Water activity in Venus’s uninhabitable clouds and other planetary atmospheres

John E. Hallsworth1,2, Thomas Koop1, Tiffany D. Dallas1, María-Paz Zorzano3,4, Juergen Burkhardt5, Olga V. Golyshina6, Javier Martín-Torres4,7, Marcus K. Dymond8, Philip Ball9 and Christopher P. McKay10

The recent suggestion of phosphine in Venus’s atmosphere has regenerated interest in the idea of life in clouds. However, such analyses usually neglect the role of water activity, which is a measure of the relative availability of water, in habitability. Here we compute the water activity within the clouds of Venus and other Solar System planets from observations of temperature and water-vapour abundance. We find water-activity values of sulfuric acid droplets, which constitute the bulk of Venus’s clouds, of ≤0.004, two orders of magnitude below the 0.585 limit for known extremophiles. Considering other planets, ice formation on Mars imposes a water activity of ≤0.537, slightly below the habitable range, whereas conditions are biologically permissive (>0.585) at Jupiter’s clouds (although other factors such as their composition may play a role in limiting their habitability). By way of comparison, Earth’s troposphere conditions are, in general, biologically permissive, whereas the atmosphere becomes too dry for active life above the middle stratosphere. The approach used in the current study can also be applied to extrasolar planets.

There is currently a surge of interest in terrestrial aerobiology, and we now know that airborne microorganisms can be metabolically active1. As long as temperatures are biologically permissive, the abundance of liquid water within Earth’s atmosphere favours physiological activity. The thermodynamic parameter water activity—the ratio between the water-vapour pressures of the solution and of pure water under the same conditions—is used to quantify the availability of water. This parameter applies to all solutions and phases—liquid, solid and gas. For planetary atmosphere applications, water activity is equivalent to relative humidity. The maximum possible value of equilibrium relative humidity is arbitrarily designated as 100%, whereas the maximum possible water activity is attributed a value of 1, for a given temperature and pressure combination. Water activity acts as a potent determinant of functionality for microbial cells1, so is also a key determinant of habitability4.

This raises the question of possible life in atmospheres beyond Earth. The atmospheres of other planetary bodies exhibit various combinations of temperature, pressure and relative humidity—parameters that can be obtained through either calculations or direct measurements. Even if temperatures within the atmospheres of other planets permit the formation of liquid-water-containing droplets and may seem permissive for life as we know it, we must still ascertain the water activity of these droplets. This parameter is not only influenced by temperature and pressure but also by thermodynamic effects of ice and/or the presence of any solutes or co-solvent(s).

The recent suggestions of biogenic substances such as phosphine in the Venusian clouds16 is continuing a history of speculation about life on Venus13–15. Venus’s surface is considered too hot for organic life forms but the lower cloud layer, at an altitude of ~40 to 70 km, has a temperature range that makes it potentially habitable based on our knowledge of terrestrial-type life. Earlier studies have suggested the lack of liquid water, or at least the low availability of water, as a potential barrier to life16. Although several recent analyses have queried whether adequate water is available, they also propose active cellular metabolism in the sulfuric acid-rich droplets of the Venusian atmosphere13–15.

A thorough assessment of biophysical limits for life on Earth was carried out in the context of planetary protection by a 2013–2014 committee of the Mars Exploration Program Analysis Group (MEPAG) of NASA that aimed to identify ‘special regions’ of Mars; that is, places that are biologically permissive for active terrestrial-type life. The MEPAG report identified that some metabolic processes occur down to ~40 °C, that is, below the recognized (~18 °C) limit for cell division, and stated that microbial metabolism and cell division had been documented only down to a water activity of 0.605 (the limit for cell division of the fungal xerophile Xeromyces bisporus). From a more recent study, we now know that metabolism, differentiation and cell division can occur down to a water activity of 0.585 (from a study of the fungal halophile Aspergillus penicillioides)17. We also know that microbes can remain dormant at water-activity values below their window for biotic activity, and then resume metabolism when water activity increases16. At the upper end of the water-activity scale, many microbes are active at a value of 1 (ref. 18); and at high temperatures, microbial growth has been observed up to about 121 °C (ref. 19), but circumstantial evidence hints at possible metabolism close to 130 °C.

1Institute for Global Food Security, School of Biological Sciences, Queen’s University Belfast, Belfast, UK. 2Faculty of Chemistry, Bielefeld University, Bielefeld, Germany. 3Centro de Astrobiología (CSIC-INTA), Madrid, Spain. 4Department of Planetary Sciences, School of Geosciences, King’s College, University of Aberdeen, Aberdeen, UK. 5Plant Nutrition Group, Institute of Crop Science and Resource Conservation, University of Bonn, Bonn, Germany. 6School of Natural Sciences and Centre for Environmental Biotechnology, Bangor University, Gwynedd, UK. 7Instituto Andaluz de Ciencias de la Tierra (UGR-CSIC), Armilla, Spain. 8Division of Chemistry, School of Pharmacy and Biomolecular Sciences, University of Brighton, Brighton, UK. 9, London, UK. 10Space Science Division, NASA Ames Research Center, Moffett Field, CA, USA. E-mail: j.hallsworth@qub.ac.uk
Here, in the light of this knowledge, including recent revisions onto our understanding of acidity and water-activity limits for activity of terrestrial microbes (see also below), we focus on Venus as a case study to quantify the water activity of clouds and determine whether terrestrial-type life is feasible there. However, the possibility of life in clouds can extend beyond Venus, so we also consider whether clouds on Jupiter and Mars have temperature and water-activity values consistent with habitability.

**Water activity and uninhabitability of Venus’s clouds**

There is no a priori reason to suppose that putative Venusian life would have the same biochemical basis as that on Earth. In the absence of any concrete proposal for an alternative biochemistry, however, several studies have considered whether living systems comparable to those on Earth might find viable niches on Venus, suggesting that this might be possible within the droplets of sulfuric acid clouds.\(^{1,2,13}\)

Concrete information about biophysical limits for cellular function comes primarily from laboratory-based studies of terrestrial extremophiles (see ‘Acidity and water-activity limits for active life on Earth’ and ‘Determination of habitability for Venus’s acid clouds’ in Methods, and Supplementary text on biophysical limits of terrestrial microbes). These data indicate that microbial growth and metabolism cannot occur anywhere near the chemical conditions relevant for Venusian clouds, as revealed below (in this section). Much of the discussion of potential life in the atmosphere of Venus, both in the light of recent work\(^{14}\) and previous studies, focuses on the extreme acidity of sulfuric acid clouds.\(^{12,13,17}\) This is not in itself an obvious obstacle because we know that some extreme acidophiles are capable of metabolism close to, and even below, pH 0 (see references within ref. 13). Indeed, it is sometimes assumed that the most acidophilic microbe can even grow in concentrated sulfuric acid. However, the record holder, the archaeon *Picrophilus torridus*, grows down to a pH of \(-0.06\) (at 60°C)\(^18\), which is equivalent to only about 11.5% (w/w) sulfuric acid\(^19\).

Given that a permissive water activity is a prerequisite for active metabolism of terrestrial life forms, we considered the water activity even at modest sulfuric acid concentrations. We employed two independent thermodynamic models of H\(_2\)SO\(_4\)–H\(_2\)O mixtures. The first model was from a study of Gmitro and Vermeulen\(^20\) and is particularly well suited for medium to high concentrations of (and up to pure) sulfuric acid over the entire temperature range of relevance to the current study. The second, the Extended Aerosol Inorganics Model (E-AIM) by Clegg et al.\(^21\) describes water activity and ion activities in multicomponent solutions, including pH, and is applicable to sulfuric acid solutions of between 0 and \(-80\)% (w/w) at temperatures from \(-73^\circ\text{C}\) to 55°C. For Fig. 1, water-activity values at temperatures that are pertinent to life (that is, those from \(-40\) to 130°C) were determined from the data presented in water-vapour-pressure tables, calculated by Gmitro and Vermeulen from their model\(^20,21\), at sulfuric acid concentrations between 10% and 100% (w/w); intermediate values were then obtained by interpolation (Supplementary Table 1 and Methods).

