Perspective

Exploring extremophilic fungi in soil mycobiome for sustainable agriculture amid global change

Luis Andrés Yarzábal Rodríguez[1], Peggy Elizabeth Álvarez Gutiérrez [2], Nina Gunde-Cimerman [3], Jimmy Casto Ciancas Jiménez [4], Adrián Gutiérrez-Cepeda[5,6], Ana María Fernández Ocaña [7] & Ramón Alberto Batista-García [7,8] ✉

As the Earth warms, alternatives to traditional farming are crucial. Exploring fungi, especially poly extremophilic and extremotolerant species, to be used as plant probiotics, represents a promising option. Extremophilic fungi offer avenues for developing and producing innovative biofertilizers, effective biocontrol agents against plant pathogens, and resilient enzymes active under extreme conditions, all of which are crucial to enhance agricultural efficiency and sustainability through improved soil fertility and decreased reliance on agrochemicals. Yet, extremophilic fungi's potential remains underexplored and, therefore, comprehensive research is needed to understand their roles as tools to foster sustainable agriculture practices amid climate change. Efforts should concentrate on unraveling the complex dynamics of plant-fungi interactions and harnessing extremophilic fungi's ecological functions to influence plant growth and development. Aspects such as plant's epigenome remodeling, fungal extracellular vesicle production, secondary metabolism regulation, and impact on native soil microbiota are among many deserving to be explored in depth. Caution is advised, however, as extremophilic and extremotolerant fungi can act as both mitigators of crop diseases and as opportunistic pathogens, underscoring the necessity for balanced research to optimize benefits while mitigating risks in agricultural settings.

The Earth is warming much faster than ever[1]. At this trend, global warming will have severe consequences at the planetary level much earlier than expected, many of which will be even worse than predicted only a couple of years ago[2]. Some of these outcomes will seriously jeopardize the stability of many regions worldwide and, most notably, the adequate and sufficient food supply to feed a population estimated to reach 9.3 billion people by 2050[3]. Thus, feeding humans and livestock will only be possible with substantial modifications to our agricultural practices that, in addition, must have minimal environmental impacts. Indeed, although the "Green Revolution" made it possible to

[1]Carrera de Bioquímica y Farmacia. Grupo de Microbiología Molecular y Biotecnología (GI-M2YB). Unidad de Salud y Bienestar, Universidad Católica de Cuenca, Cuenca, Ecuador. [2]Tecnológico Nacional de México/IT de Tuxtla Gutiérrez, Tuxtla Gutiérrez, Chiapas, Mexico. [3]Departament of Biology, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia. [4]Fundación PROINPA, Cochabamba, Bolivia. [5]Instituto de Investigación en Salud, Facultad de Ciencias de la Salud, Universidad Autónoma de Santo Domingo, Santo Domingo, Dominican Republic. [6]Instituto de Química, Facultad de Ciencias, Universidad Autónoma de Santo Domingo, Santo Domingo, Dominican Republic. [7]Departamento de Biología Animal, Biología Vegetal y Ecología. Facultad de Ciencias Experimentales, Universidad de Jaén, Jaén, Spain. [8]Centro de Investigación en Dinámica Celular, Instituto de Investigación en Ciencias Básicas y Aplicadas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, Mexico. ✉e-mail: rabg@uaem.mx

BOX 1.

Agroecosystem models for the future I: Olive groves and plant probiotic-extremophilic fungi

Although they have already begun to be impacted at a global scale by extreme environmental conditions, traditional agroecosystems will be impacted even more in the coming years. The new environmental circumstances will impose further challenges to designing novel plant probiotics. One major bottleneck in this quest is testing their performance under field conditions[10]. On the opposite side, many microbial strains are prematurely discarded because of their poor performance in vitro[93].

A few proposals have been advanced to select the best PGPM to be applied in the field[94]. Nevertheless, the ultimate decision still relies on the analysis of results obtained from longitudinal field- studies. Thus, to select the best candidates among many extremophilic/extremotolerant fungi as plant probiotics we propose conducting long-term field trials on olive groves (*Olea europaea* L. subsp. *europaea*), as model agroecosystems for the future agriculture.

Olive groves dominate the landscapes of the Mediterranean Basin, where drought episodes are increasingly frequent and severe[95]. Different varieties of olive trees have evolved there for centuries under poly-stressful conditions: extreme soil oligotrophy, water scarcity, and wide temperature fluctuation across the year, among others. On the other hand, olive trees are frequently challenged by *Verticillium dahlia* and *Xylella fastidiosa*[96–98], two pathogenic fungi that cause severe plant damage and significant economic losses in Italy and Spain[98].

Arbuscular mycorrhiza fungi (AMF) are crucial in alleviating water scarcity in olive trees. Indeed, mycorrhized trees can withstand at least 40 days without irrigation because the osmotic response of the plant is faster than recorded in non-mycorrhizal trees, due to proline accumulation and an improved stomatal conductance[99–101]. The fungi that colonize the roots of olive trees are specific to the soil in which they grow, producing a more efficient plant-fungus symbiosis[102,103]. Therefore, olive groves represent a favorable setting to test new plant probiotics.

Interrogating the olive tree-extremophilic fungi symbiosis before implementing fungal probiotics in crop fields can help us answering interesting questions like: How do these extremophilic fungi elicit plant mechanisms to overcome water scarcity and other abiotic stresses? In the specific case of AMF, important questions also arise: Do these symbiotic relationships also trigger immune-type reactions in the plant that benefit both organisms? Is the secretion of exudates by mycorrhizal roots different depending on the type of fungus or the type of soil in which they grow? Do these exudates aim to attract extremophilic fungi to carry out symbiosis, or could they also be beneficial substances that prevent or attenuate other types of stresses, such as water scarcity? Does a AMF-colonized plant develop some memory to promote mycorrhization with other species of fungi? Could a mycorrhized plant develop a memory that defends it against future drought episodes? Does the benefit occur exclusively because the water absorption area is more significant as the plant is mycorrhized? Is it the fungus or the plant (or both) responsible for altering the composition of the rhizosphere?

