The Global Air Microbiome

It's raining cats and dogs!
Now that's a funny phrase, but does rain consist only of water??

Photo by Oleksandr Pidvalnyi: https://www.pexels.com/photo/photo-of-kid-wearing-raincoat-while-walking-on-park-3036397/

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Storyline

About 150 years ago, microbes were discovered floating in the air with dust, as *aerosols*. Since then, they have been found everywhere in the atmosphere, from vegetated areas to the poles, at high altitudes up to several tens of kilometers above the ground, in clouds and in rainfall. But they are generally more abundant in indoor air, where they accumulate after being released by us, our activities and pets. Every day, each of us breathes about 11,000 liters of air, including the various microbes it carries. There are many examples of human, animal and plant diseases associated with microbes that are naturally airborne (influenza, tuberculosis, mildew, etc.), but pathogens are only the tip of the iceberg of airborne microbes. In fact, most of them usually live as commensals of plants and animals, and thrive in soils, fresh water or oceans. Once *aerosolized*, they can stay aloft for several days and travel across continents. Although not all survive their atmospheric journey due to the harsh conditions of temperature, oxidants, UV light, and humidity, some do, maintain activity in clouds and interact with atmospheric processes (chemistry and physics), before falling back to the ground where they can eventually establish themselves in the conditions are favourable. Environmental *feedbacks* linking certain bacteria capable of inducing the formation of ice with rainfall and vegetation were proposed (*bioprecipitation*), illustrating the fundamental importance of airborne microbes in regulating the functioning of our planet, such as hydrological cycles.

The Global Air Microbiome: the Microbiology

1. *The air we breathe is not just "air".* The air we breathe is obviously mostly a mixture of gases (78% nitrogen N_2, 21% oxygen O_2, nearly 1% argon Ar, carbon dioxide, water vapor, and others). But not only: numerous dust particles called '*aerosols*' float in the air. Depending on their size, these can be intercepted in the nose, throat or trachea during breathing, or reach lungs, which can be associated with serious health problems (rhinitis, asthma, hay fever, etc.).

About 30% of aerosol particles larger than 0.2 µm are biological, among which are pollen, debris from plants and animals, and microbes such as bacteria, fungi and viruses. Pollen grains are not microbes, but *propagules* emitted by trees, grasses, and weeds for reproduction. Allergies related with airborne pollen or animal debris are experienced by nearly 10% of the population. Combined with air pollution by gases, such as ozone or nitrous oxide that irritate and perturb the mucous membranes of our respiratory system, allergens are becoming more harmful. Pollution also has negative impacts on the survival of pollen, and this may affect the capacity of plants to reproduce and spread by air.

At each breath, about 0.5 liters of air circulates in our lungs, along with the tens to hundreds of microbes it carries. Some, not the majority, referred to as pathogens or opportunists, can cause disease in plants (for example the necrosis of leaves), animals or humans. The fact that microbes can spread in the air has attracted a lot of attention with the current COVID-19 pandemic. Fortunately, most microbes are not harmful. They are part of our environment and many are beneficial or even vital to plants, animals and humans, and essential for healthy functioning of ecosystems. The "super organism" constituted of a plant or an animal plus its beneficial microbes is called a *holobiont*.