Concentrations of 35.0, 37.5, 40.1 and 42.3% (w/w) sulfuric acid reduce water activity to the currently recognized (0.585) limit for life at \(-40\), 0, 50 and 100°C (233, 273, 323 and 373 K), respectively (black isoline in Fig. 1). These sulfuric acid concentrations are consistent with the E-AIM\(^21\) for temperatures at \(-40\), 0 and 50°C (35.6, 37.7 and 40.3% (w/w)) and those published elsewhere for temperatures between 0 and 75°C (273 and 348 K)\(^22\) (see Supplementary Fig. 1 and Supplementary Table 2a,b for comparisons).

Here we derive the water-activity levels in Venus’s clouds from direct observations and then determine the sulfuric acid concentration that corresponds to this water activity according to the solution chemistry. The relative humidity of the atmosphere can be calculated directly using observations of temperature, pressure and water-vapour mixing ratio\(^23\). At the altitudes pertinent to biology (40 to 70 km; that is, about 130 to \(-40^\circ\text{C}\)), the relative humidity of the atmosphere varies yet remains less than 0.40% throughout this range. Because of the small droplet size, the water of the droplets and the ambient water vapour are assumed to be in equilibrium\(^27,28\) (Methods); hence, these relative humidity values correspond to water activities in the droplets below 0.004 (that is, from 0.00003 to 0.0037; Table 1 and Fig. 2). Using data from Gmitro and Vermeulen\(^20,21\) (Methods), we observe that these water-activity values correspond to sulfuric acid concentrations of 77.8 to 99.2% (w/w) throughout the putative habitable zone, as indicated by the grey circles in Fig. 1 (see also Table 1). These concentrations are consistent with those of Clegg et al.\(^21\) in the temperature range \(-40\) to 25°C (even though they lie beyond the stated validity range of the E-AIM). Our results for water activity are consistent with published observations and published model calculations of acid content in Venus’s clouds\(^23\). Given that Earth’s entire functional biosphere spans only about 0.415 water-activity units, from 1 to 0.585 (ref. 19),...
the thermodynamic distance between the 0.585 water-activity limit and the water activity of Venus’s cloud droplets seems unbridgeable (Fig. 1). In other words, there is an enormous distance on the water-activity scale between the limits for metabolism of terrestrial extremophiles and the conditions of the Venusian cloud layer (Fig. 3). Furthermore, terrestrial life cannot survive extreme acid concentrations equivalent to those found in the Venusian clouds (see below; Fig. 3).

For cloud droplets to be habitable, their water activity would have to be strongly out of equilibrium, meaning that the water activity is not determined by ambient relative humidity. Indeed, their water activity would have to be enhanced by a factor of about 150 with respect to the ambient water vapour. In general, authors of different studies (ourselves included) agree that the droplets making up Venus’s clouds are in equilibrium with the atmosphere; both data and theoretical evidence support this view (Supplementary text relating to the equilibration of droplets).

Note that even at temperatures below 0 °C, no ice can form in the cloud layer at such low water-activity values. In the binary-phase diagram of sulfuric acid and water, several crystalline sulfuric acid hydrates are stable at lower temperatures, but at the high acid concentrations considered here (of >78% (w/w)), in principle only the sulfuric acid monohydrate or pure crystalline sulfuric acid can form. However, laboratory experiments have shown that neither of these phases crystallizes readily, even in bulk samples, and that they instead form metastable-solution droplets. Furthermore, observations in Earth’s stratospheric aerosol layer support this notion.

Seager et al. speculated that Venusian microbes would have adaptations to capture and retain water, but we have yet to identify any terrestrial microbe able to obtain and accumulate water from the vapour phase at <0.40% relative humidity. Furthermore, we believe that under the hostile conditions in the Venusian atmosphere any cells would probably perish (even dormant cells); see ‘Acidity and water-activity limits for active life on Earth’ in Methods. The water-activity limits for active life are determined by thermodynamics and the need for water as the biophilic solvent for complex macromolecules. At low water activity, microbial cells adapt to retain their functionality by changing the composition of the plasma membrane; by accumulating stress metabolites; by preferentially accumulating chaotropic substances at low temperatures.
to retain flexibility of their macromolecular systems\cite{36}; and in other ways. Such adaptations mitigate against stresses induced by low water activity, osmotic stress, and other biophysical activities of solutes but this mitigation only extends the windows for cellular functionality within finite limits and cannot circumvent the need for a biologically permissive water activity\cite{37–39}. In their analysis of cloud habitability, Seager et al.\cite{13} state that cells can be destroyed due to chemical modifications to metabolites and cellular macromolecules (these are detailed in our Fig. 3). This is consistent with studies showing that extremely acidic solutions rapidly kill the cells of many microbes at pH < 1 (ref. \cite{38}). However, we argue that the problems go far deeper. We can see that sulfuric acid, at concentrations thought relevant to Venusian cloud droplets, reduces water activity far below a level where the water can function as a biophilic solvent for complex macromolecules (Table 1 and Figs. 1 and 3). Sulfuric acid dehydrates the cellular systems, removes water from biomacromolecules, reduces hydrophobic interactions and damages plasma-membrane integrity (Fig. 3). For both the polyeextremophile Acidithalobacter aeolianus (Acidity and water-activity limits for active life on Earth in Methods) and the thermoacidophile P. torridus, sulfuric acid tolerance limits for growth are an order of magnitude lower than those found in the clouds of Venus (Fig. 3).

It is important to remember what the hydration shell of a protein actually does for functionality. There is evidence that the surface of a typical protein (lysozyme, for example) must have at least 50% water coverage to be functional\cite{36}. This is thought to correspond to 66% of the purely hydrophilic regions, and to coincide with a percolation threshold in two dimensions. Of course, one cannot assume that macromolecules in a Venusian organism would share the same features as those of terrestrial organisms, but the real point is what role this water coverage plays. The dynamics of proteins and their hydration spheres are closely coupled, and it is thought that fluctuations of the solvent (due to spontaneous rearrangements of the hydrogen-bonded network) are needed to ‘awaken’ those in the protein and give it the plasticity required for functionality\cite{36}. For additional information, see ‘Determination of habitability for Venus’s acid clouds’ in Methods and Supplementary text for Fig. 3.

### Analyses for clouds of Jupiter, Mars, Earth and exoplanets

Determinations of water activity, as an important first step in assessing habitability of clouds, can also be made for Jupiter, Mars, Earth and exoplanets. For Jupiter, there has been only one entry probe and it appears to have entered into an unusually dry region of the Jovian atmosphere. Furthermore, dry and wet regions are present in a complex pattern of local meteorology\cite{42}. Here we use the temperature–pressure profiles from this probe, the Galileo Atmospheric Entry Probe\cite{43}. The water-vapour mixing ratio, that is, the molar ratio of water gas to all other gases present, is not well constrained. The Galileo Atmospheric Entry Probe measured water-vapour mixing ratios of $(4.7 \pm 1.5) \times 10^{-3}$ at 11–11.7 bar and $(4.9 \pm 1.6) \times 10^{-3}$ at 17.6–20.9 bar (ref. \cite{44}). These values are about 3% and 30%, respectively, of the water-vapour mixing ratios expected if water on Jupiter had the same relative abundance of oxygen and hydrogen as the Sun. Conversely, Li et al.\cite{45} used the results from the Juno mission, which orbited Jupiter, to infer that the water-vapour mixing ratio in the range of approximately 0.7 to 30 bar is about 2.7 times the value expected for solar abundances. Although it is clear that the water-vapour mixing ratio is variable and the measurements uncertain, the value set by solar abundances deep in the Jovian atmosphere is plausible. This value is $1.71 \times 10^{-3}$ (ref. \cite{46}).

