The poly-extreme tolerant black yeasts are prevalent under high ultraviolet light and climatic seasonality across soils of global biomes

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Summary

Black yeasts are among the most stress-tolerant organisms of the planet, thriving under all types of terrestrial habitats and extreme environments. Yet, their global patterns and ecology remain far less studied, limiting our capacity to identify the main environmental drivers of these important organisms across biomes. To fill this knowledge gap, we analysed topsoils from 235 terrestrial ecosystems across and within globally distributed climate groups (i.e. dry, temperate and continental). We found that soils are important repositories of black yeasts, and that ultraviolet light, fine soil texture, and precipitation seasonality are the most consistent environmental factors associated with their diversity across biomes. Finally, we identified *Exophiala* and *Cladophialophora* as the most dominant black yeasts genera in soils across the globe. These findings provide novel evidence of global distribution of black yeasts and their key environmental predictors, giving

new insights for speculating the evolution and spreading of these extreme-tolerant organisms throughout both natural and human associated extreme environments.

Introduction

Within the Fungal Kingdom, the terms black yeasts refers a group of taxonomically heterogeneous ascomyceotus fungi, from taxonomic and phylogenetic perspectives, belonging to three classes (i.e. *Dothideomycetes*, *Eurotiomycetes*, and *Arthoniomycetes*). Yet, these highly melanized fungi (or black yeasts) are unified by some morpho-physiological traits that are infrequent in the fungal kingdom such as meristematic growth (i.e., conversion towards isodiametric expansion), thick multi-layered cell walls, and exo-polysaccharide production (Sterflinger, 2006; Dadachova and Casadevall, 2008; Sterflinger *et al*., 2012; Selbmann *et al*., 2015; Cordero and Casadevall, 2017; Mattoon *et al*., 2021). Most of them are also very slow growing, forming microcolonies on hard surfaces as rocks; for all these reasons, they are also named as microcolonial or meristematic fungi. These characters enable black yeasts throughout specialization in poly extreme-tolerance (Gostinčar *et al*., 2010), and capacity to exploit extremely inhospitable environments, including anthropogenic polluted environments, attesting evidence of a resistance to poly-extreme conditions that is even higher than other life-forms (Gostinčar *et al*., 2010; Vázquez-Campos *et al*., 2014; Gümral *et al*., 2016; Onofri *et al*., 2020; Schultzhaus *et al*., 2020).

The discovery of these constitutively melanized yeasts in extreme environments contributed to inform us on the origins of life on our planet by tremendously expanding our knowledge on how life can adapt and reproduce in the harshest conditions (e.g. dryness, UV and ionizing radiation, contamination from oil, hot and cold temperature, oligotrophy) (e.g. Gunde-Cimerman *et al*., 2004; Dadachova and Casadevall, 2008; Ametrano *et al*., 2019). Past and ongoing works have broadened the boundaries of habitability far beyond those considered possible until a few decades ago. Such studies reported that black yeasts

are not only able to thrive under a such a broad spectrum of parameters on Earth but a few of them, globally considered the best eukaryotic test organisms for astrobiological studies, can also survive in the dried state space environment characterized by cosmic and solar radiation, high vacuum, as well as Mars-like conditions (e.g. Zakharova *et al*., 2014; Selbmann *et al*., 2018; Malo and Dadachova, 2019). Their persistence in extreme habitats also represent a paramount resource in addressing major global challenges, playing an essential role in geological processes in harshest ecosystems, including organic and inorganic transformations and element cycling, bioweathering, and mycogenic mineral formation (Gorbushina, 2007; Gadd, 2017). It was considered that these melanized organisms were sparse, and their presence limited to extreme ecosystems such as polar and tropical environments, acidic and hydrocarbon-contaminated sites, radioactive sites such as the reactor 4 of Chernobyl, in the bottom of the Dead Sea, and exposed bare rocks (e.g. Perini *et al*., 2019; Selbmann *et al*., 2021; Baron *et al*., 2021). Yet, for many species, their natural habitat is still unknown and hence their actual ecology remains enigmatic. Recent studies reported them also as fundamental inhabitants of Antarctic soils (Canini *et al*., 2021). Despite their prominent contribution to key terrestrial processes, the proportion of black yeasts has been largely neglected in both regional, continental and global-scale soil surveys (Maestre *et al*., 2015; Cox *et al*., 2016; Eldridge and Delgado-Baquerizo, 2018; Egidi *et al*., 2019; Větrovský *et al*., 2019; Regmi and Huettmann, 2020). Thus, we are still lacking a systematic and comprehensive assessment of the global patterns and environmental factors associated with their diversity and community composition in soils across biomes, which may allow us to better understand the ecology and environmental preferences of these important organisms.