Addressing these questions could help us updating agricultural practices to enhance olive crop resilience and productivity. Understanding these symbiotic mechanisms opens new avenues for sustainable agriculture, especially in arid and semi-arid regions facing climate change challenges.

meet the food needs of humanity in the second half of the 20th century, it is not feasible to continue with this production model based on the use of large amounts of agrochemicals (fertilizers and pesticides) that have caused so many environmental disturbances[4].

The use of inputs of microbiological origin has been proposed as a viable and promising alternative to intensifying agriculture sustainably, based on the rational exploitation of the ecological functions displayed by the so-called "plant-growth promoting microorganisms" (PGPM)[5]. Among these inputs stand out biofertilizers (i.e., products containing live microorganisms that participate in the process of supplying nutrients or hormones to plants)[6] and biopesticides (i.e., products containing microorganisms capable of antagonizing plant pathogens or inducing their defense response against these same pathogens)[7]. Nowadays, the term "plant probiotics" is increasingly used to refer to all types of PGPM[8,9].

Unfortunately, an increasing amount of evidence indicates that the efficiency of commercial plan probiotics depends on the ability of PGPM to deal with many abiotic- (temperature, acidity, salinity, among many others) and biotic factors (including the capacity to colonize roots or aerial parts of plants, the ability to survive and thrive in the soil, or the ability to outcompete native microorganisms that are part of the natural microbiome, among others), when released in the field[10]. In this context, extremophilic and extremotolerant fungi, which can grow and tolerate a wide range of extreme conditions[11–13], represent a promise for the future agriculture in the context of global change. For instance, besides controlling several pathogens, a few halotolerant fungi act as promoters of plant crops' growth under saline stress[14–19]. Drought can also be alleviated by xerotolerant fungi belonging to

Trichoderma, *Fusarium*, *Piriformospora* or *Alternaria* genera[20–22]. Similarly, some thermophilic fungi, like *Thermomyces lanuginosus and Curvularia protuberata*, can protect plants from heat[23,24]; on the opposite side, psychrotolerant strains of *Rhodotorula* sp., *Mrakia* sp., and *Naganishia* sp. can promote growth of *Solanum lycopersicum* at low temperatures[25]. Notwithstanding these emblematic examples, the field is still in its early stages, and it will be imperative to redirect its focus to speed up the exploration of novel PGP fungi (PGPF) adapted to poly-extreme environments, like the ones that will dominate future soil agroecosystems. (Boxes 1, and 2).

Extremophilic fungi stand out as key players in the quest for sustainable agricultural innovations, particularly due to their ability to thrive and multiply in conditions that are typically detrimental to most life forms[11–13]. These fungi have evolved to survive in environments with extreme temperatures, high salinity, or acidity among other challenging environmental conditions[26], making them highly valuable for agricultural use in soils and climates that challenge conventional crop production. By incorporating extremophilic fungi into plan probiotics, researchers and farmers can significantly enhance crop resilience and productivity[27]. Such fungi not only improve plant growth directly through symbiotic relationships but also contribute to soil health by facilitating its remediation when contaminated. Moreover, the unique stress-resilient traits found in extremophilic fungi, including their novel molecular mechanisms[11,28–34] and genes encoding stress-related proteins and extremoenzymes that help alleviate various stresses in other organisms, offer promising avenues for genetic transfer to crop plants[35,36]. This transfer would confer enhanced stress tolerance in crops, providing a robust defense against the

BOX 2.

Agroecosystem models for the future II: Quinoa cultivation in the Bolivian Altiplano and fungal plant probiotics

Quinoa (*Chenopodium quinoa*, Willd.) is a high-quality protein pseudocereal originating in the Andean region, whose main virtue as a food crop lies in its remarkable nutritional profile[104]. Quinoa contains higher amounts of protein, lipids, calcium, iron, zinc, and magnesium than regular cereals. These are among the reasons why the Food and Agriculture Organization of the United Nations (FAO) considers quinoa essential to eradicate hunger, malnutrition and poverty[105].

Still considered an underutilized crop, quinoa is expected to contribute to food security under current and future climate scenarios, because it can grow on arid, saline and nutrient deficient soils which, in addition, contain sand and volcanic ash, and low levels of organic matter (around 0.7%). Quinoa grows also at high altitudes (from 3600 to 4800 meters above sea level), under severe water scarcity (annual precipitation between 60 and 270 mm) and high Evapotranspiration Potential (between 357 mm and 577 mm). Finally, quinoa tolerates wide daily temperature ranges (between –11 °C and – 30 °C), and periodic frosting episodes (between 160 and 257 annually)[106]. These characteristics justify the proposal of quinoa as a model crop for tomorrow's agriculture[107].

Some quinoa-microbe interactions improve grain yields, and are especially relevant for quinoa cultivation expansion to different agronomical areas elsewhere in the world[105]. For instance, native strains of *Azotobacter* spp., *Bacillus* spp., *Flavobacterium* spp., *Pseudomonas* spp., and *Rhizobium* spp. have been isolated from farmer plots in Bolivia. Some of these strains are tolerant to extreme environmental conditions, can fix nitrogen and solubilize phosphorus, and produce secondary metabolites able to promote quinoa growth[108]. Even though quinoa-colonizing fungi have received much lesser attention, various *Trichoderma* species have been isolated from quinoa plants grown in traditional lands[108–110]. A few endophytici fungi, mainly belonging to the genera *Fusarium*, *Penicillium* and *Phoma* well known for alleviating abiotic stresses in other plant species, have also been detected in the root tissues of quinoa plants[110].

