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Impact of Climatic Variations on Fungi, Mycorrhiza and Lichens –An appraisal

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Abstract

Approximately 2.5 million fungi are estimated to be live on Earth, and the updated estimate confirms fungi as the second only to invertebrates concerning species diversity. These are an important group of microbes that play crucial roles in various ecosystems in the biosphere, from decomposing organic matter to forming symbiotic relationships with plants. These functions are significantly affected as the temperature rises and precipitation patterns shift. Over the years since industrialization started, the earth's climate has changed due to increasing human intervention. The changing climate has adversely impacted the delicate web of life, and fungi and lichens are no exception. Climate change can alter fungal diversity, distribution, and activity. Warmer temperatures and increased precipitation in some regions could boost fungal decomposition rates, aiding soil fertility and potentially increasing plant productivity. Rising temperatures allow some mycorrhizal fungi, vital plant partners, to colonize new frontiers, potentially aiding plant expansion and ecosystem adaptation. However, this warming tide threatens cold-adapted fungi, pushing them closer to extinction. While offering some benefits, rising CO_2 and temperatures create a perfect storm for mycotoxin production by stressed fungi, jeopardizing food security and health. The potential risks to food security and health are significant, and it's crucial to understand and address these issues. Climate-driven extremes like droughts, floods, and wildfires threaten fungal networks, triggering die-offs and ecosystem domino effects. Climate change acts like a geographical shuffler, disrupting established mycorrhizal communities and favoring opportunistic, potentially invasive species. This reshuffling could lead to less efficient partnerships, impact plant growth, and create ecological imbalances. This review offers a comprehensive and insightful analysis of the complex interplay between climate change and fungi and explores how climate change disrupts various fungal realms, from terrestrial fruiting to marine ecosystems, unraveling impacts on fungal pathogens, symbiosis, and food security.

Keywords – Carbon dioxide emissions – global warming – greenhouse gases – mycorrhiza – pathogenic fungi – phenology

Introduction

All life forms, including fungi on this planet, from polar to tropical and terrestrial to aquatic habitats, are exposed to the unprecedented effects of climate change. Microbes, including fungi and fungi–like organisms, are nature's replenishers and scavengers and play an important role in maintaining ecological balance. Fungi are enigmatic organisms, ubiquitous yet hidden. Due to their

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versatile nature, fungi can be found in a variety of habitats such as on dead matter (saprotrophs), within living organisms and not causing any disease (endophytes) or on living organisms (biotrophs) as parasites or symbiotrophs, on leaf litter or dead wood (lignicolous), on soil (terrestrial) and in water bodies (aquatic). Fungi also exist in a mutualistic association with the roots of higher plants, which is known as mycorrhiza, and in a symbiotic relationship with algae, and this association is known as lichens (Lutzoni & Miadlikowska 2019, Niskanen et al. 2023). Being one of the largest groups of organisms, fungi are rich in diversity and distribution. With the advancement in studies, estimates for the fungal diversity are made by mainly four methods – scaling laws, fungus: plant ratios, actual versus earlier known number of species, and DNA–based studies (Antonelli et al. 2023, Niskanen et al. 2023). Their global richness is known to affect everything, be it a living organism or nonliving material, and in turn, there are also a number of factors that drive their species abundance at local as well as global scales. Climate change is one of the main factors which are affecting their distribution, diversity and phenological patterns (Tedersoo et al. 2022, Niskanen et al. 2023). Changes in the growth and distribution of fungi due to climate change are reported to have considerable subsidiary effects on the ecosystem and its functions (Bidartondo et al. 2018). For example, plant diseases are one of the biggest threats posed by climate change to global food security and productivity (Pequeno et al. 2024). Climatic variations are the direct result of increasing global temperatures. With its continuous increase at the present rate, the global temperature will likely reach or surpass 1.5°C between 2021 and 2040 across the studied scenarios (Boehm & Schumer 2023). This change will affect all groups of organisms, including fungi, by influencing their distribution, reproduction, genetic makeup, evolution, ability to adapt to the ecosystem, and ultimate survival (Burdon 1999, Bidartondo et al. 2018, Pietras et al. 2021) (Fig. 1). Patterns of rainfall and snowfall are shifting, and extreme disturbance events such as floods, droughts, and storms are increasing (IPCC 2022). All such changes are reported to have a direct effect on the evolution of species and their ability to adapt to migrate between and reside within the ecosystem (Fisher et al. 2012, Andrew et al.2018). Therefore, the rapid changes in climate and the consequences thereof are worrisome and require some serious thinking to work out solutions for the long–term sustenance of life forms in front of such global challenges. Mycologists are using different types of latest technologies for studying these effects. The relationship between environment and fungal diversity is also being studied using PCR–based, nucleic acid hybridization-based techniques and transcriptome analysis (Mitchell & Zuccaro 2006). Besides this, various ecological models and statistical tools are also being used by the investigators for studying the influence of meteorological variables on fungi such as projection to latent structure regression, general circulation model of climate, generalized linear model, specific statistical models, the generic model CLIMEX, and species distribution modeling (Desprez–Loustau et al. 2007, Wollan et al. 2008, Yang et al. 2012, Shrestha & Bawa 2014). In this review, data has been compiled that indicates how the changing climate is affecting the distribution and abundance of terrestrial, aquatic (particularly marine), and pathogenic fungi globally. The paper also reflects on the impact of climate change on the association of mycorrhizal fungi with that of higher plants and on the richness of lichens in various parts of the world. Besides this, emphasis has also been laid on the possible threat to global food security, which is being predicted due to the alterations in fungal abundance. In the last part of the paper, some measures have been suggested to deal with climate change.

Terrestrial fungi

Undoubtedly, scientists are trying to explore each nook and corner of the universe to find and study new life forms. A number of new species are being added to the database every day. But simultaneously, a large number of already described species are threatened or are being lost, primarily due to changes in the climatic conditions around them. A number of studies are available in different parts of the world that outline the effects of climate change (Fig.1) on the distribution, sporulation, reproduction, and fruiting patterns of terrestrial fungi (Boddy et al. 2014, de Sousa et al. 2017, Gonçalves et al. 2017, Alves et al. 2019). Climate change directly affects fungi by altering their growth rate, species richness, distribution, reproductive patters, and mycotoxin production and indirectly by disrupting ecosystems and the symbiotic relationship fungi have with plants and animals (Fig. 2).

