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The Last Possible Outposts for Life on Mars

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Abstract

The evolution of habitable conditions on Mars is often tied to the existence of aquatic habitats and largely constrained to the first billion years of the planet. Here, we propose an alternate, lasting evolutionary trajectory that assumes the colonization of land habitats before the end of the Hesperian period (*ca.* 3 billion years ago) at a pace similar to life on Earth. Based on the ecological adaptations to increasing dryness observed in dryland ecosystems on Earth, we reconstruct the most likely sequence of events leading to a late extinction of land communities on Mars. We propose a trend of ecological change with increasing dryness from widespread edaphic communities to localized lithic communities and finally to communities exclusively found in hygroscopic substrates, reflecting the need for organisms to maximize access to atmospheric sources of water. If our thought process is correct, it implies the possibility of life on Mars until relatively recent times, perhaps even the present.
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1. Introduction

Habitability models of Mars often tie the potential for life to the existence of aquatic habitats such as lakes or oceans (*e.g.*, McKay and Davis, 1991). Along these lines, current and planned robotic missions mainly focus on the study of sedimentary deposits formed in aquatic environments billions of years ago. The discovery of ancient lake sediments deposited in a geochemical environment compatible with life (Grotzinger *et al.*, 2014), together with the certainty that such environments were widespread during the Noachian and Hesperian periods (*e.g.*, Bibring *et al.*, 2006; Mustard *et al.*, 2008; Ehlmann and Edwards, 2014), has so far validated this strategy.

However, this vision of habitability is incomplete, and the above paradigm ought to be reconsidered because the fate of an early martian biosphere was not necessarily tied to the duration of aquatic habitats. An alternative evolutionary trajectory would have opened with the colonization of land, at which point a portion of the martian biosphere would have become dependent solely on atmospheric sources of water. In this synthesis paper, we consider this second trajectory by addressing two aspects of the problem: (1) the probability that early life on Mars would have colonized land and (2) land ecosystems' response to increasing dryness. We focus our analysis on forms of life on, or near, the surface that ultimately rely on atmospheric sources of water. The possibility of life in the deep subsurface is not discussed.

2. The Colonization of Land

The three domains of life on Earth contain both aquatic and terrestrial groups, but among the prokaryotes there appears to be a major evolutionary group with a common ancestor on land, the so-called Terrabacteria, which includes members of the cyanobacteria, the Gram-positive phyla, and the Chloroflexi and Deinococcus-Thermus (Battistuzzi and Hedges, 2009). Representatives of this group possess specific adaptations to land environments such as resistance to desiccation, high salinity, and high UV radiation. Phylogenetic, cytological, and environmental data suggest that the Terrabacteria and Hydrobacteria could have diverged as early as 3.54 Ga (Battistuzzi and Hedges, 2009), relatively fast after the origin of life. To date, possible evidence of land ecosystems have been found in late Mesoproterozoic to early Neoproterozoic paleosols (*ca.* 1.2–1 billion years ago) (Prave, 2002) in 2.9–2.7 billion-year-old ephemeral ponds (Rye and Holland, 2000) and alluvial sequences, some of which bear microfossils (Hallbauer and van Warmelo, 1974; Mossman *et al.*, 2008), and in paleosols that formed between 2.7 and 2.6 billion years ago (Watanabe *et al.*, 2000). Considering that the geological record of land environments is sparse,

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the colonization of land might have occurred earlier than what the fossil record suggests.

Resistance to desiccation, high salinity, and UV radiation, the trademarks of the Terrabacteria, are also survival adaptations of aquatic microorganisms in coastal areas, such as those that inhabit benthic mats periodically exposed to air-drying and UV radiation during cycles of evaporation and flooding (*e.g.*, Garcia-Pichel, 1998; Pattanaik *et al.*, 2007; Beraldi-Campesi, 2013). Perhaps not surprisingly, the cyanobacteria, a deeply rooted taxonomic group often found in aquatic environments, include some of the most desiccation-resistant organisms known, which are adapted to survive in the driest regions on Earth (Friedmann, 1980; Friedmann and Ocampo-Friedmann, 1995; Warren-Rhodes *et al.*, 2006; Pointing and Belnap, 2012; Wierzchos *et al.*, 2012b). The above suggests that the colonization of land could be a relatively straightforward evolutionary step once aquatic habitats are established.