Higher in Jupiter’s atmosphere, the water-vapour mixing ratio is likely to be reduced due to the removal of water by condensation. However, in the region of interest between 0.1 bar and 20 bar, the atmospheric temperature profile decreases smoothly with decreasing pressure so there is no temperature minimum to act as a cold trap\cite{47}. Thus, a uniform mixing ratio of water vapour throughout this region is plausible (see, for example, ref. \cite{47}). If anything, this assumption will overestimate the water activity at lower pressures on Jupiter. Figure 4 shows water activity in the Jovian atmosphere as a function of temperature, from $-50^\circ$C to 70 $^\circ$C. Condensation occurs at about 10 $^\circ$C (at 5.5 bar) and becomes ice below 0 $^\circ$C (strictly, there is also an effect of pressure on water and ice activity, but this is probably negligible given the other uncertainties). With further decreases in temperature, the water activity of ice decreases. In this analysis, we have neglected the effects of ammonia (NH$_3$) or other atmospheric components on the water activity of liquid water or on the freezing-point depression of the ice. These effects become more important near the ammonia clouds found at higher elevations (lower pressures and lower temperatures) that are not pertinent to the current analysis. The water activity is suitable for life (>0.585) for temperatures between approximately 10 $^\circ$C and $-40^\circ$C. According to these parameters, the atmosphere of Jupiter may therefore be more suitable for hosting terrestrial-type life than that of Venus (but whether it could serve as a suitable location for initiating life is another matter).

For Mars, even a casual inspection of the in situ conditions reveals that the clouds are not biologically permissive due to the low temperatures that are inconsistent with cellular function (there is also high ultraviolet radiation that can be lethal for atmospheric microbes\cite{37}). Whereas clouds have been observed in the atmosphere...
of Mars, the temperatures are less than −73°C (200 K) regardless of altitude or location as determined by entry probes and global remote sensing. Therefore, at best, there are ice clouds, and microbial cells are not known to be able to access water at these extremely low temperatures. Furthermore, the water activity of ice at −73°C is about 0.537, and then drops sharply with decreasing temperature (computed from vapour-pressure formulae of liquid water and ice in ref. 48), so the water activity is also below the limit for active terrestrial-type life.

For Earth, typical water-mixing ratio profiles show that the upper stratosphere and mesosphere are too dry to be permissive for active life, while in the troposphere water activity is very variable spanning the entire range between 0 and 1, depending on location, season and daily weather (Figs. 5 and 6; see Methods for details). Nearly all clouds in Earth’s atmosphere are composed of either liquid water or water ice; the water activity of liquid-water droplets is practically 1 (see Supplementary text for Fig. 6b) so is permissive for active life. The water activity of ice clouds, such as tropospheric cirrus clouds, depends on temperature and is in theory biologically permissive down to −58°C (215 K). We note that temperatures below this −58°C limit typically occur only in the upper troposphere, polar stratosphere, and in the mesosphere. Our analysis suggests that the vast majority of clouds in the troposphere are above the water-activity limit of 0.585 and, thus, consistent with active life.

Our approach of using temperature, pressure and water-vapour mixing ratio profiles to determine water activity can be applied to exoplanets. In principle, values for these three parameters can be

---

**Fig. 3 | Schematic showing the implications of the water-activity values of H$_2$SO$_4$–H$_2$O mixtures, including those found within the cloud layer of Venus, for cellular terrestrial-type life.** The narrow red zone (which looks like a thick red line) indicates the water activity of the H$_2$SO$_4$–H$_2$O droplets of Venus’s lower cloud layer (altitude about 40 to 70 km) within the temperature range that is consistent with habitability, based on knowledge of Earth’s microbial biosphere (Table 1 and refs. 41,42). The approximate sulfuric acid concentrations at 25°C relating to the water activities given on the right were calculated using the E-AIM$^{19}$, and Gmitro and Vermeulen$^{20,21}$, at 25°C and the average concentration is given here (Methods). For details, see main text. The thermoacidophile, *P. torridus*, is not known to grow at lower water activity than that of 11.5% (w/w) sulfuric acid (about 0.95019, pink arrow; Methods). For further information about H$_2$SO$_4$–H$_2$O mixtures, see Supplementary text for Fig. 3. This polyextremophile (*A. aeolianus*) is halotolerant and acidophilic but grows only down to pH 2 at high NaCl at 30°C, with a culture-medium water activity of 0.955 (grey arrow; see also main text). These are two haloarchaea able to grow down to 0.635 water activity (green arrow) at high salt concentrations and the acidotolerant xerophile/halophile *A. penicillioides* can grow down to 0.585 water activity (black arrow) at high glycerol concentration. These microbes cannot tolerate high sulfuric acid concentrations but are shown here as they represent the water-activity limits for active prokaryote and eukaryote life, respectively (note that at 24°C, 0.585 water activity is equivalent to 39.0% (w/w) sulfuric acid (pH<1.55) according to Clegg et al.$^{49}$).

**Fig. 4 | Water activity in the atmosphere of Jupiter over the altitude range that may be suitable for life.** These temperatures correspond to pressures of 2.5 to 10 bar. Temperature and pressure are taken from the Galileo Atmospheric Entry Probe data.$^{31}$ A constant water-vapour mixing ratio is assumed to be set by the solar ratio of O/H$^+$. The water activity decreases for temperatures less than 0°C due to the reduction in water activity of ice with temperature.
calculated from transit measurements as an exoplanet moves in front of its star. Considering the problem in general, we can work out the case for an exoplanet atmosphere assuming that the water-vapour mixing ratio is set by the solar ratio of O/H. For example, Kreidberg et al. found the water-vapour abundance of a Jupiter-sized exoplanet to be equal to the value for the Sun within the measurement uncertainties. Figure 7 shows a generalized water-activity analysis for exoplanets: the curve of pressure and temperature corresponds to the water activity currently regarded as the minimum for active life (0.585) (see also Supplementary text for Fig. 3). Profiles to the right of this curve will have a lower water activity, whereas profiles to the left will have a higher water activity. Ice clouds will have a lower water activity set by their temperature. The lowest temperature considered here is −59 °C because below that value the water activity of ice is less than 0.585.

Implications and perspectives

For a desiccated environment, whether a planetary atmosphere, surface or subsurface, the presence of liquid water does not necessarily indicate habitability. Temperature must be permissive for cellular integrity and function, energy sources and nutrients must be available and, critically, water activity must also be permissive for life. This is illustrated by our case study of Venus’s clouds where viable microbe–water relations are a key prerequisite that—in based on our knowledge of life on Earth—cannot be ignored. Indeed, it is only the two parameters of temperature and water activity that are considered determinants of habitability for the purposes of planetary protection1. It has been suggested that the droplets of Venus’s clouds can act as a protective environment for microorganisms13, but we believe that cells could not retain their integrity and/or functionality there due to the low water activity and biophysical and chemical effects of the highly concentrated sulfuric acid. Whereas we find the Greaves et al.1 report of phosphine to be highly intriguing, other studies refute this finding, for example, refs. 32–34. On the basis of the current study, we must imagine a qualitatively new type of organism to invoke a plausible story about life in the atmosphere of Venus, at least for life as we know it.

We found that, in relation to water activity and temperature, the in situ conditions make Jupiter’s clouds the most likely cloud formations in which life could exist in our Solar System apart from those of Earth. A similar analysis would be of interest for Saturn, Uranus or Neptune, once entry-probe missions have been conducted. At present, we lack empirical data for suitable exoplanet atmospheres. However, we mapped out an approach whereby water-activity determinations can be made. It may be that such analyses form a key part of assessments in future to identify exoplanets based on determinations of their habitability. The James Webb Space Telescope (JWST) will be able to determine atmospheric profiles of temperature, pressure and water abundance in exoplanet atmospheres15, and these will allow assessments of water activity in their atmospheres using our approach.

