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Early Mars habitability and global cooling by H₂-based methanogens

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 Check for updates

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During the Noachian, Mars' crust may have provided a favourable environment for microbial life^{1,2}. The porous brine-saturated regolith^{3–5} would have created a physical space sheltered from ultraviolet and cosmic radiation and provided a solvent, whereas the below-ground temperature² and diffusion^{6,7} of a dense, reduced atmosphere^{8,9} may have supported simple microbial organisms that consumed H₂ and CO₂ as energy and carbon sources and produced methane as a waste. On Earth, hydrogenotrophic methanogenesis was among the earliest metabolisms^{10,11}, but its viability on early Mars has never been quantitatively evaluated. Here we present a probabilistic assessment of Mars' Noachian habitability to H₂-based methanogens and quantify their biological feedback on Mars' atmosphere and climate. We find that subsurface habitability was very likely, and limited mainly by the extent of surface ice coverage. Biomass productivity could have been as high as in the early Earth's ocean. However, the predicted atmospheric composition shift caused by methanogenesis would have triggered a global cooling event, ending potential early warm conditions, compromising surface habitability and forcing the biosphere deep into the Martian crust. Spatial projections of our predictions point to lowland sites at low-to-medium latitudes as good candidates to uncover traces of this early life at or near the surface.

To assess and quantify the habitability of early Mars and the evolution of its surface conditions under the influence of methanogenic hydrogenotrophy, we use a state-of-the-art one-dimensional (1D) photochemical climate model combined with a crust model to self-consistently compute the atmospheric chemical composition, climate and thermal profile of the crust and crust–atmosphere gas exchanges (Methods, Fig. 1 and Extended Data Fig. 1). The geophysical chemical model is coupled with a depth-structured model of a chemoautotrophic ecosystem adapted from our previous work^{12,13} to (1) evaluate the habitability of the Martian subsurface to populations

of methanogenic hydrogenotrophs, (2) resolve the dynamics of these populations and (3) quantify the corresponding biological feedback on the planet's atmosphere and climate.

Only the fraction of the surface left free of ice (measured by ρ) allows crust–atmosphere gas exchanges, as a consequence of ice forming in the regolith pores blocking gas pathways into the crust⁶. We assume that the planet's ice coverage is determined by surface temperature and by the freezing points of saline brines (Methods and Extended Data Fig. 2). The brines' freezing points are poorly constrained (estimates range from 203 to 273 K) as they depend on the

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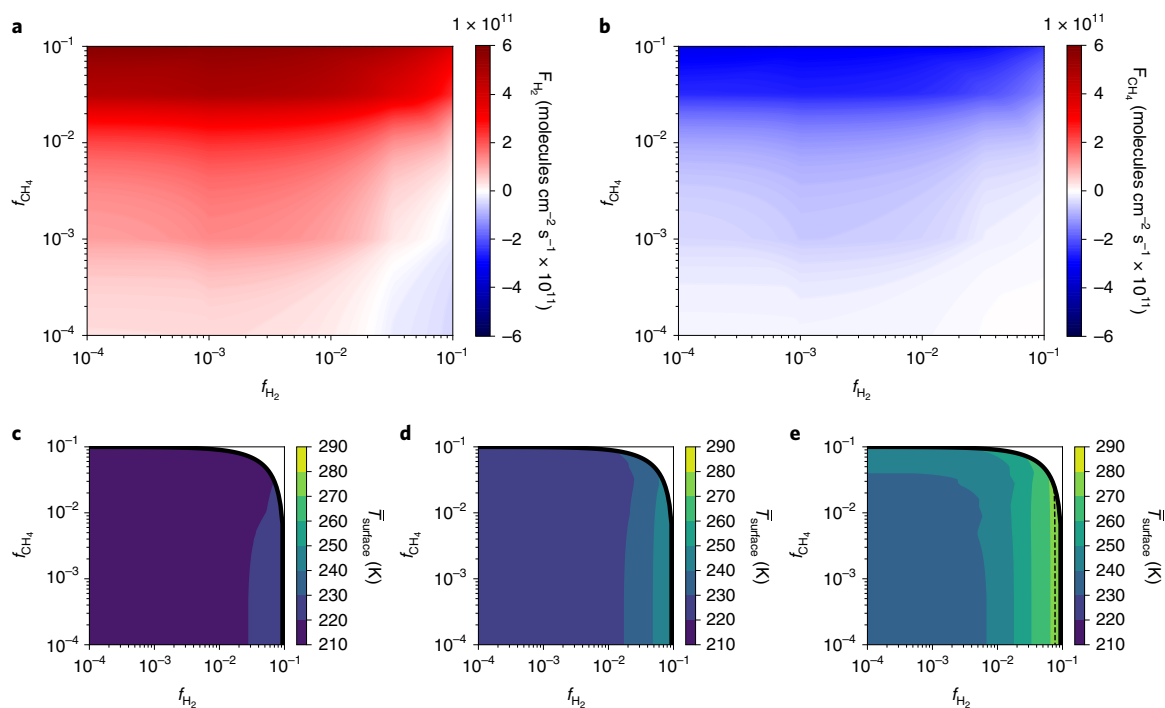


Fig. 1 | Modelled photochemistry and climate of early Mars. a, b, Rates (denoted by F) of destruction/production of H₂ (a) and CH₄ (b) as a function of H₂ and CH₄ mixing ratios (denoted by f). **c–e**, Average surface temperature (\bar{T}_{surface}) as a function of H₂ and CH₄ mixing ratios, f_{H_2} and f_{CH_4} , for an atmospheric

pressure of 0.5 (c), 1 (d) and 2 (e) bars. Our simulations were constrained by $f_{\text{H}_2} + f_{\text{CH}_4} < 0.1$ (thick black boundary curve in c–e). Dashed black line in e: $\bar{T}_{\text{surface}} = 273$ K. See Methods for details.

brine's composition^{3–5}. We therefore simulated initial and steady-state characteristics of Mars for three values of the freezing point—203, 252 and 273 K—corresponding respectively to perchlorate brines, NaCl brines and pure water⁴.

From our climate–atmosphere model (Fig. 1) we resolve Mars' initial features (Fig. 2a–c). The initial distribution of average surface temperature, \bar{T}_{surface} , ranges from 216 to 294 K, with a median at 256 K (Fig. 2c). Below the surface, a general pattern is that temperature increases with depth, whereas diffusivity decreases. For brines freezing at 203, 252 and 273 K, Mars is fully covered with ice (hence uninhabitable) in 0, 10 and 40% of the cases, with median ρ of 100%, 75% and 0.15%, respectively (Fig. 2d). Thus, the nature of the brines would have strongly constrained the geographic extent of Mars' initial habitability. Note that our model shares with other recent models of Mars climate^{14,15} the assumption that albedo remains low and constant in spite of changing ice coverage (Methods). We will further discuss this assumption and argue that our results are conservative with respect to the triple interaction between surface temperature, albedo and biological activity.