Our study aimed to provide novel insights into the identity, global distribution, and environmental drivers of black yeasts in natural ecosystems at a global scale. To achieve this aim, we analysed soils from 235 natural ecosystems across six continents, and identified the consistent environmental drivers of black yeasts across and within biomes. This database includes a wide variety of bioclimatic regions (e.g. dry, temperate, and continental), covering ~73% of the environmental conditions found on Earth (Supporting Information; Egidi *et al*., 2019) and have been previously used to understand the distribution of dominant bacteria and fungi globally (Delgado-Baquerizo *et al*., 2018; Egidi *et al*., 2019).

Results

Using amplicon sequencing targeting the fungal internal transcribed spacer (ITS) region, we identified 24 391 fungal phylotypes in our global survey. We found 2732 phylotypes belonging to the ecological group of black yeasts (see Methods and Supplementary Table S1 for a complete list). Together, black fungal taxa represented between 2% and 21% of all the ITS sequences at a given site, contributing to ca. 14% of the total reads identified as fungi. The largest percentage of black yeasts belonged to *Eurotiomycetes* (ca 7% of the total sequences identified as fungi), followed by *Dothideomycetes* while a few *Arthoniomycetes* were scarcely retrieved in our global survey (ca. 3% and 1% of the total sequences identified as fungi, respectively). Black fungal orders with the highest relative abundances included *Chaetothyriales* (5.8%, *Eurotiomycetes*) and *Capnodiales* (2.5%, *Dothideomycetes*), followed by *Dothideales* (1%, *Dothideomycetes*), *Lichenostigmatales* (0.8%, *Arthoniomycetes*), and *Venturiales* (0.3%, *Dothideomycetes*). At finer taxonomic level, we found that *Herpotrichiellaceae* was by far the most predominant family (Fig. 1A).

We detected the presence of soil black yeasts at 98% of surveyed locations, with a significant, albeit weak, substantial variation in richness across the sites (Fig. 1B). The distribution of black yeasts in soils slightly differed across biomes (Fig. 1C), although the richness was particularly high in the dry biome, and differed markedly even across continents; the highest richness was found in Australia, while the lowest in Africa (Fig. 1D). Yet, some areas exhibited a high number of black fungal phylotypes; in particular, temperate forests, dry forests and cold grasslands had much greater richness compared with other ecosystems (Fig. 1B). Conversely, less diverse black fungal communities were detected in the soil of cold and tropical forests.