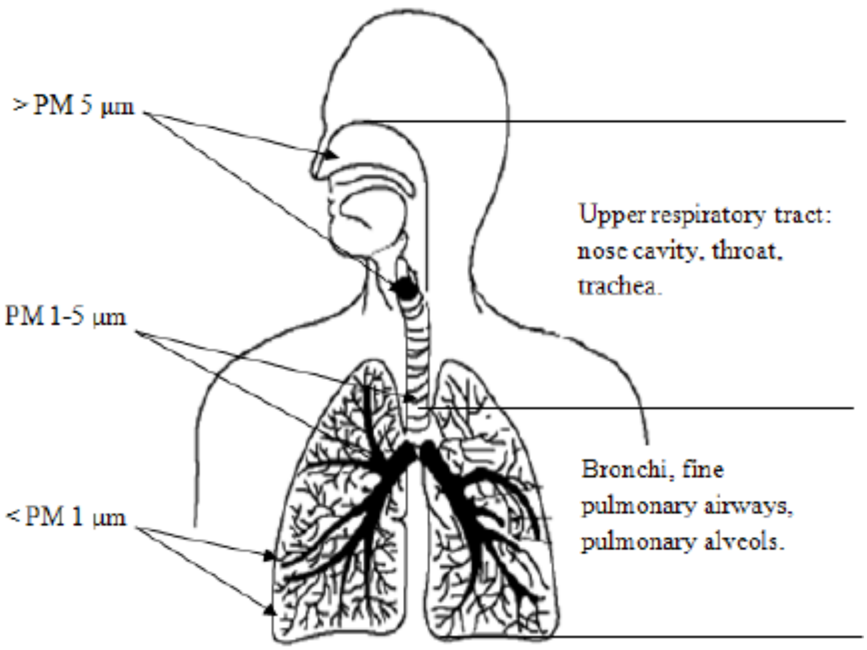


Figure 1: Size-dependent penetration of particulates in human lung. PM: particulate matter related with different sizes of aerosol particles. From Zhang et al. 2015 (https://doi.org/10.1590/0104-6632.20150323s00003510), under licence CC BY-NC 4.0 (https://creativecommons.org/licenses/by/4.0/).

2. ***The discovery that air carries microbes put an end to the spontaneous generation theory, and later extended our vision of the Earth's boundaries of life.*** Aerosol particles include microbes, *i.e.* fungal spores, bacteria and viruses. At the end of the XVIIth century, one of the fathers of *aeromicrobiology*, Antoni van Leeuwenhoek (1632-1723), observed conspicuous tiny forms of life in rain water using an ancestor of modern optical microscopes. It took two centuries and many other observations by pioneer microbiologists (such as Lazzaro Spallanzani 1729-1799, Christian Gottfried Ehrenberg 1795-1876 and Miles Joseph Berkeley 1803-1889), before Louis Pasteur (1822-1895) demonstrated more formally the presence of microbes in the air in 1862, putting an end at the *spontaneous generation theory* largely accepted at that time, the belief that life could appear anywhere from non-living objects.

His observation can easily be reproduced: he allowed boiled liquids (*i.e.* sterilized) to be exposed to air directly, or indirectly through a curved hose (swan-neck flask). Only the former became cloudy due to the growth of microbes, while the other remained clear - sterile, thereby providing evidence that air itself was not responsible for *creating* life but rather air is responsible for *transporting existing life* and bringing live microbes in the flasks.

Since then, microbes have been investigated and discovered in the most remote places in the world. They have been shown to be essential to the lives of essentially all organisms and the functioning of our planet as a whole.

In the 1930's, Charles Lindbergh and his wife Anne Morrow investigated the air above Greenland from their Lockheed Sirius airplane, using their "Sky hook" system specially designed for collecting airborne particles while flying; they reported the presence of diverse microorganisms. Much later in the 1970's, using a rocket, living microbes were found at an altitude of 77 km above ground, in the mesosphere (for comparison, planes typically fly at ~10 km above ground). More recently in the 2000's, other studies attempted to define the upper limit of the biosphere on Earth using modern methods that have once again revealed the presence of living -or surviving- microbes at high altitudes (between 12 and 50 km above ground). Today, NASA is considering exploring other planets' atmospheres, such as that of Venus, for the presence of life or a signature of it.

3. ***Humans and pets strongly influence indoor air microbes.*** Both inside and outside air are exposed to microbes. Indoor, where humans spend 90% of their time, each cubic meter of air carries about one million of them. Some originate from outside, depending on ventilation systems and habits. The rest comes from humans, pets, plants, plumbing systems (toilets mostly) and, in large amounts, from decaying walls, wood etc., in dwellings where humidity is not well managed (mold) and causes sanitary issues.

Our mere presence as humans has strong impacts on the number of microbes floating in the indoor air and therefore those in dust on the ground. Humans naturally carry thousands of billions ($\sim 10^{12}$) of microbes on their skin. Every hour, each of us sheds tens of millions of bacteria and fungi into the air, up to 30mg of microbes. Persons with respiratory diseases such as influenza, COVID-19 or other infections, exhale large numbers of viruses, which contributes to their rapid spread. However, it has to be kept in mind that, in general, large numbers of viruses must be inhaled by healthy people before they become ill.

By simply observing the microbes in the air, it is possible to determine if someone is, or was recently, in the room. Our habits also have impacts on indoor microbes. Plumbing systems, notably toilets and showers, are among the greatest sources of microbes in the air in built environments. Each toilet flush suspends thousands of microbes, bacteria and viruses from feces which can remain suspended for several hours in the room before landing on walls or floors. It goes without saying that regular cleaning is mandatory to prevent the spread and emergence of disease.

Pets such as cats and dogs also greatly influence indoor air microbe numbers and diversity. Just like Humans, they carry huge numbers of microbes, and in addition their movements resuspend dust on the floor.