The atmospheric redox disequilibrium and its accessibility in the Martian crust make the hydrogenotrophic ecosystem viable in all of our simulations in which Mars is not fully covered with ice. Consistently with microbial data from permafrost ecosystems on Earth¹⁶, our model predicts that the lowest temperature for hydrogenotrophs to exist and reproduce is approximately 253 K (Fig. 2e–g). For warmer surface temperatures, methanogens can colonize the first layer of the Martian crust. When the surface is colder, methanogens are limited upward at the depth at which the limit temperature of 253 K is reached (Methods). The deeper end of the microbial vertical distribution is bounded ca. 320 K (lower than the maximum temperature at which methanogenic extremophiles can grow on Earth¹⁷). At such depths the atmospheric redox potential diffusing from the surface has been entirely exploited by the ecosystem above.

As they colonize the Martian subsurface, methanogenic hydrogenotrophs drive atmospheric CH₄ up and atmospheric H₂ down. At

steady state, the biogenic rates of CH₄ production and H₂ consumption, combined with H₂ atmospheric escape, balance out the loss rate of CH₄ by photochemistry and the production rate of H₂ by photochemistry and volcanic outgassing (Fig. 1). Typically, the planetary system reaches this new steady state in 100,000 to 500,000 years. As a result, the median f_{H_2} drops from 5% to between 0.35% and 2.75%, depending on the brine's freezing point (Fig. 2a), whereas the median steady-state atmospheric concentration of CH₄ rises to between 0.075 and 1% (Fig. 2b). Due to the respective effects of H₂ and CH₄ on climate^{14,15,18} (Fig. 1), the global atmospheric shift triggered by the microbial biosphere drives a strong global cooling effect (Fig. 2c). Even though the biological impact on Mars' surface conditions markedly depends on the brine's freezing point and initial ice coverage (Fig. 2a–d), methanogenic hydrogenotrophs make a warm early Mars unlikely, as the maximum temperature plummets under their planetary influence from 294 K to between 260 and 250 K across the range of brine freezing point values (Fig. 2c).

Reciprocally, the global cooling feeds back to the biosphere. First, when the average surface temperature in ice-free regions drops below 253 K, methanogens are forced deeper into the Martian crust (Fig. 2e–g). Second, as the biosphere uses up the atmospheric redox potential, the atmospheric change entails that the planet's global thermodynamic favourability to methanogenesis declines. As a consequence, the total biomass productivity at steady state falls 100-fold (Fig. 2h). Finally, the ice-free (hence potentially habitable) regions of Mars can shrink dramatically (Fig. 3 and Supplementary Video 1). For example, for brines freezing at 252 K, the median ρ drops from 83% to 2% under the influence of methanogens (Fig. 2d). In spite of this biologically induced reduction of Mars habitability, the predicted planetary biomass production at steady state is similar to biomass production estimates for the same (H₂-based methanogenic) primitive biosphere in the Archaean Earth's ocean^{12,19}.

The best validation of our predictions would come from the discovery on present-day Mars of methanogenic life descending from the early metabolism modelled here. When run for atmospheric conditions

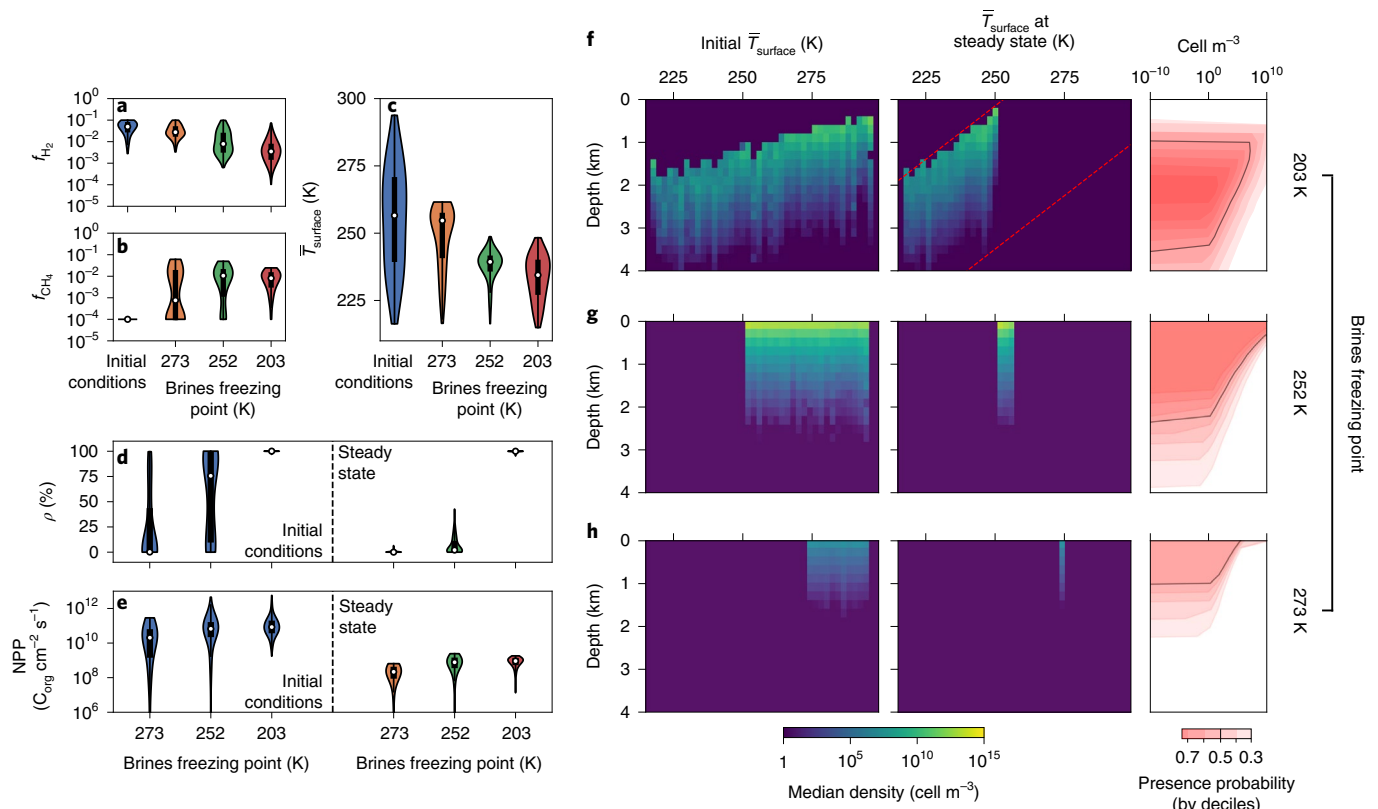


Fig. 2 | Initial and steady-state characteristics of Noachian Mars under the influence of hydrogenotrophic methanogens, for brines freezing at 203, 252 and 273 K. a, b, Atmospheric composition for H_2 (a) and CH_4 (b). c, Average surface temperature. d, Ice coverage. e, Biomass production (in molecules of carbon fixed as biomass $\text{cm}^{-2} \text{ s}^{-1}$, averaged over the whole Martian surface, only when Mars is habitable). f–h, Depth profile of the subsurface methanogenic ecosystem at steady state (median cell density in cells m^{-3}) as a function of the initial average surface temperature (left) and of the steady-state average surface temperature (middle) and corresponding vertical probabilistic distribution of cell density (right) for brines freezing at 203 K (f), 252 K (g) and 273 K (h). In a–e, the distributions corresponding to the initial characteristics of Mars are plotted in blue and the distribution at steady state in orange, green and red, when brines freeze at 273, 252 and 203 K, respectively. The white dots correspond to the median of the distributions, the thick black vertical lines correspond to their

