HABITABILITY OF CLOUDY WORLDS: INTERSECTING CONSTRAINTS AND UNKNOWNS.

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Introduction: "Follow the water" has long been a theme of astrobiology. Where there are terrestrial worlds with water, there are likely to be clouds. Earth's clouds carry active microbes [1], in addition to inactive life that comprises a significant minority of dry dust. Both Venus and Mars are believed to have had significant early water; on Venus, the limited water retained in the clouds has been suggested as a potential refuge for life, a parallel to Mars's subsurface water. Conversely, as microbes on Earth do not stay airborne for very long, a hypothetical exoplanet with more persistent cloud cover could be even more favorable to an airborne biosphere than Earth.

Airborne microbiology is significant at a planetary scale for Earth. Effects include weather (microbes as condensation and ice nuclei), climate (alteration of cloud and surface albedo), and water and air chemistry (through metabolic processing) [2]. Some of these effects, if present on exoplanets, could be detectable through remote observation. Understanding the parameters that constrain the habitability of clouds is therefore necessary to help guide the search for life.

Physical Constraints: The physical requirements for life (as we know it) are often broken down as a solvent (water), nutrients (C, H, N, O, P, S, and trace elements like Fe), energy (chemical or photonic), and a stable environment (temperature, pH, radiation, etc.). We focus on water clouds below, but much of the same reasoning applies to non-water clouds when considering the potential of non-water biochemistries.

Water availability is particularly important in aerobiology. (If the water is mixed with another solvent, as on Venus, *water activity* may be limiting instead.) Because Earth's atmosphere is generally not water-saturated, most aerosolized microbes are rapidly and fatally desiccated. However, warm, low-altitude clouds serve as roaming water 'hot spots', where microbes suspended in water droplets can stay hydrated and metabolically active as long as the cloud persists. Some microbes can remain active below 0 ºC, though ice clouds are less well studied. Some types of microbes also have surface properties that trap water, making them particularly effective nuclei for cloud formation even at lower humidities [2].

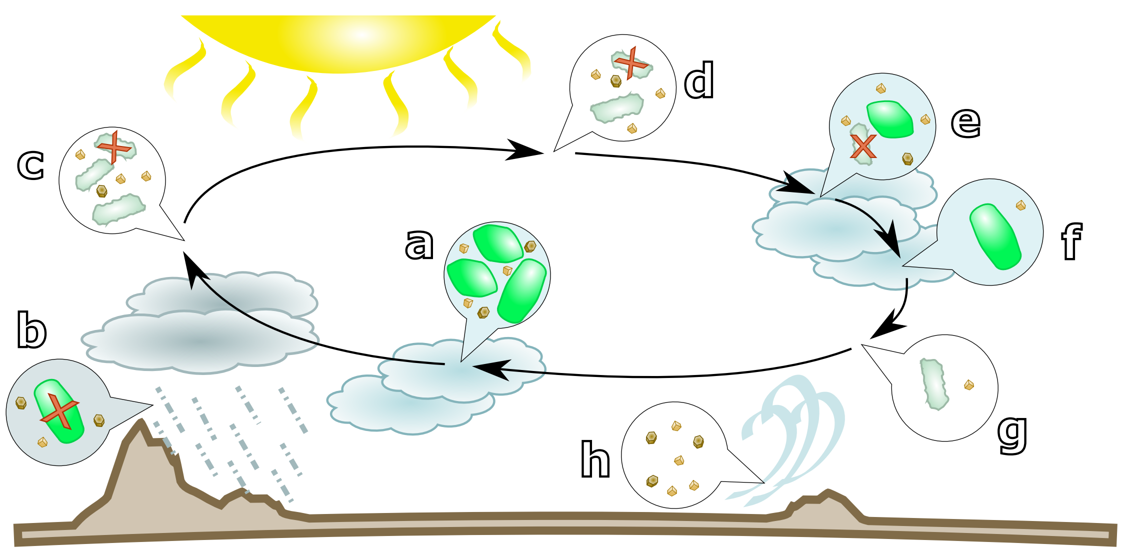

Figure 1: Notional life trajectory of microbes within a cloudy (water) aerobiosphere. **[a]** Microbes (green) accumulate enough nutrients (brown) in a warm, wet cloud to divide. **[b]** Some "rain out" to the surface; **[c]** others are lofted to a drier region where some will be able to transition to desiccated, inactive forms. **[d]** These inactive forms accumulate damage, including from radiation. **[e]** Some are carried back into a high-humidity region, and a few are able to rehydrate and repair the damage. **[f]** Survivors grow, potentially exhausting available nutrients. **[g]** Depending on the density and frequency of cloud cover, they may undergo multiple cycles of dehydration. Eventually, the combination of wet periods and available energy and nutrients (including **[h]** sources of minerals and salts from the surface) may become sufficient to allow division, beginning the cycle anew.