On Mars, the established existence of aquatic habitats during the late Noachian about 3.8 billion years ago (Grotzinger *et al.*, 2014) and the inferred existence of aquatic environments at the end of the Hesperian *ca.* 3 billion years ago (McKay and Davis, 1991), together with the cumulative evidence of episodic aquatic environments during the Early Amazonian (Fairén *et al.*, 2009; Rodríguez *et al.*, 2014, 2015), suggest that an early martian biosphere could have had sufficient time to colonize land, assuming a similar pace of colonization as life on Earth. But contrary to Earth, most of the surface of Mars was emerged land even when liquid water was abundant (Carr and Head, 2015). The inferred existence of tens of thousands of crater lakes in the martian southern highlands, and possibly a large northern ocean, implies a potentially large net shoreline area with shallow aquatic environments that could have propelled the emergence of land microorganisms. The absence of a magnetic field since the late Noachian (Acuna *et al.*, 1998; Carr and Head, 2010) along with the continued decline in atmospheric pressure in the first 2 billion years (Lammer *et al.*, 2013) would have exerted strong selective pressures on martian organisms to adapt to desiccation, UV radiation, and high salinity, thus paving the way for the colonization of land. After the colonization of land, long-term habitability on Mars would no longer have been tied to the existence of aquatic environments but to atmospheric sources of water. This could have significantly expanded the martian habitability window beyond the Hesperian period.

3. Ecological Transitions in Dryland Ecosystems

Important lessons regarding the possible adaptations of land ecosystems to increasing dryness can be learned from the study of life in dryland environments on Earth. Drylands are one of the largest terrestrial biomes, and more than 35% of Earth's land mass is permanently or seasonally arid (Pointing and Belnap, 2012). Dryland ecosystems encompass a broad hydrological range, typically measured as the Aridity Index (AI), defined as the ratio of mean annual precipitation to potential evapotranspiration. Based on the AI scale, drylands are categorized as semiarid ($0.20 < \mathrm{AI} < 0.50$), arid ($0.05 < \mathrm{AI} < 0.20$), and hyperarid ($\mathrm{AI} < 0.05$). Research conducted over the past 40 years suggests that there is a predictable pathway of ecological change with increasing dryness, driven by the need of organisms to maximize exposure to liquid water during sporadic wet events.

Many desert organisms are capable of desiccation tolerance, the ability to dry up without dying (Potts, 1994; Alpert, 2005) and to resume metabolic activity quickly after rehydration, even after years of complete desiccation (*e.g.*, Potts, 1994; Proctor *et al.*, 2007). In arid regions, these poikilohydric microorganisms colonize the top few centimeters of soil and rock substrates between a patchy vegetation cover (Belnap and Lange, 2003; Pointing and Belnap, 2012), and relatively complex microbial communities largely sustained by phototrophic organisms can develop as biological soil crusts (BSC) (Fig. 1A). In arid deserts, BSC can cover up to 70% of the total soil surface (Belnap and Lange, 2003), leading to relatively high concentrations of organic carbon (OC) that is recycled relatively fast, within decades to several centuries (Amundson, 2001).

However, a significant ecological collapse occurs in soils at the transition from arid to hyperarid conditions (Fig. 2). This transition signals a dramatic reduction in vegetation cover, which becomes almost entirely confined to ephemeral runoff channels (washes) and episodic and transient blooms that follow rare rainfall events. Biological soil crusts in hyperarid soils become increasingly fragmented or patchy, and there is a significant decline of both cell abundance and species richness (Pointing *et al.*, 2007; Pointing and Belnap, 2012; Crits-Christoph *et al.*, 2013). Soil microbial communities and BSC in both temperate and cold hyperarid environments become discontinuous and are gradually replaced by regolith and desert pavements (Pointing and Belnap, 2012; Colesie *et al.*, 2013). This is reflected in the distribution of soil OC and biomass (Fig. 2B), which fall to the lowest levels found anywhere on Earth (*ca.* 10^3 to 10^5 cells g^{-1} soil), concurrent with an increase in mean residence time of soil OC to tens of thousands of years (Ewing *et al.*, 2008).