interquartile and the thin ones to their whole range. The red dotted lines in f correspond to the median depths at which temperature equals the lower and upper limits to viability, 253 and 320 K, respectively. To resolve Mars' initial features, we followed previous work^{14,15,18} and assumed atmospheric pressure ranging from 0.5 to 3 bars, a volume mixing ratio of H_2 , f_{H_2} , from 3,000 ppm to 0.1, corresponding to a volcanic outgassing rate of 10^{10} to 2×10^{12} molecules $\text{cm}^{-2} \text{ s}^{-1}$, and a low f_{CH_4} of 100 ppm corresponding to a production rate through serpentinization of 8×10^8 to 10^{10} molecules $\text{cm}^{-2} \text{ s}^{-1}$. The rest of the atmosphere was taken to be 95% CO_2 and 5% N_2 (ref. ⁸). We drew the characteristics of the crust (porosity, tortuosity and temperature profile) from the same ranges as in ref. ⁹ and inferred the posterior distributions of the depth profiles of temperature and diffusivity of the atmospheric gases (Extended Data Fig. 1). See Methods for more detail.

corresponding to modern Mars, our model predicts the atmosphere to be an insufficient source of electron donors for H_2 -based methanogens to survive. As Mars' atmosphere became thinner during the Hesperian and early Amazonian, a putative biosphere persisting throughout the Noachian would have had to shift its main energy source from the vanishing atmospheric redox gradients to hydrothermal or radiolytic ones, deeper in the Martian crust. Deep chemotrophic ecosystems exist on Earth; an extant ecosystem on modern Mars might be of that kind^{20,21} and could explain the repeated²¹ yet highly debated²² detection of CH_4 traces in the lower Martian atmosphere. Our model could be adapted to quantify the habitability of modern Mars' crust to such ecosystems and to constrain their depth and productivity.

In the meantime, our model can help inform the search for fossilized biomarkers of Noachian H_2 -based methanogens. Among the many types of biosignatures that have been proposed to identify ancient metabolic activity^{2,23–25}, isotopic fractionation seems to be the most reliable and commonly used²⁵. Detecting isotopic signatures of anaerobic chemotrophic life on Noachian Mars and even of specific metabolic activity (for example, methanogenesis) might indeed be possible in the light of the analysis of 3-to-4-yr-old Archaean fossils from terrestrial Mars analogues (reviewed in refs. ^{2,25}). Near-surface populations would

have been the most productive ones (Fig. 2e–g), therefore maximizing the likelihood of biomarkers preserved in detectable quantities. The first few metres of the Martian crust are also the most easily accessible to exploration given the technology currently installed on Martian rovers. The probability of life traces at or near the surface is strongly dependent on the freezing point of Martian brines (Fig. 2e–g); to identify regions where this probability is highest and to evaluate current exploration sites, such as Isidis Planitia and Jezero Crater, we performed spatial projections of the model outputs (Figs. 3 and 4, and Extended Data Fig. 3; Methods).

Temperature drops with latitude and elevation²⁶ (Methods). Thus, initial ice coverage was most likely in poleward regions and highlands and least likely in lowlands located at low-to-medium latitudes, such as Isidis and Hellas Planitiae and in the Noachian lakes scattered along the north–south dichotomy²⁷ (including Jezero Crater). With a low brine freezing point (203 K), the Martian surface is initially ice-free and globally habitable. As the early biosphere expands, the biological feedback is massive and cools the planet down dramatically (Fig. 2c), leaving the surface ice-free (due to the low brine freezing point) but driving the biosphere deep into the crust (Fig. 2e). The probability of near-surface methanogenic life at steady state is ca. 0.5 in Hellas Planitia, 0.2 in Isidis Planitia

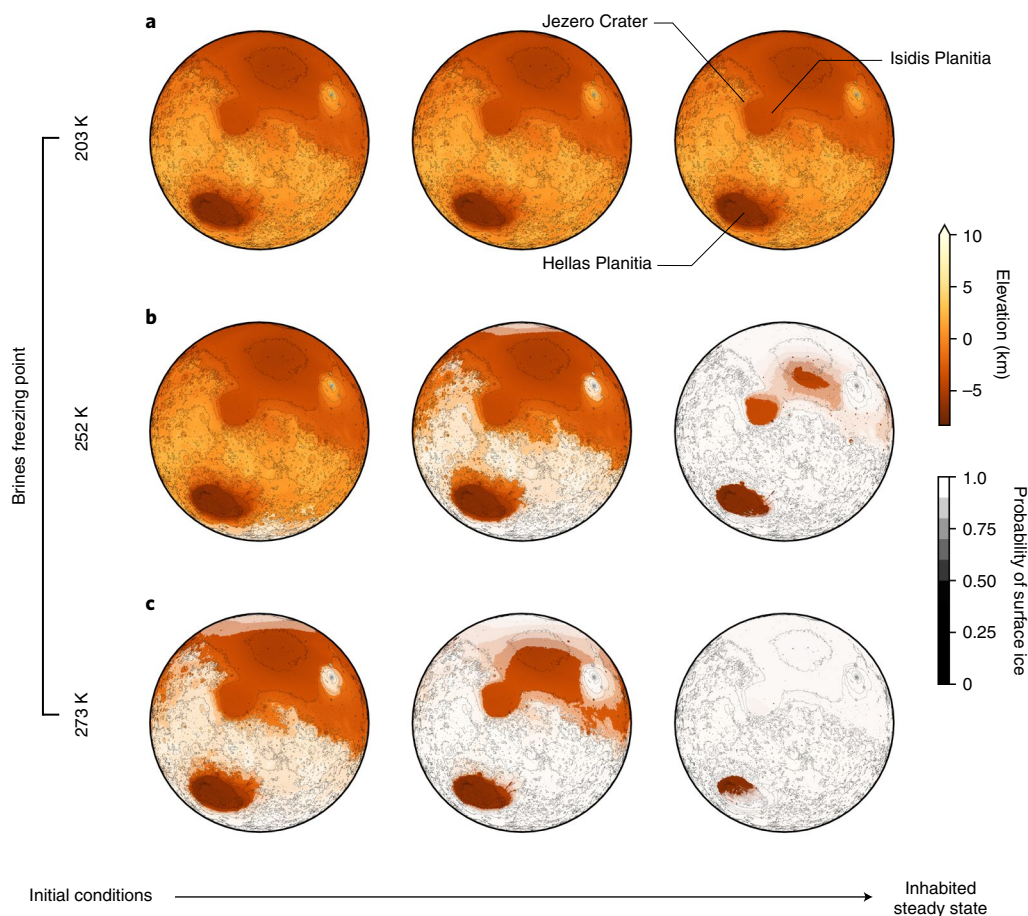


Fig. 3 | Median evolution of the ice coverage of Noachian Mars under the influence of hydrogenotrophic methanogens. a–c, Time evolution for brines freezing at 203 K (a), 252 K (b) and 273 K (c). The orange colour-scale represents