Nutrient availability is largely dependent on surface fluxes and mixing dynamics. On Earth, nutrients in fog and cloud water are typically similar to sparsely inhabited lakes, but this can vary widely (e.g., land vs. marine cloud water sources). Unless a nutrient is effectively absent, low nutrient levels are likely to slow or limit population growth rather than prevent inhabitation entirely; as a parameter, this becomes more important in aerobiology when combined with residence time (see below).

Energy availability, as a constraint, is similar to nutrient availability: while there are theoretical lower bounds, even in environments within those bounds, a low level of bioavailable energy will translate to a slower-growing population. Earth aerobiology usually has ample photosynthetically-active radiation.

Environmental stability in aerobiology includes a unique threat: gravity. The speed at which particles, including cells or cell aggregates, 'fall out' of the air is determined at the microscale (gravity, air density and viscosity, effective radius, electrical charge); the mean length of time a particle remains airborne, or residence time, is further affected by larger-scale dynamics such as thermal lofting, gravity waves, scavenging due to precipitation ('raining out'), and turbulence. Small particles may remain aloft indefinitely, but on Earth, microbe-scale particles (0.2 - 1 µm) have residence times of hours to days [3].

(Aero)biological constraints: For a biosphere to have long-term stability, its population gains must outweigh its losses. Thus, habitability of a (cloudy) atmosphere goes beyond individual organisms to a further constraint derived from the constant losses to gravity (see above): the reproduction rate of the population must be faster than the settling rate ($r_r > r_s$), or, conversely, the overall mean generation time must be less than the overall mean residence time ($t_g < t_r$). This is likely one of the reasons that we have not yet observed airborne microbial reproduction in the field, despite promising laboratory evidence: many of the hardiest microbes most likely to survive aerosolization also have generation times of hours or days, exceeding typical Earth cloud durations.

This constraint becomes even stricter when population losses due to other stresses (pH, temperature, radiation, etc.) and any periods of limited or inactive metabolism are included. Water availability is again key. Repeated bouts of desiccation are highly damaging to most microbes. On Earth, only a few types of desert microbes are able to thrive in environments where such cycles are typical, having developed the ability to repeatedly go in and out of protective dehydrated states [4]. Even such specialized adaptations have limits; during inactive periods, biomolecular damage continues to accumulate, and will eventually reach a threshold where the organism is unable to repair itself even after rehydration in a clement microenvironment.

Interactions between constraints: Figure 1 shows a notional life trajectory of an airborne microbe on an Earth-like cloudy world highlighting how these factors affect one another. Depending on microphysical and macrophysical parameters, microbes may go through multiple cycles of dehydration and rehydration, losing a percentage of the population each time; that percentage gets higher if the periods of dehydration pass through areas with unfavorable irradiation or temperature. Within wet droplets, combinations of stressors (pH, harsh chemistry, temperature, etc.) may slow the growth rate further. Even when all else is favorable, the small size of wet aerosol droplets means that growing microbes are at risk of exhausting the local supply of dissolved nutrients before they have accumulated enough resources to reproduce, delaying division until the host droplet merges with another or undergoes another cycle of condensation.

Knowledge gaps: There is a clear need for coordination between atmospheric modellers, especially with expertise in cloud microphysics, and microbiologists, especially with expertise in aero-biology. Key questions to be answered include:

- What observations are required to estimate, for microbe-sized particles, typical residence times, trajectories, and hydration cycles in planetary atmo-spheres, taking into account potential differences in nucleation?
- What are typical generation times for microbes, especially those able to survive repeated desiccation, irradiation, and other stresses often encountered while airborne, and how are these affected by limitations on bioavailable nutrients and energy? Which factors are most limiting?
- How long can microbes tolerant of such conditions remain viable while inactive under the combinations of accumulating stressors typically encountered while airborne (high UV, varying RH, low temperature, etc.)? Which factors are most limiting?
- How do the answers combine to constrain the habitability space of potential cloudy worlds?

The biology of Earth's atmosphere is significantly underexplored compared to its land, oceans, and even subsurface. Field, lab, and modelling work must be combined to address these basic questions in order to understand the extent of life on Earth as well as the potential for life elsewhere in the universe.

References: [1] Amato, P. et al. (2019) *Sci. Rep.* DOI:10.1038/s41598-019-41032-4 [2] Delort, A.-M. et al. (2010) *Atm. Res.* DOI:10.1016/j.atmosres.2010.07.004. [3] Burrows, S.M. et al. (2009). *Atm. Chem. & Phys.* 9:9281–9297. [4] Potts, M. (1994) *Microbiol. Rev.* 58(4):75