Plant probiotics developed with some of the abovementioned strains have been tested in the greenhouse and also under field conditions to validate their utility. The resulting products, well adapted to the soils surrounding Uyuni salt flat, have been certified and included in a crop management strategy and are now commercialized and available to farmers growing organic quinoa[108]. Nonetheless, research on this largely unexplored microbial biodiversity remains marginal, with almost nothing known yet concerning quinoa-associated extremophilic/extremotolerant fungi. Thus, there is plenty of room to test the potential of extremophilic fungi on quinoa growth and development in long-term assays, under extreme conditions in real-world settings.

environmental stresses associated with global climate change. Thus, exploiting the adaptive capabilities of extremophilic fungi could transform agricultural practices and foster sustainable food production on a global scale.

In contrast, extremotolerant fungi, while capable of surviving in harsh conditions, do not necessarily grow or metabolize optimally under such stresses[12]. These fungi are also tolerant to various extreme conditions like high temperatures, UV radiation, and desiccation, yet they are often found in a wide range of environments, not exclusively in extreme ones. This adaptability is largely due to their ability to switch on their stress response mechanisms only when needed, conserving energy and resources during less challenging periods. Poly-extremotolerant fungi, in particular, demonstrate a remarkable capacity to adapt to multiple types of extreme environments, reflecting their versatility (reviewed in ref.[12]). However, in their native extreme environments, both extremotolerant and extremophilic fungi tend to exhibit slower growth rates due to the demanding nature of these habitats. Interestingly, when placed in more favorable conditions, some of these fungi can significantly accelerate their growth rates, highlighting their latent potential for exploitation in more benign agricultural settings. This dual ability to endure extremes while also adapting to moderate conditions emphasizes the strategic advantage of extremotolerant fungi in developing environmentally friendly agricultural practices.

Recently, our research group published a comprehensive review that provided a variety of examples to illustrate the ecological functions of extremotolerant and extremophilic fungi, with a particular emphasis on their use as plant probiotics (reviewed in ref.[37]). Additionally, the review briefly touched upon ongoing projects that aim to harness the capabilities of these fungi to develop innovative biofertilizers[37]. In the end, we outlined a viewpoint on the significance of conducting a thorough examination of the molecular mechanisms that facilitate the interactions between plants and extremophilic/

extremotolerant fungi in extreme ecosystems. Nevertheless, our previous published review fails to offer a comprehensive perspective on this subject[37] (refer to the subsequent section), rendering this in-depth analysis a unique feature of the current review.

Here, we identify some areas that warrant further investigation to explore neglected aspects in the field of study. Additionally, we address some crucial factors that should be taken into account when considering extremophilic fungi as essential tools to develop plant probiotics. Even so, we equally caution against the potential threat posed by some of these fungi: their possible dual role as both biological control agents and opportunistic pathogens of mammals. Finally, we advocate for performing field-level investigations in long-term trials to fully explore these extremophiles' true potential. These two critical aspects represent a distinctive focus of the current Perspectives, addressing gaps from our previous work[37].

Knowledge gaps in the study of the interactions between plants and extremophilic fungi: a perspective analysis