4. ***Outdoors, microbes circulate up to clouds.***

Microbes can reach high altitudes and clouds simply through wind and air turbulence. (photo: P. Amato).

The air outdoors also transports great numbers of diverse microbes. On a global scale, it has been estimated that at any moment 10^{26} bacteria are present in the atmosphere. This huge number actually represents only a small fraction of the total bacteria on Earth, around 0.05%, and is more than 1,000 times smaller than the numbers of microbes in soil or aquatic habitats, for example. Moreover, microbes do not stay aloft long: once in the air, they can last up to 10 days, 3.2 days on average. This is still long enough to be carried by the wind to high altitude and clouds, and across regions and continents. For example, there have been several reports of microbes from the Saharan Desert being carried across the Atlantic Ocean on dust (easily traceable) and reaching America.

Closer to the ground outside, there are thousands to millions of microbes per cubic meter of air. Their abundance and diversity relate to the underlying surface: forest, grassland, road, bare soil, ocean etc. Fungi and molds can form spores that can be actively released for aerial dissemination. In the absence of such structures, bacteria and the mycelium of fungi can be pulled out from surfaces through mechanical disturbances caused by wind, raindrops impacting the ground, animals or human activities, especially agriculture. In aquatic environments, aerosols are generated by bubble-bursting caused by wind or agitation. These can include microbes from the often microbe-rich and organic-rich water:air microlayer interface. It has been observed that droplets *aerosolized* from the surface of water may contain more microbes than the water itself, and that the biodiversity they carry may be distinct, suggesting that some microbes get more easily aerosolized than others. These could have evolved to better spread in the air and disseminate.

The highest densities of microbes in the outdoor air are found over vegetated areas, where each square meter can emit up to several hundred microbial cells per second. The phyllosphere, the aerial parts of plants, is indeed literally covered with microbes, mainly on their leaves which provide moist and nutritious habitats. The majority of these microbes are beneficial to the plant and consume the volatile organic compounds (the "smell" of plants), sugar etc., it releases. At mid-latitudes, microbial diversity of outdoor air thus largely reflects the seasonal changes encountered by vegetation. Conversely, the lowest amounts of microbes are observed in the air of polar regions, above the oceans and seas, and, as one might guess, at high altitudes.

5. *The atmospheric journey of microbes.* Not all microbes equally survive their journey in the air. While fungi and certain groups of bacteria produce dissemination and resistance spores, acting as sorts of armor intended to resist stressful conditions, most bacteria lack this armor. Hence, they must react and acclimate for survival, which is not easy in the air.

Desiccation (absence of liquid water), starvation (lack of nutrients), high levels of oxidants (reactive oxygen species, *i.e.* free radicals) and solar light (UV), along with the sudden changes of these conditions, indeed impair survival, characterize air, so cells must quickly adapt to a range of simultaneous stresses in order to maintain their vital functions. Because of these hostile conditions, most airborne microbes recovered alive at high altitude are pigmented because they contain yellow to red carotenoids, which allow them to better resist cold, oxidants and solar light. Others are particularly efficient in detoxifying free radicals, or can tolerate temporary dryness and low levels of available nutrients. Yet, very little is known about how microbes function in the atmosphere: what they eat and release, and how they react and influence their direct environment.

The mean half-life of non-sporulating epiphytic microbes (the time before half of them lose viability), such as species of bacteria affiliated with *Pseudomonas*, was estimated from experiments in atmospheric simulation chambers at about 5 hours. This suggests that, on average, only 1 in a million such microbes survive for the duration of their stay in the air and are still alive when they reach the ground again. During this time, they react to the presence of organic compounds indicating that they acclimate to their temporary aerial environment.