On Earth, life in the atmosphere has co-evolved with life in the oceans, on the surface and in the subsurface. Terrestrial microorganisms are known to influence the atmospheric composition, hydrological cycle and meteorology. For example, microbes produce and consume various greenhouses gases; synthesize the stress metabolite dimethyl sulfide that volatilizes and influences climate56; nucleate ice57; and drive cloud formation and precipitation. According to the findings of the current study, Earth’s troposphere is for the most part biologically permissive, but the middle- and upper atmosphere becomes too dry for active life. Follow-on studies are also needed to consider the type of intimate relationship that can occur between the atmosphere’s microbiome and other aspects of the planetary atmosphere, including climate and weather.

It should also be noted that on Earth (and to a lesser extent on Jupiter and possibly on Venus), atmospheric conditions can be dynamic. Therefore, the calculations presented here should be considered as representative rather than fixed. This said, the temperature, pressure and composition can be determined by direct measurements of planetary atmospheres (from probes or by...
Temperature and pressure profile that corresponds to a water activity of 0.585—the limit for active life—for a water-vapour mixing ratio set by the solar ratio of O/H. For values to the right of the curve, the values of water activity are less than the 0.585 water-activity limit whereas for values to the left of the curve, the water activity is greater than this limit. The lowest temperature considered is −59 °C; below that value, the water activity of ice is less than 0.585.

remote-sensing methods) and these data provide a way to assess water activity. This methodology has planetary protection implications in relation to the potential designation of planetary atmospheres as ‘special regions’. We believe that the quantitative tools developed here can also be used to determine the water activity in exoplanet atmospheres thereby narrowing the search for life within our Solar System and beyond.

Methods

Water activity of H₂SO₄–H₂O mixtures. All solutes/co-solvents depress the water activity of solute- or co-solvent–water mixtures. We sought to identify datasets and models that enable quantification of water activity for H₂SO₄–H₂O mixtures over a range of temperatures and sulfuric acid concentrations. For this purpose, we used two independent, semi-empirical thermodynamic models. Gmitro and Vermeulen used experimental data to provide a comprehensive model dataset for vapour pressures of water, sulfuric acid and sulfur trioxide for aqueous sulfuric acid solutions from 10 to 100% (w/w) at temperatures from −50 to 400 °C. These were tabulated in a supplement to the paper, and we extracted the water-vapour pressures from −40 to 130 °C. These data were then converted to water activity by dividing them by the water-vapour pressure over pure water at the same temperature (the values for pure water were obtained from Murphy and Koop (up to and including 0 °C) and Wagner and Pruss (higher than 0 °C)).

These water-activity values were used in the current study to produce Fig. 1 by interpolation using the contour plot function of OriginPro 2021 (version 9.8.0.200). We also present four isobars of constant water activity in Fig. 1. For the 0.585 water-activity isoline, the corresponding sulfuric acid concentrations were obtained by linear interpolation between the nearest water activity: sulfuric acid concentration data pairs from Supplementary Table 1. For the 0.01 and 0.0001 water-activity isobars, linear interpolation between the nearest log(activity):sulfuric acid concentration data pairs were used because water activity changes by several orders of magnitude in that concentration range. The Gmitro and Vermeulen data were also used to calculate interpolated sulfuric acid concentrations in Venus cloud droplets from water activity (see below and Table 1), again by linear interpolation between the nearest log(activity):sulfuric acid concentration data pairs.

The E-AIM was employed to calculate water activities at predefined sulfuric acid concentrations and vice versa, as well as corresponding pH values. For that purpose, we employed model I (either option 1, ‘simple’, or option 3, ‘aqueous solution’) of the online version of the E-AIM. The E-AIM is valid from −93.2 to 56.9 °C (180 to 330 K) and up to sulfuric acid concentrations of about 80% (w/w).

For the pH calculations, the E-AIM provides the mole-fraction-based H⁺ activity coefficient, which was converted to the molality-based activity coefficient and then the molality-based H⁺ activity in solution, from which the molality-based pH (the negative decimal logarithm of H⁺ activity according to International Union of Pure and Applied Chemistry (IUPAC) convention) is derived. The E-AIM was used to calculate the pH ±0.06 isoline shown in Fig. 1 for temperatures between −40 °C and 56 °C. Between 25 °C and 56 °C, there was a perfectly linear behaviour for corresponding sulfuric acid concentrations, which enabled a linear extrapolation to 130 °C. The E-AIM was also used to calculate sulfuric acid concentrations in Venus’s cloud droplets from water activities, for comparison with those calculated from the Gmitro and Vermeulen data. Although the agreement is very good for temperatures up to about 25 °C, we note that all these values are outside the stated validity range of the E-AIM (sulfuric acid concentrations less than ~80% (w/w) and water activity higher than 0.01). See also Supplementary text relating to validation of water activity for H₂SO₄–H₂O mixtures.

Relative humidity and water activity of Venus’s atmosphere. Small droplets within clouds rapidly equilibrate with relative humidity (as shown in this section, below), so it was imperative to quantify relative humidities of the Venusian atmosphere for the altitude/temperature range that is potentially habitable according to our knowledge of life on Earth. Between about 40 and 70 km altitude, the atmosphere of Venus has temperatures and pressures similar to those of the lower atmosphere of Earth. To compute the physical properties in this region for Venus, we used the direct measurements of pressure and temperature from entry probes for equatorial latitudes, ±30° (ref. 23). These datasets report values for every kilometre of altitude and the reported uncertainties in this profile are ±15 km for altitude, ±5 K for temperature and ±5% for pressure11. Day-to-night temperature differences are only about ±5 K (ref. 1). The water-vapour mixing ratio is taken from the parameterization of Gao et al., which is based on observations from Bertaux et al. and the Venera 11, 13 and 14 missions.

Atmospheric relative humidity is a ratio, calculated according to the partial pressure of the atmospheric water vapour divided by the saturation vapour pressure of liquid water at the corresponding temperature, which we computed with the parameterization of Murphy and Koop. The results (Table 1) are shown pictorially in Fig. 2 where the uncertainty in altitude is smaller than the size of the data-point markers. The uncertainty in relative humidity was determined by combining the uncertainties in temperature, pressure and water-vapour mixing ratio. It was dominated by the uncertainty in the water-vapour parameter which, based on the comparison of the fit to observations shown in Gao et al., we estimate to be ±30% of the plotted values (Fig. 3). It is relevant to note that the data directly determine the water-vapour mixing ratio to be 1 ppm at 70–90 km and 30 ppm below 60 km. In the Gao et al. parameterization, the transition is smooth, and the water-vapour mixing ratio decreases sharply above 60 km resulting in a peak in the relative humidity at about 65 km. If instead the water-vapour mixing ratio is held at 30 ppm through the cloud layer until 70 km, the atmospheric relative humidity would rise monotonically to 0.07% at 70 km.

The water activity of the droplets (Table 1) is taken as equivalent to the relative humidity of the atmosphere. This is because the time constant for growth of droplets (due to collisions with the ambient water vapour) is short compared with droplet transport times. This assumption is common in Venus atmospheric models. The droplets are large enough (radius approximately 1 μm) that the reduction of water activity due to curvature in the droplet—the Kelvin effect—is negligible12. The timescale for water-vapour molecules to accrete on a cloud droplet can be estimated from the collision rate as derived from kinetic theory.

In the kinetic approximation, the number of atoms sticking on a droplet of radius \( r \) per unit time is approximately \( 4\pi r^2 n \alpha_k r_Z t_mn^2 \) (ref. 16), where \( n \) is the mass accommodation coefficient, \( t \) is the time to grow a particle from the size of a small droplet to a size where the particles grow as a mean free path. Over the range of altitudes considered here, the mean free path varies from 0.02 to 1.2 μm which is smaller than, or comparable to, the droplet size of about 1 μm radius.