Impact on fungi

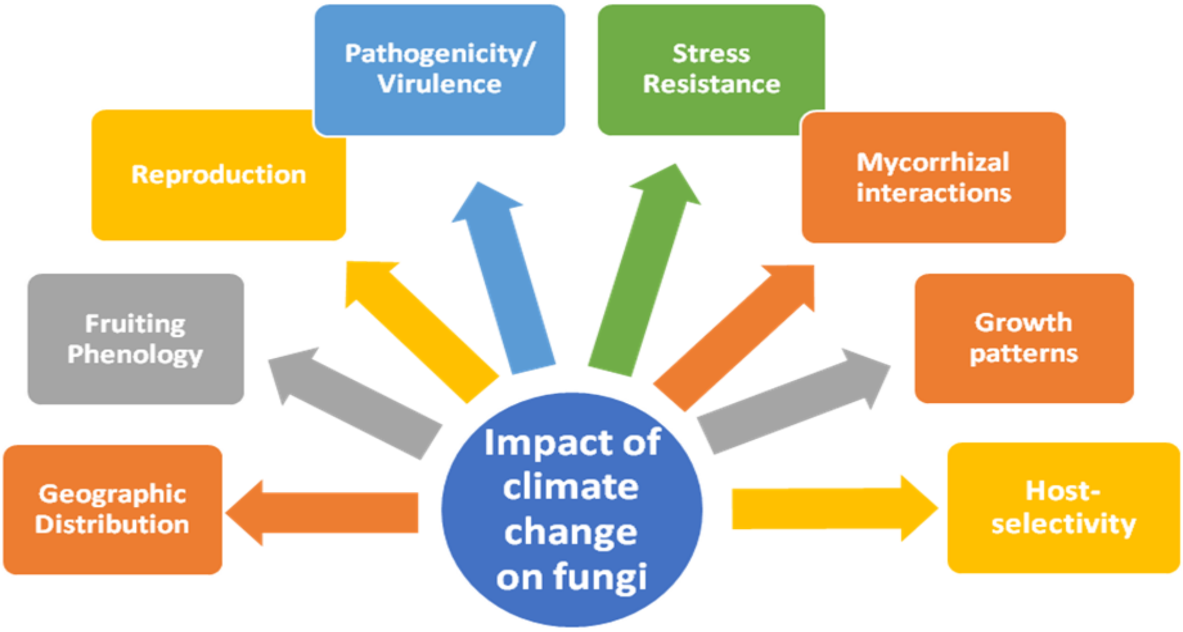

Fig. 1 – Different aspects of fungi affected by global climate changes.

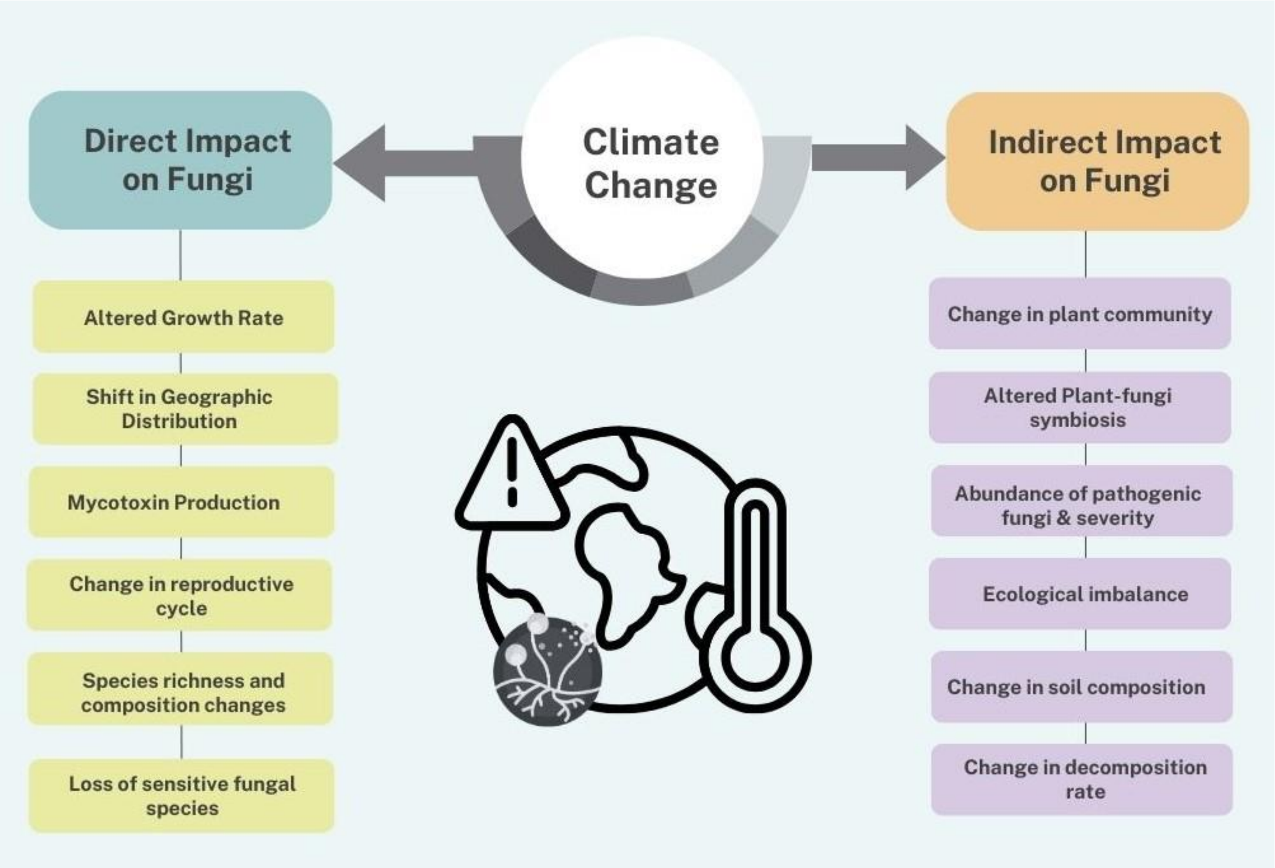

Fig. 2 – Direct and Indirect impact of climate change on different aspects of Fungi.