In these hyperarid environments, soil communities are largely replaced by rock-inhabiting (lithobiontic) communities (*e.g.*, Friedmann, 1980; Pointing and Belnap, 2012; Wierzchos *et al.*, 2012b). Lithobiontic communities comprise epilithic microorganisms that colonize the surface of rocks, hypolithic microorganisms that colonize the underside of translucent substrates such as quartz rocks and gypsum crusts (Fig. 1C), and endolithic microorganisms that colonize the interior of porous substrates such as sandstone rocks and salt crusts (Fig. 1D). The colonization of lithic substrates is a direct response to water deficit. Hypolithic and endolithic habitats extend the range of conditions under which liquid water can occur, and at the same time, surface tensions in the rock matrix slow the evaporation of water and thus prolong access to moisture after a wetting event. This is critical for microbial communities whose long-term survival hinges on their capacity to sustain a net positive carbon balance in the course of repeated cycles of wetting and drying (Alpert and Oechel, 1985; Friedmann *et al.*, 1993; Coe *et al.*, 2012). In temperate deserts, this is not trivial, because liquid water often occurs during the night, when respiration, but not photosynthesis, can occur. The net flux of CO_2 is negative in these first hours of dark metabolic activity and can only be balanced via photosynthesis if water still persists in the early morning (Noy-Meir, 1973; Alpert and Oechel, 1985; Alpert, 2005). Due to their water retention, lithic substrates expand the window for photosynthesis