Expressed in terms of the \( z \)-folding time, for the droplet to grow in size by a factor of \( Z \), the time \( t = t_mn^2/Z^2 \) (ref. 20), where \( n \) is the density of the droplet and \( d \) is the rate of change of the radius with time, \( \tau \) if we evaluate this for representative conditions in the atmospheric profile, pressure ~1 atm, temperature ~0 °C and water-vapour concentration ~20 ppm, we obtain a value of \( \tau = 0.42 \) ms for \( \alpha = 1 \). The mass accommodation, \( \alpha \), is typically assumed to be unity in models of Venus clouds physics. However, Gardner et al. reported a lower limit to \( \alpha \) of \( 0.4 \) to 0.6 \( \times 10^{-3} \) based on laboratory experiments, which gives a value of \( \tau = 0.82 \) ms. These values of \( \tau \) can be compared to the time for a 1-μm-radius droplet to settle 1 km, which is the step size in our atmospheric model. The settling velocity of a 1-μm-radius droplet at standard pressure is ~10 cm s\(^{-1} \) giving a time of 10 s to cover 1 km. Eddy mixing will be more important for droplet transportation through the clouds of settling. Zhang et al. give an eddy coefficient \( D \) at a latitude of 0° as \( 4 \times 10^{4} \text{cm}^2\text{s}^{-1} \). Transport across a distance \( Z \) will occur over a timescale of \( Z^2/D \). For \( Z = 1 \) km, giving a transport time of 2.5 \( \times 10^4 \) s. This calculation supports the conclusion that the cloud droplets are in balance with the local atmospheric water abundance, and we equate the water activity with the atmospheric...
relative humidity in Table 1. The low values of water activity that we find (Table 1) are consistent with atmospheric models (Fig. A4 in ref. 29).

**H₂SO₄ concentration in the droplets of Venus’s clouds.** The functional capability of cellular systems is determined by the biophysical and physicochemical conditions to which the cell—not least, the plasma membrane—are exposed, assuming that biocidal factors are absent, and nutrients and energy sources are available. Therefore, it is imperative to consider habitability at a scale that is pertinent to the microbial cell and its macromolecular systems rather than confining analyses to a macro level or planetary scale, or an anthropocentric viewpoint. Factors such as availability of nutrients, energy sources, temperature, cosmic rays and ultraviolet radiation have been considered elsewhere (for example, refs. 31,32,33), so here we focused on quantifying the sulfuric acid concentration and water activity of the droplets in Venusian clouds.

The sulfuric acid concentration within cloud droplets was calculated assuming that the primary sulfate species is sulfuric acid. We used the Gmitro and Veerman34 data to calculate the sulfuric acid concentrations that are in equilibrium with the relative humidity in Venus’s atmosphere, indicated by grey circles in Fig. 1; see also Table 1. We also used the E-AIM35, although the relative humidity values are below 0.01 water activity (1% relative humidity), which is the lower water-activity limit at which the model runs. The values that we obtained agreed with those calculated using the Gmitro and Veerman34 data, to within ±1% (w/w) sulfuric acid for temperatures between −40 °C and 25 °C. The formation of solids is believed not to occur, so was suppressed in the model. If we assume that uncertainty of ±30% in relative humidity, this leads to only minor changes in sulfuric acid concentrations, which were always less than the symbol size of the grey circles in Fig. 1.

**Acidity and water-activity limits for active life on Earth.** No individual terrestrial microbe is likely capable of metabolism under the combined conditions of 0.585 water activity, extraterrestrial, high glycerol, high ultraviolet radiation, and limited close-range energy sources. Some archaea can grow down to pH 1 in the range 70 °C to 80 °C, so here we focused on quantifying the sulfuric acid concentration and water activity of the droplets in Venusian clouds.

The sulfuric acid concentration within cloud droplets was calculated assuming that the primary sulfate species is sulfuric acid. We used the Gmitro and Veerman34 data to calculate the sulfuric acid concentrations that are in equilibrium with the relative humidity in Venus’s atmosphere, indicated by grey circles in Fig. 1; see also Table 1. We also used the E-AIM35, although the relative humidity values are below 0.01 water activity (1% relative humidity), which is the lower water-activity limit at which the model runs. The values that we obtained agreed with those calculated using the Gmitro and Veerman34 data, to within ±1% (w/w) sulfuric acid for temperatures between −40 °C and 25 °C. The formation of solids is believed not to occur, so was suppressed in the model. If we assume that uncertainty of ±30% in relative humidity, this leads to only minor changes in sulfuric acid concentrations, which were always less than the symbol size of the grey circles in Fig. 1.

**Acidity and water-activity limits for active life on Earth.** No individual terrestrial microbe is likely capable of metabolism under the combined conditions of 0.585 water activity, extraterrestrial, high glycerol, high ultraviolet radiation, and limited close-range energy sources. Some archaea can grow down to pH 1 in the range 70 °C to 80 °C, so here we focused on quantifying the sulfuric acid concentration and water activity of the droplets in Venusian clouds.

The sulfuric acid concentration within cloud droplets was calculated assuming that the primary sulfate species is sulfuric acid. We used the Gmitro and Veerman34 data to calculate the sulfuric acid concentrations that are in equilibrium with the relative humidity in Venus’s atmosphere, indicated by grey circles in Fig. 1; see also Table 1. We also used the E-AIM35, although the relative humidity values are below 0.01 water activity (1% relative humidity), which is the lower water-activity limit at which the model runs. The values that we obtained agreed with those calculated using the Gmitro and Veerman34 data, to within ±1% (w/w) sulfuric acid for temperatures between −40 °C and 25 °C. The formation of solids is believed not to occur, so was suppressed in the model. If we assume that uncertainty of ±30% in relative humidity, this leads to only minor changes in sulfuric acid concentrations, which were always less than the symbol size of the grey circles in Fig. 1.

**Acidity and water-activity limits for active life on Earth.** No individual terrestrial microbe is likely capable of metabolism under the combined conditions of 0.585 water activity, extraterrestrial, high glycerol, high ultraviolet radiation, and limited close-range energy sources. Some archaea can grow down to pH 1 in the range 70 °C to 80 °C, so here we focused on quantifying the sulfuric acid concentration and water activity of the droplets in Venusian clouds.

The sulfuric acid concentration within cloud droplets was calculated assuming that the primary sulfate species is sulfuric acid. We used the Gmitro and Veerman34 data to calculate the sulfuric acid concentrations that are in equilibrium with the relative humidity in Venus’s atmosphere, indicated by grey circles in Fig. 1; see also Table 1. We also used the E-AIM35, although the relative humidity values are below 0.01 water activity (1% relative humidity), which is the lower water-activity limit at which the model runs. The values that we obtained agreed with those calculated using the Gmitro and Veerman34 data, to within ±1% (w/w) sulfuric acid for temperatures between −40 °C and 25 °C. The formation of solids is believed not to occur, so was suppressed in the model. If we assume that uncertainty of ±30% in relative humidity, this leads to only minor changes in sulfuric acid concentrations, which were always less than the symbol size of the grey circles in Fig. 1.
One must assume that, at the acid concentrations found in Venus’s clouds, sulfuric acid molecules would hydrogen-bond to biological macromolecules (Fig. 3) if these are at all comparable to hydrophilic proteins in as much as they are water soluble; certain hydrogen bonding to water and ethanol is possible\textsuperscript{4,5}. In this case, solvation would more closely resemble that in the presence of concentrated macromolecular cryoprotectants such as trehalose, where the role of the protectant co-solvent is more to immobilize the protein and prevent denaturation than to sustain function.