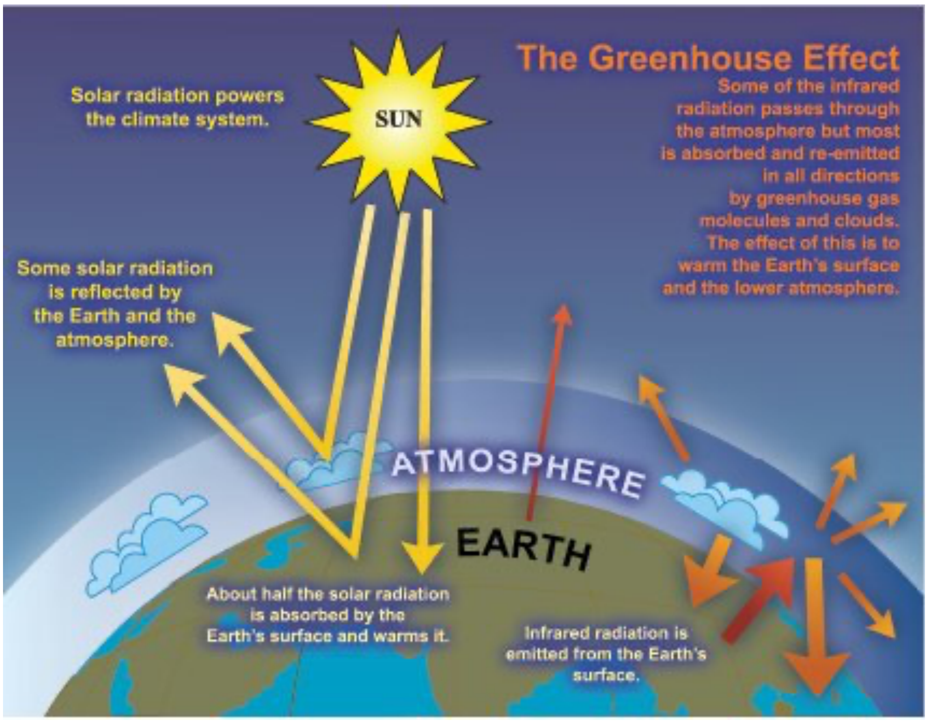
Once deposited back on Earth, a temporarily-airborne microbe can in principle re-establish itself if its new environment is compatible with its requirements (appropriate nutrients, hospitable humidity and temperature conditions, etc.), and if it is able to efficiently compete with the microbes already present in the new habitat.

Rainfall contributes largely to the deposition of *aerosols* and airborne microbes, as it literally washes them out of the air column. It was estimated that 10 to 100 million bacteria per square meter per hour are deposited on the ground by precipitation, a fraction of which comes directly from clouds that bring microbes from eventually very distant sources.

Precipitation brings microbes from high altitudes, clouds and the air column back to the surface. Certain bacteria are suspected to trigger precipitation from clouds by inducing the formation of ice. (Photo: P. Amato).

In many regards, clouds are major environmental phenomena. They occupy roughly 15% of the volume of the troposphere (first atmospheric layer of ~10 km height). They are composed of tiny droplets of liquid water or ice crystals (~5-20 µm in diameter) that have condensed on the surface of aerosol particles due to a decrease in temperature, similar to the formation of dew on grass on a cold morning, or steam on the mirror after a hot shower. Cold air can hold less water vapor than warm air, so when warm air cools it deposits water as condensation on surfaces, such as those of *aerosol* particles.

Clouds intercept sunlight and *infrared radiation* (heat) emitted from Earth' surface, and thus contribute greatly to climate regulation and the *greenhouse effect*. Fog and cloud droplets also provide temporary aquatic micro-habitats for airborne microbes. In such micro-habitats, bacteria and fungi have been shown to be able to exhibit some metabolic activity, partly in order to react against cold, osmotic shocks, and oxidants, and in some cases even to produce biomass and multiply. Cloud water contains numerous chemical compounds from natural sources and human activities that can be utilized as nutrients: organic acids, alcohols, aldehydes, sugars, amino acids, etc. To some extent, microbes may also contribute to the detoxification of pollutants in clouds (phenol, formaldehyde, etc.). Microbial activity has therefore multiple potential impacts on the complex chemical reactivity of the atmosphere, and thus on its composition, and hence on climate.



The *greenhouse effect*. Incoming solar light (in yellow) is partly reflected by the atmosphere, clouds and the surface of Earth (*albedo*), while the remaining fraction is absorbed by the surface and warms it. Earth's surface reemits heats under the form of *infrared radiation*, which partly escapes to space, and partly gets absorbed by clouds and the atmosphere, thus getting trapped in the Earth system and contributing to warm Earth to a temperature near 15°C on average. In the absence of *greenhouse effect*, the temperature on Earth would be -18°C. Source: IPCC Fourth Assessment Report: Climate Change 2007, from https://archive.ipcc.ch/publications_and_data/ar4/wg1/en/faq-1-3.html.

Clouds intercept solar light and contribute to the *greenhouse effect* (photo: Min An via Pexels.com).

Clouds are also at the origin of rainfall, when droplets or crystals grow up to a size where they cannot float in the air anymore. Due to a physical phenomenon by which ice crystals tend to grow at the expense of liquid droplets, referred to as *Wegener–Bergeron–Findeisen process*, freezing often triggers precipitation.