Despite years of successful agricultural application of PGP bacteria, many bacteria-plant interaction mechanisms remain poorly understood (i.e., bacteria-mediated plant-epigenome modifications, bacterial inheritance via seeds, bacteria-virus interactions in soil and plants, potential effects of extracellular bacterial granules, secreted metabolites involved in the interspecies interaction, plant-microorganism signaling pathways, regulation of gene expression in plant stress responses, among others). In the case of fungi, the paucity of comprehension of the crosstalk mechanisms between microorganisms and plants is even more significant. Species of the genus *Trichoderma* are the most studied fungi concerning their beneficial interactions with different types of plants[38]. A closer look at these interactions has enabled the depiction of important molecular and cellular mechanisms that govern the fungal colonization of roots, the endophytic
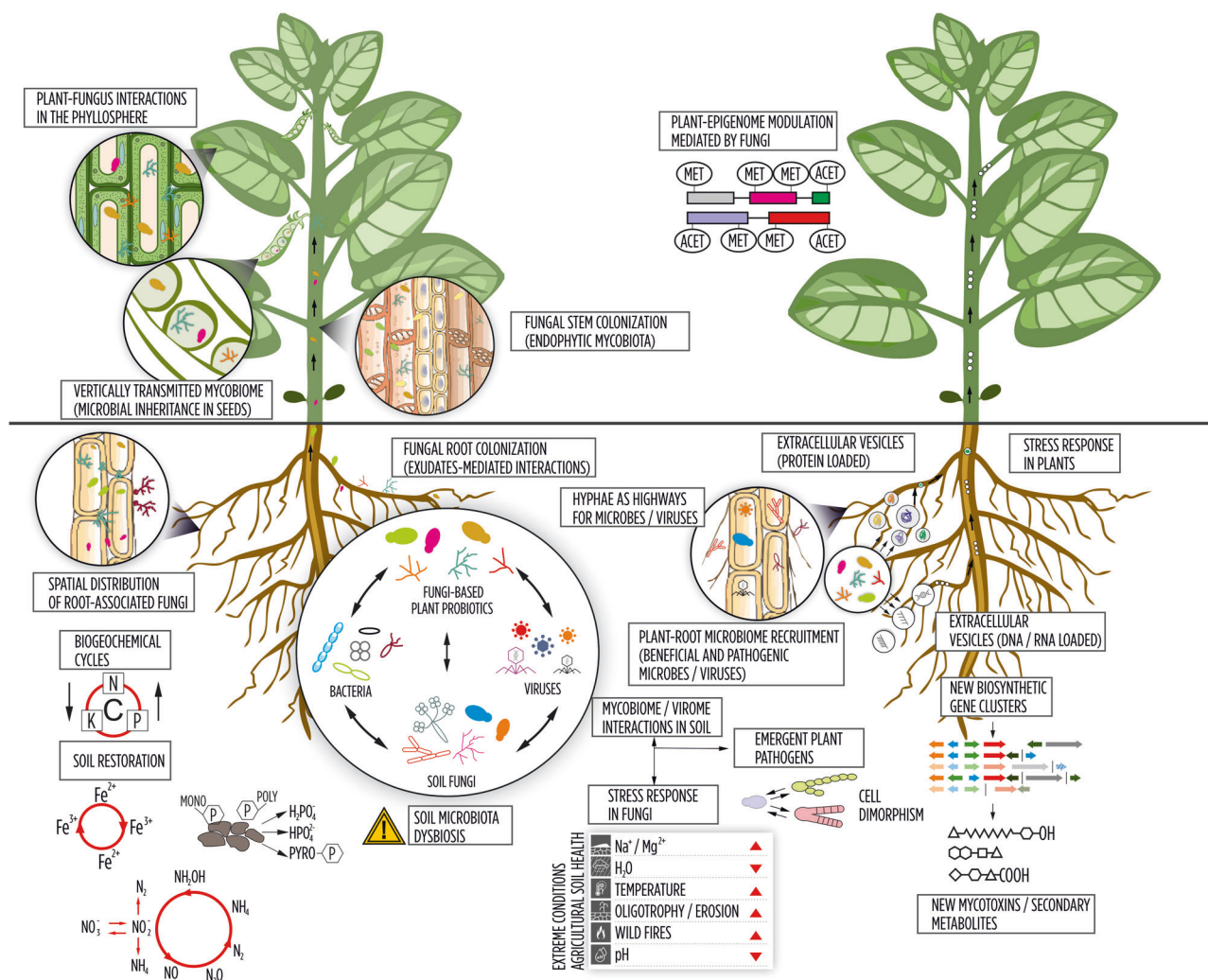
Fig. 1 | Unexplored or poorly investigated mechanisms in the context of plant-extremophilic fungi (*ExF*) interactions. These interactions occur at the phyllospheric, endospheric, and rhizospheric compartments and are discussed in detail in the main text. Eighteen subjects, including some molecular and cellular mechanisms, were identified and proposed as crucial to be explored in depth to understand these interactions. These subjects, presented here in a visual form, are: i) phyllosphere: presence/functions of *ExF*; ii) endosphere: plant epigenome modulation mediated by *ExF*, vertical inheritance of *ExF*, stem colonization by *ExF*, spatial distribution of *ExF*, microbial trafficking through *ExF* hyphae; iii) rhizosphere: *ExF* colonization and root exudates, *ExF* functions in biogeochemical cycles, interactions of *ExF* with the native soil microbiome and potential disturbances arising from such interactions, molecular cross-talk between *ExF* and native soil microbiome, outcomes of stressful conditions in *ExF* physiology, production and release of extracellular fungal vesicles (DNA/RNA/protein loaded), activation of repressed biosynthetic gene clusters, production of mycotoxins and emergence of extant plant pathogens. Digging into such subjects is critical to producing the fundamental knowledge needed to assist in rationally developing agricultural plant probiotics from (poly)extremophilic fungi in light of present and future global change scenarios.

behavior of some fungal species, and the repertoire of molecules that participate in the crosstalk between both partners, among other processes. However, numerous mechanisms still need to be studied, particularly in the case of (poly) extremophilic fungi. Understanding their significance during the interaction between these fungi and their plant hosts (Fig. 1) will unquestionably lead to a more rational design of novel fungal plant probiotics under the current global change scenario.

Within the context of microbial ecology and evolution, the roles played by pathogens and mutualists must be thoroughly reconsidered, particularly from the perspective of symbiotic relationships. Indeed, some symbioses established between microbes and plants can result in either mutually beneficial or detrimental effects, depending on factors like the environment and the life stage of the plants. However, there are still limitations in understanding how the continuum approach is applied to host-microbe pairs across different environmental and ecological conditions (reviewed in ref.[39]). Still, we know that variations

of the environmental conditions prevailing in a given agroecosystem can lead to changes in soil microbiomes' composition, structure, and functioning (= dysbiosis)[40,41]. The consequences of this phenomenon on the ecological services provided by a microbial community may be severe. Microbial dysbiosis may induce, for instance, some microbiome members to occupy different ecological niches. The most feared of these unexpected consequences in an agroecosystem is likely the switch from commensalism or mutualism to pathogenicity. By facilitating the emergence of new pathogenic strains and altering host-pathogen interactions and evolution, climate change exacerbates the dangers of outbreaks[42]. Therefore, further studies are urgently required to investigate the impact of global change, and specifically climate change, on the fungal populations present in the rhizosphere, endosphere, and phyllosphere of plants growing in extreme habitats and their potential as novel phytopathogens. The scientific value of this hypothesis is growing in the context of global change (see next section).