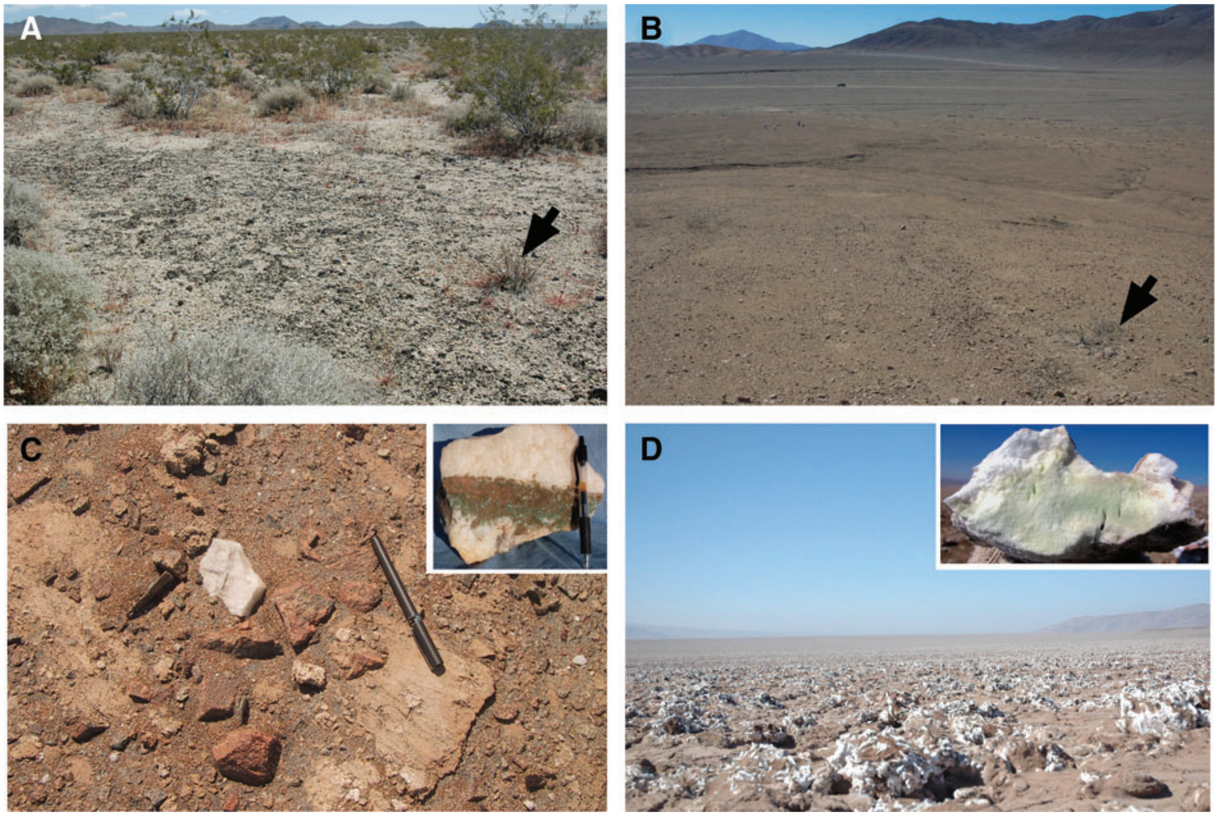

FIG. 1. Successions of dryland ecosystems with increasing dryness. (**A**) Vegetated arid site in the Mojave Desert, with a continuous cover of BSC. (**B**) Nonvegetated hyperarid site in the Atacama Desert devoid of BSC. (**C**) Hypolithic microbial community under a translucent quartz stone in the hyperarid Namib Desert. (**D**) Microbial community inside a hygroscopic salt crust in the hyperarid core of the Atacama Desert. Black arrows in A and B point to features of similar size, for scale. (Color graphics available at www.liebertonline.com/ast)

in the morning and enable the communities to balance respiration with carbon fixation. The protected lithic microenvironment also provides shelter against erosion and wind, amelioration of extreme temperature changes, and shielding against UV radiation (Friedmann, 1980). Colonized lithic habitats are found in all deserts, including regions once considered to be too dry for life (Friedmann, 1982; Warren-Rhodes *et al.*, 2006; Wierzchos *et al.*, 2006, 2012b; Pointing *et al.*, 2009; Cary *et al.*, 2010; Khan *et al.*, 2011; Pointing and Belnap, 2012). Despite the diversity of lithic habitats and the broad range of dryland environments where they are found, community structure in hypolithic and endolithic habitats is remarkably similar, although the composition of the community might be very different (Pointing *et al.*, 2007). A key concept with regard to lithic habitats is that the physical properties of the substrate generate local habitable conditions in environments that might otherwise be too harsh for life (Friedmann and Ocampo-Friedmann, 1984).

Yet there are also trends of extinction within lithic habitats with increasing dryness. For example, in the Dry Valleys of Antarctica endolithic microbial communities are found primarily in the interior of south-facing sandstone rocks and cliffs, where microorganisms take advantage of meager snowmelt that percolates into the rock during warm summer days (Friedmann, 1982; McKay and Friedmann, 1985). However, the sandstone endolithic community in the Dry Valleys appears to be at the brink of extinction, and in some of the coldest and driest valleys the endolithic colonies are largely fossilized (Friedmann *et al.*, 1994; Wierzchos *et al.*, 2004, 2005; Sun, 2013). A similar trend of extinction is observed in hypolithic habitats with decreasing rainfall in hyperarid deserts. Hypolithic colonization of translucent rocks is typically 100% (*i.e.*, all suitable rocks are colonized) in semiarid regions, dropping to <50% in arid areas and to <1% in hyperarid regions, where the hypolithic habitat becomes practically nonexistent (Warren-Rhodes *et al.*, 2006, 2007) (Fig. 2A) except in local areas of recurrent fog (Azúa-Bustos *et al.*, 2011). The disappearance of hypolithic colonies with diminishing rainfall is mirrored by epilithic lichens (Wierzchos *et al.*, 2011), despite the fact that some can supplement liquid water with water vapor and restore photosynthesis with high (>75%) humidity only (Lange, 1993).

At the driest end of hyperaridity, where soils and most lithic substrates can no longer sustain active biology (*e.g.*, Warren-Rhodes *et al.*, 2006; Ewing *et al.*, 2008; Crits-Christoph *et al.*, 2013), relatively complex and abundant communities of autotrophic and heterotrophic bacteria and archaea (de los Ríos *et al.*, 2010; Robinson *et al.*, 2015) are still found inside porous, hygroscopic salt crusts (Wierzchos *et al.*, 2006) (Fig. 1D). The communities inside the salt nodules use liquid brines that form in the interior of the salt substrate from the vapor phase via deliquescence and capillary condensation (Davila *et al.*, 2008, 2013; Wierzchos *et al.*, 2012a). Because the salt substrate retains water

