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The relevance of fungi in astrobiology research – Astromycology

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Abstract

Since the very first steps of space exploration, fungi have been recorded as contaminants, hitchhikers, or as part of missions' crews and payloads. Because fungi can cause human disease and are highly active decomposers, their presence in a space-linked context has been a source of major concern given their possible detrimental effects on crews and space structures. However, fungi can also be beneficial and be used for many space applications. The exact effects on fungi are not always clear as they possess high adaptability and plasticity, and their phenotypes and genotypes can undergo several changes under the extreme conditions found in space, thus leading to different results than those we would have on Earth. Understanding and analysing these aspects is the subject of astromycology, a research field within astrobiology.

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The impending situation of a resurgent space race is expected to boost astromycology's visibility and importance. However, researchers lack both a framework and a solid base of knowledge from which to contextualise their work. This critical review addresses this gap by conceptualising the field of astromycology, covering key research and current questions pertaining to the field, and providing a relevant research instrument for future work.

Keywords – Fungi – Mycology – Planetary Protection – Space Exploration – Space Microbiology

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1. Introduction

1.1 Astromycology – an Emergent Research Topic

Fungi are ubiquitous on Earth (where they play unique ecological roles) and in its atmosphere (DasSarma et al. 2020, Šantl-Temkiv et al. 2022), and can even be found in the most extreme environments (Gostinčar et al. 2022a), such as the frigid soils of Antarctica (Durán et al. 2019), the irradiated walls of the Chernobyl Nuclear Power Plant (Zhdanova et al. 2004), and in the saline and hypersaline waters of our oceans (Gunde-Cimerman et al. 2000, Amend et al. 2019). It is thus not surprising that fungi have even been found in seemingly unusual and nutrient-deprived outer-space environments. Various moulds and yeasts have been found hitchhiking aboard the International Space Station (ISS) (Novikova et al. 2006) and have been regularly reported in several missions since the early days of space exploration.

As increasingly stronger interest and resources are being spent exploring scientific and technological capabilities in space, it is imperative to understand the ecological roles of fungi and their full impact on human activity outside our planet. Research dealing with the intersection between astrobiology and mycology – astromycology – is nascent and still growing as more researchers begin to explore questions regarding this area and as the space economy continues to grow (De Middeleer et al. 2019, Horne et al. 2022, Urbaniak et al. 2022). The research field of

fungal systems in space has been developed for quite some time, ever since biological processes were taken into consideration in space science. However, researchers lack both a framework and a foundational basis of knowledge that they can draw to contextualise their work examining fungi and space.

Astromycology is at the interface between astrobiology and mycology. However, the field of astrobiology does not fully encompass the applied and concrete nature of astromycology that examines current-day microbes (Case et al. 2022). Whereas astrobiology studies the fundamental questions of life, its origin, and its evolution on Earth and potentially elsewhere (see section 1.2), astromycology concerns the presence, evolution, implications, and applications of fungi in extraterrestrial environments. This emerging discipline applies space science to mycology and incorporates ideas and tools from diverse areas of research (e.g., geology, biology, genetics, immunology, plant pathology, and agriculture) to better understand how fungi will continue to evolve and play a role in space environments, especially with regard to potential benefits and threats to human space presence.

Defining "astromycology" as a specific field will help to increase visibility and promote further opportunities for collaboration and funding, as well as support critical research and understanding of astrobiology, biophysics, and fungal ecology. The field has substantial breadth and depth, touching on topics ranging from contamination and human health to extremophiles and radiobiology. Nowadays, more than ever, inter- and multi-disciplinarity are key to scientific development as no research field develops on its own.

Therefore, here we discuss astromycology as the interdisciplinary and multidisciplinary scientific subfield of astrobiology (detailed in Section 1.2) that focuses on fungal life (addressed in Section 1.3). To demonstrate the expanding research being done in this discipline, we highlight all key research topics within astromycology (Section 2).

1.2 The Advent of Astrobiology

The question of whether life may exist elsewhere in the universe is as old as humanity itself, and, from the beginning of space exploration, a consequent scientific interest arose: the exploration of life in space. Ary J. Sternfeld wrote about "the birth of a new science whose main objective is to assess the habitability of the other worlds" in his 1935 article "Life in the Universe", which is one of the early references to the word "astrobiology" (Sternfeld 1935, Briot 2012). Later references to this field include a 1941 article by Laurence J. Lafleur, entitled "Astrobiology" and published in Leaflet No. 143 of the Astronomical Society of the Pacific (Lafleur 1941), while Gabriel Tikhov published the paper "Astrobiologii" in 1953 (Tikhov 1953).

Defining scientific fields can be a complex task and it is not always a relevant asset when knowledge and science constantly evolve, change, and expand their breadth and depth. Moreover, if we have not found a precise definition of life (Cockell 2020), how can we properly define a field that is focused on its study? Interestingly, up until now, there has been no agreement on a consensual definition of astrobiology.

Many well-known dictionaries give somewhat different astrobiology definitions, such as a "multidisciplinary field dealing with the nature, existence, and search for extraterrestrial life beyond Earth" (Encyclopaedia Britannica) or a "branch of biology concerned with the search for life outside the Earth and with the effects of extraterrestrial environments on living organisms" (Merriam Webster), presenting it as a synonym of exobiology. In turn, exobiology has also been used since the 1960s, when Joshua Lederberg defined the objective of exobiology as "to compare the overall patterns of chemical evolution of the planets, stressing those features which are globally characteristic of each of them" (Lederberg 1960). Pioneer sampling and studies analysed life at high elevations, but eventually ended up extending to the different layers of our atmosphere and into space (DasSarma et al. 2020). These were the early days of space biology, now referred to as Astrobiology (Soffen 1997, Chyba & Hand 2005, DasSarma et al. 2020).

Astrobiology, defined by Soffen (1997) as "the scientific study of the origin, distribution, evolution, and future of life in the universe", is a highly interdisciplinary field that relates several

disciplines such as biology, chemistry, geology, astronomy, physics, engineering, planetary sciences, and Earth sciences. In 2001, with the start of the National Aeronautics and Space Administration (NASA) Astrobiology Program, astrobiology was defined as "the study of the origin, evolution, distribution, and destiny of life in the universe" (Morrison 2001). In "The Astrobiology Primer: an outline of general knowledge, version 1, 2006", astrobiology is defined as "the study of life as a planetary phenomenon", aiming to "understand the fundamental nature of life on Earth and the possibility of life elsewhere" (Billings et al. 2006). Ten years later, "The Astrobiology Primer v2.0" (Domagal-Goldman et al. 2016), defined astrobiology as "the science that seeks to understand the story of life in our universe". More recently, in the document "Origins, worlds, and life: a decadal strategy for planetary science and astrobiology 2023-2032" (National Academies of Sciences, Engineering, and Medicine 2022), astrobiology is simply defined as "the study of the origin and evolution of life on planetary bodies".

A critical impulse for the nascent field of astrobiology took place in 1996, with the discovery of potential evidence of life in the Martian meteorite ALH 84001 (McKay et al. 1996); the first astrobiology scientific conference was also held in that same year. Then, in 1998, the NASA Astrobiology Institute (NAI) was established "to develop the field of astrobiology and provide a scientific framework for flight missions" (Blumberg 2003). Ending in 2019, the NAI was a successful virtual organisation that integrated astrobiology and training programs with the international science communities for two decades. NASA's 2000 Space Science Strategic Plan (NASA 2000) explains that "astrobiology intends to expand exobiology research and encompass areas of evolutionary biology to further our understanding of how life may persist and evolve to exert a global environmental influence", defining three main questions (How does life begin and develop? Does life exist elsewhere in the universe? What is life's future on Earth and beyond?) along with ten related main goals, listed at www.hq.nasa.gov/office/codez/plans/SSE00plan.pdf.

Over time, several focus areas for astrobiology research have been identified by different publications: the NASA Astrobiology Roadmap (Des Marais et al. 2008), the European Astrobiology Roadmap (Horneck et al. 2016), the Astrobiology Primer (Domagal-Goldman et al. 2016), as well as more recent, equivalent discussions in China (Lin et al. 2020). Those areas include: research on extreme environments, life-detection missions on Mars, the composition of icy moons of our solar system (e.g., Enceladus and Europa) (O'Rourke et al. 2020), and the search for potentially habitable exoplanets (Brack et al. 2010).

Since first mentioned in the 1930s, astrobiology has grown to have its own peer-reviewed focused journals (Section 3.2) and more than eleven thousand publications, which include more than five hundred reviews according to Clarivate Analytics (ISI Web of Knowledge, www.webofscience.com/wos/woscc/basic-search).

One of the main pillars of astrobiology is the study of the limits of life and how terrestrial organisms survive and adapt to extreme extraterrestrial conditions, namely in the so-called terrestrial analogue environments. Microorganisms are the best survivors and thrivers in conditions that we consider extreme in the context of life in space (Cockell 2020). They can affect and take a toll on: astronauts' health (e.g., Landry et al. 2020, Simões & Antunes 2021), habitat safety (e.g., Pierson 2001, Yamaguchi & Nasu 2015, Landry et al. 2020), and planetary protection (e.g., Benardini & Moissl-Eichinger 2022, Horne et al. 2022). Microorganisms are also major assets for the study of the origin of life (e.g., of fungal life – Onofri et al. 2007, Berbee et al. 2017, Loron et al. 2019, Berbee et al. 2020, Saxena et al. 2021) and its limits (e.g., Rothschild & Mancinelli 2001, Pikuta et al. 2007).

With an ever-expanding list of potentially habitable exoplanets (Krissansen-Totton et al. 2022) and a very active exploration program of the planets of the solar system (Enya et al. 2022), astrobiology is currently a healthy scientific field, expected to enter a golden age in the near future, when the first signs of life beyond our planet might be finally detected (Impey 2022).

1.3. Fungi (on Earth)

1.3.1. Fungal Diversity and Evolution

The number of fungal species on Earth is still subject to debate. One of the first and most accredited appraisals was proposed by Hawksworth (1991), who estimated 1.5 million based on, among other metrics, a ratio of about six fungal species per plant. With the advent of molecular approaches for species delimitation, and after the publication of primers targeting the fungal nuclear ribosomal internal transcribed spacer (ITS) region in 1990 (White et al. 1990), the rate of species discovery increased dramatically. Estimates were revised to values between 2 and 13.2 million fungal species on Earth (Blackwell 2011, Simões et al. 2013, Hawksworth & Lücking 2017, Wu et al. 2019). Whatever the true number of fungal species might be, the number of formally described taxa, even though it is continuously increasing, currently stands at 51,568 species according to the global catalogue of microorganisms (https://gcm.wdcm.org, accessed on Jul, 2023), and this accounts for a negligible portion of total fungal diversity (Simões et al. 2013, Hawksworth & Lücking 2017, Phukhamsakda et al. 2022).

Fungi have always been controversial organisms. Initially, researchers struggled to even define which organisms should be included in this kingdom, as most traditional classification systems were based solely on morphology, leading to some ambiguity in this group. Certain fungi, such as yeasts, do not show enough differentiating morphological features (e.g., shape, colour, and size of various structures), while others display different characteristics depending on their asexual or sexual states. Deoxyribonucleic acid (DNA) sequencing initiated a cascade event that allowed a wider understanding of the differentiation and polymorphisms of these organisms (Blackwell 2011), but the highly diverse morphological features (Fig. 1) can still be highly valuable for species recognition.

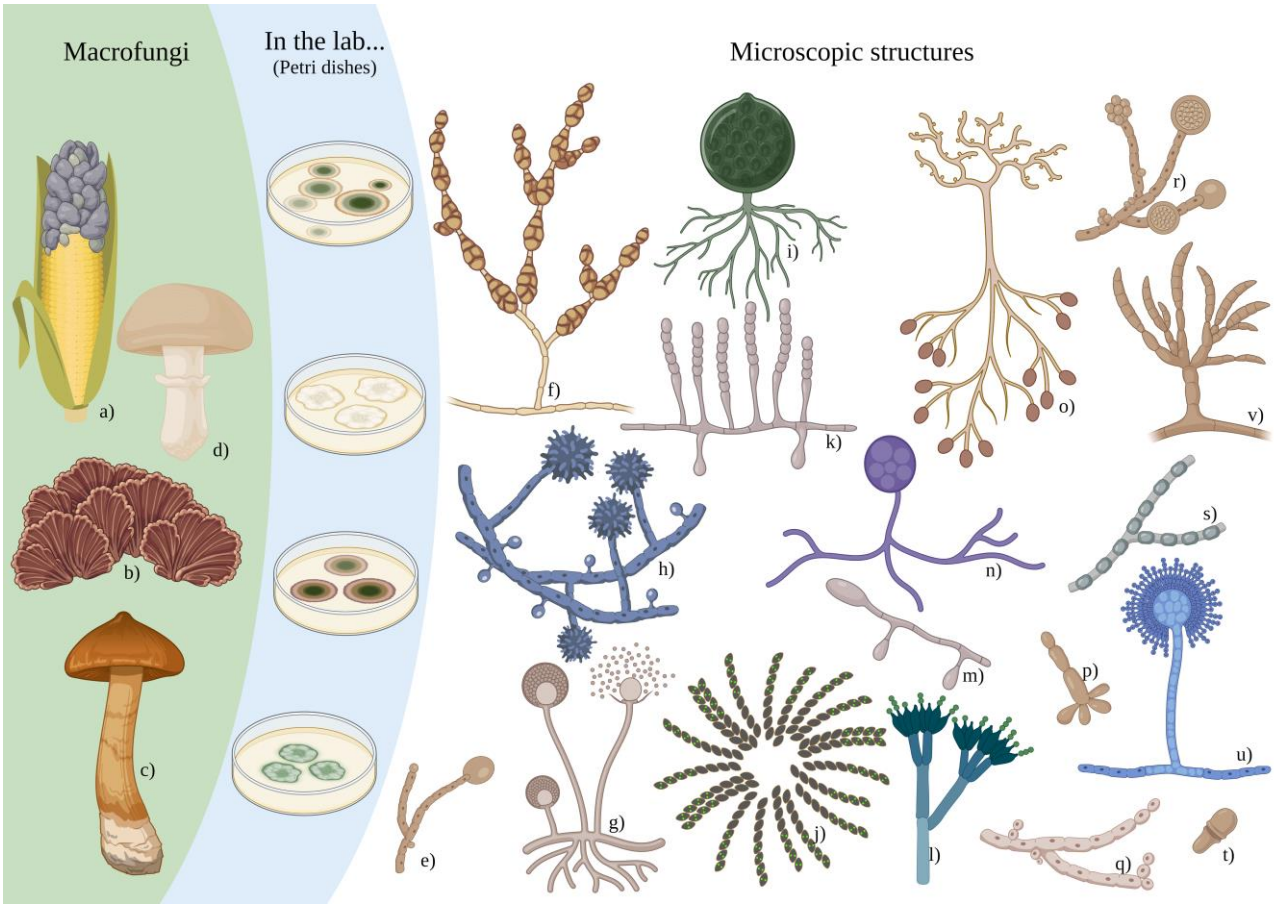


Figure 1 – Morphological diversity of fungi, showcased by several examples of species schemes available at BioRender.com. a) Corn infected with *Ustilago maydis*. b) *Schizophyllum commune*. c) *Cortinarius rubellos*. d) *Leucoagaricus leucothite*s. e) *Candida* sp. f) *Alternaria alternate*. g) *Mucor* sp. h) *Histoplasma* sp. i) Chytridiomycota division species, with rhizomes. j) *Neurospora crassa*. k) Powdery mildew fungus conidia. l) *Penicillium* sp. m) Powdery mildew fungus

germinating spore. n) Arbuscular mycorrhiza. o) Oomycete (sporulation). p) *Metschnikowia gruessii*. q) Hypha. r) *Candida* sp. s) *Coccidioides* sp. (arthroconidia). t) *Malassezia* sp. u) *Aspergillus* sp. v) *Fusarium* sp. Created with BioRender.com.

Physiological characteristics, such as growth rate and production of pigments, are also used for the recognition of some species (Geiser et al. 2007), while traditional dichotomous keys are still widely used in fungal taxonomy (e.g., Navi et al. 1999, Watanabe 2010, Tsurykau & Etayo 2017, Corazon-Guivin et al. 2019, Zheng et al. 2020).

We now have a clearer perception of the boundaries of the kingdom Fungi and its taxonomic diversity (Fig. 2).