Both the Arctic and Antarctic regions are the two most rapidly changing areas of the earth which are responsible for some changes in both marine and terrestrial ecosystems (Clarke et al. 2006). The fungal species belonging to these regions are reported to be highly adapted to various kinds of environmental stresses, such as freeze-thaw cycles, strong winds, high UV irradiation, varying pH levels, dryness, low nutrient concentrations, and osmotic stresses (Fell et al. 2006). A study by Newsham (2016) has shown that the diversity of soil fungi is increasing with the increase in maritime temperature in the Antarctic region. According to this report, surface air temperature directly affects the diversity and composition of soil fungal communities, as in regions like Antarctica, higher temperatures increase access to water and also enhance the metabolic activities of fungi. A rapid rise in temperature by about 0.34°C per decade has been predicted to lead to a 20–27% increase in fungal species richness. Various investigators recovered some species of fungi from rocks and ornithogenic soil nests of some bird species in continental Antarctica and experimentally tried to grow them at 37°C. It was found that *Acremonium* spp., *Debaryomyces hansenii, Penicillium. chrysogenum, P. citrinum, P. tardochrysogenum, P. tardochrysogenum,* and *Fusarium* spp. are able to grow at 37°C. Further, some species are reported to produce spores and show hemolytic activity (de Sousa et al. 2017, Gonçalves et al. 2017, Alves et al. 2019). These studies explain that the fungal taxa with potential pathogenicity occurring in the habitats of Antarctica can possibly disperse to other regions due to climate change effects (Rosa et al. 2019). Another investigation was undertaken on the most abundant fungus of maritime Antarctic fellfield soil, *Pseudogymnoascus roseus*. It has been documented that warming of the soils above 20°C reduces the abundance of fungi by 1–2 orders of magnitude (Misiak et al. 2021). Further, it has also been reported that in laboratory experiments, the hyphal extension rates and the activities of five extracellular enzymes in *P. roseus* also decreased by 54–96% at high water accessibility on exposure to temperature cycling every day from 2 to 21°C and 2 to 24°C, relative to temperature cycling from 2 to 18°C (Misiak et al. 2021). Thus, the study indicates that elevated levels of global warming can potentially have inhibitory effects on the abundance and metabolism of fungi in cold regions.

In a study undertaken during the period 1960–2010 by Diez et al. (2020), significant changes in the phenology of fungi fruiting have been reported in the European Alps. They have recorded an average trend of 2.2 m per year upward shift in mycorrhizal species and litter or soil-inhabiting species, while 0.66 m per year shift in the case of wood–rotting fungal species due to climatic variation in the European Alps. An increase of 0.36°C temperature per decade between 1979 and 2019 (Klein et al. 2017) and, on the other hand, extreme drought events associated with the heat waves are reported to have led to vegetation damage (Corona–Lozada et al. 2019, Schuldt et al. 2020). More intense and less frequent rainfall, as well as reduced snow depth in the region, has also been documented by various investigators (Appenzeller et al. 2011, Fischer et al. 2019, Matiu et al. 2021). All these factors are reported to significantly affect fungal growth. Boddy et al. (2014) have also documented that speedy and continuous variations in the climate are changing the fruiting phenology of the fungal species. Different groups and species of fungi are reported to respond differently to such climatic variations. On account of such climatic variations, an extension has been documented in the fruiting season in some of the species, while in others contraction in the fruiting season has been reported. Kauserud et al. (2010) studied the spatial and temporal variation in the fruiting of fungal species in the United Kingdom and Norway. They observed that high winter temperatures led to the early fruiting of spring fungi. A five–day shift with an increase in 1°C temperature has been documented. A similar report also documents the fruiting patterns of 315 autumnal fruiting species in England which was recorded over a period of 20 years (Gange et al. 2007). This study reflects that the average date of the first fruiting was preponed, and that of the last fruiting was delayed significantly. A more than double increase in the fruiting period was noticed from the 1950s to the 2000s. It has been observed that temperature and moisture dominantly influence the growth and reproduction of fungi (Eveling et al. 1990). In a study undertaken by Damialis et al. (2015) on six fungal species, namely *Alternaria alternata, Aspergillus niger, Botrytis cinerea, Cladosporium cladosporioides, C. oxysporum*, and *Epicoccum* *purpurascens*, it was demonstrated that these fungi grew vigorously under high temperatures and are not affected by or produce a lower number of spores with further increases in temperature. As a result, it is expected that with the change in climate in the future, as per the reports of the IPCC, an increase in temperature may enhance the growth of fungal mycelium with a lower rate of sporulation. A common fungus, *Auricularia auricula–judae*, is known to be host–specific. Gange et al. (2011) studied the fungus on a woody plant, *Sambucus nigra*, over a record period of 59 years and found that, of late, this species has switched hosts as well as some changes in its fruiting pattern has also taken place. It has also been reported that interspecific mycelial interactions vary depending on the microclimate (Boddy 2000).