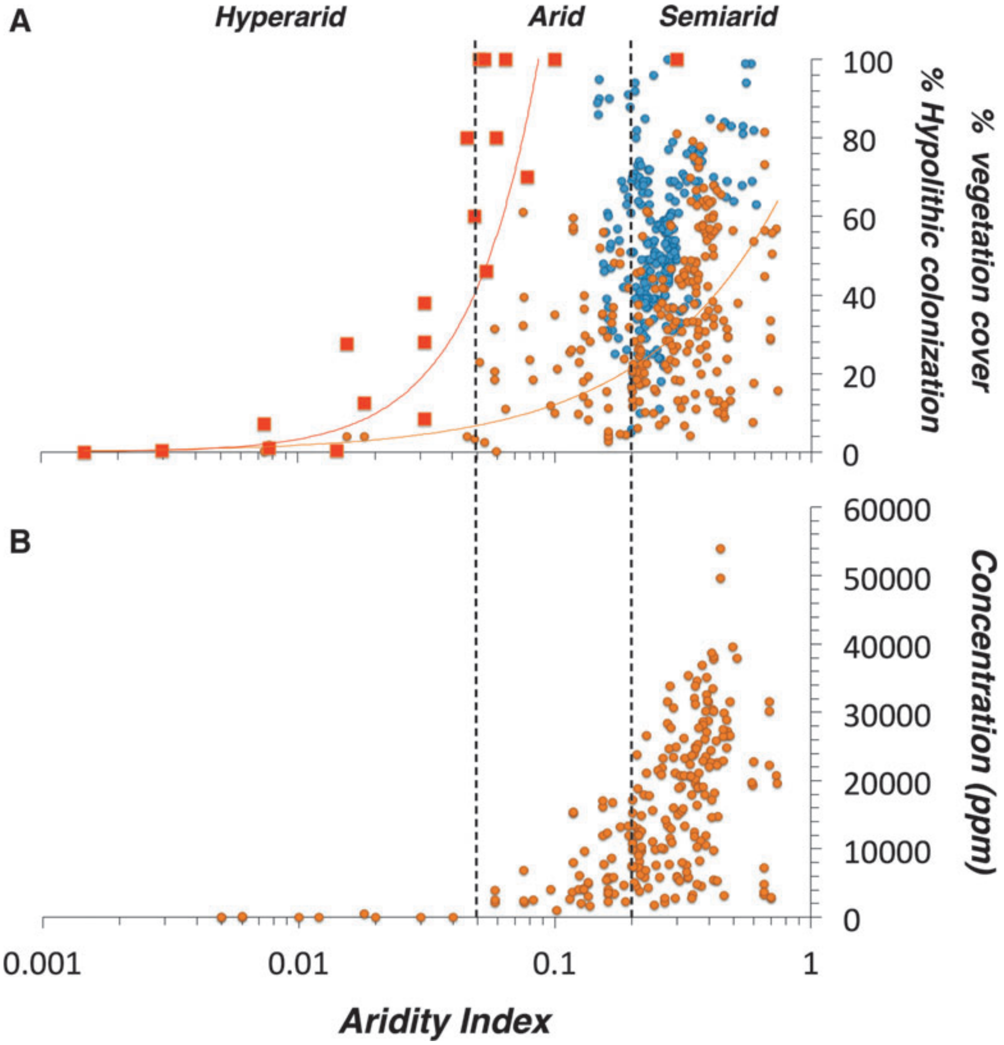

FIG. 2. (**A**) Percent vegetation cover (dots) and percent hypolithic colonization (squares) as a function of aridity (expressed as AI). Blue dots are actual field observations (data from Delgado-Baquerizo *et al.*, 2013). Orange dots are from satellite data. Percent hypolithic colonization data was obtained from Allen (1997), Warren-Rhodes *et al.* (2006, 2007, 2013), Khan *et al.* (2011), Al-Thani (2014) and references therein. (**B**) Soil OC concentration as a function of aridity (data from Delgado-Baquerizo *et al.*, 2013).

efficiently, cyanobacteria inside the salt nodules can fix CO_2 for days after a wetting event (Davila *et al.*, 2015), and the community is capable of carbon cycling rates in timescales of decades (Ziolkowski *et al.*, 2013) even in the absence of atmospheric precipitation. Such deliquescent substrates provide a minimalistic habitat for survival under extremely dry conditions, and in the driest place on Earth they likely represent the last available habitat for life.