elevation. The superimposed white shaded areas correspond to the probability (from 0.5 to 1 by steps of 0.1) of surface ice. See Supplementary Video 1 for an animated version of the 252 K scenario.

and less than 0.15 at Jezero Crater (Fig. 4a; see Extended Data Fig. 3 for median minimum depth of methanogenic life). With an intermediate or high brine freezing point (252 K or 273 K), a substantial fraction of the Martian surface may have initially been frozen (Fig. 3), reducing the habitable region but also the biological feedback to climate. At life-atmosphere steady state, the relatively high brine freezing point and relatively weak biological feedback balance out with a large ice coverage yet relatively warm ice-free surface, resulting in methanogenic life being limited to small ice-free regions but at or very close to the surface. With brines freezing at 252 K, Hellas and Isidis Planitiae and Jezero Crater are among the few regions that may remain free of ice, where the median minimum depth of Noachian methanogens would then be within the top few metres (Extended Data Fig. 3). The probability of near-surface life reaches 1 in some areas of Hellas Planitia, 0.5 in Isidis Planitia and 0.3 at Jezero Crater (Fig. 4b). With brines freezing at 273 K, the biological feedback, albeit weak, would have caused Isidis Planitia and Jezero Crater to freeze, thus compromising these areas' habitability. Only Hellas Planitia would have probably remained ice-free at steady state, in which case the probability of near-surface habitability would have been 1 (Fig. 4c and Extended Data Fig. 3).

We conclude that, somewhat counterintuitively, the condition that makes Mars' initial habitability to methanogens least likely (high freezing point of Martian brines) is also the condition under which signs of early Martian methanogenesis might be easiest to detect today. With early Mars brines' freezing points high enough, Hellas and Isidis Planitiae and Jezero Crater appear to encompass the best candidate sites to search for signs of methanogenic life that might have persisted

near the surface throughout the Noachian. Access to these biomarkers may, however, be obstructed by the accumulation of sediments from the Late Hesperian and later^{28,29}, which are unlikely to have trapped later biomarkers because life would have, by then, either disappeared or migrated deep into the crust.

Habitability and climate feedback of hydrogenotrophic methanogens were recently quantified for the early Archaean Earth¹². The results reported here for the Noachian Mars show striking similarities and differences. On the one hand, models predict very likely habitability to hydrogenotrophic methanogens on both young planets, with similar biomass production. On the other hand, climate feedbacks work in opposite directions. Although hydrogenotrophic methanogens may have contributed to maintaining temperate conditions on Earth^{12,19}, they would have cooled the early Martian surface, with a reduction of the maximum possible temperature by 33–45 K. Such divergence in climate evolution is the consequence of different prebiotic atmospheric compositions. For a CO₂-dominated atmosphere as on early Mars, H₂ has a stronger greenhouse effect (from CO₂-H₂ collision-induced absorptions) than CH₄, in contrast to a N₂-dominated atmosphere as on the early Earth^{14,15,18}. Contrasted planetary responses of Earth and Mars to metabolic activity might have occurred repeatedly as their biospheres evolved and diversified. On Earth, the evolution of methanotrophy (biological consumption of methane) could have transiently offset the warming effect of methanogenesis¹²; by contrast, methanotrophy could have driven a warming event on the Late Noachian/Hesperian Mars. The co-evolution of Martian surface conditions with a diversifying methane-cycling biosphere therefore adds to