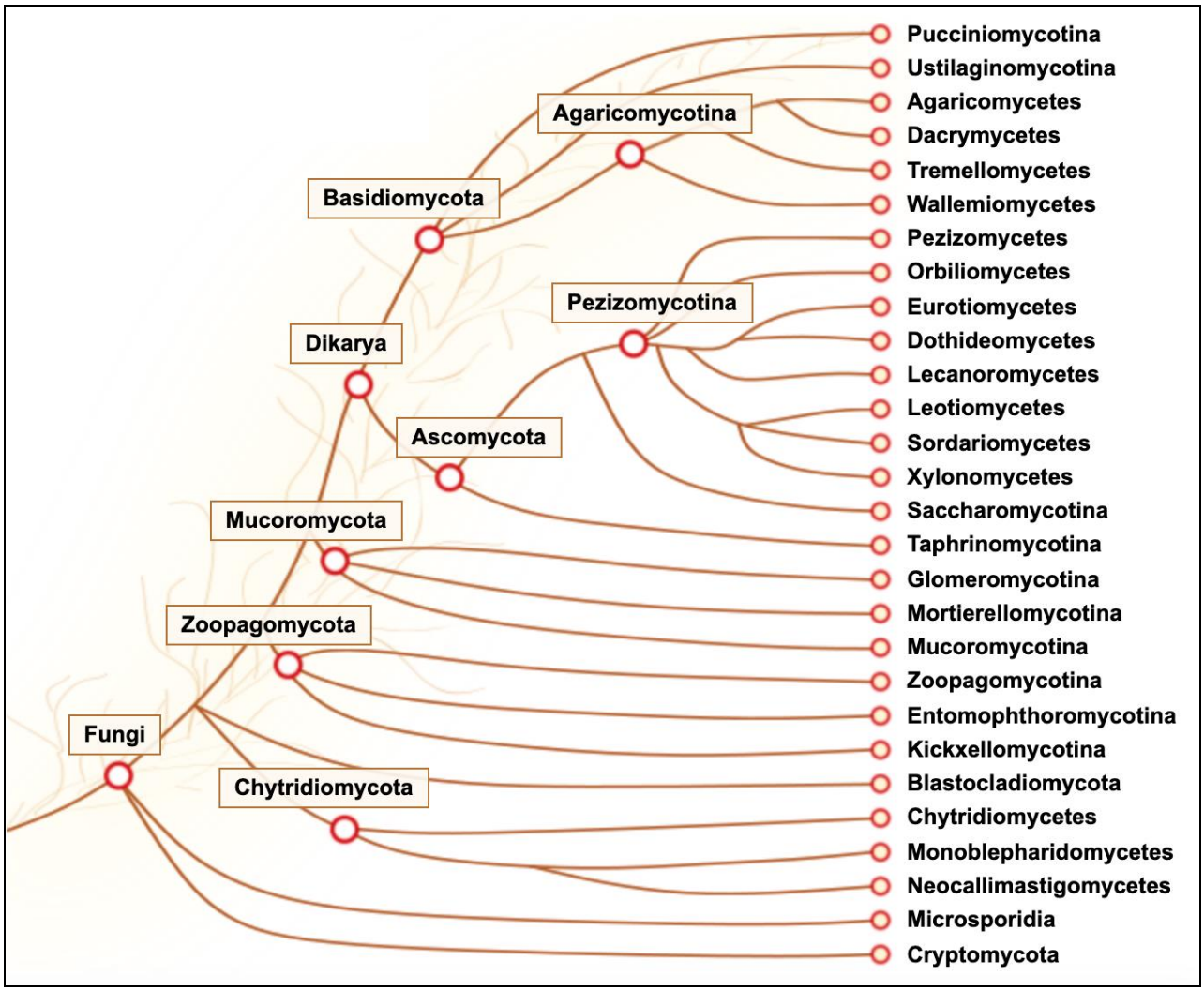


Figure 2 – Fungal taxa and relationships between major fungal groups, derived from the Joint Genome Institute (JGI) database, the MycoCosm Fungal Portal (https://mycocosm.jgi.doe.gov/mycocosm/home), accessed on March 11, 2023 (Grigoriev et al. 2014).

Divergence time studies suggest that almost all true fungi have a single common ancestor. Also, the earliest terrestrial fungi may have evolved around 1000 million years ago (MYA) (Heckman et al. 2001), originating from aquatic fungi and becoming the dominant life forms on Earth around 250 MYA (Loron et al. 2019). Adaptation to the terrestrial environment may have been facilitated by symbiotic associations, as suggested by evidence of arbuscular mycorrhizae in the earliest fossil fungi (460 MYA) (Berbee et al. 2017). Fossil traces of early fungi, morphologically very close to Glomeromycota, are known to have formed the first

endomycorrhizal symbiotic associations (Harper et al. 2020). The remarkable frequency of fossil fungi increasing in the Tertiary Period suggests that their proliferation is related to the diversification of angiosperms, which occurred around 400 MYA (Blackwell 2000, Webster & Weber 2007, Massini et al. 2012, Taylor et al. 2014, Wijayawardene et al. 2020). Many studies have proven that, although the first fungi were unicellular and probably marine, their evolution co-occurred with an increase in size, complexity, structure, and functions (Webster & Weber 2007). Furthermore, their interactions with other organisms, such as plants, were the main reason for the development of Earth's atmosphere, as mentioned by Blackwell (2000) and reviewed by Berbee et al. (2017).

The undeniably broad effects of fungi on Earth's ecosystems can be noted in the genomes of plants, on the chemistry of soils, and even in the function of animals' immune systems (Peay et al. 2016).

1.3.2 Fungi General Characteristics

Fungi are eukaryotic organisms with a cell structure showing a few peculiarities, such as the presence of ergosterol (a type of cyclic lipid) in their cell membranes. Their cell walls are composed of polysaccharides, such as glucans (fibrillar glucose polymers with ß-1,3 ß-1,6 glycosidic bonds) and chitin (N-acetylated glucosamine units linked by ß-1,4 glycosidic bonds) (Garcia-Rubio et al. 2020), which are important targets in antifungal therapies.

Fungi are known for their wide metabolic competences and the capability to produce a vast number of secondary metabolites. They release a wide range of extracellular enzymes that are fundamental for breaking down the matter that serves as their substrate, followed by further digestion and product absorption through the cell wall. These enzymes also play an important role in biodeterioration and biocorrosion (Gutarowska 2010), reasons for which fungi are used in various applications.

Fungal secondary products can also have a direct impact on health. Fungal pathogens rely on their digestive enzymes to penetrate natural host barriers (Hoffmeister & Keller 2007, Lavrin et al. 2020), while some secondary metabolites can also act as mycotoxins, which are low-molecular-weight substances that may have carcinogenic, mutagenic, nephrotoxic, hepatotoxic, or neurotoxic effects. On the other hand, many important pharmaceuticals have been developed from fungal secondary metabolites (Bills & Gloer 2016, Keller 2019). The best-known examples are the β-lactam antibiotics, including penicillins and cephalosporins. Among the roughly 33,500 bioactive microbial metabolites that have been described, about 47% (15,600) are of fungal origin (Bills & Gloer 2016).

Fungi are extremely adaptable organisms, with a striking tendency to explore new environments. They can exploit new resources, form novel associations, and take advantage of the suite of traits that they carry when encountering a new condition (Zalar et al. 2011, Selbmann et al. 2013). Fungi display a considerable degree of morphological plasticity and may, for instance, promptly shift from one growth form to another according to physical or chemical conditions. They are unicellular (yeasts) when immersed in rapidly fermentable sugar or when they are in their infective phase (as seen for most human pathogens or during vascular plant invasion). Alternatively, they may exhibit filamentous growth, a "search for food" growth form that allows them to inspect their surroundings, or they may even switch to meristematic growth to optimise the surface/volume ratio when exposed to stressful conditions. Fungi have complicated life cycles with sexual, asexual, and parasexual phases (Gostinčar et al. 2022b). These phases can differ morphologically and often ecologically, displaying different requirements. In another unusual characteristic, fungi do not need to complete their life cycle. Depending on the surrounding environmental conditions, sometimes they can focus only on a part of their life cycle to successfully autoperpetuate and disseminate via spores (Peraza-Reyes & Malagnac 2016).

Fungal spores play a vital role in the fungal survival strategy and their overall resilience. These microscopic structures may remain metabolically inactive if they do not meet proper environmental conditions for germination and persist in a quiescent or dormant state even after

prolonged periods (Blatzer & Latgé 2021). Under the proper environmental circumstances, spores can then germinate and become vegetative cells (Sephton-Clark & Voelz 2018, Blatzer & Latgé 2021).

Fungal spores can have a wide variety of morphologies (Van Leeuwen et al. 2010) and are largely distinguished by their reproduction process (Samanta 2015), which can be asexual (arthrospores, blastospores, chlamydospores, conidiospores or conidia, and sporangiospores) or sexual (ascospores, basidiospores, oospores, and zygospores). As an example, *Aspergillus niger* spores are formed asexually via conidiophores, which can extend up to 460 µm due to the formation of aerial hyphae (Cortesão et al. 2022). Due to this morphological property, chains of fungal spores can be lifted above the laminar airflow, which makes it easier for the spores to be released via high airflow and liquid streams.

Fungal spores can survive extreme temperatures and germinate as soon as optimal temperatures prevail, with the need for only very low water activity to germinate compared to bacteria (Gibson et al. 1994). Light and the composition of the surrounding atmosphere may also play a role in spore germination (Fuller et al. 2015). Additionally, most spores, e.g., of highly abundant filamentous fungi, such as *Aspergillus* spp. and *Penicillium* spp., are highly stress-resistant against environmental factors like drought, ultraviolet (UV) radiation, heat (Cortesão et al. 2020a), or cold (Sonjak et al. 2006). Due to their often pigmented, thick cell walls and their already mentioned ability to go into a dormant (low metabolism) state, they are essential for fungi to withstand harsh conditions and are one of the main factors ensuring their survival fitness (Dantigny & Nanguy 2009).

Filamentous fungi (also known as moulds) are a distinct group of fungi that are of particular relevance for several fields. They are spore formers (i.e., they reproduce and disperse by sporulation), mycotoxin emitters, biofilm producers, and material degraders, and may create complex hyphal networks, which are the substantial basis for the fungus to colonise very diverse substrates. Fungi can grow in a wide range of temperatures, and according to their optimum, they are classified as psychrophiles, mesophiles, and thermophiles. Some filamentous species are eurytherms, and they may adapt well to environments experiencing wide temperature variations (0–40 °C) (Dix & Webster 1995).

1.3.3 Fungal ecology in space-relevant environments

In general, fungi have been recognized as essential components in terrestrial, aerial, and aquatic environments. Their vital roles in the processes and functioning of our planet's ecosystems are becoming clearer as more details are constantly uncovered (Berbee et al. 2020, Anees-Hill et al. 2022). In terrestrial environments, fungi are major decomposers of woody and herbaceous substrates, as well as of dead animals and animal parts. Fungi produce organic compounds contributing to soil carbon storage, transform organic nitrogen or phosphorus, and form symbiotic associations that increase net primary productivity rates (Treseder & Lennon 2015). They are also important pathogens of plants and animals and may form symbiotic relationships with a wide range of organisms (Hyde et al. 1998, Perini et al. 2022). In particular, in oligotrophic environments, their role is fundamental in contributing to primary production and efficiently recycling the limited resources available (Perini et al. 2019, 2022).

Some species, known as (poly)extremophiles, best represented by polyphyletic black yeasts (Selbmann et al. 2020), have evolved a variety of morphological and physiological adaptations that allow them to thrive in multiple extremes and even survive exposure to space conditions. Adaptations to extreme conditions (e.g., pH, temperature, salinity, hydrostatic pressure) are complex and interconnected. They include morphological changes, such as polymorphic changes that enable switching from filamentous form to unicellular yeast cells and meristematic clumps, increase and remodelling of extra polymeric substances (EPS), and ability to form biofilms. The molecular responses involve rigorous changes in gene expression that lead to subsequent synthesis of compatible solutes, changed composition of the cell membrane, regulation of intracellular alkali-metal cations, and changed cell-wall ultrastructure and morphology. The high osmolarity glycerol

(HOG) branched mitogen-activated protein kinase (MAPK) signal-transduction system is used for sensing increased osmolarity of the medium, and heavy-metal and temperature stress. Increased expression of genes involved in energy production and oxidative damage protection was seen under different extreme conditions along with a lack of the classical heat and cold shock response (HSR and CSR, respectively) and in some cases even decreased levels of common stress proteins (Tesei 2022). Moreover, additional cellular strategies with potential roles in these fungi polyextremotolerance involve the modulation of non-coding and circular RNAs (circRNAs), and fusion transcripts, as recently brought to light by transcriptomics analyses (Blasi et al. 2015). These conditions also induce changes in the level or production of extracellular metabolites and enzymes active at extreme physicochemical values in the environment. Within such organisms, we can have true extremophiles, which display an obligate need for one or more extreme conditions to grow (Gostinčar et al. 2019a), and extremotolerant organisms, which can tolerate extreme values of one or more physico-chemical parameters (Rampelotto 2013, Gostinčar et al. 2019b, Zajc et al. 2019).

Understanding these patterns of tolerance provides us tools for defining the boundaries for habitability on our planet and may help us understand how life evolved on Earth and what types of life forms might, or might not, be found on other planetary bodies in our solar system and beyond. Among the environments that are considered optimal models for studying adaptations of life in analogue conditions of extraterrestrial environments, the Antarctic, Atacama deserts, and polar glaciers have attracted considerable attention for being considered current Mars analogues (Azua-Bustos et al. 2017, Perini et al. 2019, Azua Bustos et al. 2022, Touchette et al. 2022) and have been the targets of different mycological studies.

Microorganisms dominate terrestrial and glacial environments in the polar regions. Fungal diversity has been intensively studied in different regions of Antarctica and Arctic, from permafrost to ice sheets and glaciers (Flint & Stout 1960, Lawley et al. 2004, Cowan et al. 2014, Czechowski et al. 2016, Canini et al. 2020, Canini et al. 2021, Perini et al. 2021, 2022). Most researchers reported specificities in the diversity influenced by local environmental parameters and without consistent latitudinal trends (Cowan et al. 2014, Canini et al. 2020, Malcheva et al. 2020). The soil communities are mainly dominated by the divisions Ascomycota, (with Dothideomycetes and Eurotiomycetes, two close classes, as the most abundant), followed by Basidiomycota, Mortierellomycota, and Chytridiomycota (De Menezes et al. 2019, Canini et al. 2021), while in glacial environments basidiomycetous yeasts prevail (Perini et al. 2019, 2011) (check Fig. 2, for a clear picture of relationships between different groups). However, as confirmed by many studies, our knowledge of Antarctic fungal diversity is still partial, as many of the sequences retrieved in recent molecular studies do not correspond to any known taxa, further confirming that our knowledge of global fungal diversity is still limited (Lawley et al. 2004, Scalzi et al. 2012, Selbmann et al. 2015, Czechowski et al. 2016, Selbmann et al. 2017, Coleine et al. 2018, De Menezes et al. 2019, Durán et al. 2019, Perini et al. 2019, Canini et al. 2020, Coleine et al. 2020, Canini et al. 2021).

Where the climatic conditions become too harsh for life exposed on the rock or soil surfaces, fungi retreat to subglacial environments or the interior of rocks (Perini et al. 2019). Porous rocks enable better protection, creating hotspots of microbial diversity. Antarctic rocks have been suggested to contribute to soil microbial diversity since rock powder generated by bio-weathering processes is easily blown away by winds (Friedmann 1982). Whereas the porosity of rocks provides a more protected niche, it is still not clear if microorganisms can survive in the soil. It was hypothesised that only the most resistant ones would survive, but it has yet to be determined whether they are metabolically active or present as dormant or dead wind-transported spores and propagules (Carini et al. 2016). On the other hand, subglacial environments harbour rich communities of basidiomycetous yeasts and fungi of the genus *Penicillium*, that are released into the adjacent environment, either permafrost or the ocean, as a result of accelerated glacial thawing (Sonjak et al. 2006, Butinar et al. 2007, Sonjak et al. 2007). Dothideomyces and Eurotiomycetes were reported as the most abundant components of Antarctic cryptoendolithic fungal communities, mostly colonising sandstone rocks distributed throughout Victoria Land and beyond (Zucconi et al.

2016, Selbmann et al. 2017, Coleine et al. 2018, 2020), while basidiomycetous yeast from the genera *Cryptococcus*, *Naganishia*, and *Rhodotorula*, to mention just a few, are released in glacial forefields and in the sea environment (Selbmann et al. 2017).

Such prior studies reported the existence of a noticeable, rather peculiar group of melanized, microcolonial, slow-growing, and morphologically poorly differentiated fungi, highly adapted to Antarctic and Arctic environmental constraints, which attracted the attention of scientists due to their bewildering physiological flexibility. Fungi of this morphological group identified in polar areas belong to two main classes: Dothideomycetes (with the order Capnodiales, and in particular families Teratosphaeriaceae and Cladosporiaceae) and Eurotiomycetes (with the order Chaetothyriales) (Selbmann et al. 2015, Perini et al. 2021, 2022, Zajc et al. 2022).