4. The Late-Stage Evolution of Land Ecosystems on Mars

The transition from widespread edaphic communities to localized lithic communities and finally to communities exclusively found in hygroscopic substrates reflects the need for land organisms to maximize access to atmospheric sources of water. We propose that, if life colonized martian land, a similar sequence of ecological transitions would have occurred as the planet became increasingly dry (Fig. 3).

First, relatively diverse microbial communities would have been widespread in the top centimeters of the regolith, with metabolic cycles tuned to episodes of rainfall, dew, fog, snow, or glacier melt. Pigmentation and community structure could be adequate solutions for UV protection, and proximity to the surface would have granted access to sunlight and an abundant carbon source in the atmosphere. These communities would likely be comprised of poikilohydric organisms capable of desiccation tolerance, analogous to BSC and soil bacteria found in terrestrial arid deserts and in permafrost in polar regions. Other possible early land habitats could have been seasonal or perennial snow banks, debris-rich glacier ice, ice-bearing permafrost (Jakosky *et al.*, 2003; Córdoba-Jabonero *et al.*, 2005; McKay *et al.*, 2013), or protected habitats near the surface such as caves (Boston *et al.*, 2011; Northup *et al.*, 2011).

With increasing dryness, regolith communities would have become discontinuous and gradually replaced by desert pavements. Wind erosion or dust deposition would have