There are a number of reports available documenting the fruiting patterns of fungi in various regions of Asia. A thirty–year survey in a Japanese Oak Forest reveals that the phenology of mushroom fruiting is highly driven by meteorological factors. Besides this, the response of fungi to such factors is variable among different groups and taxa (Sato et al. 2012). In another study done over an 11–year period from 2000 to 2010, it was emphasized that increasing temperatures and reduced rainfall in May and June caused delayed fruiting of *Tricholoma matsutake* (Matsutake mushroom) in West Yunnan, China (Yang et al. 2012). Based on another study on the Chinese caterpillar fungus (*Ophiocordyceps sinensis*) in China, it is predicted that there will be a potential reduction in the distribution of this species in the future due to unfavorable climatic changes (Wei et al. 2021). Contrary to this observation, Shrestha & Bawa (2014) have suggested that due to the change in climate, there would be an extension in the potential distribution of *O. sinensis* as new additional habitats would be created in the Himalayas. Further, on the basis of an analysis, it is also suggested by Hopping et al. (2018) that production of the caterpillar fungus has reduced due to a variety of reasons, including overexploitation, habitat destruction, and climate change. Guo et al. (2019) evaluated the impact of climate change on the incidence of *Polyporus umbellatus* and found that this fungus requires an optimum mean annual temperature of 13°C and an annual precipitation of 1000 mm for its growth. Further, it is predicted that the increasing temperature and rainfall in the future are likely to increase the number of suitable habitats for this fungus in northeastern and southwestern China, while habitats are likely to decrease in central China.

Pathogenic fungi

The effect of climatic variations on pathogenic fungi, which are the causative agents of numerous diseases in plants and animals, is of real concern. Like other groups of fungi, scientists have also undertaken investigations into the impact of climatic changes on the pathogenic fungi infecting crop plants and humans (Lyon & Broders 2017, Gadre et al. 2022, Money 20024, Pequeno et al. 2024). Climatic variation is reported to alter the magnitude of their virulence, host susceptibility, dispersal, geographic distribution, emergence of new variants, and even new species. Despite some fungi being tolerant to body temperature, the rise in human mycoses is unlikely directly linked to climate change's minor temperature increase. Instead, the overuse of antifungal agents in medicine and agriculture likely plays a bigger role (Money 2024). The appearance of a novel species, *Candida auris*, discovered in 2009 in the ear canal of a patient in Japan, is reported to be an example of a newly emerged species under the influence of climate change (Nnadi & Crater 2021). Being multi-drug resistant, this species is reportedly a potential threat to public health and hygiene (Satoh et al. 2009, Rhodes & Fisher 2019). Its resistance, pathogenicity, and virulence may also be directly linked with the changing climate (Simões 2021). Similarly, some fungal species are reported to have become more virulent due to changing climates. One such species is *Batrachochytrium dendrobatidis,* which causes chytridiomycosis in amphibians, leading to the extinction of various amphibian species (Bosch et al. 2007). Further, Olson et al. (2021) have documented mean temperature as a chief factor affecting the occurrence of this fungal species. They observed that the probability of *B. dendrobatidis* increased with the increase in temperature, with a peak nearly at 18°C and decreased when the mean temperature exceeded ~20°C. Fisher et al. (2009) reported that the distribution pattern and host-pathogen interaction of *B. dendrobatidis* are linked to changing climatic variables. Similar is the case with another basidiomycetous yeast species, *Cryptococcus gattii*, previously known as *C. neoformans*. It is a human and animal pathogen that affects mainly immunocompetent and immunocompromised patients, causing serious illness and even death. For a long period, *C. deuterogatti* was recognized as an endemic pathogen in Australia, but in the 1990s, it was reported to have spread to Canada and the Pacific Northwest region of the United States (Chen et al. 2014). It is reported that climate change is a potential driver for the emergence and spread of *C. gattii* in the Pacific Northwest region of the United States and Canada (Kidd et al. 2007, Greer et al. 2008, Datta et al. 2009). Another study by Bharathi et al. (2007) in South India from 1999 to 2002 suggests that the prevalence of fungal keratitis has increased due to the hot and windy climate in the tropical zone. Warmer temperatures and shifting precipitation patterns are expanding the distribution ranges of some fungi, allowing them to colonize new territories. This can be catastrophic, like the Coccidioides fungus, infamous for Valley fever, now creeping northward in the US. This "geographical shuffling" is reported to disrupt the existing ecological balances, potentially endangering native species and introducing new fungal–borne threats (Gorris et al. 2019). Besides this, it has also been documented that natural disasters such as volcanic eruptions and wildfires are giving rise to new niches leading to the emergence of new fungal species (Seidel et al. 2024).

The plant pathogens are known to serve as indicators of climate change. Like animal pathogens, plant pathogens have also shown differences in their distribution patterns caused by climate change. *Puccinia striiformis*, which is one of the major problematic pathogenic fungi, causing stripe rust in wheat, was earlier reported from cold areas, but since the 2000s, it has spread to warmer areas as the species is becoming thermotolerant (Prashar et al. 2007, Lyon & Broders 2017). It has been documented that, due to the continuously increasing global temperature and aberrant precipitation pattern, a shift of *P. striiformis* and many other fungal pathogens from southern to northern latitudes is reported to have occurred (Bebber et al. 2013). These climatic changes are reported to impact sporulation, latent growth period, and host resistance in the life cycle of a fungus (Severns et al. 2014, Ma et al. 2015). A similar shift has also been reported in the case of *Fusarium* spp. In warm and humid weather, increased infection of cereal crops by *F. graminearum* is reported to have adversely affected the yield and quality of grains (Sarver et al. 2011, Leplat et al. 2013). Plant diseases, which are more severe at high temperatures, are expected to be favored by climate warming. For instance, *Phytophthora cinnamomi*, which is one of the most invasive species in the world, causes root rot and die–back disease (Brasier et al. 1994, Martín–García et al. 2015), and *Ophiostomanovo–ulmi*, which causes elm disease (Sutherland et al. 1997), are reported to get more virulent in a number of plant species at higher temperatures. Future temperatures are predicted to be warmer and more humid, which will expand the region susceptible to wheat blast infection caused by the fungal pathogen *Magnaporthe oryzae* especially in the Southern Hemisphere (Pequeno et al. 2024).