Fungal studies in the Atacama Desert, the driest and oldest desert on Earth (Hartley et al. 2005, Sun et al. 2018), and a well-known Mars analog model (Azua-Bustos et al. 2022), have been recently reviewed by Santiago et al. (2018). These authors reported a list of all the lichenized and free-living fungi isolated in different substrata, highlighting their metabolic and biotechnological potentialities, and suggesting their application as model organisms in astrobiological studies. Among other species reported in this desert from its Coastal Range, through the hyperarid core, to the Andes Mountains, there are epilithic species such as *Hortaea werneckii* (Zalar et al. 2019), non-lichenized fungi such as *Alternaria*, *Ascobolus*, *Aspergillus*, *Cladophialophora*, *Cladosporium*, *Eupenicillium*, *Gibberella*, *Leptosphaerulina*, *Monodictys*, *Penicillium*, *Periconia*, *Ulocladium*, and *Ustilago* (Conley et al. 2006), and species like *Cladosporium halotolerans*, *Penicillium citrinum* and *Penicillium chrysogenum* reported in epilithic and endolithic environments (Gonçalves et al. 2016). Other species, such as *Neocatenulostroma*, also found inside gypsum rocks, have been studied in search of detectable biosignatures such as melanin (Culka et al. 2017), while others, such as *Caloplaca orthoclada* (synonym: *Follmannia orthoclada*), have been reported as part of lichens (Castillo & Beck 2012), with a number of other species (*Cryptococcus*, *Cladosporium*, *Ulocladium*) been reported around fumaroles up to 6000 m high in the Andes Mountains in front of the Atacama (Costello et al. 2009). In turn, a yet to be identified species of fungi was found growing as epi- and endoliths in gypsum rocks (Wierzchos et al. 2011) of another site of the hyperarid core, while *Aspergillus atacamensis* and *Aspergillus salisburgensis* were reported growing inside a cave of the Coastal Range (Martinelli et al. 2017). Interestingly a diversity of viable cells of fungal species (*Ophiosphaerella herpotricha*, *Aspergillus versicolor*, *Chaetomium globosum*, *Cladosporium bruhnei*, *Aspergillus nidulans*, *Penicillium chrysogenum*) have been shown to use wind-transported dust particles (Azua-Bustos et al. 2019), and able to traverse, thus colonise, the entire Atacama in but a few hours.

Yeasts are common inhabitants of extreme environments, including Antarctic and Arctic regions, deserts, glaciers, ice sheets, and space stations like the ISS (Buzzini et al. 2018, Checinska Sielaff et al. 2019, Perini et al. 2019, 2021). A recent study isolated and identified 21 yeast species, including five new species, from the Qaidam Basin desert in China, the highest desert in terms of altitude and one of the driest deserts on Earth, which harbours Mars-like extreme environments (Wei et al. 2022). The yeasts isolated were dominated by basidiomycetous species and strains isolated from hypersaline soil samples exhibited elevated salt-tolerance (Wei et al. 2022).

Although the vast majority of fungi do not exhibit pathogenic traits, a limited number, including those that populate extremely cold environments, can cause infections in plants and animals (including humans) (Perini et al. 2019, Sun et al. 2020). According to the Leading International Fungal Education (LIFE, http://en.fungaleducation.org/) platform estimations, over 80% of the world's population (more than 5.7 billion people) are affected by serious fungal infections (Bongomin et al. 2017). Given that space exploration is frequently linked with crewed missions, fungal infections also need to be considered in these alternative extreme environments, particularly as many microbes (including fungi) have been recorded in space stations as Earth contaminants or as crew members' microbiota (as discussed in Section 2.2).

2. Astromycology roadmap and research developments

2.1 Fungi, Planetary Protection, and Cleanrooms

Planetary protection is a major concern for space agencies and governments, as sought by the Committee of Space Research's (COSPAR) Planetary Protection Policy (COSPAR 2020). COSPAR defends responsible exploration of other worlds by safeguarding space and planetary bodies from Earthly microbes (forward contamination), and avoiding the Earth's contamination with (potentially harmful) extraterrestrial agents (backward contamination) (Rummel et al. 2020, Horne et al. 2022). The increasing number of space agencies and public and private space sector start-ups makes regulatory mechanisms critical to prevent potential contamination of unexplored celestial bodies and backward contamination of our planet. In fact, while it is unlikely that Earthly life could easily proliferate in the inhospitable conditions of other planets, any type of contamination by terrestrial microbes could seriously compromise the search for biological signatures of extant or extinct life forms. Therefore, it is crucial to refocus worldwide efforts to safeguard the space and extraterrestrial environments (Cheney et al. 2020, Gunde-Cimerman et al. 2018) and to evaluate microbial survivability in spacecraft or planetary analogues of possible astrobiology-relevant targets (Moissl-Eichinger et al. 2016, Cassaro et al. 2021a), for a more accurate assessment and regular refinement of actual contamination hazards (Rettberg et al. 2019).

The principle of "planetary protection" was established in 1967 within the "Outer Space Treaty" (which acts as the legal framework and basis for international space law) when it was (originally) signed by the three depository Governments (the Russian Federation, the United Kingdom, and the United States of America). Signatory countries (which currently extend to 112 and include all major spacefaring nations) agreed on nine essential principles for conducting activities in space (https://treaties.unoda.org/t/outer_space). One of these principles mentions that "no foreign planet should be influenced in its development by the entry of terrestrial flora and fauna" (Dittel & Vogt 2021). To meet this objective, COSPAR officially suggests strict planetary protection measures for extraterrestrial missions.

The most rigorous protocols of planetary protection and consistent contamination control guidelines have been in place for many years now, meeting high standards of biological cleanliness. Almost all activities and preparations for space travel are done in International Organization for Standardization (ISO) 8 – ISO 5 cleanrooms while adhering to rigorous European Cooperation for Space Standardization (ECSS) classifications such as those set forth in standards like ISO 14644 and ECSS-Q-ST-70-58C (http://esmat.esa.int/ecss-q-st-70-58c.pdf), as is the case at the NASA Jet Propulsion Laboratory (JPL)'s spacecraft assembly facility (SAF) (Danko et al. 2021). Many planetary protection-sensitive missions, including the Mars 2020 Perseverance rover that was launched in 2020, were built using such cleanroom facilities.

The protocols and guidelines currently in place include extensive and routine microbial monitoring (Mora et al. 2016a), state-of-the-art high-efficiency particulate air (HEPA) filters, as well as consistent measures of control to prevent or reduce any existing bioburden. The standard guidelines for decontaminating cleanroom interiors include the usage of 70% isopropyl alcohol (IPA), 7.5% hydrogen peroxide in wipes, and ultraviolet C (UVC) light (Lalime & Berlin 2016). For validating any applied sterilisation measures, official planetary protection policies suggest considering specific sterilisation bioindicator organisms. These usually consist of bacterial endospores of *Bacillus* spp., as they show high resistance to radiation-based decontamination measures as well as space and other extreme environmental conditions (Nicholson et al. 2005, Moeller et al. 2014, Cortesão et al. 2019). Current regulations limit the detected bioburden found during spacecraft assembly, integration, and testing. For example, sensitive missions like the robotic lander systems being used to investigate extant Martian life have restricted surface bioburden to 3,000,000 spores (COSPAR 2020).

Despite these control efforts, research on the microbiome of SAFs has found distinct and mostly human-associated microbial communities within and around cleanroom environments (Venkateswaran et al. 2014a, Moissl-Eichinger et al. 2015, Bashir et al. 2016, Mora et al. 2016b, Regberg et al. 2018, Hendrickson et al. 2021). It is worth noting that, in most of these studies, the microbial profiling was focused on bacterial populations and that most planetary protection

programs are based specifically on bacterial spore resistance (Nicholson et al. 2012, Onofri et al. 2012). However, a few studies have investigated fungal presence. This was the case in a recent study on surfaces from the assembly, testing, and launching facility of the OSIRIS-REx, a spacecraft that collected samples from the near-Earth asteroid (101955) Bennu (Regberg et al. 2020). Fungal DNA was detected, although for this mission there were no bioburden restrictions in place. Detected fungi included: *Articulospora proliferata*, *Cladosporium delicatulum*, *Itersonilia pannonica*, *Phaeosphaeria caricicola*, *Sistotremastrum* spp., *Udeniomyces pyricola*, and *Zymoseptoria* spp.

In general, filamentous fungi traces and spores were and are still underrepresented in most research when it comes to microbial monitoring, despite being recognized as acceptable bioindicators for planetary protection. This under-representation is particularly puzzling, as it has been proven that the spores of these widely prevalent eukaryotes can be equally or even more robust to harsh environmental conditions than bacterial endospores (Onofri et al. 2007, de Vera et al. 2012, Pacelli et al. 2017a, Coleine et al. 2022a), namely in terms of resistance to UVC (Onofri et al. 2007, Dadachova & Casadevall 2008, Neuberger et al. 2015, Cortesão et al. 2020a, Cortesão et al. 2021), UVB (Selbmann et al. 2011), gamma and E-beam radiation (Blank & Corrigan 1995, Pacelli et al. 2017a, 2017b), desiccation (Onofri et. al, 2012, 2015, Dijksterhuis 2019), vacuum and other atmospheres (Silverman et al. 1967, Sarantopoulou et al. 2011, Neuberger et al. 2015, Pinto et al. 2020), temperature (Onofri et al. 2007, Pacelli et al. 2019, Dijksterhuis 2019, Coleine et al. 2022b), acid (Van Laere 1986, Zuo et al. 2022), and peroxide-based cleaning agents (Visconti et al. 2021).

Prevention and sterilisation of fungal contamination have become increasingly relevant also because some common fungal genera can germinate, grow, and tolerate environments with a low water activity (Segers et al. 2016, Gunde-Cimerman et al. 2018) and low oxygen (Perrone & Susca 2017). Thus, understanding fungal spore resistance, especially under decontamination procedures, should be recognized as essential for planetary protection, as it already is for the food and medical sectors (Sharma et al. 2015, Misra et al. 2019). These sectors have provided helpful insights into the resilience of fungal spores to decontamination, such as surface sterilisation using plasma-ionised gas and UV radiation in the food and medical industries (Sharma et al. 2015, Misra et al. 2019). Given the variety of fungi identified in all space missions analysed so far, it is critical to develop appropriate containment measures for fungal growth and to select the most practical materials. This will aid in avoiding unwanted fungal growth, minimise health risks, and prevent the contamination of structures and spacecraft components.

Although an Earth-analogue of the ISS habitat is not available, the amount of data on microbial species available in NASA cleanrooms makes these facilities the best-characterised closed environments with limited human traffic (Checinska et al. 2015). Earth cleanrooms have a lower prevalence of cultivable microorganisms than the ISS, implying that: 1) regular cleaning is required to reduce microbial burden in closed habitats; and, 2) accurate estimations of viable population size can help identify potential contaminations (e.g., as done through the coupling of propidium monoazide – PMA treatment with Next-Generation Sequencing – NGS) (Checinska et al. 2015).

The risks of failing to assess and contain fungal contamination are obvious. As an example, terrestrial fungal contaminants, mostly *Penicillium* spp., were found inside the cleanroom storing meteorite samples at NASA's Johnson Space Center (JSC) in Houston, Texas (Regberg et al. 2018). This underscores the possibility that the search for life in off-world samples may be highly affected by fungal contamination.

2.2 Fungal contaminants in space habitats

There is a long historical record of fungal detection in space habitats. Fungi were first detected aboard Salyut 6, a Soviet orbital space station, the eighth station of the Salyut programme (Makimura et al. 2001). Later, they were also found aboard the first modular space station, the Soviet Mir, and its mycoflora was examined in several studies. Viktorov et al. (1992) isolated

filamentous and yeast-like fungi and identified 36 species belonging to 12 different genera. In a later study, the fungi *Penicillium rubens* and *Aspergillus* sp. were identified among the responsible for the degradation of a navigation window at Mir (Klintworth et al. 1999). Makimura et al. (2001) isolated six strains from air collected on board the Russian 1997 Mir-Space Station (mission J/MM), and identified them by morphological analysis and molecular techniques (18S- and ITS1-rDNA sequences) as *A. versicolor*, *Penicillium* sp., and *Penicillium chrysogenum* (renamed *P. rubens*). Shnyreva et al. (2001) also analysed samples from Mir using random amplified polymorphic DNA (RAPD) markers and found 21 fungal strains, isolated from different polymeric materials and air inside the station, all belonging to the Eurotiales order, mostly *Aspergillus* and *Penicillium* genera.

Fungi were also detected in several NASA missions. Numerous fungal species from diverse genera (*Alternaria*, *Aspergillus*, *Botrytis*, *Candida*, *Cephalosporium*, *Cladosporium*, *Fusarium*, *Mucor*, *Penicillium*, *Phoma*, and *Trichoderma*) were recovered, up to 1998, from spacecraft belonging to the Apollo missions (10, 11, 14, and 15), Skylab, shuttles, and astronauts (Schuerger 1998). During the Apollo 14 and 15 missions to the moon, despite a three-week quarantine, 57 fungal and actinomycetes genera were found on human and spaceship surfaces (Gonzales et al. 1996).

More recently, several studies have also been conducted at the ISS. Novikova et al. (2006), analysed the microbial load on air and surface samples during nine missions and seven Soyuz flights to the station, over a period of six years. They found over 30 different fungal species, with *Aspergillus* and *Cladosporium* being the most dominant genera. Several of those species were found to be opportunistic contaminants involved in the biodegradation of structural materials (polymers and metallic surfaces), affecting their integrity and leading to potential short circuits and malfunctioning (Novikova et al. 2006). According to Haines et al. (2019), the main sources of fungi detected in aerosols collected at the ISS were foods and plants, justifying the detection of a higher abundance of the species *Cyberlindnera jadinii* (common food additive) and *Penicillium paczoskii* (now *Penicillium glabrum*), followed by less abundant: *Acremonium alternatum*, *Aspergillus pseudodeflectus*, *Rhodotorula mucilaginosa* (an emerging opportunistic pathogenic yeast), *Fusidium griseum*, *Fusarium oxysporum* (specifically found infecting experimental plants in an ISS experiment), *Gibberella intricans* (now *Fusarium equiseti*), *Gyrothrix verticiclada* (now *Peglionia verticiclada*), *Idriella rara*, *Neoascochyta paspali*, *Papiliotrema laurentii*, and *Penicillium digitatum* (Haines et al. 2019).

The ISS air and surface microbiome has been studied using both culture-based and molecular methods. During the ISS Expedition 31, after reports of excessive dust and allergic symptoms from several crew members, the mycobiome of several areas was analysed. Several opportunistic pathogenic fungal species of the genera *Aspergillus*, *Candida*, *Cryptococcus*, and *Trichosporon* were found, representing 32% of the total number of sequences. Allergen species from the genera *Aspergillus* and *Penicillium* were also found, representing an additional 17% of the total sequences. Besides these, other disease-associated species were found at this time: *Candida parapsilosis*, *Penicillium spinulosum*, and *Penicillium aurantiogriseum*, associated with sepsis and wound infection, lung inflammation, and renal disease, respectively. Furthermore, the plant pathogenic species *Dothidiomycetes* spp., *Fusarium equiseti*, and *P. digitatum* were also detected (9% of the total sequences), probably due to the existing experiments with plants at that time (Venkateswaran et al. 2014b).

Aspergillus candidus, *A. niger*, *Aspergillus terreus*, and *Aspergillus unguis*, along with *Penicillium* as the second most dominant genus, were among 19 strains isolated from ISS dust samples (Checinska et al. 2015). The same genera, with the species *P. chrysogenum* and *A. versicolor*, were also found as the commonest contaminants on the Mir space station (Makimura et al. 2001). These genera have also been commonly reported as the most abundant contaminants isolated from two SAFs at the JPL and Kennedy Space Center (KSC) (Blachowicz et al. 2022a). A viable fungal community with a predominance of *R. mucilaginosa* and *P. chrysogenum* was found on different ISS surfaces collected during three flight missions and analysed upon return to

Earth (Checinska Sielaff et al. 2019). *Aspergillus fumigatus*, an opportunistic fungal threat to human health, was also found on ISS surfaces (Checinska Sielaff et al. 2019), raising concerns about the potential health impact on astronauts. Even though comparative genomics of *A. fumigatus* ISS isolates and clinical Earth strains revealed no significant differences, the former demonstrated enhanced lethality in a vertebrate model, implying higher virulence in space environments (Knox et al. 2016).

Satoh et al. (2021) analysed the fungal diversity at the Japanese Experiment Module KIBO (ISS; experiments Microbe-I, II, III, and IV) over a period of seven years. They found *Aspergillus* and *Penicillium* to be the dominant genera when using culture-dependent methods, and *Malassezia* (a monophyletic genus commonly found on human skin) when using DNA analysis. From those strains, they studied the species *Aspergillus sydowii*, *Penicillium palitans*, and *R. mucilaginosa*, which grew in the microgravity environment of KIBO, and they found no novel phenotypic characteristics or significant differences in antifungal susceptibility from prior reports of the corresponding fungi.