Fascinatingly, some bacteria that live on plant leaf surfaces, and that are swept up into the atmosphere by wind, probably the best known and most studied being *Pseudomonas syringae*, can initiate ice formation via a membrane protein at temperatures higher than any other natural compounds (~-2°C). And: just for the record, the ice nucleation protein produced by this bacterium is also used as a commercial snow-making product in ski resorts, snomax®. The presence of this bacterium in the air, clouds and precipitation has been reported worldwide. It is though to be involved in the triggering of precipitation and be responsible for a fragile interaction existing between vegetation and rain, called *bioprecipitation*, in which vegetation and the microbes it emits attract rainfall in a positive *feedback*. Such capacity of initiating rain can be seen as beneficial to the related microbes, because it leads to their early deposition along with rain, therefore increasing their chances to escape the harsh conditions encountered in the high atmosphere.

The Evidence Base, Further Reading and Teaching Aids

- **Vulgarization articles**

Amato, P. (2012). Clouds provide atmospheric oases for microbes. Microbe 7, 3, 119-123. http://www.microbemagazine.org/index.php/02-2012-home/4547-clouds-provide-atmospheric-oases-for-microbes

The New York Times – The Opinion Pages, article by Olivia Judson, 2008: When life goes cloudy. https://archive.nytimes.com/opinionator.blogs.nytimes.com/2008/02/19/when-life-goes-cloudy/

Sofpedia News, article by Tudor Vieru, 2011: Microorganisms influence the weather. https://news.softpedia.com/news/Microorganisms-Influence-the-Weather-202148.shtml

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Youtube, video by Seeker, 2014: Are clouds full of bacteria? https://www.youtube.com/watch?v=46_0SQDh9Sk

Youtube, video by SciHow: Bioprecipitation: How Bacteria Makes Snow. https://www.youtube.com/watch?v=mFJLFXhycSQ

Youtube, video by SciHow: Bacteria and Viruses Are Raining Down on Us All the Time. https://www.youtube.com/watch?v=KBRyyCc9mLE

- **Scientific publications (reviews)**

Delort, A.-M., Vaïtilingom, M., Amato, P., Sancelme, M., Parazols, M., Mailhot, G., Laj, P., and Deguillaume, L.: A short overview of the microbial population in clouds: Potential roles in atmospheric chemistry and nucleation processes, Atmospheric Research, 98, 249–260, https://doi.org/10.1016/j.atmosres.2010.07.004, 2010

Després, V. R., Hufffman, J. A., Burrows, S. M., Hoose, C., Safatov, A. S., Buryak, G., et al. (2012). Primary biological aerosol particles in the atmosphere: a review. *Tellus B*, *64*(0). https://doi.org/10.3402/tellusb.v64i0.15598

Šantl-Temkiv, T., Amato, P., Casamayor, E. O., Lee, P. K. H., & Pointing, S. B. (2022). Microbial ecology of the atmosphere. FEMS Microbiology Reviews, fuac009. https://doi.org/10.1093/femsre/fuac009.

- **Scientific publication (book)**

Delort, A.-M. and Amato, P.: Microbiology of Aerosols, John Wiley & Sons, 324 pp., 2017.

Glossary

Aeromicrobiology: field of microbiology interested in microbes in the air.
Aerosolization: action of being aerosolized, that is to say to pass from a fixed state on the surface (ground, water, living organism…) to a suspension in the air.
Aerosols: liquid or solid particle passively suspended in the air.
Albedo: fraction, or percentage, of incident light that is reflected from a surface. For example, snow reflects much more light than asphalt (it is brighter) and its albedo is therefore much higher: up to 0.90 (90%) versus 0.15 (15%).
Bioprecipitation: environmental feedback linking vegetation and precipitation, through ice-nucleation active bacteria that develop at the surface of plants. The development of plants and bacteria is promoted by water supplied by precipitation, which, in turn, favors precipitation by emitting water and ice nucleators responsible for triggering precipitation.
Feedback: intimate positive of negative loop relationship between two or more processes, by which they are mutually enhanced or attenuated.
Greenhouse effect: by analogy with the processes occurring in greenhouses, this term refers to the trapping of light (and so heat) in the Earth system due to the presence of the atmosphere.
Holobiont: Super-organism composed by a living pluricellular organism and the microbes associated with it.
Infrared radiation: light of long wavelength (not visible to the eye) associated with heat.
Propagules: biological structures designed to disseminate, in general referring to plants.
Spontaneous generation theory: theory largely accepted until the late 19th century, by which life can emerge spontaneously from non-living material.
Wegener–Bergeron–Findeisen process: physical process discovered in 1935 by the 3 eponymous scientists, by which ice crystals grow at the expense of droplets in clouds. This is often associated with precipitation.