The fluxes associated with carbon metabolism in soil microbiomes may also be altered by dysbiotic events, induced by extreme environmental conditions. New metabolic functions might emerge, ultimately leading to a modification of the microbial metabolism in the soil, all of which may adversely affect the rates at which organic matter is turned over in soil ecosystems. Thus, it is necessary to conduct long-term mesocosm experiments to gain a better understanding of the types of microbial interactions and host-microbial associations that may occur in future soils[39,43], and how, within the context of biogeochemical cycles, these microbial relationships could modify the recycling of organic matter and the metabolic fluxes in the soil.

The idea of microbial consortia as the functional workforce of the rhizosphere, examined recently by Williams et al.[44], should be thoroughly understood to design new plant probiotics to increase food production in the era of global change. Toward reaching this goal, we must first fully comprehend the complicated interactions between extremophilic fungi and other members of the soil microbiome not only in terms of the microbial associations established in the soil, but also at the phyllosphere, rhizosphere, and endophyte levels. Thus, in-depth investigations of the intricate dynamics within the soil microbiome are required.

Extremophilic fungi's hyphae could play a crucial role in transporting both helpful and harmful microorganisms to the rhizosphere of plants, i.e. microbial trafficking through hyphal highways. How extreme environmental conditions will determine which microbial populations would be attracted to plants—and thus determine which ecological functions will be promoted or disfavored—must be investigated. The nature of the interactions taking place between native archaeal, bacterial, and fungal populations and the newly introduced fungal probiotics in an agroecosystem also represents a gap that should be investigated. In addition, we need to fully understand the processes that mediate how extremophilic fungi colonize the plant's stem, leaves, and roots, and how they are assisted in this process by the soil- or plant microbiota.

At present, we know little or almost nothing about the relationships established between fungi and their viruses in soil[45]. We know, for instance, that viruses linked to extremophilic fungi can significantly affect plant physiology and survival under stressful conditions, alleviating the impact of a specific abiotic stress[46]. Even though it is almost certain that fungal plant probiotics will also interact with the soil virome, biology inadequately covers these interactions and their biological significance. For example, it is unknown how viruses can infect plant probiotic fungi and how viral populations change over time due to a molecular link with fungi. All these gaps need to be comprehended urgently, including the possibility to genetically manipulating mycobiomes and viromes, which appears as an exciting avenue to explore.

While our understanding of the role played by the epigenetic machinery in modulating the plant's response to environmental stresses is increasingly growing, less attention has been given to the role of epigenetics in establishing and regulating beneficial interactions between plants and other organisms (reviewed in refs. 47,48). Recent studies have emphasized the significance of DNA methylation in symbiotic and commensal interactions. However, comprehensive and consistent information regarding the involvement of epigenetic mechanisms in mycorrhizal symbiosis is scarce[48]. Investigating the modifications induced in the plant epigenome by the microbial partners colonizing the rhizosphere, the endosphere, and the phyllosphere is imperative, particularly in the case of extremophilic fungi. Further investigations are required to comprehend the molecular interdependencies among various regulatory layers and the influence of naturally occurring epigenetic variations in plants on their interactions with other organisms.

The production of extracellular vesicles by extremophilic fungi could be one of the primary mechanisms enabling them to modify the genetic expression of their plant hosts[49,50]. These vesicles can contain non-coding RNAs, such as lncRNA and microRNA, which could alter plants' transcriptional and protein expression profiles, altering, in turn, their resilience towards environmental challenges. On the other hand, vesicles containing DNA or proteins may also significantly determine how plants respond to stressors; thus, they may contribute to the expression of resistance mechanisms against biotic and abiotic stresses. We must, therefore, dig into how the environmental -(poly)-extreme- conditions prevalent in agroecosystems could also influence the production of fungal extracellular vesicles, modify their content, and consequently, influence the type of epigenetic regulation that fungi can trigger on their plant hosts.

The metabolism of extremophilic fungi is extraordinarily versatile, highly flexible, and adaptable, and it is influenced by environmental conditions[28,51,52]. Owing to these features, extremophilic fungi provide many valuable ecological services—for instance, degradation and recycling of soil´s organic matter—by producing extracellular enzymes such as cellulases, hemicellulases, peroxidases, proteases, or amylases, and other stress-tolerant proteins (i.e., hydrophobins), adapted to extreme pH, temperature, salinity, and low water activity conditions, among others (reviewed in ref.[53]). In global change scenarios, we must examine the possible metabolic changes that extremophilic fungal ecotypes will experience and how these changes might impact biogeochemical cycles, nutrient mobilization, and further improve soil health.

Secondary metabolism also plays a crucial role in modulating the interactions of fungi with their plant hosts. Environmental conditions influence the expression of numerous clusters of fungal biosynthetic genes[54], many of which could be essential for promoting plant health and growth[55]. The aforementioned becomes pertinent in a context of global change, if we consider that environmental conditions that induce microbial stress may promote the expression of dormant biosynthetic genes and enable the synthesis of metabolites possessing unique chemical structures and, consequently, functions unknown in the interplay between fungi and plants. How the produced metabolites will interfere with the promotion of plant growth, how will these metabolites contribute to reprogramming metabolic processes that affect or improve the plant's physiology, and how will these metabolites influence the soil microbiota, among other questions, must be answered to consider the formulation of new fungal plant probiotics. It is foreseeable that beneficial crosstalk between extremophilic fungi and plants would result in plant transcriptional reprogramming, activating numerous host genes associated with resistance to fungal pathogens, insect pests, and drought, among other desired effects. Particular attention should be devoted to understanding the molecular changes occurring in plants when colonized by extremophilic fungal endophytes and how these changes relate to the control of microbial metabolism at various levels.