Climate change, it seems, is also stirring up a toxic brew. Warmer, wetter conditions favor the production of mycotoxins, fungal metabolites that can contaminate crops and sicken humans and animals. Aflatoxin contamination in food crops, for example, poses a serious health risk, particularly in developing countries (Perrone et al.2020). For example, a study undertaken by Mikušová et al. (2012) on berries in Slovakian vineyard regions showed an abundance of spoilage of the crop due to the increased magnitude of aflatoxin and ochratoxin–producing fungal infections in the crop. The most important of these are *Aspergillus* spp., followed by *Fusarium* spp., and *Penicillium* spp. Scientists are also concerned about the potential for fungal adaptation and evolution in response to changing temperatures. Could some fungi develop heat resistance, allowing them to colonize our bodies or even become more virulent pathogens? While the answer remains unclear, it's a chilling prospect requiring further research.

Marine fungi

Fungi exist in almost every marine habitat, such as surface waters, hydrothermal vents, salt marshes, sandy beaches at low tide, subsurface deep-sea sediments, and arctic ice (Gladfelter et al. 2019). These are generally found living inside or on the body surfaces of other organisms, such as algae, fungi, corals, sponges, dinoflagellates, and diatoms. They play a pivotal role in the aquatic ecosystem, similar to that of terrestrial fungi, like in nutrient cycling and carbon sequestration (Amend et al. 2019). Marine fungi are adapted to a broad range of environmental stresses specific to the aquatic habitat, such as high salinity, hydrostatic pressure, and ultraviolet light exposure (Velez et al. 2019, Gladfelter et al. 2019). Marine fungi, like *Hortaea werneckii* and *Aspergillus terreus*, are reported to adjust to shifts in temperature, salinity, and oxygen levels, which is crucial for mitigating risk and preserving marine health (Kumar et al. 2021). Therefore, these fungi have many unique characteristics, including the development of mechanisms for maintaining the accumulation of ions in the vacuoles, the elimination of high levels of sodium chloride, maintaining turgor pressure in the mycelium, increased growing capacity at alkaline pH, and a broad temperatures range from lower temperature in polar waters to higher temperatures in sand dunes or intertidal periods as well as growth in deep water and under anoxic conditions (Jones et al. 2022). Thus, this group of fungi is expected to respond well to environmental changes. There is a large degree of uncertainty in predicting the environmental effects (Harvell et al. 2002). Still among various types of environmental changes, an increase in CO_2 levels seems to be a major one. Most of the CO_2 emissions are dissolved by the oceans, which lowers the pH of the water (Houghton et al. 2001). A study undertaken by Caldeira & Wickett (2003) indicated that a continuous increase in the CO_2 level in the atmosphere due to anthropogenic activities will lead to a reduction of 0.7 units in the pH of the ocean, which is bigger than what has been experienced in the past 300 million years. To predict the response of marine fungi to this situation, an investigation undertaken by Krause et al. (2013) can be referred. In the laboratory experiments, these investigators noticed the effect of pH on the growth and abundance of fungal colonies. The outcome of the study showed significantly higher colony–forming units at lowering pH as compared to pH *in situ*. Therefore, it is predicted that oceanic water with a low pH might be beneficial for the active growth of the fungal colonies, which ultimately would also affect the biogeochemical cycles, microbial food webs, and interactions of fungi with other marine organisms (Krause et al. 2013). Another investigation was carried out by Pang et al. (2020) on ten fungal species collected from the marine shallow–water Kueishan Island Hydrothermal Vent Field, Taiwan. Out of these ten species (*Aspergillus terreus*, *A. aculeatus*, *A. sydowii*, *Pencillium matriti*, *P. sumatrense*, *P. oxalicum*, *Fodinomyces uranophilus*, *Verticillium dahlia*, *Trichoderma harzianum,* and *Microascus brevicauli*), only *Aspergillus terreus* has been reported to show adaptability for growth even at high temperatures (45°C), high salinity (30%), as well as acidic pH 3. Further transcriptome analysis of this species demonstrated that the differential expression of stress–related genes, such as mannitol biosynthetic genes, is responsible for the active growth of this fungus at 45°C. Together with this, it was observed by Pang et al. (2020) that pH–related genes were down-regulated at pH 3, while genes related to salt tolerance, like glycerol lipid metabolism and mitogen-activated protein kinase, were up-regulated. Therefore, with respect to this study, it can be predicted that *Aspergillus terreus* responds positively to changing climatic conditions. There are reports which reflect the role of genes in controlling the salt tolerance in marine fungi. For example, Aggarwal et al. (2005) and Prista et al. (2007) have cloned the genes *DHAL2,* which encodes a 420 amino acid protein and *DhTRK1* and *DhHAK1* encoding K^+ transporters in halotolerant yeast *Debaryomyces hansenii*. These had sequences similarities with TRK and HAK transporters from *Debaryomyces occidentalis* and *Candida albicans*. They have concluded that *DHAL2* & DhTRK1 genes perform very well in the presence of Na and K ions, which could be an important factor responsible for salt tolerance in *D. hansenii*.