2.2.1 Fungal contamination sources, monitoring, and control

Space stations provide useful case studies on sources of fungal contamination, monitoring, and control. The main reason for the transmission of diseases related to filamentous fungi and, moreover, for the accumulation of fungal contaminants on touch surfaces and building materials at the ISS is the human-carried contamination (Venkateswaran et al. 2014a, Mora et al. 2016b). In addition to this factor, food and plants are other well-established sources of fungal contamination, particularly in aerosols (Haines et al. 2019)

In space habitats, the relative air humidity of the cabin environment is kept at about 60% (three times higher than in regular aircrafts), which facilitates fungal growth. Other factors inside the ISS enhance the development of fungi: air ventilation, water circulation, and oxygen and nitrogen distribution, all of which run as closed systems. Once a fungal colony colonises life-support systems, decontamination and sterilisation are highly challenging, especially since microgravity facilitates fungal spores' dispersal. Therefore, moisture control, ventilation, and air filtration systems with HEPA filters serve as countermeasures against air pollution in aircraft and spacecraft. According to the International Air Transport Association (IATA), HEPA filters are used as recirculation filters and can effectively capture 99 % of the airborne microbes in the filtered air. However, some studies have reported limitations of these filtration systems, suggesting that they can become point sources of contamination (since fungi were detected growing inside HEPA filters in use at the ISS) and highlighting the need for regular and continuous environmental monitoring (Price et al. 2005, Vesper et al. 2008).

Efforts to prevent microbial growth inside the ISS are directed towards reducing moisture and free water. Moreover, astronauts are forced to regularly decontaminate commonly touched surfaces and wet areas (such as toilet surfaces) (Vesper et al. 2008, Yamaguchi et al. 2014), combined with weekly cleaning with a vacuum cleaner and antiseptic towelettes containing 0.4% benzalkonium chloride (Satoh et al. 2021). Unfortunately, some common and effective disinfectants used in terrestrial indoor environments are not an option. One prime example is hydrogen peroxide (used as a liquid or as vapour), a chemical that cannot be freely used in space as it could form dangerous droplets that could disperse throughout the spacecraft, due to microgravity. To guarantee the maintenance of water and air quality at the ISS, the following measures are put in place: supplementation of water with iodide or ionic silver compounds, and HEPA filters as an integral part of all air distribution systems (Satoh et al. 2021). As recently stated by the World Health Organization (2018) and several other studies (e.g., Ottoni et al. 2017, da Silva et al. 2022, Khan et al. 2022), using silver as a disinfectant for drinking water is a preventative approach that can minimise microbial development.

Another risk associated with fungal contaminants is the production of certain harmful compounds. This was noted early on, as studies have found that the high concentration of airborne fungi on Mir (which fluctuated between 2 x 10^4 and 5 x 10^4 CFU/m^3; Novikova 2004) were

associated with high levels of detectable mycotoxins (ochratoxin A – OTA) (De Middeleer et al. 2019). Strategies to control fungal exposure in space are specifically stated in the ISS medical operations requirements document (ISS MORD SSP 50260, https://emits.sso.esa.int/emits-doc/ESTEC/AO6216-SoW-RD9.pdf). State-of-the-art strategies to control and monitor fungal and mycotoxin exposure in space habitats are almost exclusively directed towards risk assessment and risk management of mycotoxins within the environment.

The main methods used for monitoring fungal agents inside enclosed space habitats are similar to those used in terrestrial environmental settings. Microbial detection is conventionally done through culture-dependent methods, usually through surface swabs for sample collection (Van Houdt et al. 2012). In addition to swabbing surfaces, sampling can also involve the collection of air with an air sampler. Culture-independent methods have become more relevant due to the growing awareness of mycotoxins and fungal products like volatile organic compounds (VOCs), which are low-molecular-weight organic compounds that easily evaporate at room temperature (Pennerman et al. 2016, Inamdar et al. 2020). Furthermore, as culture-dependent methods are time-consuming and unable to detect low microbial contamination levels, culture-independent molecular methods are more adequate for spaceflight and aviation because they facilitate rapid analysis and allow for consistent and frequent screening. However, regular screenings have not been reported for all types of detection, e.g., mycotoxin levels on the ISS or in aircrafts, as part of systematic air quality controls.

Spaceflight is known to enhance microbial proliferation, activity, and virulence (Benoit & Klaus 2007, Rosenzweig et al. 2010, Taylor 2015), and there is ample evidence that increased biomass and biofilm thickness are generated under microgravity conditions (Crabbé et al. 2013, Sathishkumar et al. 2016, Wang et al. 2021). Not only are highly proliferating microorganisms more difficult to keep at bay, even under strict cleaning protocols, but spacecraft-associated species can also be resistant to antimicrobial agents and have the potential to degrade spacecraft cleaning reagents (Mogul et al. 2018).

2.3 Fungi exposed to space

Fungi have been exposed to space under several different circumstances, including real space conditions (Section 2.3.1), as well as simulated conditions for single or multiple parameters, similar to those found in real space (Section 2.3.2).

Several types of environmental extremes are considered relevant for exposure experiments and have been the subject of a range of targeted experiments aimed at assessing different microbial groups and relevant conditions in different parts of the solar system (e.g., Wu et al. 2022). Such testing has traditionally been split into experiments conducted in orbit and under simulated conditions in ground-based experiments. These started with balloon experiments with fungal spores around 1935s, rocket experiments in the 1950s and 1960s, satellite and moon expeditions, and long-time orbit experiments followed by space missions in the 1980s and 1990s (Kern & Hock 1993).

2.3.1 Exposure experiments to real space conditions

Radiation and oxidant species are considered major challenges to the search for life beyond Earth. The Earth's magnetic field and its atmosphere protect the terrestrial surface, but the space environment and the surfaces of other planets in our solar system are reached by various types of radiation. High-energy electromagnetic waves from our sun (UV, gamma, and X-rays) and subatomic particles from the universe characterise the radiation environment (electrons, protons, neutrons, and heavy ions). A heavily ionising core and a penumbra where energy is transferred by far-reaching secondary electrons can be found in high-energy radiation (Baltschukat et al. 1986). When this energy collides with microorganisms or biomolecules, it can cause cellular damage by generating direct energy absorption effects on biomolecules (such as nucleic acids and proteins) and secondary effects from radiation-induced radicals (radiolysis) (Moeller et al. 2010). Numerous studies have been done and are still being done under specific conditions, such as microgravity, galactic cosmic radiation, solar UV radiation, and space vacuum, to better understand the survival

or development of life in space (Horneck et al. 2010). These were analysed in both real and simulated laboratory settings.

Regarding fungal characteristics that allow them to survive such exposure testing, we highlight a few examples. The ability of melanin-producing fungi (i.e., from the genera *Aspergillus*, *Penicillium*, and *Cryomyces*) to survive the vacuum of space and Mars-simulated conditions in low Earth orbit (LEO) has been associated in part with the protective effects of melanin (Horneck et al. 1999, Panitz et al. 2001, Onofri et al. 2012, 2015, 2019, Pacelli et al. 2019, Cortesão et al. 2020a). The importance of melanins in fungal resilience to exposure experiments is worth stressing and is further discussed in Section 2.3.4.

In addition to melanin, it has been proven that filamentous fungi and yeasts possess complex regulatory networks and molecular processes that ensure a sophisticated DNA damage repair system, based on nucleotide excision (NER), mismatch repair (MMR), and the mechanism of homologous recombination (HR). In this process, a defective site is cut out of the DNA by enzymes (recombinases) and repaired. In non-homologous end joining (NHEJ), the two fragments are rejoined after a DNA double-strand break without a homologous DNA sequence acting as a template (Sinha & Häder 2002).

Spacecraft, space stations, and shuttles have closed environments that allow for many different mycological experiments and have been used for these scopes (summarised in Table 1). Understandably, such experiments with exposure to real space conditions are somewhat limited and conducted in small numbers. Not all researchers have access to space facilities or outer space environments, and concerns regarding biological load are always too wide-scoped and rarely focused on fungi. Although this perspective is now changing, there are still clear gaps in coverage that need to be addressed.

So far, there are only reports of two fungal species belonging to the phylum Basidiomycota being exposed to space conditions. Furthermore, within the phylum Ascomycota, studies tend to focus on a limited number of species, with most studies focusing on the genera *Cryomyces*, *Aspergillus*, and *Penicillium*.

2.3.2 Studies using ground-based simulations

Space conditions can be simulated in laboratory settings. These are a more accessible way of assessing fungal adaptations to space-like conditions and are thus better studied (Table 2).

It is clear that environmental stress can affect fungal strains' growth and survival, and that the space environment can favour the growth of some fungal species. However, the number of fungal species tested is still very limited, with almost all strains analysed belonging to the phylum Ascomycota. Among all species, only three yeasts were studied: *C. albicans*, for being a common human-pathogen; *Saccharomyces cerevisiae*, for being a well-known and researched budding yeast species; and *Debaryomyces hansenii*, for being a well-known halotolerant yeast. More tests are necessary; different species need to be analysed, especially now that there is a boom in planning for long-term missions.

2.3.3 *Cryomyces antarcticus* – a detailed case-study of fungal survival under real and simulated space exposure

One noteworthy fungal species regarding exposure experiments and fungal resilience is *Cryomyces antarcticus*. This cryptoendolithic endemic black fungus, first isolated from sandstone collected at Linnaeus Terrace, McMurdo Dry Valleys, Southern Victoria Land (Antarctica), has been selected for several space exposure experiments. Taking advantage of the possibility to allocate samples outside the ISS by the European Space Agency (ESA) exposure facility EXPOSE, the fungus was exposed to real space conditions in LEO, in two ESA experiments: LIchen and Fungi Experiment (LIFE, Scalzi et al. 2012) and BIOlogy and Mars EXperiment (BIOMEX, de Vera et al. 2019), detailed in Table 3.

Table 1 Mycological experiments under real space conditions.

Fungi			Space condition	Exposure details	Effects observed	References
Phylum	**Class**	**Species**				
Ascomycota	**Dothideomycetes**	***Cryomyces antarcticus***	Microgravity, Radiation, simulated Mars conditions, Mars artificial regoliths	Dried colonies outside the ISS (EXPOSE-E, EXPOSE-R2)	12% survival to full outer space exposure, including cold, ionising and UV radiation up to 900 kJ. Growth on phyllosilicatic (78% of the samples) and sulfatic (40% of the samples) Mars artificial regoliths. Survival under Mars simulated atmosphere and radiation.	de Vera et al. (2019), Onofri et al. (2012, 2015, 2019)
			Microgravity, Radiation, simulated Mars conditions, Mars and lunar artificial regoliths	Dried colonies outside the ISS (EXPOSE-R2)	Preservation of DNA and melanin – still detectable after exposure (can be used as biosignatures).	Pacelli et al. (2021a), Cassaro et al. (2022a, b)
		Cryomyces minteri	Microgravity, Radiation	Dried colonies, outside the ISS (EXPOSE-E)	Extensive DNA mutations after 1.5-year exposure.	Onofri et al. (2018)
		Ulocladium chartarum	Microgravity, Radiation	ISS (Solid media)	Formation of microcolonies, changes in colony growth, but no changes in spore viability.	Gomoiu et al. (2013, 2016)
	Eurotiomycetes	***Aspergillus fumigatus***	Microgravity, Radiation	ISS isolate	Enhanced growth and increased virulence.	Knox et al. (2016)
			Microgravity, Radiation	ISS isolate	Increased abundance of proteins involved in stress responses, carbohydrate and secondary metabolism.	Blachowicz et al. (2019a)
		Aspergillus nidulans	Microgravity, Radiation	ISS	Changes in stress response and secondary metabolites.	Romsdahl et al. (2019)

Table 1 Continued.

Fungi			Space condition	Exposure details	Effects observed	References
Phylum	**Class**	**Species**				
		Aspergillus niger	Microgravity, Radiation	ISS isolate	Enhanced production of naphtho-γ-pyrones and secondary metabolites (bicoumanigrin A, aurasperones A and B, and pyranonigrin A).	Romsdahl et al. (2020)
			Microgravity, Radiation	ISS	No changes in spore viability.	Gomoiu et al. (2013)
		Penicillium expansum	Microgravity, Radiation	Outside the ISS	Increase of polysaccharide capsule and melanin layer.	Dadachova & Casadevall (2008)
		Penicillium rubens (formerly *P. chrysogenum*)	Microgravity, Radiation	Outside the ISS	No changes in morphology or antifungal susceptibility.	Satoh et al. (2016)
			Microgravity	Biofilms in several surface materials, ISS	No changes in the shape of biofilms, on the biomass growth, thickness, and surface area coverage in stainless steel 316, aluminum alloy, titanium alloy, carbon Fiber, quartz, silicone, and nanograss.	Hupka et al. (2023)
	Saccharomycetes	***Saccharomyces cerevisiae***	Microgravity, Radiation	Soyus and ISS	Up-regulation of proteins linked to anaerobic conditions. Random budding patterns. Reduced invasive growth.	Van Mulders et al. (2011)
	Sordariomycetes	***Fusarium oxysporum***	Microgravity, Radiation	ISS isolate	Higher abundance of PKS domains.	Urbaniak et al. (2019)
		Sordaria macrospora	Microgravity	Space Shuttle and Mir	No changes in crossing-over frequencies under microgravity. Increased gene recombination frequencies under heavy ion radiation.	Hahn & Hock (1999)

Table 1 Continued.

Fungi			Space condition	Exposure details	Effects observed	References
Phylum	**Class**	**Species**				
Basidiomycota	**Agaricomycetes**	***Polyporus brumalis***	Microgravity	Orbital space flight aboard the uncrewed Soviet biosputnik	After 20 days aboard, the fruiting body presented negative gravitropism.	Zharikova et al. (1977)
		Flammulina velutipes	Microgravity	D-2 mission, Space Shuttle Columbia	Grown in space for 8 days. Gravimorphogenesis of developing fruiting body with random orientation (flat and helically twisted stipes), with an accumulation of cytosolic vesicles at the lower part of the stipe.	Kern & Hock (1996)
	Tremellomycetes	***Cryptococcus neoformans***	Microgravity, Radiation, space flight general conditions	ISS	Melanized yeasts survived 50% more than non-melanized yeasts following roundtrip and 29 days inside the ISS.	Cordero et al. (2022)

ISS = International Space Station, DNA = deoxyribonucleic acid, PKS = polyketide synthase, UV = Ultraviolet Radiation.

Table 2 Mycological experiments under simulated space conditions.

Fungi			Space condition	Exposure format	Effects observed	References
Phylum	**Class**	**Species**				
Ascomycota	**Dothideomycetes**	***Alternaria alternata***	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 2.409 kGy, Electron beam LD_{90} = 1.099 kGy.	Blank & Corrigan (1995)
		Cryomyces antarcticus	Microgravity, Radiation, simulated Mars conditions, Mars and lunar regoliths	EXPOSE-E, EXPOSE-R2	12 % survival to full outer space, including cold, ionizing and UV radiation up to 900 kJ. Nucleic acids, melanin, and dicarboxylic acids stability after exposure.	de Vera et al. (2019), Onofri et al. (2008), Pacelli et al. (2017c, 2019), Cassaro et al. (2022b)

Table 2 Continued.

Fungi			Space condition	Exposure format	Effects observed	References
Phylum	**Class**	**Species**				
			Gamma rays, He-ions, X-rays, UVB radiation	Dried colonies	12% of survival at 56 kGy of gamma rays, survival up to 1000 Gy of He ions, survival up to 0.3 Gy of X-rays, and survival up to 240 hours of UVB irradiation. Nucleic acids and melanin stability after gamma rays exposure.	Pacelli et al. (2017a, b, c), Selbmann et al. (2011), Cassaro et al. (2022c)
			Cosmic rays (He- and, Fe-ions), Mars artificial regoliths	Dried colonies	Survival up to 1 kGy, preservation of DNA and melanin – still detectable after exposure (biosignatures).	Pacelli et al. (2020a), Aureli et al. (2020)
			Cosmic rays (Fe-ions)	Liquid culture	Survival up to 2000 Gy.	Pacelli et al. (2021b)
			Simulated radiation, Simulated Mars conditions, Mars and lunar regoliths	Dried colonies	Good viability, higher under Mars conditions than in space conditions. DNA preservation only slightly affected by radiation.	Pacelli et al. (2017c, 2019), Cassaro et al. (2021b, 2022b), Gevi et al. (2022)
			Martian relevant perchlorates	Agar culture	Good viability up to 220 mM of Na-,145 mM of Mg-, 200 mM of Ca-, and 90 mM of K-perchlorates	Cassaro et al. (2022d)
		Curvularia geniculata	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 1.798 kGy, Electron beam LD_{90} = 1.193 kGy.	Blank & Corrigan (1995)
	Eurotiomycetes	***Aspergillus carbonarius***	Microgravity (Clinostat, 20 rpm)	Solid media	No effect on cell or colony growth, but increased organic acid production.	Jiang et al. (2019)
		Aspergillus echinulatus	Ionizing radiation (Gamma and	Spore suspensions	Gamma radiation LD_{90} = 0.319 kGy, Electron beam	Blank & Corrigan (1995)

Table 2 Continued.