A relatively new and insufficiently explored area pertains to the study of metabolic remodeling of plants when colonized by beneficial microorganisms. Studying these interactions between plants and extremophilic fungi, under conditions of biotic and abiotic stress, provides unique opportunities to unravel the secrets behind these interactions. The acquired knowledge will be highly significant in future agricultural scenarios, where the plant's metabolism could be altered by both extreme conditions—resulting from global change—and the introduction of unconventional plant probiotics, such as those containing extremophilic fungi.

How extreme conditions will affect the production of mycotoxins by toxin-producing fungi[56] is an additional significant challenge that must be addressed. In addition to studying this particular aspect, the use of fungal plant probiotics in the context of global change will also require the implementation of new analytical technologies to identify and quantify these mycotoxins, as well as to develop new laboratory assays to demonstrate their biological activity and estimate their risks.

We must also learn how extremophilic fungi, including filamentous and yeast-like species, can thrive and proliferate in various soil environments. Toward this goal, we envisage it will be necessary to conduct mesocosm experiments, simulating current and more extreme environmental conditions, to investigate the impact of changes in soil properties (including moisture, particle aggregation, porosity, nutrient availability, pH, oxygen availability, or presence of emerging micropollutants, among others), on the establishment, survival, persistence, and performance of exogenous plant probiotic extremophilic fungi.

Lastly, we also identified other topics that should be addressed, such as the existence of spatial profiles of fungal colonization concerning different plant organs; the mechanisms enabling the vertical transmission of extremophilic fungi through seeds, ensuring their inheritance across filial generations; the impact of biofertilizers containing extremophilic fungi on the molecular crosstalk in the rhizosphere; the significant consequences on the microbiota and the plant with regards to cell signaling induced by fungal plant probiotics under extreme conditions; the possibility that obligate extremophilic fungi could establish mycorrhizal symbiosis; and the role of the extremophilic members of the soil and plant microbiome in establishing ecologically relevant symbiotic relationships, known and unexplored, among others.

Biocontrollers and opportunistic pathogens: The danger beneath two-faced traits

As said before, extremotolerant and extremophilic fungi are promising alternatives to manage the diseases or damages caused to crops by pathogens, pests, and herbivores on a warming planet. Alas, a kingdom-wide phylogenetic analysis suggests significant co-occurrences of opportunistic and biocontrol traits at the level of fungal orders[57]. In other words, some of the traits relevant for microbial antagonism towards plant-pathogens (= biocontrol) may also play a role in mammalian opportunism, making using extremophilic fungi for biotechnological purposes risky.

This hypothesis is well illustrated by the example of the closely related species *Aureobasidium pullulans* and *Aureobasidium melanogenum*: they are both remarkably poly-extremotolerant, being able to multiply under hypersaline (3.0 M NaCl), acidic/basic pH (3–10), low temperature (4 °C), and oligotrophic conditions[58]. On the other hand, they are markedly different: *A. pullulans* is currently considered safe from an animal health perspective and can be used to control plant pathogens. That is why commercial *A. pullulans*-based biocontrol agents (e.g., Blossom Protect®, Boni Protect®, AureoGold®) are available to prevent preharvest and postharvest fruit and vegetable diseases. However, *A. melanogenum* causes human opportunistic infections in immunocompromised patients, in part due to its ability to grow at 37 °C[59]. Unfortunately, due to the recent redefinition of *Aureobasidium* species, distinguishing between *A. pullulans* and *A. melanogenum* is often impossible[60].

Other examples of poly-extremotolerant fungal species, proposed as potential biocontrollers but also shown to behave as opportunistic pathogens under various environmental conditions, are the halophilic yeast *Debaryomyces hansenii*, the neurotropic black yeast *Exophiala dermatitidis*, the thermotolerant yeast *Meyerozyma guilliermondii*, and the pink/red pigmented widely distributed yeast *Rhodotorula mucilaginosa* (reviewed in ref.[58]).

Based on the facts mentioned above, plus other experimental evidence, Zajc et al.[58]. noticed an overlap between traits associated with opportunism and traits desirable for biocontrol purposes. The authors proposed that thermotolerance, oligotrophism, siderophore production at 37 °C, urease activity, melanization, and biofilm formation (all traits considered beneficial for biocontrol purposes) are also characteristics that increase the likelihood that fungi will cause opportunistic infections in mammals. In the present work, we

extended this hypothesis by adding a few additional mechanisms and updating the position of others (Fig. 2). On the side of biocontrol desired traits, these newly added mechanisms include cellulase/hemicellulase and pectinase production[61,62]. On the side of "two-faced traits", we added biosynthesis of volatile compounds[63,64], capsule synthesis[65,66], protease/gelatinase activity[67,68], and *quorum sensing*[69,70].

In the current perspectives we placed thermotolerance in the intersection of both types of traits ("two-faced traits"), considering that in a warming planet, this ability will be crucial for biocontrollers to act efficiently in the field. As various studies have shown, fungi can readily acquire thermotolerance without requiring extensive genomic mutations to develop this complex phenotype. For example, experimental evolution studies allowed to develop thermotolerant strains of *Metarhizium anisopliae*, a versatile entomopathogenic fungus with significant biotechnological potential for biocontrol. The temperature-adapted variants grew better at higher temperatures, resulting in enhanced biological control efficacy[71]. However, this study left unanswered questions regarding whether the increased pathogenicity was directly linked to the thermotolerant phenotype.