At the acidity limit for terrestrial life, we believe that, paradoxically, it is water activity that is the limiting factor. The water activity of a 11.5% (w/w) sulfuric acid solution according to the Clegg et al.\textsuperscript{19} thermodynamic model is about 0.95 (we calculated 11.4% (w/v) at 56 °C (329 K); that is, near the upper limit of the model, and extrapolation of values derived from Clegg et al. to 60 °C yields 11.5% (w/v)). The majority of microbes, apart from specialist halophiles and xerophiles, have a minimum water activity of 0.950 (w/w) at high temperature (70 °C). And a likely limit in this range is consistent with the growth phenotypes and ecology of *Pichia pastoris*, which is not known in saline habitats. The sulfuric acid tolerance of *Pichia pastoris*, therefore, is probably determined by its limits of xerotolerance rather than tolerance to acidity per se. This is analogous to the growth limit of the *Saccharomyces* species in a similar range.

It is noteworthy that other studies of xerophilic fungi in a similar range have found that substituting some of the glycerol with a chaotrope (for example, sulfate ions) can stabilize cellular macromolecules at high temperature and may thereby enable growth at higher temperatures; conversely, increased temperatures probably enable tolerance to higher concentrations of chaotropes (ref. \textsuperscript{84} and references therein; ref. \textsuperscript{85}). For the ultimate terrestrial acidophile, water activity and pH may act concomitantly to curtail metabolism.

Other biophysical conditions that appear to limit the functional biosphere on Earth might also be a consequence of insufficient solvent water. For example, the growth limit of *A. niger* and *A. oryzae* at 7.7 M glycerol may be an artefact in as much as the microbe may be capable of growth at water activities below the 0.95 value. In this case, when glycerol greatly predominates over water, the cell may cease to function. It is noteworthy that other studies of xerophilic fungi in a similar range of glycerol concentrations found that substituting some of the glycerol with a chaotrope (for example, sulfate ions) could reduce the water activity limit for growth\textsuperscript{84,85}. Whereas this could have been because the kosmotropicity of the added solute mitigated against the chaotropicity of glycerol\textsuperscript{84}, it is plausible that the partial substitution of glycerol by a different solute meant that a critical concentration (where this polyol prevents water acting as the cellular solvent) was not reached.

Similarly, the most ethanol-tolerant strains of *S. cerevisiae* retain active up to almost 20% (v/v) of ethanol. For our analysis of monthly average profiles, the largest variation occurs in the polar regions (Fig. 6a). At higher altitudes, in the stratosphere and mesosphere, relative humidity is very low except for a local maximum in the winter polar mesosphere at an altitude of about 85 km latitude, and a local maximum in the winter polar stratosphere at an altitude of about 25 km latitude. Given that the stratosphere is 1000 times drier than the troposphere, and the mesosphere is 100 times drier than the stratosphere, the local maxima in relative humidity in the winter polar stratosphere and mesosphere at the equator result from high clouds. For this purpose, we used the Committee on Space Research (COSPAR) International Reference Atmosphere\textsuperscript{90} average temperature and pressure profiles and water abundance obtained from the temperature versus altitude profiles corresponding to each January and July for the polar, mid-latitude and tropical troposphere—(solid blue, solid green, and solid red respectively, in Fig. 5)—and one average profile for altitudes of 20 km (solid black circles in Fig. 5), which is based on data from Bohren and Clothiaux\textsuperscript{86}.

As the height of the interface between the troposphere and stratosphere (termed the stratospheric inversion layer, which is in turn latitude, being lower at the poles and higher in the tropics, the stratospheric inversion layer is equal to the ratio of the vapour pressure of ice to the vapour pressure of pure liquid water at water activity at a given temperature. The stratospheric inversion layer is equal to the ratio of the vapour pressure of ice to the vapour pressure of pure liquid water at water activity at a given temperature. The stratospheric inversion layer is equal to the ratio of the vapour pressure of ice to the vapour pressure of pure liquid water at water activity at a given temperature. The stratospheric inversion layer is equal to the ratio of the vapour pressure of ice to the vapour pressure of pure liquid water at water activity at a given temperature. The stratospheric inversion layer is equal to the ratio of the vapour pressure of ice to the vapour pressure of pure liquid water at water activity at a given temperature.

**Analyses of water activity and habitability of Earth’s clouds.** As a comparative case study, we applied our approach of computing the water activity from temperature and water-vapour abundance data also to Earth’s atmosphere and clouds. For this purpose, we used the Committee on Space Research (COSPAR) International Reference Atmosphere\textsuperscript{90} that acts as a model of the terrestrial atmosphere and is based on empirical temperature, pressure and altitude data. But it cannot be expected to mediate macromolecular interactions in the same way that water does. The role of water's motions and fluctuations on biological macromolecules seems to depend, for example, on the highly cooperative dynamics created by its three-dimensional hydrogen-bonding network. So, there would be little justification for extrapolating from the biochemistry of terrestrial organisms at all.

Analyses of water activity and habitability for clouds of Jupiter, Mars, and exoplanets. For Jupiter, the method employed consisted of three steps. First, a measured profile of temperature and pressure (from the Galileo Atmospheric Entry Probe) was used; second, we assumed that the water abundance is set at the value that corresponds to the solar ratio of oxygen to hydrogen; and third, water activity was calculated by computing the atmospheric partial pressure of water from the pressure and water-vapour mixing ratio, and the equilibrium vapour pressure of liquid water from the temperature. Water activity is the ratio of these. Below freezing, when the calculation indicates that ice is present, the water activity is equal to the ratio of the vapour pressure of ice to the vapour pressure of pure liquid water at water activity at a given temperature. But in the absence of water activity at a given temperature. But in the absence of water activity at a given temperature. But in the absence of water activity at a given temperature. But in the absence of water activity at a given temperature.
to estimate the typical water-activity values that occur within clouds (Fig. 6b and Supplementary text for Fig. 6b).

Data availability
We confirm that all relevant data are included in the paper and/or its Supplementary Information files. Source data are provided with this paper.