Impact on mycorrhizal interactions and biodiversity

Mycorrhizal fungi are one of the major components of the ecosystem and play a critical role in its sustenance and overall functioning. There are a number of studies supporting the fact that plant–fungus association imparts manifold benefits to the host plants, such as better water uptake, protection against several biotic and abiotic stressors, nutrient uptake, and cycling (Kumar & Atri 2018, 2023, Meddich et al. 2021, Jajoo & Mathur 2021, Xie et al. 2021). The response of host plants to the fungal symbionts is reported to be influenced by various factors such as soil fertility, functional characteristics of host plants, and complexity of the soil microbiota. (Hoeksema et al. 2010). Besides this, climatic factors and undergoing changes in these factors also influence the enormity and direction of plant responses to mycorrhizal partners (Kivlin et al. 2013, Mohan et al. 2014). Any change in the climate influences both partners individually, and they affect each other as well. Different fungal species forming mycorrhiza vary in their effects and influence on the growth and development of host plants (Smith & Read 2008, Kumar & Atri 2018, 2023). There are studies that support that enhanced CO_2 levels in the environment increase the population and fruiting of mycorrhizal fungi. Similarly increased temperature has also been reported to favor the relative degree of abundance of these fungi. Mycorrhizal fungi, besides increasing the productivity of host plants, also play an important role in reducing plant stress (Mohan et al. 2014). A substantial shift has been reported in mycorrhizal fungi, which has been directly linked with the tolerance of the host plants to climate change (Fernandez et al. 2016). There are also various studies reflecting the vulnerable effects of sub–optimum temperature on the colonization of roots with mycorrhiza, extraradical hyphal production, and the transfer of phosphorus and nitrogen to the plants (Liu et al. 2004, Chen et al. 2013). However, simultaneously, it has also been reported that the warming of the climate has a stimulatory effect on mycorrhization and all other associated activities. Studies of different plant species have shown that mycorrhizal fungi are very helpful for host plant species in combating heat and cold stress. The association of the AM fungus *Glomus fasciculatum* with *Cyclamen persicum* and *Zea mays* has been linked with an enhancement in the heat stress tolerance of the plant, a reduction in membrane lipid peroxidation, an increase in osmotic regulation of compounds, and an overall promotion of plant growth (Zhu et al. 2010, Maya & Mastubara 2013). Similar studies have also been conducted by Nogales et al. (2020) on 'Touriga Nacional' variety of grapevines by inoculating these with AM fungal species *Rhizoglomus irregulare* or *Funneliformis mosseae*. This association of grapevine with AM fungi is reported to help the plant in tolerating heat stress, especially heat shocks. Therefore, the increase in global temperature has been reported to result in increased mutual advantages to the mycorrhizal partners in particular and the proliferation of mycorrhizal associations in general (Ciais et al.2013).

Besides this, there are reports that changes in the carbon dioxide levels in the atmosphere also affect the mutual relationship between plants and fungi. It is a well–known fact that increased carbon dioxide levels in the atmosphere normally result in an increased rate of photosynthesis in plants and, thus increased availability of fixed carbon for fungi (Long et al. 2004, Walker et al. 2021). It is also reported to improve microbial activity and colonization in the soil, which in turn results in a supply of minerals like phosphorus, nitrogen, and zinc to the plants (Shao et al. 2018, Tran et al. 2021, Bhantana et al. 2021). Thus, the overall increase in atmospheric CO_2 concentration provides mutual benefits to the host as well as the associated fungal partner. All these effects of climate change on mycorrhizal fungi have been studied by investigators in the laboratory, which may not behave the same way under natural climatic conditions. A meta-analysis done by Durate and Maherali (2022) shows that there is great variability in AM responses towards temperature alteration and CO_2 concentration depending upon the species. In some cases, mycorrhizal colonization is promoted by an increase in CO_2 levels, while in the case of other species, no such effects were observed (Monz et al. 1994). There are some studies on the impact of increased temperature on the dispersal patterns of host species. In this regard, Walther et al. (2002) reported that the ECM species are shifting towards poles or higher altitudes due to the increasing temperature in the lower regions. Thus, mycorrhizal fungi give several advantages to the associated plants. They are reported to shield the plants against extinction by facilitating or retarding the dispersal of plants from unsuitable environments, alleviating the effects of abiotic stressors, or enabling such plants to adapt to new climatic situations. With changes in ecological niches and the availability of newer plant associates, fungal biodiversity will also change, which will have an immense influence on the area around. Mycorrhizal subterranean mushroom, *Tuber melanosporum*, is usually found in regions with a Mediterranean climate in a symbiotic relationship with tree roots. Over a period of time, due to the effect of drought on the Mediterranean habitat, the yield of truffles was adversely affected. To avoid drought, the investigators looked for alternative habitats in the northern maritime climate of the British Isles, where *T. melanosporum* gave an increased yield in comparison (Simões 2021).

One of the primary concerns is the impact of rising temperatures on the delicate balance between mycorrhizal fungi and their plant hosts. Some fungal species, particularly those adapted to cooler climates, may struggle to survive in warmer soils. This could lead to a breakdown in the symbiosis, leaving plants deprived of their fungal partners and potentially vulnerable to various stresses. Climate change is also predicted to bring more frequent and intense droughts, further jeopardizing mycorrhizal relationships. Warmer temperatures and altered precipitation patterns can also favor the growth of certain competitive fungal species, potentially displacing beneficial mycorrhizal fungi. This could lead to the formation of new, less efficient symbioses, limiting plant growth and nutrient uptake. The story of mycorrhizae and climate change is a powerful reminder of the interconnectedness of our planet. It highlights the urgent need for research, conservation efforts, and sustainable land management practices that prioritize healthy soil microbiomes and foster beneficial fungal partnerships. Protecting these unseen threads is not just about saving fungi, it's about safeguarding the foundation of our terrestrial ecosystems and the future of the countless species that depend on them.

The interaction between elevated CO2 levels and rising temperatures impact the diversity of arbuscular mycorrhizal fungi and their colonization of plant roots (Liu et al. 2023). Increased warmth leads to a higher allocation of biomass to roots, altering the root–to–shoot ratio, while changes in precipitation patterns and mycorrhizal partnerships affect how carbon is managed in terrestrial ecosystems. Both temperature and rainfall variations have diverse effects on the structures of mycorrhizal fungi, with warming having a more pronounced impact on ectomycorrhizal fungi compared to arbuscular mycorrhizal fungi (Zhou et al. 2022). These fungi possess traits that can help plants survive extinction risks and adapt to new environmental conditions, although these effects depend on specific contexts (Bennett & Classen 2020). Decreases in soil moisture reduce the diversity of arbuscular mycorrhizal fungal communities, leading to changes in root colonization and the density of spores. Temperature also influences the availability of water and nutrients critical for mycorrhizal interactions, although excessive heat can dry out the soil, hampering nutrient absorption. While fungal biodiversity appears to be only minimally affected by global changes, there is a noticeable increase in the abundance of plant–pathogenic fungi, particularly in ecosystems weakened by phenomena such as drought (Baldrian et al. 2022). The transition from mutualistic to pathogenic fungi poses a significant threat to ecosystem functioning, underscoring the need for further research to predict and mitigate the impacts of global changes on fungal communities.