Fungi			Space condition	Exposure format	Effects observed	References
Phylum	**Class**	**Species**				
		(synonym: *Eurotium echinulatum*)	electron beam)		LD_{90} = 0.241 kGy.	
		Aspergillus fumigatus	UVB	Spore suspensions	1.62 CPDs per 10 kb at a dose of 5400 J/m^2.	Nascimento et al. (2010)
			Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.276 kGy, Electron beam LD_{90} = 0.198 kGy.	Blank & Corrigan (1995)
			Mars, UVC (MSC)	ISS isolate, dried spores	Survived Mars-like conditions for 30 min. 20 % spore survival at 4000 J/m^2.	Blachowicz et al. (2019b)
		Aspergillus glaucus	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.250 kGy, Electron beam LD_{90} = 0.243 kGy.	Blank & Corrigan (1995)
		Aspergillus nidulans	UVB	Spore suspensions	0.04 CPDs per 10 kb at a dose of 900 J/m^2.	Nascimento et al. (2010)
		Aspergillus niger	Microgravity (HARV)	Liquid culture	No changes in stress response.	Sathishkumar et al. (2014)
			Microgravity	Solid media	No differences in morphology, growth, asexual development or antifungal susceptibility.	Yamazaki et al. (2012)
			Microgravity (Clinostat, 60 rpm)	Solid Media	General increase in colony area, spore production, and biofilm (vegetative mycelium) thickness	Cortesão et al. (2022)
			Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.245 kGy, Electron beam LD_{90} = 0.199 kGy.	Blank & Corrigan (1995)
			UVB radiation	Dried spores	24% survival up to 1.6 kJ/m^2.	Silverman et al. (1967)

Table 2 Continued.

Fungi			Space condition	Exposure format	Effects observed	References
Phylum	**Class**	**Species**				
			UVC, X-rays, Cosmic Rays: He- and Fe-ions	Dried spores and spores suspensions	UVC LD_{90} = 1038 J/m2, X-ray LD_{90} = 360 Gy. Spores dried before irradiation were more susceptible to X-ray radiation. He-ion LD_{90} = 500 Gy, Fe-ion LD_{90} = 100 Gy.	Cortesão et al. (2021)
			Mars (Trex box + Balloon flight)	Dried Spores	Survival of spore monolayer after 5-month desiccation under Mars simulated atmosphere, temperature fluctuation ([-51 °C, 21 °C]), and exposure to 1148 kJ m^{-2} UVA-UVB radiation.	Cortesão et al. (2021)
		Aspergillus ochraceus	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.209 kGy, Electron beam LD_{90} = 0.198 kGy.	Blank & Corrigan (1995)
		Aspergillus versicolor	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.282 kGy, Electron beam LD_{90} = 0.234 kGy.	Blank & Corrigan (1995)
		Knufia chersonesos	Microgravity (HARV)	Liquid culture	No changes in morphology. Upregulation of enzymes involved in the synthesis of (DHN) melanin.	Tesei et al. (2021)
		Penicillium aurantiogriseum	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.236 kGy, Electron beam LD_{90} = 0.194 kGy.	Blank & Corrigan (1995)
		Penicillium cyclopium	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.397 kGy, Electron beam LD_{90} = 0.290 kGy.	Blank & Corrigan (1995)
		Penicillium granulatum	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.416 kGy, Electron beam LD_{90} = 0.341 kGy.	Blank & Corrigan (1995)

Table 2 Continued.

Fungi			Space condition	Exposure format	Effects observed	References
Phylum	**Class**	**Species**				
		Penicillium roqueforti	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.397 kGy, Electron beam LD_{90} = 0.290 kGy.	Blank & Corrigan (1995)
		Penicillium rubens (formerly *P. chrysogenum*)	Microgravity (HARV)	Liquid culture	Changes in cell wall; increased expression of Acyl-coenzyme: isopenicillin N acyltransferase.	Sathishkumar et al. (2016)
			Microgravity (HARV)	Liquid culture	The number of mitochondria increased.	Sathishkumar et al. (2014)
		Penicillium verrucosum	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.266 kGy, Electron beam LD_{90} = 0.208 kGy.	Blank & Corrigan (1995)
		Penicillium viridicatum	Ionizing radiation (Gamma and electron beam)	Spore suspensions	Gamma radiation LD_{90} = 0.333 kGy, Electron beam LD_{90} = 0.265 kGy.	Blank & Corrigan (1995)
	Saccharomycetes	***Candida albicans***	Microgravity (HARV)	Liquid culture	Random budding phenotype occurred. Cells showing random budding were often found in clusters composed of a variety of morphologic forms, including filamentous form.	Altenburg et al. (2008)
		Debaryomyces hansenii	Liquid perchlorate brines from Mars. Sodium perchlorate (2.4 M $NaClO_4$)	Liquid culture	Presented the highest microbial perchlorate tolerance reported so far.	Heinz et al. (2020)
		Saccharomyces cerevisiae	Microgravity (HARV)	Liquid culture	Random and abnormal budding phenotype. Increased number of cells in clumps or aggregates. Increase in gene	Purevdorj-Gage et al. (2006)

Table 2 Continued.

Fungi			Space condition	Exposure format	Effects observed	References
Phylum	**Class**	**Species**				
					expression of HWP1 and decrease of YWP1.	
			Gamma radiation, freezing (-79°C)	Desiccated cells	Survival limit increased from 10 kGy to 24 kGy after desiccation and freezing.	Horne et al. (2022)
		Neurospora crassa	X-rays Cosmic Rays	Commercial radiation sources	NHEJ-deficiency led to differences in survival between X-ray and heavy ions (Ar and Fe).	Ma et al. (2018)
	Sordariomycetes	***Purpureocillium lilacinum***	Liquid perchlorate brines from Mars (1.1 M $NaClO_4$)	Liquid culture	Has the second-highest microbial perchlorate tolerance reported so far.	Heinz et al. (2020)
		Sordaria macrospora	Microgravity (Clinostat, 4 rpm)	Solid media	Changes in crossover.	Henkel & Hock (1991)
Basidiomycota	**Agaricomycetes**	***Coprinus cinereus***	Microgravity (Clinostat)	Solid media	Gravimorphogenesis observed, with longer stems and bending.	Moore et al. (1996)
		Flammulina velutipes	Hypergravity (1 and 20G), Microgravity (1 and 2 rpm) during D-2 mission	Solid media	Gravimorphogenesis. Gravistimulation, differential accumulation of vesicles (vacuole enlargement) inside the transition zone hyphae at the lower side of horizontally oriented stipes. Fruiting bodies grow with different directions.	Kern & Hock (1996), Moore et al. (1996)

CPDs = cyclobutane pyrimidine dimers, DHN = 1,8-dihydroxynaphthalene, DNA = deoxyribonucleic acid, HARV = high aspect ratio vessel, HWP1 = hyphal wall protein 1 gene, ISS = International Space Station, LD_{90} = dose at which there is 90% spore inactivation, MSC = Mars simulation chamber, NHEJ = nonhomologous end-joining, rpm = revolutions per minute, UV = ultraviolet radiation, YWP1 = yeast wall protein 1 gene.

Table 3 European Space Agency (ESA) experimental work exposing *Cryomyces antarcticus* to low Earth orbit (LEO).

The LIFE experiment

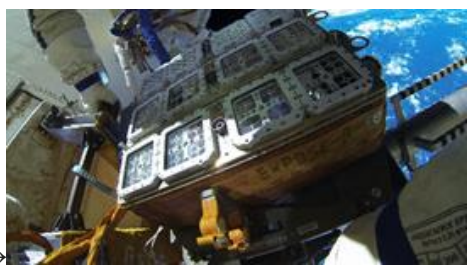
Aimed to investigate the resistance of *C. antarcticus* to space and Martian simulated conditions in space after 1.5 years of ISS external exposure. During the experiment, dried fungal colonies, accommodated in wells (1.4 cm in diameter), were either exposed to space environment (vacuum from 10^{-7} to 10^{-4} Pa, fluctuations of temperature between -21.5 and +59.6 °C, cosmic ionising radiation up to 190 mGy, and solar extra-terrestrial electromagnetic radiation up to $6.34\times10^{8}Jm^{-2}$) or shielded from insolation. The sun-exposed LIFE samples were exposed to 1,879 eSCh (estimated Solar Constant hours) (Rabbow et al. 2012). The samples were also kept in simulated Mars atmosphere (1.6% Ar, 0.15% O_2, 2.7% N_2, 370 ppm H_2O, in CO_2), pressure (10^3 Pa), and UV radiation, cutting-off the spectrum of solar extra-terrestrial electromagnetic radiation at a wavelength of $\lambda = 200$ nm (using quartz filters). Some samples were screened with neutral density filters, with fluencies of $9.19\times10^{5}Jm^{-2}$, below a 0.1% transmission, to reduce insolation irradiance by three orders of magnitude. In addition, dark flight samples were allocated beneath the insulated ones. After 1.5 years in space, fungal cells were tested for: survivability, DNA stability, and cell-membranes and cellular ultrastructure integrity. *Cryomyces antarcticus* lost colony-forming ability after exposure to full insolation (λ >110 nm, 100% insulated samples), but the percentage of culturable cells was still 12.5% (±4.11) when 0.1% insulated (Table 1, Onofri et al. 2012). Under Mars conditions simulated in space (100% solar electromagnetic radiation at λ >200 nm), the viability of the dehydrated cells was 0.8% (±0.18) (Table 1, Onofri et al. 2015).

← Expose-E facility (courtesy of ESA).

The BIOMEX experiment

Aimed at investigating the survival of selected extremophiles as well as the stability/degradation of their biological components (pigments, cell wall components, etc.) (de Vera et al. 2012, 2019), to be proposed as biomarkers for searching for life on Mars. In this frame, the black fungus *C. antarcticus* was grown on lunar regolith analogue like anorthosite, and on two Mars regolith analogue mixtures, Phyllosilicatic Mars Regolith Simulant (P-MRS, igneous rocks) and Sulfatic Mars Regolith Simulant (S-MRS, analogue for a more acidic environment with sulphate deposits), to study its resistance in space. After 531 days in space, samples were investigated on Earth to analyse fungal growth, resistance, and the resilience of its biomolecules, to be accounted for as biomarkers (Pacelli et al. 2021a, Baqué et al. 2022, Cassaro et al. 2022a). Survival and metabolic activity recovery were reported for *C. antarcticus* colonies regardless of the substratum, with no detectable DNA or cell-membrane damages (Table 1, Onofri et al. 2019). The percentage of culturable cells was 78% and 40% for samples grown on P-MRS and S-MRS, respectively (Onofri et al. 2019). Overall, these findings support the hypothesis that desiccation-tolerant life forms could survive for long periods of time in protected niches on Mars. The stability of fungal biomolecules, namely melanin, in space and under simulated Martian conditions was further investigated using Raman spectroscopy, a technique planned for the upcoming ESA ExoMars mission (Vago et al. 2017). Melanin pigment present in the fungal cell-walls was identified as stable and detectable, even after space exposure (Table 1, Pacelli et al. 2021a, Cassaro et al. 2022a, b).

EXPOSE-R2 facility (courtesy of ESA). →



Preliminary ground-based experiments evaluating *C. antarcticus* resistance under different space stressors were performed for the LIFE project (Table 3). This fungus was exposed to two sets of Experiment Verification Tests (EVT), in order to assess its responses to: i) simulated space conditions: vacuum, temperature fluctuations (-20 / +20 °C), monochromatic UVC radiation, and high polychromatic UV radiation; and, ii) simulated CO_2 Martian atmosphere and pressure, simulated space vacuum combined with polychromatic UV radiation, and simulated CO_2 Martian atmosphere combined with polychromatic UV radiation, respectively (Onofri et al. 2008). *Cryomyces antarcticus* was the most negatively affected when compared to other black fungi species, despite having a good growth ability after exposure to simulated space and Mars conditions (Onofri et al. 2008). Samples were also subjected to temperature cycles at different time intervals, and a surprising high viability of growing colonies was recorded after exposure to 80 and 90 °C for 60 minutes (Onofri et al. 2008; Table 2).

In the frame of the BIOMEX project (Table 3), *C. antarcticus* was exposed to two series of ground-based experiments, including the EVTs and the Science Verification Tests (SVTs, Rabbow et al. 2015) carried out before the space exposure. Particularly, EVTs simulated individual space conditions, while SVTs were performed within the same exposure platform used aboard the ISS (EXPOSE-R2), and simultaneously simulated all the environmental stresses expected in the LEO exposure. In these experiments, de-hydrated colonies of *C. antarcticus* were exposed to simulated Martian and space conditions after being grown on sandstone, where it naturally occurs, as well as on Martian and lunar regolith analogues (de Vera et al. 2012, 2019; Table 2). During the EVTs, *C. antarcticus* colonies were exposed to increasing doses of UV irradiation, simulating the whole Solar UV spectrum expected in LEO for the duration of the mission (up to 16 months). Firstly, samples were analysed through culture methods in order to evaluate their survival in terms of colony forming ability, and a high count was detected even after vacuum or Martian atmosphere coupled with irradiation. These results were further confirmed by the investigation of cellular membrane integrity (PMA- quantitative polymerase chain reaction – qPCR assay) and ultrastructural damages (Transmission electron microscopy – TEM). While a high percentage of survivors was detected for *C. antarcticus* colonies grown on Martian artificial regolith and exposed to SVTs treatments.

Cryomyces antarcticus had already shown capacity to retain colony forming ability and DNA integrity after ultraviolet B (UVB) exposure at doses lethal to *Saccharomyces pastorianus* (Onofri et al. 2007, Selbmann et al. 2011; Table 2). As part of the STARLIFE irradiation campaign (Moeller et al. 2017), which focused on the exposure of selected extremophilic organisms to different types of ionising radiation (x-rays, gamma-rays, heavy ions), representing part of the galactic cosmic radiation spectrum, *C. antarcticus* was exposed to gamma rays (up to 117.07 kGy), alpha particles (helium nuclei, up to 1000 Gy), and heavy ions (iron-ions, up to 1000 Gy) (Table 2). The aim of these studies was to evaluate the resistance of dehydrated colonies to photon and ion radiations that differ in their linear energy transfer (LET) values. Surprisingly, *C. antarcticus* demonstrated remarkable DNA integrity after exposure at 117 kGy of gamma radiation, which corresponds to 1.5 million years' exposure on the Martian surface and 13 million years at 2-meters beneath the surface (Hassler et al. 2014). Results reported in Pacelli et al. (2017b) clearly indicated a very high resistance to gamma radiation, with a 12% survival rate recorded even at the dose of 55.81 kGy (Table 2). Also, a good stability of nucleic acids and melanin pigments was reported up to the dose of 117.07 kGy (Cassaro et al. 2022c).

The biological effect of increasing helium-ions radiation (up to 1000 Gy) was assessed by different molecular tests, demonstrating the maintenance of high survival and metabolic activity even after the highest dose (Pacelli et al. 2017d). Similar results were reported for fungal colonies mixed with a phyllosilicatic Mars regolith simulant (up to 1000 Gy, 6% of survivors) (Pacelli et al. 2020a).

Given the high vitality reported with no evidence of DNA damage, the focus was directed to melanin pigments as radiation photoprotection, by comparing the resistance of melanized and non-melanized *C. antarcticus* strains. After demelanization, fungal colonies were treated with densely

ionising deuterons (^{2}H, up to 1500 Gy) and sparsely ionising X-rays (up to 300 Gy) in physiological conditions, and the effects were measured using cell viability colorimetric assays (XTT, and MTT) and ATP levels. Both melanized and non-melanized cells survived acute ionising radiation doses, with melanized cells being more resistant (Pacelli et al. 2017a, b; Table 2). It was recently discovered that *C. antarcticus* can produce both 1,8-dihydroxynaphthalene (DHN) and L 3-4 dihydroxyphenylalanine (L-DOPA) melanins (Pacelli et al. 2020b). In addition, the resistance of the black fungus to heavy ions was recently reported (Aureli et al. 2020, Pacelli et al. 2020a) (Table 2). *Cryomyces antarcticus* colonies were able to reactivate and grow after 1000 Gy of Fe-ions exposure, alone or in combination with two Martian artificial regoliths (phyllosilicatic and sulfatic, Aureli et al. 2020). According to these results, *C. antarcticus* showed a stunning ability to survive up to 1000 Gy of Fe-ions, when exposed in metabolically active conditions (Pacelli et al. 2021b) (Table 2).