Received: 15 October 2020; Accepted: 7 May 2021; Published online: 28 June 2021

References

1. DeLeon-Rodriguez, N. et al. Microbiome of the upper troposphere. Proc. Natl. Acad. Sci. USA 110, 2575–2580 (2013).
2. Kabir, E. et al. Recent advances in monitoring, sampling, and sensing techniques for bioaerosols in the atmosphere. ACS Sens. 5, 1254–1267 (2020).
3. Stevenson, A. et al. Is there a common water-activity limit for the three domains of life? ISME J. 9, 1333–1335 (2015).
4. Rummel, J. D. et al. A new analysis of Mars "special regions": findings of the Second MEPAG Special Regions Science Analysis Group (SR-SAG2).
5. Greaves, J. S. et al. Phosphate gas in the cloud decks of Venus. Nat. Astron. https://doi.org/10.1038/s41550-020-1174-a (2020).
6. Mogul, R., Limaye, S. S., Way, M. J. & Cordova, I. A. Venus’s mass spectra show signs of disequilibrium in the middle clouds. Geophys. Res. Lett. 48, e2021GL091327 (2021).
7. Morowitz, H. & Sagan, C. Life in the clouds of Venus? Nature 215, 1259–1260 (1967).
8. Limaye, S. S. et al. Venus’ spectral signatures and the potential for life in the clouds. Astrobiology 18, 1181–1198 (2018).
9. Izenberg, N. R. et al. The Venus life equation. Astrobiology 21, 451–475 (2021).
10. Sagan, C. The planet Venus. Science 200, 2137–2154 (1998).
11. Roos-Serote, M. et al. Proximate humid and dry regions in Jupiter’s atmosphere indicate complex local meteorology. Nature 505, 138–140 (2000).
12. Seager, S. et al. Thermal structure of Jupiter’s atmosphere near the edge of a 5-μm hot spot in the north equatorial belt. J. Geophys. Res. Planets 103, 22857–22889 (1998).
13. Wong, M. H., Mahaffy, P. R., Atreya, S. K., Niemann, H. B. & Owen, T. C. Updated Galileo probe mass spectrometer measurements of carbon, oxygen, nitrogen, and sulfur on Jupiter. Icarus 171, 153–170 (2004).
14. Li, C. et al. The water abundance in Jupiter’s equatorial zone. Icarus 397, 1539–1565 (2005).
15. Liu, C. et al. Precise water abundance measurement for the hot Jupiter WASP-43b. Astrophys. J. Lett. 793, 1–7 (2014).
16. Schwenker, T. E. Newcombe, D. A. & Venkateswaran, K. Rapid inactivation of seven Bacillus spp. under simulated Mars UV irradiation. Icarus 181, 52–62 (2006).
17. Withers, P. & Smith, M. D. Atmospheric entry profiles from the Mars exploration rovers Spirit and Opportunity. Icarus 185, 133–142 (2006).
18. Fedorova, A. et al. Stormy water on Mars: The distribution and saturation of atmospheric water during the dusty season. Science 297, 290–300 (2000).
19. Murphy, D. M. & Koop, T. Review of the vapour pressures of water, ammonia, carbon dioxide, nitrogen, and sulfur on Jupiter. J. Phys. Chem. Ref. Data 31, 713–1015 (2002).
20. Sagan, C. The planet Venus. Science 200, 2137–2154 (1998).
21. Roos-Serote, M. et al. Proximate humid and dry regions in Jupiter’s atmosphere indicate complex local meteorology. Nature 505, 138–140 (2000).
22. Seiff, A. et al. Thermal structure of Jupiter’s atmosphere near the edge of a 5-μm hot spot in the north equatorial belt. J. Geophys. Res. Planets 103, 22857–22889 (1998).
23. Wong, M. H., Mahaffy, P. R., Atreya, S. K., Niemann, H. B. & Owen, T. C. Updated Galileo probe mass spectrometer measurements of carbon, oxygen, nitrogen, and sulfur on Jupiter. Icarus 171, 153–170 (2004).
24. Li, C. et al. The water abundance in Jupiter’s equatorial zone. Icarus 397, 1539–1565 (2005).
25. Krivtsov, I. L. et al. Precise water abundance measurement for the hot Jupiter WASP-43b. Astrophys. J. Lett. 793, 1–7 (2014).
26. Villanueva, G. et al. No phosphine in the atmosphere of Venus. Preprint at https://arxiv.org/abs/2009.06499 (2020).
27. Snellen, I. A. G., Guzman Ramirez, L., Hogerheijde, M. R., Hygate, A. P. S. & van der Tak, F. E. S. Analysis of the 267 GHz ALMA observations of Venus—no statistically significant detection of phosphine. Astron. Astrophys. 644, L2 (2020).
28. Witze, A. ‘Life on Venus’ claim faces strongest challenge yet. Nature 590, 19–20 (2020).
29. Grene, T. P. et al. Characterizing transiting exoplanet atmospheres with JWST. Astrophys. J. 817, 17 (2016).
30. Hoffmann, E. H. et al. An advanced modeling study on the impacts and atmospheric implications of multiphase dimethyl sulfide chemistry. Proc. Natl. Acad. Sci. USA 113, 11776–11781 (2016).
31. Altard, E. et al. Effects of atmospheric conditions on ice nucleation activity of Pseudomonas. Atmos. Chem. Phys. 12, 10667–10677 (2012).
32. Wacker, W. & Pruss, A. International equations for the saturation properties of spanning water networks via 2D percolation transition. J. Phys. Chem. A 108, 1998–1998 (2005).
33. Arcangeli, C., Bizzarri, A. R. & Cannistraro, S. Role of interfacial water in the molecular dynamics-stimulated dynamical transition of plasticoycin. Chem. Phys. Lett. 291, 7–14 (1998).
34. Romano, S. et al. Proximate humid and dry regions in Jupiter’s atmosphere indicate complex local meteorology. Nature 505, 138–140 (2000).
35. Seiff, A. et al. Thermal structure of Jupiter’s atmosphere near the edge of a 5-μm hot spot in the north equatorial belt. J. Geophys. Res. Planets 103, 22857–22889 (1998).
36. Wong, M. H., Mahaffy, P. R., Atreya, S. K., Niemann, H. B. & Owen, T. C. Updated Galileo probe mass spectrometer measurements of carbon, oxygen, nitrogen, and sulfur on Jupiter. Icarus 171, 153–170 (2004).
37. Li, C. et al. The water abundance in Jupiter’s equatorial zone. Icarus 397, 1539–1565 (2005).
38. Kuiper, G. P. et al. Precise water abundance measurement for the hot Jupiter WASP-43b. Astrophys. J. Lett. 793, 1–7 (2014).
39. Villanueva, G. et al. No phosphine in the atmosphere of Venus. Preprint at https://arxiv.org/abs/2010.14505 (2020).
40. Snellen, I. A. G., Guzman Ramirez, L., Hogerheijde, M. R., Hygate, A. P. S. & van der Tak, F. E. S. Analysis of the 267 GHz ALMA observations of Venus—no statistically significant detection of phosphine. Astron. Astrophys. 644, L2 (2020).
41. Wittke, A. ‘Life on Venus’ claim faces strongest challenge yet. Nature 590, 19–20 (2020).
42. Grene, T. P. et al. Characterizing transiting exoplanet atmospheres with JWST. Astrophys. J. 817, 17 (2016).
43. Hoffman, E. H. et al. An advanced modeling study on the impacts and atmospheric implications of multiphase dimethyl sulfide chemistry. Proc. Natl. Acad. Sci. USA 113, 11776–11781 (2016).
44. Altard, E. et al. Effects of atmospheric conditions on ice nucleation activity of Pseudomonas. Atmos. Chem. Phys. 12, 10667–10677 (2012).
45. Wacker, W. & Pruss, A. International equations for the saturation properties of ordinary water substance. Revised according to the International Temperature Scale of 1990. Addendum J. Phys. Chem. Ref. Data 16, 893 (1987). J. Phys. Chem. Ref. Data 22, 783–787 (1993).
46. Wacker, A. S. & Clegg, S. L. Atmospheric aerosol models for systems including the ions H+, NH4+, Na+, SO42−, NO−3, Cl−, Br−, and H2O. J. Geophys. Res. 107, ACH1-14–ACH1-14 (2002).
47. Jia, S. Technical note: Comparison and interconversion of pH based on different standard states for aerosol acidity characterization. Atmos. Chem. Phys. 18, 11125–11133 (2018).
61. International Union of Pure and Applied Chemistry IUPAC Compendium of Chemical Terminology 2nd edn (compiled by McNaught, A. D. & Wilkinson, A.) (Blackwell Scientific Publications, 1997); https://doi.org/10.1351/goldbook.

62. Lasn, D. & Verhild, J. Physics and Chemistry of Clouds (Cambridge Univ. Press, 2011).

63. Camuffo, D. Physics of drop formation and micropore condensation. In: Microclimate for Cultural Heritage Conservation, Restoration, and Maintenance of Indoor and Outdoor Monuments (2ed. Camuffo, D.) 165–201 (Elsevier, 2014).

64. Wix, A., Bracht, L., Sinanis, S. & Schaber, K. A simulation tool for aerosol formation during sulphuric acid absorption in a gas cleaning process. J. Aerosol Sci. 41, 1066–1079 (2010).

65. Gardner, J. A. et al. Measurement of the mass accommodation coefficient of SO2 (g) on water droplets. J. Geophys. Res. 92, 10887–10893 (1987).

66. Schütte-Makuch, D., Grinspoon, D. H., Abbas, O., Irwin, L. N. & Bullock, M. A. A sulfur-based survival strategy for putative phototrophic life in the Venusian atmosphere. Astrobiology 4, 11–18 (2004).