We then aimed to determine the main environmental factors associated with black yeasts across and within dominant biomes in our dataset (dry, continental and temperate). Our Random Forest (RF) models explained 56%, 37%, 43% and 47% of the variation in the distribution of black yeasts diversity in the whole global dataset, dry, temperate and continental climates, respectively (Fig. 2). These models provided evidence that UV light, fine texture (Clay + Silt), and precipitation seasonality (PSEA) were consistent predictors ($P < 0.05$) of black yeasts distribution across three major biomes (i.e. dry, continental and temperate climates) (Fig. 3). These environmental variables were also important predictors at global scale. Thus, UV light, Clay + Silt, and PSEA were the most important universal predictors of black yeasts diversity for both the entire globe and temperate, continental and arid biomes. On the contrary, ecosystem type (e.g. forests and grasslands) was not linked ($P > 0.05$) with the richness and relative abundance of black yeasts. Significant associations ($P < 0.05$) were also obtained
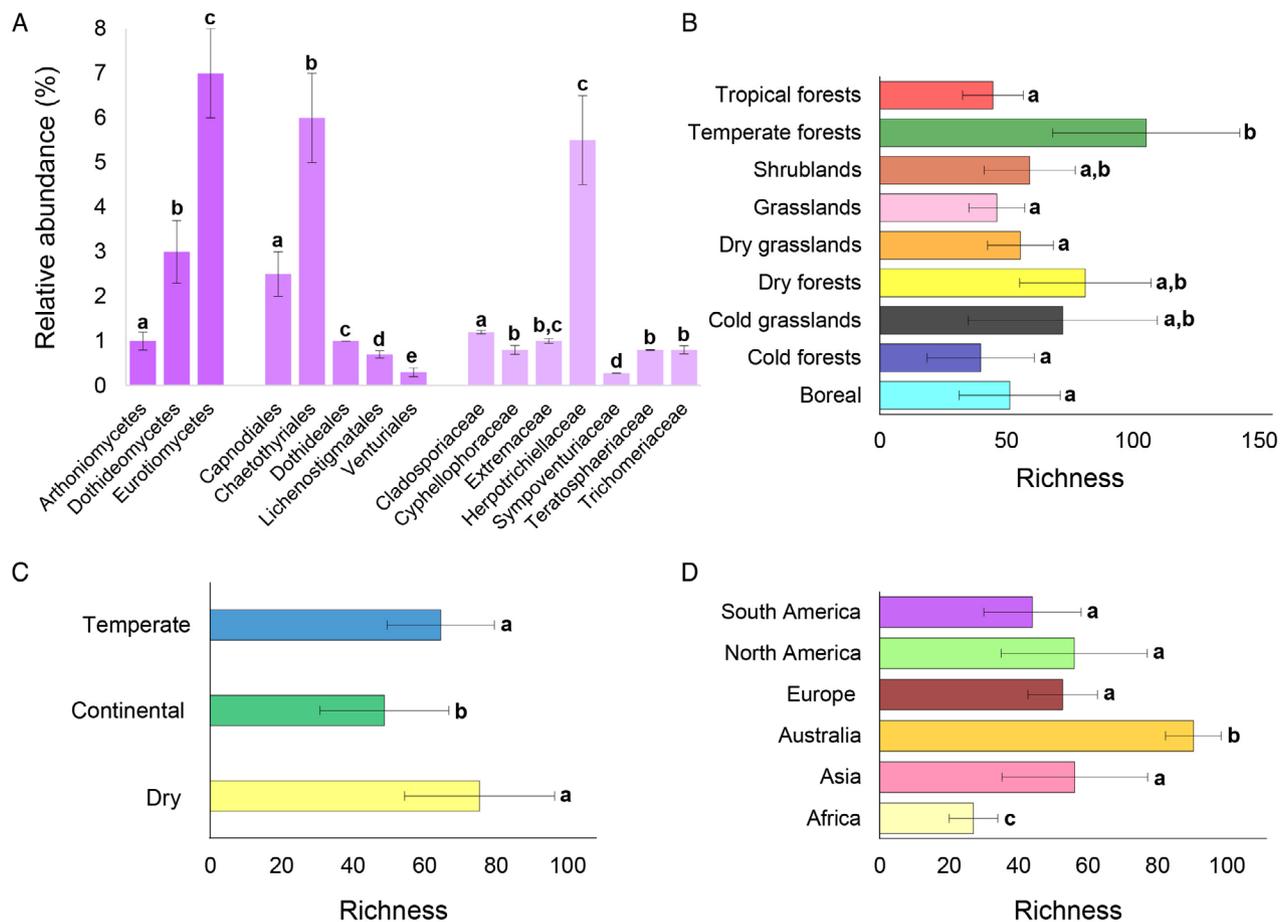
Fig. 1. Relative abundance and diversity of black fungi worldwide ($n = 237$).
A. Relative abundance (percentage of all ITS sequences; mean $\pm$ s.e.) of the most common black yeasts identified at class, order, and family taxonomic level across all sites.
B–D. Mean ($\pm$ SE) black yeasts richness across major ecosystem types (B), three globally distributed biomes (C), and continents (D). Ecosystem type classification followed the Köppen climate classification and the major vegetation types found in our database. Grasslands include both tropical and temperate grasslands. Shrublands include polar, temperate and tropical shrublands. Dry grasslands include dry ecosystems dominated by different levels of grass and shrub cover. Letters indicate differences found through post hoc PERMANOVA.