Since radiation is not the only stressor encountered in space or on the surfaces of extraterrestrial planets, the fungus was also tested for its resistance against perchlorate species as a part of the Italian "Life in Space" project (Onofri et al. 2020). The project was funded by the Italian Space Agency (ASI), in the wake of the proposal for the development of a network of institutions and laboratories conceived to implement Italian participation in space astrobiology experiments. One of the project's primary goals was to investigate the origin and evolution of life in the universe, spanning from prebiotic chemistry to astrobiology and astrophysics (Onofri et al. 2020).

Perchlorate ions are known to damage the main functions of terrestrial living organisms, they break off a number of metabolic processes, and also act as oxidising agents causing cell membrane damage (Urbansky 1998). Although these compounds are rarely seen on Earth, high concentrations have been detected in several locations on Mars. The fungus demonstrated the ability to withstand up to 220 mM of Na-, 200 mM of Ca-, 145 mM of Mg- and 90 mM of K-perchlorates, and 0.4-0.6 wt% of $Mg(ClO_4)_2$ and $Ca(ClO_4)_2$, concentrations similar to those found on Mars by the Phoenix lander (Cassaro et al. 2022b,d; Table 2). Also, a considerable metabolic activity was detected even at higher perchlorate concentrations, while ultrastructural investigations reported scarcely distinguishable internal structures (Cassaro et al. 2022d). This study provides, for the first time, insights about the resistance of the black fungus *C. antarcticus* to different perchlorate species that might have implications on habitability in other planetary bodies.

Furthermore, during the BIOMEX project mentioned in Table 3, the stability of fungal biomolecules was investigated using techniques similar to those included in the Perseverance and Rosalind Franklin rovers (Raman and Fourier transform infrared – FTIR spectroscopies and Gas Chromatography-Mass Spectrometry – GCMS). In addition, PCR and qPCR techniques were applied to detect any damages in nucleic acids, suggesting their potential use as life-detection instruments in new-generation rovers. Indeed, nucleic acids may be considered a potential biomarker of life, despite their high sensitivity to degradation, as good amplification was recorded even at the high dose of 5.5×10^5 kJ/m^2 of EVT treatments (Pacelli et al. 2020a; Table 2). Compared to EVT treatments, SVT samples showed a decrease in copy numbers amplification, even if no noticeable damages were reported (Cassaro et al. 2021b). Since one of the main goals of the ongoing and future space exploration missions is the detection of extant or recently extinct signs of life, the studies concerning the stability of terrestrial biomolecules after exposure to space stressors are critical.

2.3.4 Relevance of melanins for space exposure

Melanins are a class of multifunctional and acid-resistant pigments (or biochromes) that are widely known for their protective properties (Malo et al. 2019). In the fungal kingdom, we can observe different types of melanin, as well as numerous examples of how these biochromes protect fungal organisms against a plethora of abiotic and biotic stressors (Cordero & Casadevall 2017). From an abiotic perspective, they are associated with protection against different types of ionising radiation (Wang & Casadevall 1994a, Robertson et al. 2012, Shuryak et al. 2015, Pacelli et al. 2017a, c, Cortesão et al. 2020a), oxidative stress (Jacobson & Tinnell 1993, Wang & Casadevall

1994b, Jahn et al. 2000), heat/cold stress (Rehnstrom & Free 1996, Rosas & Casadevall 1997, Paolo et al. 2006), osmotic stress (Kogej et al. 2007, Fernandez & Koide 2013, Kejžar et al. 2013), toxic metals (García-Rivera & Casadevall 2001) and antimicrobial organic compounds (Wang & Casadevall 1996, van Duin et al. 2002, Nosanchuk et al. 2004). In terms of biotic stressors, fungal pathogens of animals and plants are known to use melanin to aid during infection and resist host-immune defence mechanisms, making melanin an important virulence factor and antifungal drug target (Nimrichter et al. 2005, Černoša et al. 2021).

Beyond protection, fungal melanin serves as an energy-harvesting biological pigment, absorbing electromagnetic radiation with conversion into thermal energy (Cordero et al. 2018) and/or chemical energy associated with enhanced fungal growth and metabolic activity (Dadachova et al. 2007, Robertson et al. 2012). Considering all the examples in which melanin protects against different stressors, it makes sense that melanin would play a role in the ability of fungal organisms to survive space environmental conditions.

A direct link between melanin and protection against spaceflight conditions was recently demonstrated. This was achieved by comparing the viability of melanized and non-melanized clones of *Cryptococcus neoformans* cells after a roundtrip to the ISS and spending 29 days inside the Japanese Experimental Module (Cordero et al. 2022). Following the 29 days, colony-forming unit (CFU) analysis showed that, while Earth-bound control samples exhibited similar viability, ISS-bound melanized cells exhibited 50% higher viability than non-melanized clones (Cordero et al. 2022). The higher viability of melanized cells following spaceflight is consistent with the known protective properties of melanin. In addition to protection, melanin may also confer a growth advantage under spaceflight conditions related to its energy-harvesting properties (Dadachova et al. 2007, Cordero et al. 2018).

Since spaceflight conditions comprise a combination of stressors such as radiation, low gravity, temperature shocks, and hypervelocity, identifying which specific properties of melanin are important for viability in space, as well as specific mechanisms of melanin-mediated survival, would require the analysis of such spaceflight stressors, individually, and in combinations, using real and/or simulated conditions. The conclusion that melanin can protect fungi from spaceflight effects suggests that biological melanization and/or melanin-containing products could eventually be exploited as a strategy to protect and increase the lifespan of biological assets in space (Section 2.4).

It is also worth noting that the detectability of melanin pigments, even in the presence of a multitude of biomolecules and their discernibility from amorphous carbon spectra, has been demonstrated (Cassaro et al. 2021b, Pacelli et al. 2021a; Table 2). This body of evidence encourages their inclusion in the list of biomarkers used in the search for Earth-like life elsewhere in our solar system. This is further emphasised by the general importance of these pigments in fungal stress tolerance under space-relevant conditions and in the model organism *C. antarcticus* (Section 2.3.3).

2.4 Fungal threats for space exploration

Fungi can constitute formidable threats to space exploration. The isolation of opportunistic fungal human pathogens and mycotoxin-producing species from space habitats has been extensively documented (Novikova 2004, Checinska Sielaff et al. 2016, De Middeleer et al. 2019). Numerous studies have demonstrated spaceflight associated changes in both the astronauts' immune system (i.e., immune dysregulation) (Cervantes & Hong 2015, ElGindi et al. 2021) and microbial physiology (e.g., enhanced virulence and biofilm formation) (Bijlani et al. 2021, Urbaniak et al. 2021). Monitoring of the mycobiome is crucial to maintain sanitary and microbiological optimum condition; however, it is also necessary to prevent the process of bio-destruction of spacecraft materials (Rcheulishvili et al. 2020). Corrosion and degradation of different materials depend on the ability of several fungi to use a great variety of substrates as a source of nutrients for growth, by enzymatic hydrolysis and hyphal penetration (Sanchez-Silva & Rosowsky 2008). In addition to the potential damage to space equipment, the growth of fungal

communities may cause genetic adaptations to stressors encountered in space conditions, which have the potential to lead to the emergence of virulence traits and increase risks to the crew's health (Wilson et al. 2007, Rosenzweig et al. 2010, Crabbé et al. 2013, Cortesão et al. 2020b).

2.4.1 Habitat contamination and material biodegradation

Microorganisms-mediated biodeterioration is observed in various settings on Earth. Mechanical and chemical damage resulting from fungal physiological features and metabolism have been largely reported for diverse types of materials, including rock, plastic, metal, fabric, and glass, among others (Gutarowska 2014, Borrego et al. 2018, Schmidt et al. 2020). These phenomena have severe economic impact in several industries, along with jeopardising the cultural heritage, as they challenge the physical integrity of substrates (Sterflinger & Pinzari 2012, Kavkler et al. 2022, Ul-Abdin et al. 2022) through processes known as bioweathering, erosion, decay, and decomposition (Gadd 2007).

Biodegradation of organic substances is a natural process that acts on leaves, grass, and food scraps, and is correlated with fungal ability to secrete extracellular enzymes with hydrolytic properties (DSouza et al. 2021). Physical and chemical similarities of some natural polymers (e.g., lignin, starch, cellulose, and hemicelluloses) with synthetic polymers, enable fungi to breakdown artificial products such as plastic, and use them as carbon and energy sources (Kumar et al. 2013, Srikanth et al. 2022). Acidic metabolic by-products of fungal metabolism can, on the other hand, create an accelerated environment for corrosion, leading to metal dissolution and loss of structural integrity (Rcheulishvili et al. 2020, Okorie & Chukwudi 2021). Fungal-mediated corrosion has been documented in mixed biofilm formation in both water environments and humid atmospheres (Coetser & Cloete 2005, Kauffmann-Lacroix et al. 2016, Babič & Gunde-Cimerman 2021). Types of microbiologically influenced corrosion include biofouling – the accumulation of microorganisms and microbial products on natural and man-made surfaces – which represents a major problem for the industrial, medical, and marine fields (Bixler & Bhushan 2012). The fungal-led biofouling is characteristic of indoor environments, such as spacecraft, aircraft, hospitals, and industrial systems (Coetser & Cloete 2005, McNamara et al. 2005, Kokilaramani et al. 2021). Induced corrosion deriving from the biofilm build-up and secretion of EPS can lead to material degradation, mechanical blockages, and product contamination, issues often faced in industrial settings (e.g., water treatment systems and food/beverage industries) (Coetser & Cloete 2005, Luo et al. 2017, Dobretsov et al. 2021, Kokilaramani et al. 2021). Biofouling-dependent structural integrity reduction of medical devices and implants can instead cause malfunctions, implant rejection, and the spread of infectious diseases (LoVetri et al. 2010, Bixler & Bhushan 2012). Also due to microbial contaminants in aeronautical aluminium alloys and aircraft fuel tanks (e.g., *A. niger*), the aerospace industry has been facing increased corrosion, fuel filter clogging, and fuel deterioration for many years (McNamara et al. 2005, Jirón-Lazos et al. 2018, Hu et al. 2020).

Biodeterioration is also a major issue in space, linked to the rich fungal communities that are found in spacecrafts, space stations, and other structures and materials in space missions. This problem proved to be particularly acute in the case of the orbital station Mir, where a unique microbiocenosis remained viable during the space station's 15-year existence, resulting in visible fungal growth and biological damage to structural materials (e.g., cable insulation, window seals, space suits), leading to cases of malfunctioning and even breakage of certain units, and thus endangering the safety and reliability features of space equipment (Novikova 2004, Blachowicz et al. 2017, Mohan et al. 2017).

Although the diversity of fungal species isolated from spacecraft and space stations appears not to be significantly different from the strains isolated on the ground (Makimura et al. 2001, Satoh et al. 2016, Blachowicz et al. 2018, Satoh et al. 2021), discrepancies have emerged between spaceflight species and their ground counterparts, especially concerning biodegradation ability and virulence (Satoh et al. 2021). In terms of colonisation and biodeterioration activity, for instance, several of the fungal species isolated on Mir were more aggressive against structural and decorative materials than reference isolates of the same species (Novikova 2004, Gutarowska 2014). This

resulted in an overrun of “dangerously aggressive”, radiation resistant, fast growing fungi and bacteria, which proved to be extremely hard to eradicate due to their high resistance to common antimicrobial agents (Novikova et al. 2006).

The damaging activity of Mir fungal isolates (e.g., *Penicillium* spp., *Aspergillus* spp., *Cladosporium* spp., *Aerobasidium* spp.) was visible *in situ*, but also confirmed by ground-based studies, testing the deterioration of thermoplastic polymers (polyethylene terephthalate, PET) and metal corrosion (aluminium-magnesium alloys) (Alekhova et al. 2005). Organisms known to colonise and attack a large variety of polymeric and metallic surfaces have also been detected in samples originating from the ISS, where monitoring of biological contamination is regularly carried out in order to avoid microbiological problems (Novikova et al. 2006). A number of studies indicated that *Aspergillus, Cladosporium, Fusarium* and *Penicillium* are predominant fungal genera on both Mir and the ISS and possess an acid-producing capability (Rcheulishvili et al. 2020) that can contribute to the potential corrosion and degradation of stainless steel and other materials associated with electronic equipment and life support systems (Checinska et al. 2015, Kip & van Veen 2015, Amalfitano et al. 2020). Additionally, degradation of high heat-resistance plastic material used for insulation (i.e., polyimide) was reported for the ISS isolates *A. versicolor*, *Cladosporium cladosporioides*, and *Chaetomium* sp. (Gu 2007). Growth of *Cladosporium* spp. was also observed on synthetic polymer materials (Nomex and cable labelling material; Reidt et al. 2014) in the Russian segment of the ISS and on spacesuits from the Apollo mission (Breuker et al. 2003), and their ability to degrade the same polymers was also demonstrated. Finally, the fungal ability to degrade military assets such as paints and fuel storage containers has also been reported (Little et al. 1997, Little & Ray 2001).

Maintaining microbial contamination in the space habitat within regulated levels is paramount to reducing concerns about spacecraft integrity and function (Liu 2017). Albeit the polymeric structural and insulation materials used in spacecraft are chemically synthesised with exceptionally high strength and resistance against both chemical and biological degradation processes (Gu 2007), the spacecraft-mycobiome biodeterioration potential should not be underestimated.

Fungal growth on indoor vehicle surfaces and equipment is supported by organic and inorganic components required for their manufacturing, such as additives and plasticizers from polymeric material and additional nutrients (e.g., dust) (Gu 2007). As mentioned earlier, condensate atmospheric moisture, accumulated in the habitable pressurised cabins, is another crucial aspect of microbial colonisation (Novikova 2004). Alongside decreasing the efficiency and lifetime of the spacecraft equipment, microbial attack of polymeric material can also be associated with the release of toxic VOCs (e.g., alcohols, esters, hydrocarbons, terpenes, ketones, compounds containing sulphur), as well as polymer particles, which, when accumulated, can impair the sanitary and hygienic properties of surfaces (Wang et al. 2021). It follows that microbial activity has a profound impact on the success of space missions, in terms of both the structural stability of the spacecraft and the well-being of the crew (Kim et al. 2013).

To reduce the risks associated with microbial contamination of the spacecraft habitat, the deposition of antimicrobial coatings on indoor spacecraft surfaces, combined with strict cleaning protocols and continuous monitoring, is implemented as a prevention strategy (Paton et al. 2020, Wang et al. 2021). Similarly, protective organic coatings have been used to slow the effects of corrosion by stabilising metal surfaces (Rcheulishvili et al. 2020). Despite the implementation of these techniques, the dynamic and persistent spacecraft microbiomes harbour a biochemical potential to tolerate cleaning procedures and survive the oligotrophic spacecraft environment (Mogul et al. 2018), resulting in serious microbial biodeterioration problems for both crewed and uncrewed space missions. Hence, understanding how microbes adapt to utilise different resources in a controlled built environment is essential to implementing prevention strategies. Such strategies encompass the design and optimization of spacecraft materials with antimicrobial properties that aid in the prevention of unwanted microbial growth, which will be essential for long-term crewed missions (Tesei et al. 2022).

2.4.2 Fungal threats for astronaut health

Space microbiology studies indicate that the environmental conditions on board spacecraft and space stations allow the growth of potentially pathogenic fungi, which could result in contamination with allergenic or toxic secondary metabolites (such as mycotoxins) and cause opportunistic infections, allergies, and intoxication in space, as on Earth (Yamazaki et al. 2012, Satoh et al. 2016, De Middeleer et al. 2019). Opportunistic pathogens encountered on spacecraft and space stations encompass several moulds of the genus *Aspergillus* (e.g., *A. fumigatus*, *A. niger*, and *A. flavus*), while other species identified as potential producers of mycotoxins and allergens include, along with *Aspergillus* spp., *Alternaria* spp., *Fusarium* spp., *Cladosporium* spp., and *Penicillium* spp. (Alekhova et al. 2005, Novikova et al. 2006, Gu 2007, Vesper et al. 2008, Satoh et al. 2011, Checinska Sielaff et al. 2019). The opportunistic pathogenic yeasts and main causative agent of mucosal disease, *Candida albicans* (Bongomin et al. 2017) and *R. mucilaginosa*, are also commonly detected among the predominant spacecraft species (Geltner et al. 2013, Wang et al. 2020).

Infections due to *Aspergillus* spp. cause significant morbidity and mortality (Person et al. 2010). The illnesses resulting from aspergillosis usually affect the respiratory system, but their signs and severity vary greatly, ranging from an allergic reaction to mild and serious lung disease. Invasive aspergillosis can additionally occur if the infection spreads to blood vessels and beyond, as observed in patients with severely compromised immune systems (Gletsou et al. 2018). The majority of the infections (~90%) are attributed to *A. fumigatus*, the most significant airborne opportunistic pathogenic mould on Earth (Bongomin et al. 2017, Knox et al. 2016), followed by *A. flavus* and *A. niger*, which, although less pathogenic to humans than other *Aspergillus* spp., have been associated with ear infections and cases of invasive infection (e.g., pulmonary aspergillosis, tracheobronchitis) in immunocompromised patients (Schuster et al. 2002, Person et al. 2010, Atchade et al. 2017).