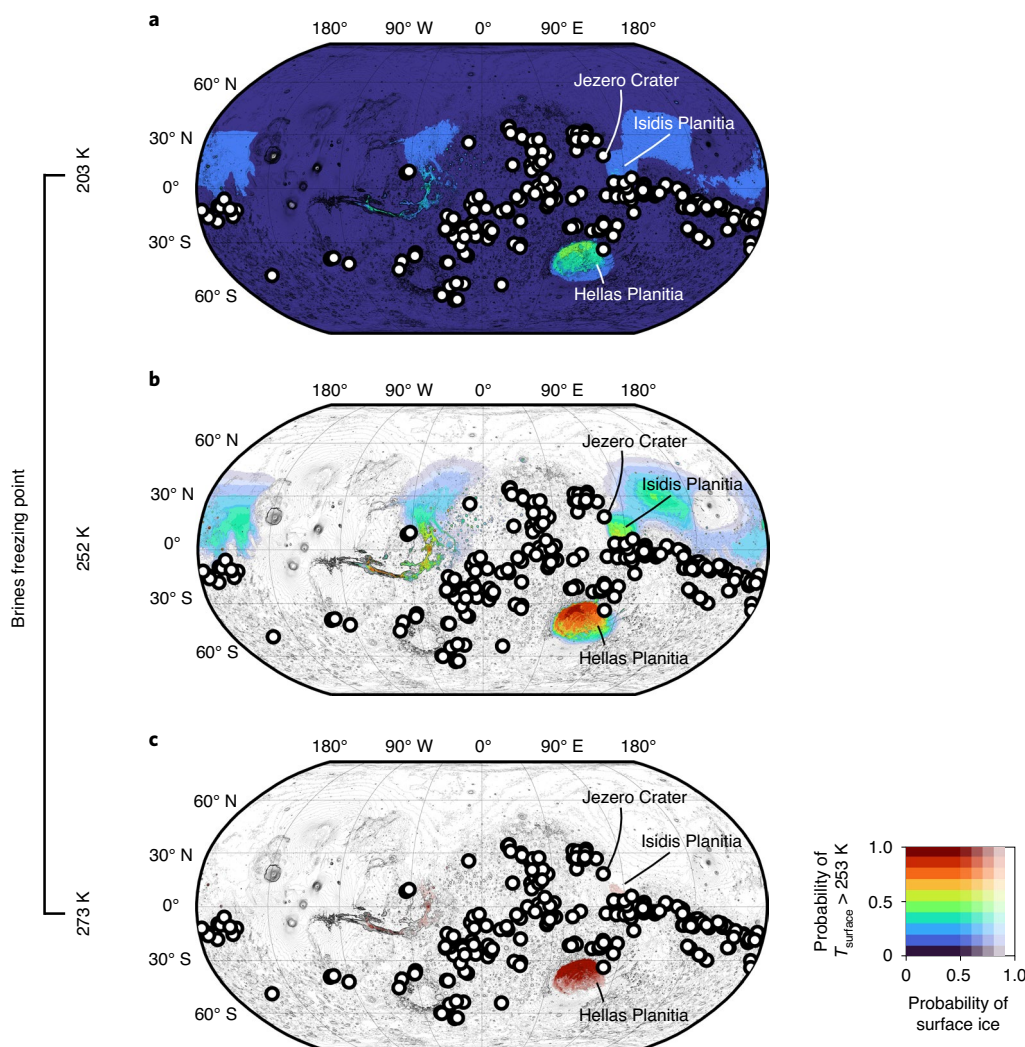


Fig. 4 | Steady-state distribution of habitable conditions and ice on the surface of Noachian Mars. a–c, Spatial projection of the probability of surface ice (shades of white, from 0.5 to 1 by increments of 0.1) superimposed on the probability of habitable surface temperature (that is, $T_{\text{surface}} > 253$ K, represented

by the colour gradient), for brines freezing at 203 K (a), 252 K (b) or 273 K (c). Open circles indicate the Noachian lakes distributed along the north–south dichotomy. See Methods for more detail.

mechanisms possibly explaining an early global cooling event, as well as the transient warming episodes that seem to have punctuated the early Martian climatic history⁸.

Our model does not take into account the biology-to-climate feedback specifically driven by albedo increasing with surface ice formation. As a consequence, the model probably underestimates the cooling effect of hydrogenotrophic methanogens on early Mars¹⁵. This additional feedback could have amplified the direct atmospheric impact of methanogenesis on Mars' climate and triggered a global glaciation. Although quantification of this effect warrants further development of Mars climate models^{14,15,18}, the mechanism in and of itself points to the possibility that life–environment feedbacks can compromise habitability at planetary scale. This Medean scenario³⁰ (self-destructive life–planet feedbacks) adds conceptually to Gaian bottlenecks (life–planet feedback failing to counter the geophysical loss of habitability³¹) as a potential limit to the long-term habitability of planets and planetary bodies in our solar system and beyond.

Methods

Atmospheric and climate model

To evaluate the photochemical destruction/production of H_2 and CH_4 (the two main atmospheric species in our planetary ecosystem model),

we ran the latest version of the 1D photochemical model of Mars developed in the Virtual Planetary Laboratory³², on grids of atmospheric compositions. The results are in line with previous estimates³³ and, based on them, we interpolated the photochemical rates as functions of the atmospheric composition (Fig. 1a,b).

Similarly, we evaluated the dependence of the Martian climate on its atmospheric composition and pressure based on the Virtual Planetary Laboratory's 1D climate model, updated to account for the latest data on the respective collision-induced warming effects of H_2 and CH_4 (refs. 14,15,18). Again, we used the outputs of the model to interpolate the mean surface temperature as a function of the atmospheric composition (f_{H_2} , f_{CH_4} , f_{CO_2}) and total atmospheric pressure (Fig. 1c–e). Because of the collision-induced absorption resulting from the CO_2 -saturated atmosphere of early Mars, H_2 appears to be a more potent greenhouse gas than CH_4 , in line with previous studies^{14,15,18}. Methane may even produce an anti-greenhouse effect at low atmospheric pressure and low f_{H_2} .

Following previous work^{14,15}, the climate model was run assuming a constant low planetary albedo of 0.2, corresponding to low ice coverage. Note, however, that a low temperature is expected to be associated with an extended ice coverage (Methods, 'spatial projections' section) and a high planetary albedo. It was previously shown¹⁸ that a high planetary albedo can cool the Mars climate down considerably. Therefore,

in the case of Mars global cooling, the resulting expansion of surface ice and increase in planetary albedo may have mediated positive feedback, strengthening the cooling event and potentially triggering a cold runaway scenario. To our knowledge, this climate–surface ice feedback loop remains to be integrated and evaluated dynamically in climate models of Mars.

Crust model

Subsurface temperature is expected to increase with depth, whereas the availability of diffusing atmospheric gases drops. Following ref. ⁷, we assume a linear temperature gradient with depth, starting from the surface temperature and warming as depth increases:

$$T(z) = T_{\text{surface}} + a_7 z \tag{1}$$

where z is the depth in kilometres and a_7 the rate at which temperature increases with depth, ranging between 10 and 40 K km⁻¹ (ref. ⁷). The decrease with depth of the diffusivity (in cm² s⁻¹) in the water-saturated crust depends partially on the temperature depth profile, according to ref. ⁷:

$$D_i(z) = \frac{\epsilon(z)r(z)}{3\tau(z)} \sqrt{\frac{8RT(z)}{\pi m_i}} \tag{2}$$

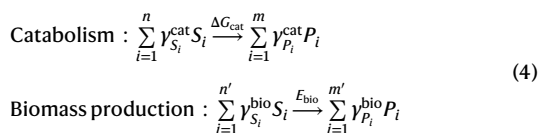
where i is the considered chemical species X_i ($X_i = \text{H}_2, \text{CO}_2, \text{CH}_4$ or N_2), m_i its molar mass, $\epsilon(z)$ the porosity of the crust, $r(z)$ the radius of the pores (in cm) and $\tau(z)$ the tortuosity. The pore radius $r(z)$ follows a linear decrease with depth $r(z) = r(0) - a_r z$ with $a_r = \frac{r(0)}{z_{\text{max}}}$, so that $r(z) = 0$ when $z = z_{\text{max}}$ the depth of pore closure. The crust porosity and tortuosity both follow an exponential decrease with depth, respectively $\epsilon(z) = \epsilon(0) e^{-\frac{z}{z_{\text{max}}}}$ and $\tau(z) = \tau(0) e^{-\frac{z}{3z_{\text{max}}}}$. The vertical flux (in molecules cm⁻² s⁻¹) can then be written as

$$F_i = D_i(z) \frac{\partial n(X_i)}{\partial z} \tag{3}$$

$n(X_i)$ being the density of species X_i (in molecules cm⁻³). The envelopes and distribution of depth profiles for the temperature and diffusivity of H₂ corresponding to the soil parameter ranges explored (Extended Data Table 1) are shown in Extended Data Fig. 1.