Unfortunately, the available evidence shows that thermotolerance in extremotolerant or extremophilic fungi with biocontrol activities would act as an additional virulence factor in the event of becoming pathogenic. As previously noticed by Casadevall[72], fungal adaptation to higher temperatures is one of the most important factors explaining the emergence of new fungal pathogens, like *Candida auris*. Even though the origin and emergence of *C. auris* remain unclear due to limited knowledge of its ecology and distribution, a working hypothesis suggests it may be the first fungal disease linked to global warming[73]. The recent isolation of *C. auris* from samples collected in the coastal wetlands of the tropical Andaman Islands, India, supports this idea, indicating that the pathogen can persist in the environment and that human infections could stem from environmental sources[74].

Besides *C. auris*, other fungal pathogens have surfaced, leading to notable outbreaks that correlate with climate change[75–77]. For instance, *Batrachochytrium dendrobatidis*, an aquatic chytrid fungus, is a pathogen that has emerged as a significant threat to amphibian diversity in Australia, North America, and South America, especially in areas undergoing warming trends[78]. This fungal pathogen is increasingly prevalent in tropical regions, where higher temperatures enhance its pathogenic fitness[79,80]. *Cryptococcus deuterogattii* is also a thermotolerant fungus that has emerged in temperate regions of western Canada and the Pacific Northwest of North America, leading to numerous infections in humans and animals[81]. This species demonstrates a notable level of thermotolerance compared to other members of the *C. gattii* complex[82].

Rhodotorula mucilaginosa, is another thermotolerant basidiomycetous yeast, able to tolerate a wide temperature range from near freezing to human body temperature[83,84]. The species has been found in various environments such as cold and hypersaline conditions, but is also present in plant surfaces, uranium mineral heaps, acidic and oligotrophic settings and contaminated water sources (reviewed in ref.[51]). Despite its potential use as a biocontrol agent for fruit preservation, and a plant probiotic[25,85], *R. mucilaginosa* is considered as an emerging opportunistic pathogen, capable of causing severe infections in humans[86]. Similarly, *Meyerozyma guilliermondii*, formerly known as *Pichia guilliermondii*, is a versatile and thermotolerant yeast, capable of growing at 40 °C[87,88]. Although it can act as an antagonist of some fungal pathogens[89], it also behaves as an opportunistic pathogen in immunocompromised individuals, causing skin lesions and osteomyelitis[87,89].

Climate change has also been proposed as a catalyst for the emergence of new thermotolerant and virulent fungal lineages. For example, *Puccinia striiformis*, the etiologic agent of the most devastating global wheat disease, is increasingly prevalent in warmer
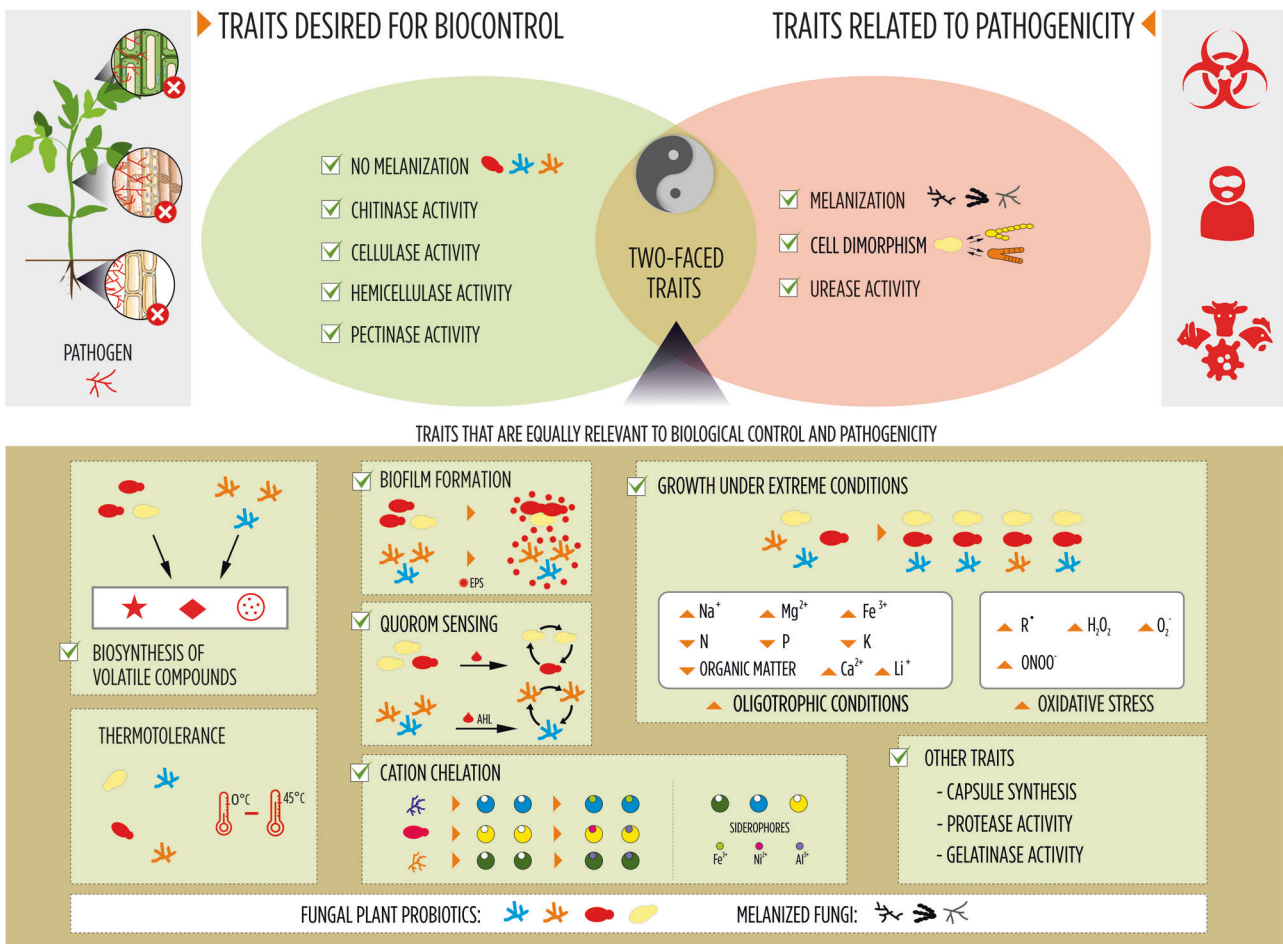
Fig. 2 | Traits of extremophilic/extremotolerant fungi desirable for biocontrol of plant/fruit pathogens/spoilers in extreme environments under climate change scenarios, which can lead to pathogenesis in animals and humans (adapted and extended from Zajc et al.)[58]. Three types of traits are presented: i) traits desirable for the biocontrol of plant pathogens; ii) traits involved in pathogenesis in animals and humans; and, iii) two-faced traits, displayed by pathogenic fungi and also relevant for biocontrol.