Of no less importance is the production, by these and other species, of contaminants that are extremely harmful to the health of humans and animals. Mycotoxins, for instance, can cause acute and chronic toxic effects that range from nausea, diarrhoea, gastrointestinal problems, nephropathies, hepatitis, and hyperestrogenism to immunotoxicity and carcinogenicity (Klintworth et al. 1999, Bennett & Klich 2003, De Middeleer et al. 2019). Species found on ISS surfaces and/or on dust, such as *A. flavus*, *A. ochraceus*, *A. versicolor*, and *Penicillium expansum*, are known to produce carcinogenic mycotoxins – aflatoxins (AFs) and foodborne mycotoxins – OTA (also produced by *A. niger*), sterigmatocystin, and patulin (Novikova et al. 2006). ISS sampling also revealed potential producers of the nephrotoxin citrinin (*Penicillium corylophilum*) and rubratoxin B (*Penicillium purpurogenum*), the immunosuppressive compound mycophenolic acid (*Penicillium brevicompactum*) (Ndagijimana et al. 2008), and several genotoxic and mutagenic mycotoxins like alternariol and tenuazonic acid (*Alternaria alternata*) (Ostry 2008, Vesper et al. 2008).

The actual impact of opportunistic pathogens and mycotoxins on astronauts' health depends on many factors, including the susceptibility and health state of the crew members and the type and extent of the contamination (e.g., skin, airways, or bloodstream) (De Middeleer et al. 2019, Simões & Antunes 2021). Additionally, the growth and metabolite production of fungi on humans and spacecraft materials and equipment is regulated by factors like specific atmospheric fluid condensates and contaminants of chemical or human origin (e.g., metabolic products) (Klintworth et al. 1999). Due to moisture accumulation and environmental protection, material types with higher hygroscopicity and porosity tend to be associated with higher microbial diversity, including microbes having higher abundance of antimicrobial and virulence-associated genes (Gadd 2017, Mohan et al. 2020, Tesei et al. 2022). Another factor influencing human exposure to potentially dangerous species is microbial transfer, among crew members and between the astronauts and the spacecraft environment – where humans not only help build the spacecraft microbiome, but also uptake it as their own (Danko et al. 2020, Lee et al. 2021). This and the periodic exchange of crew members can contribute to qualitative and quantitative changes in the mycobiome composition, with fungal diversity increasing or decreasing over time (Sugita et al. 2016, Checinska Sielaff et al.

2019). Other potential contamination routes are regenerative life-support processes providing water – given that fungal biofilms have been found in tap water in private homes, hospitals, and industrial premises (Döğen et al. 2013, Babič et al. 2016, 2017) – and food, during long-term space missions (Walker & Granjou 2017).

The reported capacity of fungi to grow and adapt to stress conditions, combined with the immune dysregulation observed in humans during spaceflight, have therefore the potential to pose direct and serious threats to the health of the astronauts (Vesper et al. 2008, Abad et al. 2010, Simões & Antunes 2021). Even more so, given the effects exerted by the space stressors, microgravity and ionising radiation in particular, on gene expression, mutation rate, epigenetics, metabolite production, virulence factors, etc., that could further increase fungal virulence and antifungal resistance of opportunistic pathogens, infections and diseases may become more likely and possibly harder to treat (Nickerson et al. 2003, Nickerson et al. 2004, Dadachova & Casadevall 2008, Liu 2017, Urbaniak et al. 2019).

Alteration of fungal properties and characteristics which could contribute to increased survival and pathogenicity, have been observed following exposure to both real and ground-simulated spaceflight conditions (Prasad et al. 2021). While a number of studies pointed out little to no phenotypic and genotypic changes between causative agents of allergy and opportunistic infections and strains of the same species kept under Earth gravity (Yamazaki et al. 2012, Sathishkumar et al. 2014, Satoh et al. 2016) – e.g., Sathishkumar et al. (2014) observed no clear differences in morphology, growth, or asexual reproduction, nor significant stress influence on germination and cell wall integrity – others revealed interesting changed features, e.g., Kennedy et al. (2002) and Mahnert et al. (2019). For example, an ISS *A. fumigatus* isolate proved to be significantly more lethal than Earth-based clinical isolates when causing aspergillosis in neutrophil-deficient zebrafish (Knox et al. 2016). Increased resistance to the antifungal agent amphotericin B (AmB) was observed in spaceflight-cultured *C. albicans*, compared to ground controls (Nielsen et al. 2021), along with increased proliferation rate, biofilm formation, antioxidant capacity, cytotoxicity, and filamentous morphology (Crabbé et al. 2013, Sathishkumar et al. 2016). Whole-genome sequencing of another ISS isolate, *A. niger*, revealed the introduction of non-synonymous point mutations in specific regions of its genome (i.e., chromosomes VIII and XII) in response to space conditions, suggesting that only selected regions of the genome undergo positive selection to confer advantage while adapting to the space environment (Blachowicz et al. 2022b). Proteomics and metabolomics profiling of the same strain additionally showed an enhanced production of pyranonigrin A, a metabolite with antioxidant and UV-protective properties, as well as a higher abundance of enzymes involved in the synthesis of 1,8-dihydroxynaphthalene (DHN)-melanin (Romsdahl et al. 2020).

Pigmentation and melanization are found in several microorganisms living on space stations (Dadachova & Casadevall 2011). For example, the melanin layer and polysaccharide capsule increased significantly in the mycotoxin producer *P. expansum*, following a seven-month exposure to outer space (Dadachova & Casadevall 2008). This is consistent with the increased melanin production in fungi isolated from high-radiation environments (Singaravelan et al. 2008, Gessler et al. 2014, Shunk et al. 2022). Another study documented the unaltered viability of *A. niger* conidia, which are darkly pigmented due to their high melanin content, following up to five months of spaceflight onboard the ISS (Gomoiu et al. 2016). Fungal melanins are radioprotectors that absorb space radiation, protecting from both DNA and cell damage (Pacelli et al. 2017b, Selbmann et al. 2018). However, they are also potent virulence factors in both animal- (Wang et al. 1995, Heinekamp et al. 2012, Cordero & Casadevall 2017) and plant-pathogenic species (Steiner & Oerke 2007). DHN-melanin was found to protect *A. fumigatus* clinical strains from UVC radiation, and when using a zebrafish model for invasive aspergillosis, the pigment was confirmed to be a virulence factor also in an *A. fumigatus* ISS-isolated strain (Blachowicz et al. 2020). These authors additionally detected UVC protective properties of the *A. fumigatus* spore metabolite fumiquinazoline. Similarly, higher levels of the pigment anthraquinone were reported in *Aspergillus nidulans*, also a causative agent of aspergillosis (Corrêa-Almeida et al. 2022), flown for

four to seven days aboard the ISS (Romsdahl et al. 2019), whose role may be to shelter the cells from both oxidative stress and radiation.

Despite strict monitoring of the ISS and its astronauts to prevent risks from pathogenic infection and allergies, crew members still experience medical events of varying severity during spaceflight missions, such as conjunctivitis, acute upper respiratory tract infections, cold sores, skin infections, etc. (Institute of Medicine 2001, Crucian et al. 2016, Tesei et al. 2022). Therefore, continuous evaluation of the impact of these fungi on the ISS is essential to prevent the astronauts' health from being jeopardised, especially during long-duration missions. It is essential to monitor not only fungi but also mycotoxin levels on board spacecraft as well as to define remediation strategies (De Middeleer et al. 2019). Indeed, although the presence of fungi does not necessarily mean mycotoxins are being produced, mycotoxins can still be present even when, over time, fungi are no longer detected (De Middeleer et al. 2019). Microbial interactions can also influence mycotoxin production. Studies of fungal co-infection in maize showed that the co-presence of *Fusarium* spp. and *Aspergillus* spp. leads to enhanced production of the carcinogenic aflatoxin B1 (AFB1) by *A. flavus*, possibly due to a stress response caused by fungal competition (Camardo Leggieri et al. 2019, Giorni et al. 2019). Curiously, recent results of microbial tracking on the ISS indicate that *Aspergillus* spp. often co-occur with *Fusarium* spp. (Urbaniak et al. 2022). Given that *A. flavus* is commonly found in foods like peanuts, corn, and cereal, and because the ISS is a stressful environment for microbes, which could increase mycotoxins' production, microbial monitoring of food sources destined for space is also necessary (Urbaniak et al. 2022). Other preventive strategies may include the application of spacecraft antimicrobial surfaces and coatings (e.g., nanoparticle-based approaches; Gupta et al. 2019) to counteract biofilm formation and, as we have mentioned, prevent changes in microbial physiology that could be detrimental to both astronaut health and spacecraft integrity (Wang et al. 2021). Efforts towards the design of spacecraft materials to inhibit pathogenic growth would benefit from preventing infection rather than relying on treatments after infection, given the limited medical resources available onboard spacecrafts (Tesei et al. 2022).

While current fungal loads in spacecraft are not worthy of raising alarm, continuous monitoring will be critical to guaranteeing the success of future missions, especially those that actively utilise fungi in space (De Middeleer et al. 2019).

2.5 Fungal opportunities and applications for space exploration

We have been using fungal processes and products since the primordial days of our civilization, but innovations keep popping up in all sorts of fields and areas with multidisciplinary applications. Mycological research has been witnessing a massive development, and new fungal applications and technologies have been surfacing in our daily lives, where the use of fungal products is becoming increasingly common (Hyde et al. 2019, Meyer et al. 2020, Füting et al. 2021, Mapook et al. 2022).

Thinking beyond, applications of fungal biotechnology on Earth can be reconceptualised as pioneering tools for space exploration. As hardy forefathers of life on Earth, fungi can pave the way for beginning a new life in the vastness that is space. From jumpstarting organic life to creating versatile biomaterials and being efficient cell factories, the potential applications of fungi in space are incredibly vast. While several examples from the literature are included in this section, the list is by no means exhaustive as there are many more applications of fungi on Earth that could potentially be applicable to space (Fig. 3). Some examples include: production of pharmaceutical drugs, enzymes, preservatives, acidulants, flavour enhancers, antioxidants, beverages, detergents, cosmetics, paper, rubber, wood, textiles, leather-like materials, synthetic fibers and resins, plastics, surfactants, oil additives, as well as using fungi directly as food (Cortesão et al. 2020b).

Long-term human presence in space necessitates a wide variety of versatile materials and technologies: shields against space radiation, life support, waste processing and remediation, production of medicines and food, building materials, and more. Additionally, weight (and cost)

constraints set stringent restrictions and demands on what materials can be taken into space; thus, an optimal solution is one that allows astronauts to utilise and produce materials *in situ.*

Such *in situ* resource utilisation (ISRU) activities are most commonly associated with microbe-mineral interactions in roles that fungi excel at. Fungi can be used to extract essential mineral nutrients from extraterrestrial regolith and rock, reducing dependency on terrestrial resources. An astromycology project funded by NASA aimed to identify leading fungal species to initiate soil formation, create healthy soil matrices for plants, and enable life-support biospheres for the exploration of space (Shevtsov 2021). The use of microorganisms for both space biomining and bioremediation has been covered in depth by Santomartino et al. (2022). According to these authors, although promising, the science around space biomining and bioremediation is still relatively young, and it is pivotal to invest in terrestrial and space-based research on specific methods for space applications. Highlights of recent and current research include a focus on the possible use of microbes to extract metals from lunar or Martian soil, or even asteroids, tested with regolith simulants, namely with the projects BioRock (Loudon et al. 2018) and BioAsteroid (Santomartino et al. 2022), or the ESA Spaceship European Astronaut Centre (EAC) research on lunar regolith simulant EAC-1A (Engelschiøn et al. 2020). Fungal species of the genera *Aspergillus* and *Penicillium* seem to be particularly well suited for these activities, as they are natural producers of organic acids, which are essential for bioleaching and are now being studied for potential biomining of lunar regolith (Dusengemungu et al. 2021).

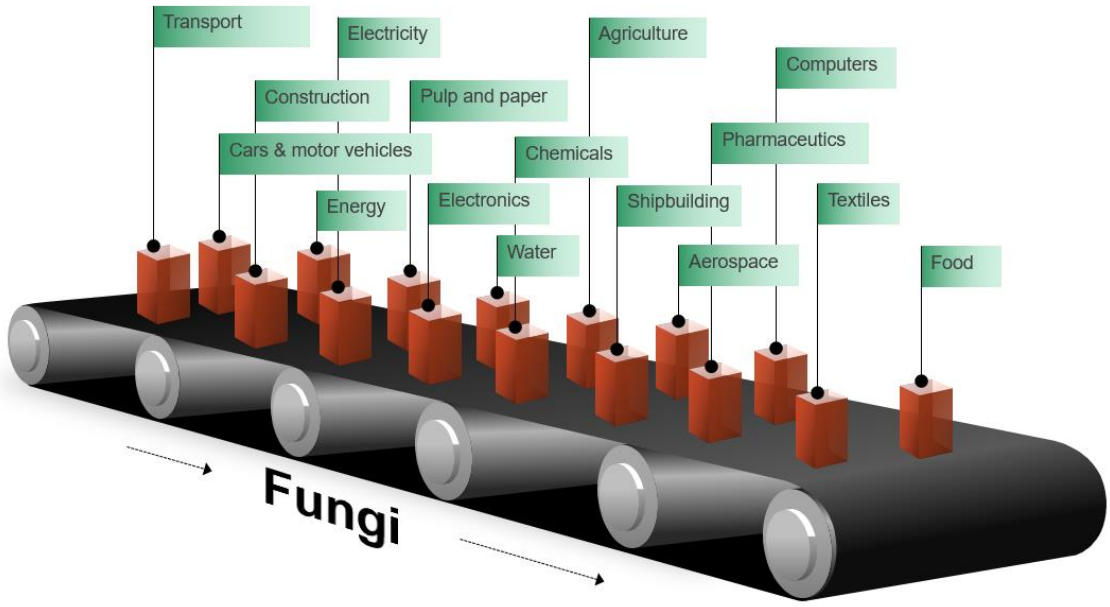


Figure 3 – Production processes supported by fungi (adapted from Meyer et al. 2020).

Space travel requires materials built to survive the various threats in space, whether it is mechanical resistance against debris or shielding against radiation. Biologically-produced nanocomposite materials provide unique advantages by increasing fatigue strength, weighing less than conventional materials, and providing more effective radiation control (Rothschild et al. 2019, Bhat et al. 2021). Here, advancements in a variety of fungi illustrate their ability to produce nanoparticle films and other fungal nanobiocomposites using metals like nickel, iron, and gold, which are more efficient and require fewer downstream purification processes than inorganic production methods (Prasad et al. 2018).

One significant advantage of developing fungal biotechnology is that, theoretically, all that is needed to bring fungal species into any location (including those beyond our planet) are few fungal

spores or cells, which have negligible mass and can then propagate in place. Some other aspects of fungal physiology could find further applications in space engineering. For example, mushrooms and yeasts are composed primarily of water and are cooler than their environment through evaporative cooling (Cordero & Casadevall 2020, Husher et al. 1999) which could potentially be exploited for passive cooling and water repurposing. Moreover, darkly pigmented fungi can absorb heat from electromagnetic radiation (Cordero et al. 2018), a property that can also be explored in space for heat capture applications. Mycoculture in space could be further engineered into human habitats to store and purify water while also increasing humidity and temperature control. Therefore, fungal biotechnology works well to establish ISRU systems, as it allows a wide variety and volume of material to be produced from a minimal initial payload, with applications in several areas, including architectural development and material improvement of future space habitats (Wösten et al. 2018).

Advantages of fungal biomaterials include lower manufacturing costs, waste reduction, recyclability of products, and lightweight materials that are very good at insulating, and versatility (they can be used to mimic even leather and brick) (Wösten et al. 2018, Pohl et al. 2022). They could also be combined and used for multiple functions. Fungi from the Ascomycota and Basidiomycota phyla can create a variety of mycelium-based biomaterials. Paired with melanin-producing fungi, an organic growth system would allow the cultivation of high volumes of biomaterials, which could even be used for printing into large structures shielding from the harsh radiation in space (Cordero 2017, Wösten et al. 2018, Shunk et al. 2020). The same melanized fungi could also be used as air purification systems to filter out VOCs (Prenafeta-Boldú et al. 2019) and melanin harvested from them could also serve as a potential tool for mycoremediation in industrial water purification systems (Panzarasa et al. 2018).

As previously highlighted, fungi can synthesise compounds with many useful properties: antibiotics, antimycotics, antivirals, anticancer drugs, antidiabetics, and immunosuppressives. They also produce a wide range of enzymes and bioactive secondary metabolites, some of which are of high biotechnological interest. Such biosynthetic activity can be influenced under real or simulated space conditions (Section 2.3). In this regard, space stations, such as the ISS, provide unique environments for the potential "guided evolution" of species, leading to the emergence of strains with novel properties (e.g., high yield, rapid growth, improved pathogen resistance, enhanced tolerance, enzymes with altered biochemistry, etc.). These space stressors, which cannot be fully duplicated on Earth, can be used for the evolution of strains that will be more robust and productive than their respective wild types on Earth (Makimura et al. 2001).