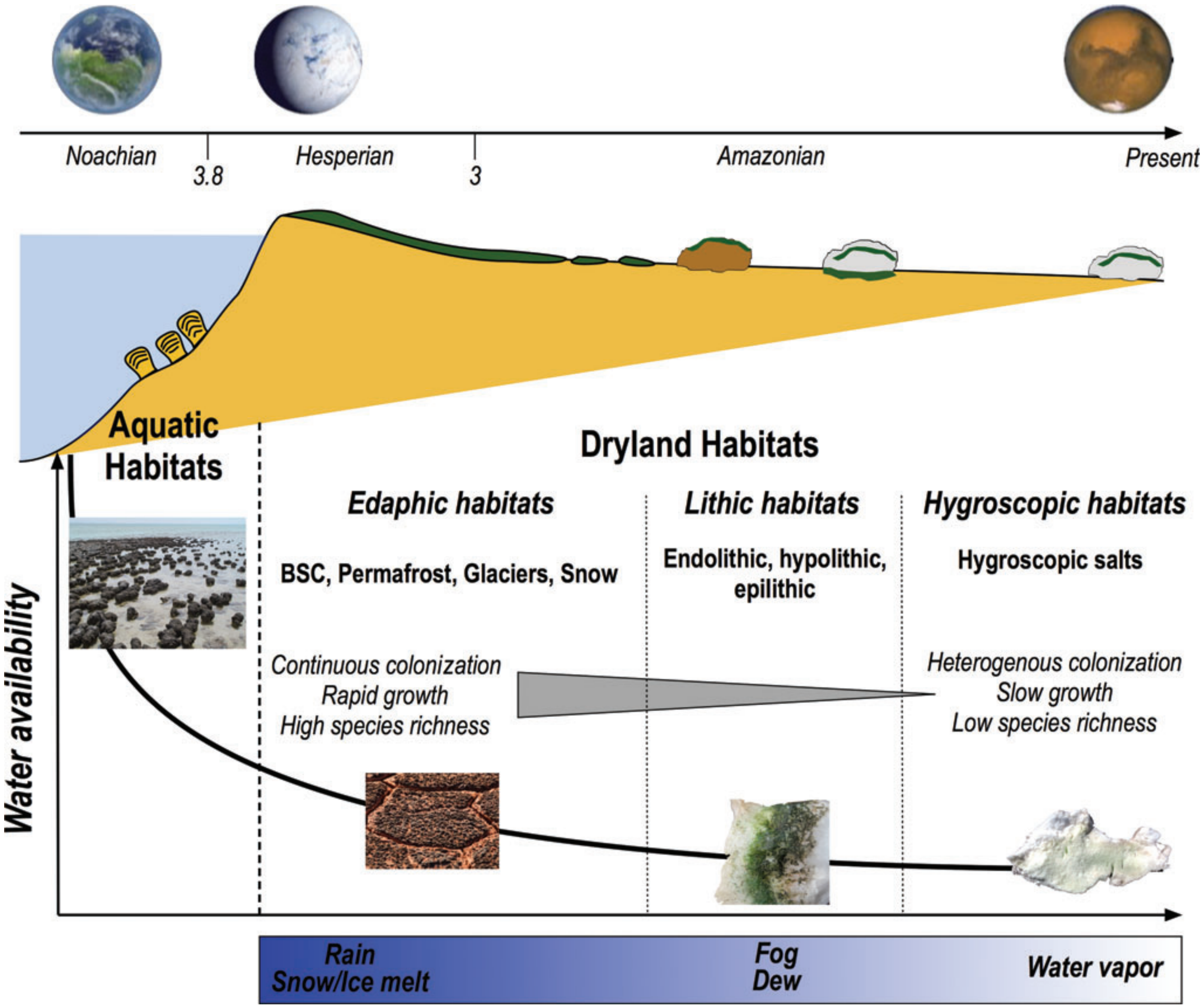

FIG. 3. Proposed sequence of ecological transitions on Mars with increasing dryness, assuming an early colonization of land. After the disappearance of aquatic environments, land habitats (edaphic, lithic, and lastly hygroscopic) would still be available, based on different sources of atmospheric water. (Color graphics available online at www.liebertonline.com/ast)

slowly erased any surface expression of such communities through dispersal or burial, although transient climate excursions toward wetter conditions, driven for example by orbital fluctuations, could have reactivated the regolith communities for relatively short periods. At this point, long-term active metabolism would have been largely constrained to lithobiontic communities, both in hypolithic and endolithic habitats selected based upon certain physical properties of the rock substrate, such as color, opacity, size, and porosity (*e.g.*, Friedmann and Koriem, 1989; McKay *et al.*, 1992). If members of these lithic communities were light-dependent, relatively translucent rocks such as sandstone, calcite, ignimbrite, gypsum, quartz, or dolomite would have been suitable for colonization, such as is observed in practically all deserts on Earth (Friedmann, 1982; Friedmann and Ocampo-Friedmann, 1984; Wierzchos *et al.*, 2011, 2013; Pointing and Belnap, 2012; DiRuggiero *et al.*, 2013). In the case of light-independent communities, other lithic substrates might have been available, such as opaque rocks. Yet the strong selective pressure to colonize lithic habitats ought to be independent of sources of energy and nutrients and instead should apply to forms of life that rely on atmospheric sources of water.

Finally, the last habitat for life near the surface would have been the interior of hygroscopic salt crusts, which could trigger the condensation of liquid water via deliquescence at relative humidity (RH) conditions well below the atmospheric condensation point. At the same time, the deliquescent brines would have acted as antifreeze, depressing the freezing point of water, and the interior of the salt substrate would have provided shelter against UV radiation. Analogues of such salt communities would be the endolithic communities found in fossil salars in the hyperarid core of the Atacama Desert (Wierzchos *et al.*, 2006; Davila *et al.*, 2010).

The proposed sequence of ecological transitions with increasing dryness is based on global trends observed in both hot and cold deserts on Earth. Our analysis does not preclude the existence today, or in the recent past, of specialized habitats typical of polar desert environments, such as debris-rich ice (Jakosky *et al.*, 2003; Córdoba-Jabonero *et al.*, 2005; McKay *et al.*, 2013), but such habitats would require local sources of water and are constrained to high latitudes, which are permanently cold, an additional constraint to life.

5. Implications for Recent Martian Habitability

If hygroscopic habitats such as those found in the Atacama Desert represent the last possible outposts for life under extremely dry conditions, then we can use them to approximate the last time when Mars might have been a habitable planet.

The habitability of hygroscopic salt crusts depends critically on the abundance of water in the atmosphere and in the nature of the salt substrate, which determines its deliquescence properties and the eutectic temperature and water activity of the deliquescence solution (Davila *et al.*, 2010). Water activity is the relevant parameter that links liquid water and habitability. Assuming long-term equilibrium conditions and the average temperature and RH on the martian surface, the water activity of an aqueous solution on present-day Mars should fall well below the conditions for habitability for any terrestrial organisms (*e.g.*, Kminek *et al.*, 2010; Rummel *et al.*, 2014). However, for a more precise assessment of habitability we must consider that the planet is not in equilibrium and determinations of water activity need to be done at the scale of the environment experienced by microorganisms, where environmental conditions can depart significantly from the average (McKay and Friedmann, 1985; Nienow *et al.*, 1988a, 1988b; Davila *et al.*, 2008; Wierzchos *et al.*, 2012a; Meckenstock *et al.*, 2014). Temperature and RH fluctuations on Mars could promote transient deliquescence inside salt crusts with low eutectic points (Chevrier *et al.*, 2009; Davila *et al.*, 2010; Martín-Torres *et al.*, 2015). For salt with very low eutectic points such as perchlorate, the water activity of the resulting transient solution—in addition to its temperature—would still fall below the known threshold for growth, but other salts such as NaCl would produce more benign deliquescent brines. These examples serve to illustrate the limitations that arise when assessing habitability assuming only large-scale equilibrium conditions.