Impact on lichen association and lichen-forming fungi

Lichens or, more appropriately, lichenized fungi are a mutualistic association of fungi, cyanobacteria, and green algae, which are highly sensitive to climatic variations and possess the capability to adapt to such changes. Among the different organisms, lichens are considered one of the best bioindicators of environmental changes and thus serve as a convenient model for monitoring climate change (Aptroot & von Herk 2007, Braidwood & Ellis 2012). Lichens are found in the most hostile environment on earth and are highly sensitive to environmental vagaries, including air quality, and show differential sensitivity towards a wide range of pollutants. Certain species are inherently more sensitive (*Usnea longissima*, *Ramalina conduplicans*, *Flavoparmelia caperata*, *Xanthoria elegans*, *Teloschistes flavicans*), while some species (*Dirinaria consimilis*, *Heterodermia diademata*, *Peltula euploca*, *Phaeophyscia hispidula*, *Pyxine cocoes*), show tolerance to high levels of pollutants (Shukla et al. 2014, Bajpai et al. 2014, 2016a, b, 2018, 2019). These characteristics make certain lichen species suitable for being utilized as indicator species (based on their sensitivity and tolerance) for various pollutants, including metals, metalloids, radionuclides, and organic pollutants. Besides this, many have been reported to have vanished in towns with poor air quality.

Lichen ecophysiology can be greatly impacted by climate change in several ways. Lichens' development, metabolism, and distribution can all be affected by variations in temperature, precipitation patterns, and air composition. The metabolism of lichens can be impacted by rising temperatures, which can alter growth rates and reproductive strategies. Changes in the distribution and composition of species may result from the success of certain lichen species in warmer climates while others may find it difficult to adjust. Lichen hydration levels can be impacted by modifications to precipitation patterns, such as changes in the quantity and frequency of rainfall. Desiccation stress in lichens can result from drier conditions, especially in species that depend on atmospheric moisture (Simões, 2021). Borge & Ellis (2024) showed decreased net growth for epiphytic lichen, *Lobaria pulmonaria* by the late 21st century, which was accounted for by prolonged climatic dryness and desiccation. On the other hand, some lichens can benefit from higher precipitation as it provides more moisture needed for development and reproduction. Changes in temperature and moisture levels may affect the symbiotic relationships within lichens, potentially altering their ecophysiology and overall fitness (Borge & Ellis 2024). There are evidences which suggest that lichens are responding to climate change in Western Europe. In these areas, epiphytic species are reported to be increasing instead of declining due to global warming, however, in comparison, terricolous species are reported to be declining. Lichen species most rapidly increasing in such forests are reported to contain green alga *Trentepholia as* a phycobiont partner (Aptroot & Herk 2007). Some lichen-forming fungi are reported to adapt to extreme environmental conditions like the surface of rocks and hot, cold, and dry areas. Such endolithic habitats provide some protection against inclement temperatures and deleterious solar radiation and help the fungi retain some amount of water, which prevents them from desiccation (Simões 2021). Despite significant advances in understanding lichen responses to climate, biases towards large high–latitude species and neglecting within–thallus dynamics hinder our predictions (Stanton et al. 2023). Overall, climate change poses significant challenges to lichen ecophysiology, with potential impacts on their growth, distribution, and ecological interactions. Monitoring and understanding these changes are crucial for predicting the future of lichen communities and their roles in ecosystems. Future work demands broader geographical and ecological coverage, to unlock the power of lichen ecophysiology for climate forecasting.

Fungi in relation to Food safety concerns under changing climate

There are a number of fungi that play a major role in the overall growth and development of plants in general and crops in particular through mycorrhization, which directly influences different agricultural practices, including irrigation requirements, crop rotation, optimal crop timing, and the propensity for crop contamination with fungal phytopathogens (Simões 2021, Pequeno et al. 2024). Although no major disruption to soil fungal communities has been observed so far, however, simulations predict significant shifts under global climate change. Under such a changing climatic scenario, plant–beneficial fungi appear to be vulnerable to decline, thus favoring plant pathogens and disease outbreaks. At the same time, an increase in global temperature has been reported to influence the abundance of soil–born plant pathogenic genera like *Alternaria*, *Fusarium*, *Venturia*, and *Phoma*. On exposure to high CO_2 concentrations and high temperatures *Fusarium verticillioides*, which is a maize pathogen, is reported to become more resilient with an increased ability to cause infection (Simões 2021). Warmer temperatures are expected to accelerate pathogens growth cycles, leading to a surge in their populations by harvest time. Higher temperatures combined with humidity empower pathogens of potato blight and Phoma stem canker, resulting in more severe infections (Gustafson 2022). At the same time milder temperatures are reported to allow fungal pathogens like *Phytophthora* spp. to remain active for a longer duration, leading to devastating tree death events like those reported in American chestnut populations (Gustafson et al. 2022, Singh et al. 2023). With the changing climate, many phytopathogens are expected to become active and affect agricultural crops leading to major economic losses. With the impact of rising temperatures, suitable tea plantation areas are expected to shrink by up to 34% by 2050 due to increased infection by fungal pathogens as these are expected to adapt and expand their range under the changed climate (Tibpromma et al. 2021). Though new regions might become available, they may harbor existing or new pathogens, further challenging tea cultivation. Therefore, agriculture–based economies will also have to change and adapt to survive the changing climate in the years to come. It is reported that the maize crop in Kenya will be largely affected in the coming decades by the increasing contamination of aflatoxins. Climatic variations have been reported to increase fungal colonization in cereal grains, dry beans, peanuts, cheese, coffee, cocoa, dried fruits, grapes, and wine, which will consequently result in an increase in the contamination of ochratoxin A in the derived products. Ochratoxin A is reported to be nephrotoxic, with health risks both for humans and animals (Simões 2021). With the changing climate, a rise in the rate of infection by *Talaromyces marneffei*, which occurs mainly in immunocompromised hosts, has been documented. This is a dimorphic fungus that grows as filamentous fungus or as unicellular yeast depending on the habitat's temperature. It is considered an emerging pathogen. *Aspergillus flavus*, another important pathogen of maize, when exposed to high CO_2 concentrations and high temperatures is reported to produce higher amounts of the carcinogenic aflatoxin B_1, with an increased risk for human and animal health. This species is reported to be highly resilient to all climate stressors (Simões 2021). Wheat blast, a devastating fungal disease, is also expected to expand its reach under the changing climate scenarios. It is observed that there will be a 13% decrease in global wheat production by 2050, primarily impacting the Southern Hemisphere due to increased suitability for infection (Pequeno et al. 2024). This highlights the urgent need for mitigation strategies to combat climate change to ensure food security in vulnerable regions. It appears that climate change is also agitating a hazardous mixture. Warmer and more humid weather encourages the growth of mycotoxins, which are fungus–produced byproducts that can poison crops and make people and animals sick. For instance, aflatoxin contamination in food crops presents a significant concern to public health, especially in underdeveloped nations (Perrone et al. 2020). As climate change progresses, the increased prevalence of mycotoxin–producing moulds, such as *Aspergillus flavus* and *Fusarium* species, poses a growing threat to global food security. Regions like Europe are experiencing shifts in mycotoxin contamination patterns, with heightened risks of cereal contamination by aflatoxins and other toxic metabolites. Urgent measures are needed to develop advanced diagnostic tools and understand the evolving biological dynamics between hosts and pathogens to mitigate the impact on agricultural cultivars and food safety (Kos et al. 2023).