Promising results are leading to increased interest in the potential production of pigments and other secondary metabolites by microorganisms exposed to spaceflight conditions. Several spaceflight and ground-simulated experiments have demonstrated enhanced production of pharmaceutically relevant secondary metabolites from different fungi (Knox et al. 2016, Blachowicz et al. 2019b, Romsdahl et al. 2019), in gene clusters that are either silent or expressed at very low concentrations under normal, terrestrial conditions. Moreover, in space, cells can produce certain secondary metabolites in suspension and in the absence of shear forces (Friedrich et al. 2007), offering unique advantages for bioprocessing applications (Bijlani et al. 2021).

The degradation capabilities of fungi can also be a point of interest. Although, generally, the breakdown of materials by microorganisms is mainly undesirable, depending on the circumstances, the same process may be harmful or beneficial (Hueck 2001). For instance, fungal biodegradation skills proved effective towards plastics (mainly aliphatic polyesters, aromatic co-polyesters, and polyethylene), as largely documented by research work investigating the use of fungal enzymatic systems for waste polymer disposal (Webb et al. 2000, Friedrich et al. 2007, Srikanth et al. 2022). Some well-known fungi showing effective degradation on plastics include several filamentous species (e.g., *A. flavus*, *A. nidulans*, *Aspergillus oryzae*, *C. cladosporioides*, *Phanerochaete chrysosporium*) and saprotrophic species (e.g., *Agaricus bisporus*, *Pleurotus abalones*, *Pleurotus ostreatus*) (Brunner et al. 2018, Muhonja et al. 2018, Daly et al. 2021, Srikanth et al. 2022). However, recent reports have indicated extremophilic species as a source of enzymes

(extremozymes) with catalytic efficacy towards degradation-recalcitrant materials and stability and activity at broader ranges of various physical-chemical parameters (Gostinčar et al. 2014, Tesei et al. 2020, Borthakur et al. 2021, Spina et al. 2021). This suggests that stress-resistant species are capable of enhanced degradation and might be of increased relevance in the context of space exploration and ensuring its sustainability.

We're still in the first steps of defining a list of helpful species for space-based applications. However, one fungal species seen as key for future application in space is *A. niger*, as it has long been explored for several applications (Cairns et al. 2018) and is now being included in many space-linked experiments. With an already-proven track record as an efficient production system of varying organic substrates, *A. niger* could help with the *in-situ* production of organic resources (Cortesão et al. 2020a). The applications of *A. niger* range from secreting enzymes useful in the hydrolysis of polymers and organic acids to producing a diverse range of proteins and secondary metabolites (Cairns et al. 2018). *A. niger* is currently used in industrial scale production of citric acid, which has wide applications in foods, beverages, textiles, biofuels, cosmetics, and pharmaceutics (Currie 1917, Tong et al. 2019, Behera 2020, Cortesão et al. 2020a).

Fungal biotechnology is a valuable tool in humanity's arsenal as we venture to explore space and can enable human sustainability and resource independence from Earth (Cortesão et al. 2020b). However, it is important to acknowledge the difficulties in transferring and applying such technologies and the fact that many questions still remain.

In what ways can fungi aid space exploration? Is the production and utilisation of fungi in space feasible? Which species of fungi are optimal for use in space? What are the setbacks to their application? How will we grow fungi in space? What equipment should be used to harness the materials? Where will the oxygen, nitrogen, phosphorus, water, etc. needed to grow the fungi come from? What will happen when materials are exposed to solar flares or radiation (Wösten et al. 2018)? These are but a few questions; there are a myriad more waiting to be asked, addressed, and answered by further research in this field.

Future astromycology research regarding application of fungal biotechnology in space should address these questions. In particular, the development of novel biotechnological processes should prioritise integration of such processes within already existing spacecraft systems (e.g., life-support, crop-cultivation and waste-recycling) in order to minimise resources and optimise sustainability. This asks for highly interdisciplinary endeavours that bring astromycologists, astrobiologists, mycologists, and space engineers together, to promote a successful and sustainable human space exploration.

3. Tools and Resources

3.1 Target journals for publishing astromycology research

There are currently several journals with dedicated space to astrobiology. The last few years have brought us an increase in the inclusion of this topic, with many special issues and topics covered in several journals. As astromycology research falls under the astrobiology umbrella, we're presenting here a wide selection of journals that currently publish astrobiology research, combined with relevant journals in the field of mycology, as viable targets for publishing astromycology papers (Table 4).

The listed journals are organised according to their impact factor, despite some increased resistance against the use of this metric. Our decision is based on the continued use of impact factor as one of the main criteria for ranking journals. Even though journal impact factor is seen by many as an inappropriate way of evaluating research, it remains one of the most relevant criteria for career progression (impacting on recruitment, promotions, and even sometimes financial bonuses) and an indicator of the quality and relevance of research (Guo et al. 2021). One should also note that the backlash against the use of impact factor as a valid metric is not yet a global phenomenon, with views in Western countries (particularly the UK and the US) contrasting with those across several Asian countries (namely China, or Korea).

3.2 Useful resources for astromycology

New findings and regular changes in taxonomic nomenclature are continuously taking place, affecting taxa across the three domains of Life (e.g., Wijayawardene et al. 2020, 2022). There are several helpful tools taxonomists can use when confirming the updated and currently accepted fungal names: Index Fungorum (www.indexfungorum.org/Names/Names.asp), MycoBank (www.mycobank.org), and the Global Biodiversity Information Facility (GBIF – www.gbif.org). There are also numerous webpages Researchers working with fungal species of clinical relevance are also affected by changes in nomenclature. There are specific tools and resources specifically addressing such changes in this group of fungi (e.g., www.adelaide.edu.au/mycology/fungal-descriptions-and-antifungal-susceptibility/name-changes-for-medical-fungi).

Table 4 Where to publish astromycology research (list presented in descending order according to impact factor available at the time of publication).

Target journals	**Impact factor***	**Official Abbreviation****	**Publisher**	**Periodicity**	**OA**	**Website**
# Nature Reviews Microbiology	78.297	Nat. Rev. Microbiol.	Springer Nature Limited	Monthly	No OA	www.nature.com/nrmicro
Nature	69.504	Nature	Springer Nature Limited	Weekly	Contains OA	www.nature.com
Science	63.832	Science	American Association for the Advancement of Science (AAAS)	Weekly	Contains OA	www.science.org
# Annual Review of Astronomy and Astrophysics	37.226	Annu. Rev. Astron. Astrophys.	Annual Reviews	Annual	No OA	www.annualreviews.org/journal/astro
Nature Microbiology	30.964	Nat. Microbiol.	Springer Nature Limited	Monthly	Contains OA	www.nature.com/nmicrobiol
Studies in Mycology	25.731	Stud. Mycol.	Centraalbureau Schimmelculture	3 issues per year	OA	www.studiesinmycology.org
Fungal Diversity	24.902	Fungal Divers.	Springer	Bimonthly	Contains OA	www.springer.com/journal/13225
Trends in Microbiology	18.230	Trends Microbiol.	Cell Press, Elsevier	Monthly	Contains OA	www.cell.com/trends/microbiology/home
Nature communications	17.694	Nat. Commun.	Springer Nature Limited	Daily	OA	www.nature.com/ncomms
Microbiome	16.837	Microbiome	BioMed Central Ltd	Daily	OA	https://microbiomejournal.biomedcentral.com
Mycosphere	16.525	Mycosphere	Mycosphere Press	Annual	OA	www.mycosphere.org
# Annual Review of Earth and Planetary Sciences	16.304	Annu. Rev. Earth Planet. Sci.	Annual Reviews	Annual	No OA	www.annualreviews.org/journal/earth
# Annual Review of Microbiology	16.232	Annu. Rev. Microbiol.	Annual Reviews	Annual	No OA	www.annualreviews.org/journal/micro
Nature Astronomy	15.647	Nat. Astron.	Springer Nature Limited	Monthly	No OA	www.nature.com/natastron

Table 4 Continued.

Target journals	Impact factor*	Official Abbreviation**	Publisher	Periodicity	OA	Website
FEMS Microbiology Reviews	15.177	FEMS Microbiol. Rev.	Oxford Academic	Bimonthly	Contains OA	https://academic.oup.com/femsre
Science Advances	14.980	Sci. Adv.	American Association for the Advancement of Science (AAAS)	Weekly	OA	www.science.org/journal/sciadv
Biological Reviews	14.355	Biol. Rev.	John Wiley & Sons, Inc.	Bimonthly	Contains OA	https://onlinelibrary.wiley.com/journal/1469185x
Microbiology and Molecular Biology Reviews	13.044	Microbiol. Mol. Biol. Rev.	American Society for Microbiology	Quarterly	No OA	https://journals.asm.org/journal/mmbr
Microbiology Spectrum	9.043	Microbiol. Spectr.	American Society for Microbiology	Not defined	OA	https://journals.asm.org/journal/spectrum
Space Science Reviews	8.943	Space Sci. Rev.	Springer Nature Switzerland AG	8 issues per year	Contains OA	www.springer.com/journal/11214
New Astronomy Reviews	8.682	New Astron. Rev.	Elsevier	Bi-annual	Contains OA	www.journals.elsevier.com/new-astronomy-reviews
mBio	7.786	mBio	American Society for Microbiology	Bimonthly	OA	https://journals.asm.org/journal/mbio
mSystems	7.328	mSystems	American Society for Microbiology	Bimonthly	OA	https://journals.asm.org/journal/msystems
Fungal Biology Reviews (journal of the The British Mycological Society)	6.727	Fungal Biol. Rev.	Elsevier	Quarterly	Contains OA	www.sciencedirect.com/journal/fungal-biology-reviews
iScience	6.107	iScience	Cell Press	Monthly	OA	www.cell.com/iscience/home
Frontiers in Microbiology	6.064	Front. Microbiol.	Frontiers Media S.A.	Daily	OA	www.frontiersin.org/journals/microbiology
Journal of Fungi	5.724	J. Fungi	MDPI	Monthly	OA	www.mdpi.com/journal/jof/instructions
Environmental Microbiology	5.476	Environ. Microbiol.	John Wiley & Sons, Inc.	Monthly	Contains OA	https://sfamjournals.onlinelibrary.wiley.com/journal/14622920
mSphere	5.029	mSphere	American Society for Microbiology	Bimonthly	OA	https://journals.asm.org/journal/msphere
Applied and Environmental Microbiology	5.005	Appl. Environ. Microbiol.	American Society for Microbiology	Bimonthly	Contains OA	https://journals.asm.org/journal/aem
Scientific Reports	4.997	Sci. Rep.	Springer Nature Limited	Daily	OA	www.nature.com/srep
NPJ Microgravity	4.970	NPJ Microgravity	Nature	Not regular (all year)	OA	www.nature.com/npjmgrav

Table 4 Continued.

Target journals	Impact factor*	Official Abbreviation**	Publisher	Periodicity	OA	Website
Microorganisms	4.926	Microorganisms	MDPI	Monthly	OA	www.mdpi.com/journal/microorganisms
Fungal Ecology (journal of the The British Mycological Society)	4.204	Fungal Ecol.	Elsevier	Bimonthly	No OA	www.sciencedirect.com/journal/fungal-ecology
Microbial Ecology	4.192	Microb. Ecol.	Springer Nature Switzerland AG	Quarterly	Contains OA	www.springer.com/journal/248
Frontiers in Astronomy and Space Sciences	4.055	Front. Astron. Space Sci.	Frontiers Media S.A.	Daily	OA	www.frontiersin.org/journals/astronomy-and-space-sciences
Astrobiology	4.045	Astrobiology	Mary Ann Liebert, Inc., publishers	Monthly	Contains OA	https://home.liebertpub.com/publications/astrobiology/99
Research in Microbiology	3.946	Res. Microbiol.	Elsevierplane	Bimonthly	Contains OA	www.sciencedirect.com/journal/research-in-microbiology
PLoS One	3.752	PLoS One	Public Library Science	Daily	OA	https://journals.plos.org/plosone
Earth and Space Science	3.680	Earth Space Sci.	John Wiley & Sons, Inc.	Monthly	OA	https://agupubs.onlinelibrary.wiley.com/journal/23335084
Life	3.253	Life	MDPI	Monthly	OA	www.mdpi.com/journal/life
PeerJ (Life & environment)	3.061	PeerJ	PeerJ Publishing	Not defined	OA	https://peerj.com/life-environment
Extremophiles	3.035	Extremophiles	Springer Nature Switzerland AG	Not defined	No OA	www.springer.com/journal/792
Microbiology (journal of the Microbiology Society)	2.956	Microbiology-(UK)	Microbiology Society	Monthly	OA (from Jan 2023)	www.microbiologyresearch.org/content/journal/micro
Acta Astronautica	2.954	Acta Astronaut.	Elsevier	Monthly	No OA	www.sciencedirect.com/journal/acta-astronautica
Fungal Biology (journal of the The British Mycological Society)	2.910	Fungal Biol.	Elsevier	Monthly	Contains OA	www.sciencedirect.com/journal/fungal-biology
Life Sciences in Space Research	2.730	Life Sci. Space Res.	Elsevier	Quarterly	Contains OA	www.journals.elsevier.com/life-sciences-in-space-research
Advances in Space Research	2.611	Adv. Space Res.	Elsevier	Bimonthly	Contains OA	www.sciencedirect.com/journal/advances-in-space-research
Microbes and Environments	2.596	Microbes Environ.	Japanese Society of Microbial Ecology / Japanese Society of Soil Microbiology / Taiwan Society	Quarterly	OA	www.jstage.jst.go.jp/browse/jsme2/-char/en

Table 4 Continued.

Target journals	Impact factor*	Official Abbreviation**	Publisher	Periodicity	OA	Website
			of Microbial Ecology / Japanese Society of Plant Microbe Interactions / Japanese Society for Extremophiles			
Planetary and Space Science	2.085	Planet Space Sci.	Elsevier	Monthly	Contains OA	www.sciencedirect.com/journal/planetary-and-space-science
Mycobiology (journal of the Korean Society of Mycology)	1.946	Mycobiology	Taylor and Francis group	Bimonthly	OA	www.tandfonline.com/journals/tmyb20
Astrophysics and Space Science	1.9	Astrophys. Space Sci.	Springer	Monthly	Hybrid, contains OA	www.springer.com/journal/10509
Microgravity Science and Technology	1.642	Microgravity Sci. Technol.	Springer Nature Switzerland AG	Bimonthly	Hybrid, contains OA	www.springer.com/journal/12217
International Journal of Astrobiology	1.358	Int. J. Astrobiology	Cambridge University Press	Bimonthly	Contains OA	www.cambridge.org/core/journals/international-journal-of-astrobiology
Mycoscience (official English journal of the Mycological Society of Japan)	1.333	Mycoscience	Elsevier	Bimonthly	Contains OA	www.journals.elsevier.com/mycoscience
Origins of Life and Evolution of Biospheres (journal of the International Astrobiology Society)	1.120	Orig. Life Evol. Biosph.	Springer	Quarterly	Contains OA	www.springer.com/journal/11084
Fungal Interactions (journal of the British Mycological Society)	-	Fungal Interactions	Elsevier	Not defined	OA	www.journals.elsevier.com/fungal-interactions
BioCosmos	-	BioCosmos	Sciendo	Annual	OA	https://sciendo.com/journal/BIOCOSMOS

*According to the Journal Citation Reports of Clarivate Analytics for 2022. **According to the Standard Journal Abbreviation (ISO4). #Only upon invitation. OA = Open Access.

Another relevant issue when discussing research in Astromycology is that of strain availability and access. While the role of Biological Resource Centers (BRCs) is widely recognised as essential for ensuring reproducibility of results and public access to type strains, among many

other key services (e.g., Antunes et al. 2016), there are clear limitations in accessing relevant non-type strains. As highlighted by Rettberg et al. 2019, microbial strains from SAFs cleanrooms and spacecrafts from ESA missions are deposited in a public collection, but the same cannot be said for NASA and other space agencies. Such strains cannot be obtained for basic research, limiting relevant studies in this field. These authors propose the establishment and maintenance of an international culture collection for all such microbes, which would constitute a valuable resource for astrobiology (and astromycology).

As a final note, the ongoing explosive increase in dispersed data about new fungal strains of relevance for astromycology, including their general properties and results of exposure tests, will increasingly make it difficult to navigate this growing pool of useful resources. The need for dedicated tools that compile such information and facilitate their exploration for identifying knowledge gaps and potential novel research directions has been recently demonstrated for the archaeal class *Halobacteria* by Wu et al. (2022). This is equally applicable to fungal strains, so community-wide efforts and the development of such tools should be set as key priorities for the astromycology community.

Declarations

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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