Ecological model

Our ecological model describes the dynamics of biological populations of chemotrophic cellular organisms. Equations for the growth and death of individual cells are derived from how, in each individual cell, energy flows from catabolism (energy acquisition) to anabolism (cell maintenance first, then biomass production). The individual metabolism is described by



where S_i and P_i are the substrates and products of the metabolic reactions that are specific to the considered metabolism, the γ are their stoichiometric coefficients, and ΔG_{cat} and E_{bio} are the energy released by the catabolic reaction and necessary for biomass production, respectively. In the case of hydrogenotrophic methanogens, the catabolic reaction is $\text{CO}_2 + 4 \text{H}_2 \rightarrow \text{CH}_4 + 2 \text{H}_2\text{O}$. The value of ΔG_{cat} is given by the Nernst relationship

$$\Delta G(T) = \Delta G_0(T) + RT \log(Q) \tag{5}$$

where R stands for the ideal gas constant, T for temperature (in K), $\Delta G_0(T)$ (in kJ per mol of electron donors, noted eD) for the standard

Gibbs free energy of the reaction and Q for the reaction quotient $\frac{\prod_{i=1}^n S_i^{\gamma_{S_i}}}{\prod_{i=1}^m P_i^{\gamma_{P_i}}}$.

The value of ΔG_0 is obtained from the Gibbs–Helmholtz relationship:

$$\Delta G_0(T) = \Delta G_0(T_S) \frac{T}{T_S} + \Delta H_0(T_S) \frac{T_S - T}{T_S} \tag{6}$$

where T is the temperature of the medium, T_S the standard temperature of 298.15 K and $\Delta H_0(T_S)$ the standard enthalpy. The catabolic acquisition of energy occurs at a rate q_{cat} (in mol eD cell⁻¹ d⁻¹). The energy obtained is first directed toward maintenance, with E_m (in kJ cell⁻¹ d⁻¹) the biomass specific energy requirements for maintenance per unit of time. The energy requirements of the cell can be expressed in terms of the rate at which the catabolic reaction must occur for the cell to function, q_m (in mol eD cell⁻¹ d⁻¹), with:

$$q_m = \frac{-E_m}{\Delta G_{\text{cat}}} \tag{7}$$

The cell maintenance requirements are met when $q_{\text{cat}} > q_m$. If they are not (that is, $q_{\text{cat}} < q_m$), a decay-related term $k(q_m - q_{\text{cat}})$ (in d⁻¹) is added to the basal cellular mortality rate, m (in d⁻¹), with $d = k(q_m - q_{\text{cat}}) + m$ the effective mortality rate (in d⁻¹). If $q_{\text{cat}} > q_m$, the energy remaining after maintenance ($(q_{\text{cat}} - q_m) \Delta G_{\text{cat}}$ (kJ cell⁻¹ d⁻¹) can be allocated to biomass production. The assimilation of each mol of carbon into biomass requires a quantity of energy E_{bio} (in kJ per mol of carbon assimilated as biomass, C_{org}) corresponding to the sum of the costs of producing the biomass, ΔG_{ana} , and organizing it, E_{diss} . The term E_{diss} is a phenomenological estimate, and its value is the same as in ref. ¹² (Supplementary Table 2). The value of ΔG_{ana} is obtained from the Nernst equation (equation (5)) and assuming the following anabolic reaction: $24 \text{H}_2 + 10 \text{CO}_2 + 1 \text{N}_2 \rightarrow \text{C}_{10}\text{H}_{18}\text{O}_5\text{N}_2 + 15 \text{H}_2\text{O}$. Note that we assume that Martian methanogens would have been able to fix N from the atmospheric N₂, as their terrestrial counterparts most probably were ³⁴. As an alternative to biological N₂-fixation, the atmospheric production and rain-out of bioavailable forms of N (ammonia, nitrate) could have been coupled to the lightning-induced breakdown of atmospheric N₂ (refs. ^{35,36}). Infiltration of those fixed nitrogen compounds into the subsurface would have been possible during the Noachian, in locations when and where there was surface liquid water. Should biological nitrogen fixation not have evolved on Mars, the exclusive use of fixed nitrogen compounds by methanogens would have imposed additional constraints on underground habitability to methanogenic life. The efficacy of the metabolic coupling λ (that is, the necessary number of occurrences of the catabolic reaction to fuel one occurrence of the reaction of biomass production, in mol eD mol C_{org}⁻¹) is the ratio between the energy produced by the catabolic reaction and the energetic cost of biomass production

$$\lambda = \frac{-\Delta G_{\text{cat}}}{E_{\text{bio}}} \tag{8}$$

Biomass is produced at a rate q_{bio} (in mol C_{org} cell⁻¹ d⁻¹) with

$$q_{\text{bio}} = \lambda(q_{\text{cat}} - q_m) \tag{9}$$

The metabolic rates q_{cat} and q_{bio} depend on the concentration of the metabolic substrates through a Michaelis–Menten term:

$$q = q_{\text{max}} \frac{S_{\text{lim}}}{S_{\text{lim}} + K} \tag{10}$$

where S_{lim} is the most limiting nutrient, q_{max} the maximum reaction rate and K the half-saturation constant (we assume the same maximum rates and half-saturation constants for all the reactions, their values being

based on phenomenological estimates; Supplementary Table 2). Rates increase with both cell size S_c (radius in μm) and temperature, which we describe with power laws. Finally, the optimal cell size, that is, the cell size that maximizes the individual ability to exploit its environment, is itself estimated through a power law (see ref. ¹² for details). The default parameter values based on empirical estimates and used in the main text are given in Supplementary Table 2 (details about these values can be found in ref. ¹³).

A key feature of the model is that it estimates both the thermodynamic and kinetic temperature dependencies of the metabolism. Typically, high temperatures result in a decreased thermodynamic coupling between energy acquisition and biomass production—that is, an energetic constraint. Lower temperatures, on the other hand, result in lower metabolic rates—that is, a kinetic constraint. The metabolic efficiency of H_2 -based methanogens is therefore optimized at intermediate temperatures, the exact value being set by the ecological context (for example, fluxes of metabolic substrates and wastes, basal mortality¹³). Note that for the sake of simplicity, we neglect the potential effect of low water activity and osmotic constraints resulting from the high salinity of the Martian hydrosphere on the physiology of methanogens. The effect of these unaccounted constraints on Martian life are hard to evaluate as they are poorly understood on Earth; any assumption on what cellular life's adaptation to such constraints might have been on Mars would be highly speculative. However, our model could be adapted to include the thermodynamic components of these constraints.

