcus furiosus* has a similar temperature range, possessing proofreading activity not present in *Taq* and superior to many other thermostable polymereases (Cline et al., 1996; Bargseid, 1991). Indeed, it is probably cases in which many of these concepts converge (SRE, EME, and biotechnological utility [BU]), such as with *Taq* and *Pfu,* that encourage biologists to run these distinctions together.

C10.P61 Biotechnological applications are perhaps one of the best cases for considering extremes as more than just physical and chemical variables and including trophic, ecological, organismal, or population-based extremes. Antibiotic resistance, for example, tends to develop in environments where there is an extremely strong selective pressure caused by antibiotics: conditions that can be anthropogenic or occur in naturally antibiotic rich competitive bacterial habitats. Indeed, Bhullar et al. (2012) have argued nutrient-limited and bacteria (species) rich environments encourage an antibiotic arms-race, suggesting this kind of extremity is of biotechnological utility. As the authors point out, "the diversity in the resistome also suggests that there are a myriad of bioactive molecules with antibiotic properties waiting to be discovered" (Bhullar et al., 2012). Put another way, we have reason to think that this corner in the intersection of the axes of species richness and nutrient density constitutes a genuine extreme of interest to biotechnologists in the business of antibiotic development. Considerations like these suggest that in context of biotechnological research something like an EME, with special attention given to rare or unexplored habitats, might be most fruitful.

C10.S12 Conclusion

C10.P62 This chapter explored the multiple, occasionally incompatible characterizations of "extremophiles." We argued that extremophily, far from being a straightforward concept, admits of multiple interpretations, each with extremely different consequences. This concept faces many of the same concerns of vagueness and arbitrariness as other areas of biology, such as defining life itself, species, or genes. Extremophile research is especially prone to these concerns, as it involves basic assumptions about life's nature, limits, and whether we can know either.

C10.P63 We considered a number of possible definitions, including indexing extremophily to the limits of human habitability (human-centric), identifying extreme organisms as those which thrive at the limit of what is inhabited by life (edge of morphospace), as well as those which thrive at the limit of what is inhabitable by life (near impossibility). Each of those definitions had a role to play in the timid pluralism we advocate. Two other definitions, dealing with the rarity of creatures able to survive in one environment (statistical rarity) and one in which extremes were identified by physical boundaries and extremophiles were creatures near those limits (objective limits), had problems that proved devastating to their continued use. One final consideration was the utility of organisms for human purposes (BU), which illustrated how widely divergent research aims may be with respect to extremophiles, although even this view may simply be the pragmatic cousin of the edge of morphospace view. We hope this conceptual exploration of extremophily will guide and buttress further research into this area.

Note

C10.N1 1. We use the terms "concept," "definition," "account," "approach," and "view" interchangeably, but note that there are scholars with strong opinions on the distinction between these terms.

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