Combating adverse effects of climate variation

Fungi play a vital role in fighting global warming in general and other associated adverse environmental vagaries plants face. These microbes are known to form symbiotic associations with the plants, which help facilitate their nutrition and protection against various stressors, including drought and pathogenic organisms. Such forest plants form rich forest cover, which plays a vital role in delaying the effects of global warming by absorbing excessive CO_2 released into the atmosphere due to anthropogenic causes. In this way, such plants with associated microbes serve as climate change warriors by sequestering the increased CO2 (Avrill et al. 2018). Fungi that thrive in changing climate conditions are reported to decompose plant cellulose more efficiently, potentially reshaping forest soil nutrient cycling across vast areas (Finestone et al. 2022). Besides releasing locked carbon, these microbes also play a significant role in the absorption of water, minerals, and nutrients. ECM also helps the trees absorb CO_2 faster and, in turn, helps offset climate change. As long as carbon molecules stay out in the forest, they stay away from the atmosphere, thus preventing them from contributing to global warming. Currently, forests are absorbing approximately one third of all the anthropogenic CO_2 emissions into the atmosphere A collaborative study from the University of Texas, Boston University, and the Smithsonian Tropical Research Institute discovered that the atmosphere receives positive gains from the relationship of plants with fungi, which helps in fighting against the stresses due to climate change impacting the growth of plants (Avrill et al. 2018). As far as fungi are concerned, in response to climatic variations, their increased adaptations have been reported at the genetic level, metabolic level, life cycle level, sporulation, behavior, modification of spore walls, melanization, formation of rhizomorphs and sclerotia and gelatinization of texture (Simões 2021). Thick walls of resting spores like chlamydospores, zygospores, and oospores provide protection from desiccation due to drought and high temperature (Aneja & Mehrotra 2015, Bidartondo et al. 2018). Many fungi are reported to form linear aggregates of parallel–running hyphae called rhizomorphs. These help the fungi survive under drought conditions. Some fungi, including *Rhizoctonia solani*, *Sclerotium rolfsii*, and *Claviceps purpurea*, produce resistant sclerotia under unfavorable climatic conditions. These structures remain dormant for a number of years and provide protection from desiccation and high temperatures (Bidartondo et al. 2018). Some of the fungal genera including *Auricularia*, *Tremella*, and *Dacrymyces*, are commonly referred to as jelly fungi, get shriveled up and become hard under drought conditions. However, upon exposure to moisture, they revive back to normal become gelatinized, and start growing. In *Pracoccidioides brasiliensis* and *Blastomyces dermatidi*, a rise in temperature serves as a morphogenetic trigger (Aneja & Mehrotra 2015, Bidartondo et al. 2018). Climate changes are reported to alter the structure of microbial communities by favoring the growth of fungi over other organisms due to the acidification of soils that tend to inhibit certain micro–organisms and favor fungal growth up to certain pH values (Simões 2021).

Conclusions and future perspectives

This review is a timely and thought-provoking read for anyone interested in the intricate dance between climate, our planet, and the often–overlooked fascinating world of fungi. It is a stark reminder that even the smallest organisms can have a profound impact on our future. If the climate keeps on changing at a present rate, fungi and lichens will exhibit a remarkable response which is important from the perspective of biodiversity and public health since climate change produces a confluence of factors that can act together to drive the emergence of new pathogenic races, increased virulence, mycotoxin production, increased resistance to fungicides and even loss of biodiversity due to change in habitats. Research on the effects of climate change on fungi, mycorrhiza, and lichens faces several limitations that warrant future investigation. Firstly, there is a lack of comprehensive long–term data on fungal populations and their interactions with other organisms in response to changing climatic conditions. Additionally, the complexity of fungal communities and their interactions with plants and other microbes makes it challenging to predict the precise impacts of climate change. Furthermore, the potential for synergistic effects between climate change and other stressors, such as habitat loss and pollution, remains poorly understood.

There are huge opportunities to undertake research for a much deeper understanding of the impacts of global climate change on fungi and their relation with other microbes and plants. While the impacts of climate change on fungi are undeniable, there are still many unanswered questions. Understanding how fungal communities shift, how they influence carbon cycling, and whether new fungal diseases might emerge are crucial research areas. The complex dance between climate, fungi, lichens, and mycorrhizae holds profound implications for our future. Future research efforts should focus on elucidating the mechanisms underlying the responses of fungi, mycorrhiza, and lichens to climate change, including their physiological adaptations and genetic variability. Long–term monitoring studies and experimental manipulations across different ecosystems are needed to assess the resilience of fungal communities and develop effective strategies for conservation and management in the face of ongoing environmental changes.

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