Physiological rates can then be implemented in a model of ecological dynamics describing the variation through time of the methanogenic population abundance B (in cells) as the balance of biomass production and death, and the abundance of each chemical species in the medium X_i as the balance of the inward/outward flux $F(X_i)$ between the local ecosystem (here a given point in the crust column) and the exterior (here provided by the crust model; equation (3)) and biological consumption/production:

$$\begin{aligned} \frac{dB}{dt} &= \left(\frac{q_{\text{bio}}}{Q_{\text{c,org}}} - d \right) B \\ \frac{dX_i}{dt} &= F(X_i) + \left(q_{\text{cat}} Y_{X_i}^{\text{cat}} + q_{\text{bio}} Y_{X_i}^{\text{bio}} \right) B \end{aligned} \quad (11)$$

where $Q_{\text{c,org}}$ is the structural carbon content of a cell. From equation (11) we obtain a quantitative criterion for habitability, which is that the initial environmental conditions must be compatible with biological population growth, that is, $\frac{q_{\text{bio}}}{Q_{\text{c,org}}} > d$. By solving for the equilibrium of

(11), we also quantify (1) the biological feedback on the local chemical composition and (2) the ability of the local ecosystem to influence the larger scale of the environment through the value of the interaction term $F(X_i)$ at steady state (equation (3)). Although the ecological model is similar to the model used in Sauterey et al.¹², its integration along the spatially structured environmental gradient provided by the crust model is unique to this study. This coupled model provides us with average surface fluxes at the crust–atmosphere interface corresponding to the planetary conditions set by the atmospheric and climate model. These fluxes are then integrated into the global planetary model over the ice-free surface of Mars; they feed back dynamically to the atmosphere and climate, driving the evolution of Mars' surface conditions over time.

Note that we made the assumption, common for chemotrophic ecosystems^{12,13,19}, that biomass production would have been limited either by the energetic yield of methanogenesis (controlled by the redox imbalance of the atmosphere) or by the availability of the key elements C, H, N and O, obtained from CO_2 , H_2 and N_2 . Although phosphorus-containing and sulfur-containing minerals are abundant on Mars^{23,35}, whether P and S may have been biologically limiting is

currently unknown. Our estimates of carbon assimilation (Fig. 2h) provide a basis to actually quantify the macronutrients' abundance that would be needed to sustain the levels of biomass production that the model predicts.

Minimum depth of the hydrogenotrophic methanogenic ecosystems

Due to the kinetic constraints on the H_2 -based methanogenic metabolism, the lowest viable temperature is approximately 253 K. The minimum depth at which the ecosystem can exist in the Martian crust, z_{bio} , can be found by considering the temperature gradient of the crust:

$$z_{\text{bio}} = \max \left(\frac{253 - T_{\text{surface}}}{a_T}, 0 \right) \quad (12)$$

where T_{surface} is the surface temperature and a_T the temperature gradient (in K km^{-1}).

Probabilistic simulations

We run the coupled crust-ecosystem-atmosphere-climate model in a probabilistic framework, by performing a Monte Carlo exploration of likely ranges for each planetary parameter in the model (Supplementary Table 1). From the simulations of 3,000 plausible versions of the young Mars, we obtain probabilistic estimates of global properties (atmosphere composition, climate, ice coverage, and the productivity and depth profile of the methanogenic biosphere) before biologically induced changes to the surface conditions, and after these changes at steady state.

Spatial projections

To obtain spatial projections, we begin with the posterior distributions of average surface temperature \bar{T}_{surface} produced by our model. Then we evaluate the probability distribution of surface temperature at any location given latitude and elevation based on Fastook and Head's model²⁶. The authors used simulations from the LMD Generic Climate Model to derive empirical relationships between local surface temperature (T_{surface}) and a base temperature, latitude (lat) and elevation (Z), for various scenarios of atmospheric pressure (0.008, 0.2 and 1 bar). We modified the relationship found for an atmospheric pressure of 1 bar so that the local surface temperature is expressed as a function of the average surface temperature instead of a basal temperature, and obtain

$$T_{\text{surface}} = \bar{T}_{\text{surface}} - 5\pi + 20 \cos \left(\frac{\text{lat} \pi}{180} \right) + 2.4Z \quad (13)$$

Based on a topographic map of Mars³⁷, this relationship is used to obtain a map of the local temperatures as a function of Mars average surface temperature. We consider that ice covers all the locations at which the local temperature is inferior to the brine's freezing point. From that, we draw the maps of the ice coverage corresponding to each of the three values of brine freezing point (Fig. 3 and Supplementary Video 1). We then evaluate the habitable (that is, ice-free) fraction ρ of Mars as a function of the global average surface temperature for each of the values of brine freezing point (Extended Data Fig. 2a). Finally, for each value of the brine freezing point, we integrate the average surface temperature over the habitable fraction of the Mars surface (Extended Data Fig. 2b). The obtained relationships between the global average surface temperature, the habitable fraction of Mars ρ and the average surface temperature in this habitable fraction are then implemented in the global ecosystem model.

Equation (13) is also used to compute temperature distributions at any location on Mars for each of the three scenarios explored, based on the average steady-state surface temperature distribution obtained from our simulations. From these distributions and equation (12),

we infer the median minimum depth of the biosphere (that is, the median depth at which the temperature reaches 253 K, the limit temperature to viability; Fig. 4) and the probability of the biomass reaching the surface (that is, the probability that the local surface temperature is higher than the 253 K threshold; Extended Data Fig. 3).

Data availability

The datasets produced and analysed in this study are available in the following repository: <https://github.com/bsauterey/MarsEcosys> (ref. ³⁸ <https://doi.org/10.5281/zenodo.6963348>).

Code availability

The planetary ecosystem model coupling climate, atmosphere, ice coverage and below-ground ecosystem and the datasets produced with it are available in the following repository: <https://github.com/bsauterey/MarsEcosys> (<https://doi.org/10.5281/zenodo.6963348>; ref. ³⁸). The photochemical and climate models are accessible on the Virtual Planet Laboratory's gitlab (<https://github.com/VirtualPlanetaryLaboratory/atmos>; ref. ³²); the adapted versions used in this study are available upon request.