regions. Indeed, some thermotolerant variants of *P. striiformis* have emerged in recent years, expanded into new geographical areas and are more virulent than the original strains[90]. *Fusarium graminearum*, a mycotoxigenic species and significant phytopathogen for cereal crops, has also emerged as a pathogen in warm agroecosystems. This species is highly thermotolerant, and produces increased amounts of mycotoxins at high temperatures and under water scarcity conditions[91]. Some researchers suggest that *F. graminearum* has expanded its range into warmer environments due to global warming[92]. Likewise, climate change seems to have influenced the distribution of other fungal pathogens, including *Coccidioides immitis*, the thermotolerant *Apophysomyces trapeziformis*, and other soil-borne fungi such as *Talaromyces marneffei*, *Blastomyces*, *Histoplasma*, and *Paracoccidioides*[75,76].

In summary, there seems to be little doubt that the emergence of thermotolerant variants of some fungal species, exhibiting significantly different disease profiles from those currently recognized[75,76], is related to climate change and represents a potential threat to human and animal health. However, as we said before there is a growing need for thermotolerant fungi able to thrive and support crop production under elevated temperatures. Therefore, as we explore using extremophilic and thermotolerant fungi for sustainable agriculture in a warming world, it is crucial also to carefully assess and manage the potential risks associated with their (potential) pathogenicity and ensure a balanced approach towards their utilization in agricultural practices.

Final comments

Fungal plant probiotics and extremotolerance: navigating alternate routes for sustainable agronomy in the era of global warming

Despite the commercial success of bacterial PGPM, fungi remain comparatively understudied, even though they display unique attributes and remarkable plant growth-promoting functions. This lack of information, even more pronounced when considering extremophilic and extremotolerant fungi, is striking if one considers their remarkable potential as plant probiotics for a warming planet. Indeed, in the face of the formidable challenges posed by global climate change, the need for sustainable agricultural practices and innovative solutions is paramount. Within this context, both extremophilic and extremotolerant fungi are notable for their ability to endure extreme environmental conditions and to promote plant growth, through direct and indirect mechanisms. Thus, using plant probiotics based on PGP-extremophilic fungi emerges as a green paradigm offering multifaceted contributions to plant well-being and environmental resilience.

However, the interactions between plants and extremophilic fungi still need to be explored, highlighting a crucial research gap. Therefore, comprehensive investigations into the underlying fungus-plant interaction mechanisms are imperative for successfully developing and deploying plant probiotics. Integrating advanced 'omics' technologies, including genomics, transcriptomics, proteomics, and metabolomics, can help us better understanding the biotechnological potential of extremotolerant fungi and could clear the way for

precision agriculture. In addition, a paradigm shift from single-strain probiotics to synergistic consortia—known as Synthetic Communities (SynComs)—, is also needed to take profit of the remarkable versatility exhibited by fungi in controlling various plant stresses and pests.

As we tread into this exciting frontier, caution is warranted. In the face of global change, the critical importance of thermotolerance in developing biocontrol agents is evident. As temperatures rise, the safe and efficient operation of extremophilic fungi becomes imperative. However, the potential adaptation of these fungi to higher temperatures introduces a need for vigilant strain selection and continuous monitoring to mitigate the risk of unintended pathogenicity.

In summary, throughout this perspective article, we insist on the urgent need to turn our attention to this fascinating group of microorganisms and join efforts to address major gaps in our current understanding of the mechanisms driving fungal-plant interactions, particularly in extreme environments. Thanks to these collective actions, we believe we will contribute to ensuring the success of sustainable agricultural practices, and to warrant food security in a planet increasingly facing extreme climatic conditions. The untapped biotechnological potential of extremophilic fungi holds one of the keys to reaching these goals.

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Author contributions

L.A.Y.-R. and R.A.B.-G. conceived and designed this work and wrote the first draft of the manuscript. J.C.-J., A.G.-C., and A.M.F.-O. prepared text boxes. P.E.A.-G., A.G.-C., J.C.-J., A.M.F.-O., L.A.Y.-R., and R.A.B.-G. prepared and edited the figures. N.G.-C. participated in writing the first draft of the manuscript and with L.A.Y.-R., R.A.B.-G., and P.E.A.-G. edited the final version. All authors commented on the figures and previous versions of the manuscript. All authors read and approved the final manuscript.

Competing interests

The Authors declare no competing interests.

Additional information

Correspondence and requests for materials should be addressed to Ramón Alberto Batista-García.

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