67. Dartnell, L. R. et al. Constraints on a potential aerial biosphere on Venus: I. Cosmic rays. Icarus 257, 396–405 (2015).

68. Winston, P. W. & Lueh, D. H. Saturated solutions for the control of humidity in biological research. Ecology 41, 232–237 (1960).

69. Lee, C. J. D. et al. NaCl-saturated brines are thermodynamically moderate, rather than extreme, microbial habitats. FEMS Microbiol. Rev. 42, 672–693 (2018).

70. Harrison, J. P. et al. Aerobiologically respiring prokaryotic strains exhibit a broader temperature–pH–salinity space for cell division than anaerobically respiring and fermentative strains. J. R. Soc. Interface 12, 20150658 (2015).

71. Benison, K. C., O’Neill, W. K., Blain, D. & Hallsworth, J. E. Water activities of acid brine lakes approach the limit for life. Astrobiology https://doi.org/10.1089/ast.2020.2334 (2021).

72. Moser-Reiterer, R. Z. & Lennon, J. T. Microbial ageing and longevity. Nat. Rev. Microbiol. 17, 679–690 (2019).

73. Khaeleque, H. N., Kaksonen, A. H., Boxall, N. J. & Watkin, E. L. J. Chloride ion tolerance and pyrite bioleaching capabilities of pure and mixed halotolerant, acidophilic iron- and sulfur-oxidizing cultures. Miner. Eng. 120, 87–93 (2018).

74. Khaeleque, H. N. et al. Genome-based classification of two halotolerant extreme acidophiles, Acidihalobacter prosperus V6 (=DSM 14174 =JCM 32253) and Acidihalobacter ferroxoxidans V8 (=DSM 14175 =JCM 32254) as two new species, Acidihalobacter aeolianus sp. nov. and Acidihalobacter ferroxoxidans sp. nov. respectively. Int. J. Syst. Evol. Microbiol. 69, 1557–1565 (2019).

75. Hallsworth, J. E. et al. Limits of life in MgCl2-containing environments: chaostrophy defines the window. Environ. Microbiol. 9, 801–813 (2007).

76. Stevenson, A., Hamill, P. G., Dijkstraus, J. & Hallsworth, J. E., Water-, pH- and temperature relations of germination for the extreme xerophiles Xeromyces bisporus (FR8 0025), Aspergillus penicillioides (JH06THJ) and Eurotium halophilicum (FR2 2471). Microb. Biotechnol. 10, 330–340 (2017).

77. Ross, L., Lobry, J. R., Bajard, S. & Flándros, J. L. Convenient method to describe the combined effects of temperature and pH on microbial growth. Appl. Environ. Microbiol. 61, 610–616 (1995).

78. Beale, E. Confidence regions in non-linear estimation. J. R. Stat. Soc. Ser. B 22, 41–88 (1960).

79. Fu, W. & Zhang, X. Global phosphorus dynamics in terms of phosphine. npj Clim. Atmos. Sci. 3, 51 (2020).

80. Rozenberg, M., Loewenschuss, A. & Nielsen, C. I. Hydrogen bonding in the sulfuric acid–methanol–water system: A matrix isolation and computational study. J. Phys. Chem. A 119, 2271–2280 (2015).

81. Rozenberg, M., Loewenschuss, A. & Nielsen, C. I. H-bonding of sulfuric acid with its decomposition products: An infrared matrix isolation and computational study of the H2SO3·H2O·SO3 complex. J. Phys. Chem. A 120, 3430–3455 (2016).

82. Stevenson, A. & Hallsworth, J. E. Water and temperature relations of Actinobacteria. Environ. Microbiol. Rep. 6, 744–755 (2014).

83. Ball, P. & Hallsworth, J. E. Water structure and chaostrophy: their uses, abuses, and biological implications. Phys. Chem. Chem. Phys. 17, 8297–8305 (2015).

84. Cray, J. A. Chaostrophy: a key factor in product tolerance of biofuel-producing microorganisms. Curr. Opin. Biotechnol. 33, 228–259 (2015).

85. Roy, C. et al. Microbiome and ecology of hot spring-microbaitite system on the Trans-Himalayan plateau. Sci. Rep. 10, 5917 (2020).

86. Stevenson, A. et al. Glycerol enhances fungal germination at the water-activity limit for life. Environ. Microbiol. 19, 947–967 (2017).

87. Williams, J. P. & Hallsworth, J. E. Limits of life in hostile environments: no barriers to biosphere function? Environ. Microbiol. 11, 3292–3308 (2009).

88. Wakisaka, A. & Matsuura, K. Microheterogeneity of ethanol-water binary mixtures observed at the cluster level. J. Mol. Liq. 129, 25–32 (2006).

89. Zhao, H., Zhang, Q. & Du, L. Hydrogen bonding in cyclic complexes of carboxylic acid–sulfuric acid and their atmospheric implications. RSC Adv. 6, 71733–71743 (2016).

90. Fleming, E. L., Chandra, S., Shoebert, M. R. & Barnett, J. J. Monthly Mean Global Climatology of Temperature, Wind, Geopotential Height, and Pressure for 0–120 km NASA Technical Memorandum TM-100697 (NASA, 1988).

91. Warneke, P. & Williams, J. The Atmospheric Chemist’s Companion (Springer, 2012).

92. Bohren, C. F. & Clothiaux, E. Fundamentals of Atmospheric Radiation (Wiley, 2006).

93. National Oceanic and Atmospheric Administration U.S. Standard Atmosphere 1976 (Governmental Printing Office, 1976).

Acknowledgements
We are grateful to S. L. Clegg (University of East Anglia, England, UK) for helpful discussions on the use of the E-AIM at low water activity and the provision of some code; C. S. Cockell (University of Edinburgh, Scotland, UK), D. Y. Sorokin (Winogradsky Institute of Microbiology, Russia) and A. Ventosa (University of Seville, Spain) for providing information about thermotolerance of halophiles; M. S. Marley (NASA Ames Research Center, CA, USA) for information on Jupiter and exoplanets; A. Méndez (University of Puerto Rico, Puerto Rico) for inputs relating to analysis of Earth’s atmosphere; J. R. Lobry (University of Lyon, France) who helped with use of the cardinal pH model; N. J. Tosca (University of Cambridge, England, UK) for discussions about thermodynamic properties of aqueous sulfuric acid solutions; and E. L. J. Watkin (Curtin University, Australia) who provided information about stress tolerance of Acidihalobacter. J.E.H. was funded by the Biotechnology and Biological Sciences Research Council (BBSRC, United Kingdom) project BB/E003471; M.-P.Z. was supported by projects PJD2019-104205GB-C21 of Ministry of Science and Innovation and MDM-2017-0373 Unidad de Excelencia ‘María de Maeztu’ Centro de Astrobiología (CSIC-INTA) (Spain); and O.V.G. was supported by the Centre of Environmental Biotechnology Project (grant 810280) funded by the European Regional Development Fund (ERDF) through the Welsh Government.

Author contributions
J.E.H., P.B. and M.-P.Z. conceived the study; J.E.H., C.P.M., T.K. and M.-P.Z. designed the author contributions.

© The Author(s), under exclusive licence to Springer Nature Limited 2021

Springer Nature remains neutral with regard to jurisdictional claims in published material and does not accept any responsibility or liability for the accuracy of the content.

Supplementary Information
The online version contains supplementary material available at www.nature.com/reprints.

The Atmospheric Chemist’s Companion (Springer, 2012). The online version contains supplementary material available at www.nature.com/reprints.

Additional information
Supplementary Information
The online version contains supplementary material available at https://doi.org/10.1038/s41550-021-01391-z.

Correspondence and requests for materials should be addressed to J.E.H.

Peer review information Nature Astronomy thanks Abel Méndez, Dirk Schulze-Makuch and Nicholas Tosca for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2021