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Author contributions

B.S., B.C., R.F. and S.M. conceptualized the study. B.S., A.A., R.F. and S.M. were responsible for the methodology. B.S. carried out the investigation and performed the formal analysis. B.S. and R.F. carried out the visualization. B.S. and S.M. wrote the software. R.F. and S.M. supervised the study. B.S. wrote the original draft of the manuscript. B.S., B.C., A.A., R.F. and S.M. reviewed and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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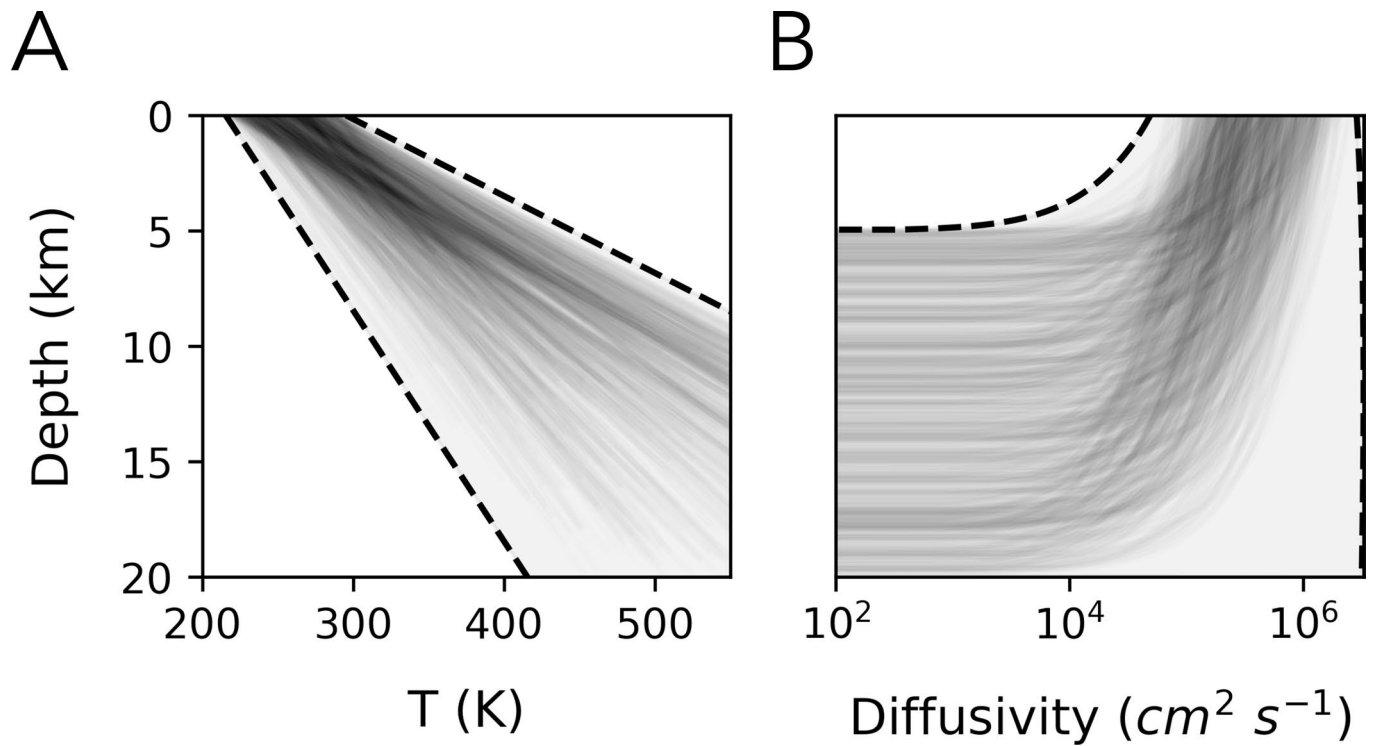
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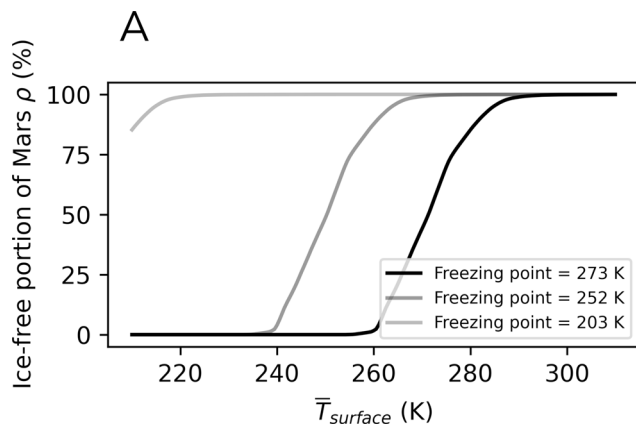
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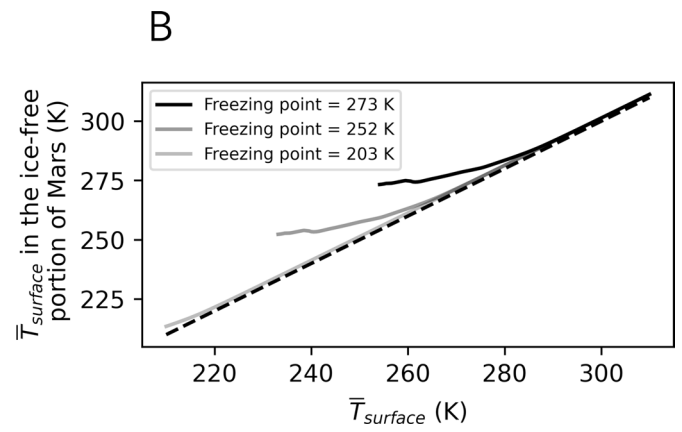


Extended Data Fig. 1 | Simulated depth profiles of (A) temperature and (B) diffusivity in Mars' Noachian regolith. Gray areas bounded by dashed lines represent the entire space in which the depth profiles can exist. Each line (here

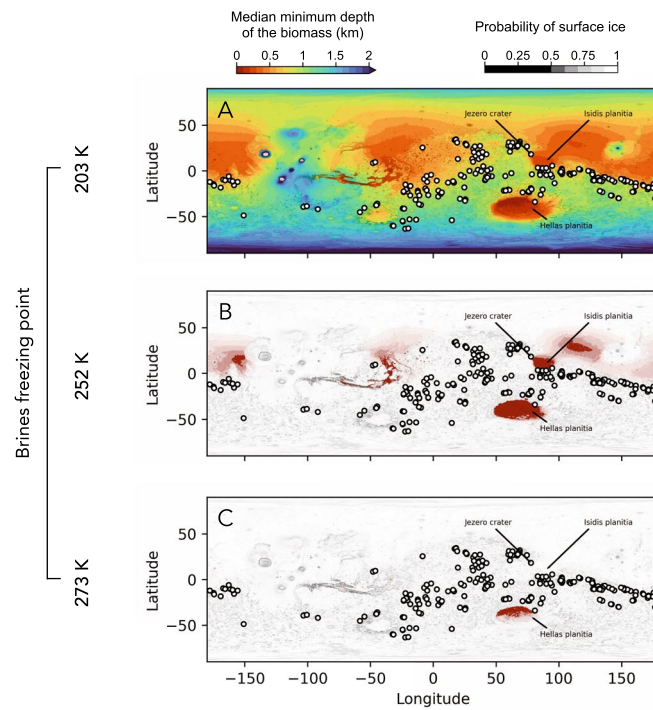
2,000 in total) represents one specific profile simulated for one set of parameters drawn from the ranges given in Supplementary Table 1.



Extended Data Fig. 2 | Ice-free surface fraction, ρ , (A) and average temperature in the corresponding region (B). Ice coverage and average surface temperature are evaluated across the spatial projection of Mars average



temperature distribution (see Methods). The black dotted line in B is the first diagonal corresponding to the planetary averaged surface temperature $\bar{T}_{surface}$.



Extended Data Fig. 3 | Surface and vertical distribution of a putative hydrogenotrophic methanogenic biosphere on Noachian Mars. Spatial projection of the median minimum depth of this biomass occurrence for three values of brines' freezing point of 203 K (A), 252 K (B), and 273 K (C). The white

shaded areas correspond to the probability (from 50% to 90% by steps of 10%) of ice-coverage superimposed to the maps by transparency. Open circles indicate the Noachian lakes distributed along the South-North dichotomy. See Methods for more detail.