A comparison of the abundance of atmospheric water on Mars and in the driest regions on Earth might give an idea of how prevalent and intense deliquescent events might be on the planet. Most of the martian water inventory is sequestered in the polar layered terrains and in the near-surface regolith at latitudes above 30–40° (*e.g.*, Head *et al.*, 2003; Feldman, 2004; Byrne *et al.*, 2009; Carr and Head, 2010; Kadish and Head, 2011). The median column of precipitable water vapor (PWV) is between <3 and 100 precipitable micrometers (pr-μm) planetwide (Jakosky and Farmer, 1982; Haberle *et al.*, 2001). Climate simulations predict that increased polar summer insolation during high obliquity leads to a water cycle that is much more intense than today's, with a column water abundance up to 3000 pr-μm above the northern polar cap around summer solstice and about 50 pr-μm in the summer tropics (Jakosky and Carr, 1985; Forget *et al.*, 2006). Assuming an average obliquity of 40° during the last 3 billion years, the long-term water content of the lower atmosphere could be 2 orders of magnitude higher than it is at present (Mellon and Jakosky, 1995), and there could be >1000 pr-μm of atmospheric water at midlatitudes and low latitudes during recent high-obliquity (*i.e.*, 45°) periods (Jakosky and Carr, 1985). In comparison, the median column of PWV above the Andean plateau in the Atacama Desert is approximately 1200 pr-μm at an elevation of 5000 m (Giovanelli *et al.*, 2001; Tremblin *et al.*, 2012), equivalent to the PWV in the hyperarid core of the desert where deliquescence-driven microbial ecosystems are found. For completeness, we note that the lowest PWV reported so far on our planet is near the South Pole and ranges between 100 and 800 pr-μm, with minimum annual values as low as 30 pr-μm (Buravo *et al.*, 1986; Chamberlain *et al.*, 2000). Hence, as a first approximation the water abundance in the present-day martian atmosphere is lower than in the driest regions on Earth by a factor of 10–100, but during high obliquity it is comparable to levels measured in the hyperarid core of the Atacama Desert. Assuming—rather arbitrarily—that a PWV of 1000 pr-μm represents the minimum atmospheric water abundance that can sustain deliquescence-driven microbial ecosystems, the abundance of water on a comparison of the martian surface to the driest deserts on Earth suggests that the habitability window in this type of substrate might have closed relatively recently, perhaps during the late Amazonian, or it may possibly still be open.

6. Conclusions

Currently, the search for ancient aqueous environments as repositories of possible evidence of life is the primary focus of robotic missions to Mars. However, the colonization of land by putative martian microorganisms could have opened a lasting evolutionary trajectory for life independent of aquatic habitats. The ecological transitions that occur in Earth's deserts with increasing dryness can inform us as to where the last martian near-surface ecosystems may have existed or still exist. In analogy with terrestrial dryland ecosystems, the physical properties of habitats with regard to water retention, rather than the physiological adaptations of microorganisms, could have directed the late-stage evolution of life on Mars. As is the case for Earth's driest regions, the last possible sources of water for life on Mars would have been the deliquescence of hygroscopic salt crusts, and this window of habitability might have closed relatively recently or may still be open. As such, and in retrospect, dry regolith samples analyzed by the Viking landers might not have been the best substrates to search for active (or extinct) biology. Future robotic missions would be advised to prioritize the study of lithic substrates.

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Author Disclosure Statement

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Abbreviations Used

AI = Aridity Index
BSC = biological soil crusts
OC = organic carbon
PWV = precipitable water vapor
RH = relative humidity