when controlling for spatial autocorrelation (i.e. using latitude and longitude as controlling matrix).

Additional correlation analyses revealed that UV light, Clay + Silt, and PSEA consistently promote or limit black yeasts richness across the three major global biomes. For instance, the negative association with Clay + Silt and PSEA is shown in the temperate and arid biomes, respectively. A positive association with UV light was found in the dry biome and also at global scale (Fig. 3). Yet, we showed that, globally, % of fine texture and PSEA had a negative relationship ($P < 0.05$) with richness. Overall, similar patterns were observed when all biomes were analysed together in the global dataset ($n = 235$; Fig. 3), which also included samples from polar and tropical biomes. Generally, we found that most of the ecological factors negatively or positively associated with the richness of black yeasts

were also correlated with their increasing or reducing relative abundance.

When the three biomes were analysed separately from the global dataset (Supporting Information Fig. S2), the elevation was the most important predictor in arid ecosystems, showing a weak negative relationship with black yeasts diversity, while total soil nitrogen was the most important soil predictor limiting fungal richness in continental ecosystems. Ultimately, the aridity index was the most important climatic predictor for temperate climates and showed a negative relationship with black yeasts richness.

We then asked whether the black yeasts phylogenetic and community composition was correlated with environmental factor we considered in this work. This analysis was based on unweighted UniFrac distances, which incorporate the phylogenetic relatedness of the
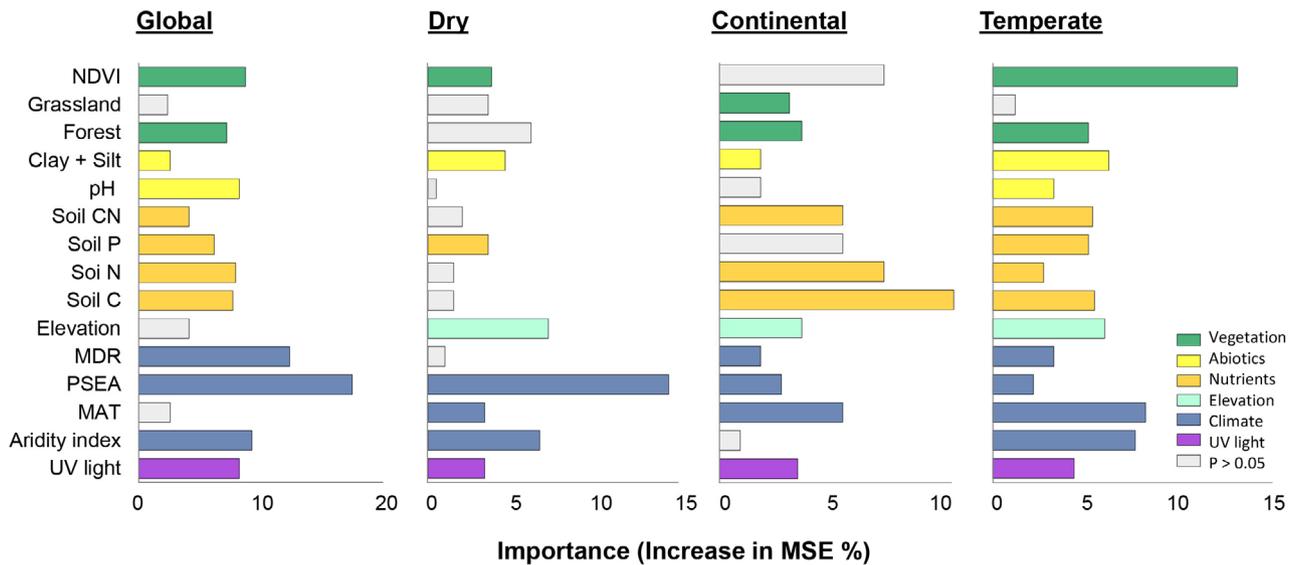
Fig. 2. Identifying the most important predictors associated with black yeasts. Results from a Random Forest model aiming to identify the main significant (*P* < 0.05) environmental predictors of black yeasts diversity (B). *MSE*, mean square error. Coloured and grey columns represent *P* < 0.05 and *P* > 0.05, respectively. MAP, mean annual precipitation; MAT, manual mean temperature; MDR, mean diurnal temperature range; PSEA, temperature precipitation seasonality; NDVI, normalized difference vegetation index. The aridity index, precipitation/potential evapotranspiration, and lower values of aridity index indicate higher aridity.
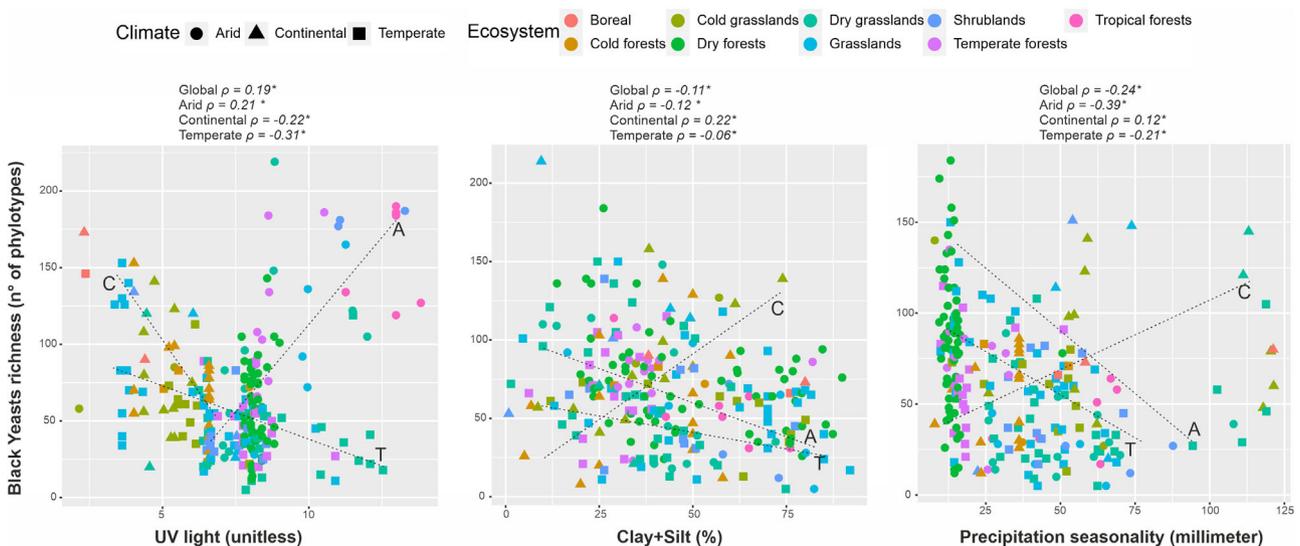

Fig. 3. Scatterplots showing Spearman correlations between universal environmental predictors and black yeasts richness across the globe. Significant (*P* < 0.05) correlation coefficients are shown in the upper part of each panel. Dashed lines indicate fitted lines expresses the relationship between points within each biome (A: arid; C: continental; T: temperate).

taxa in the dataset when comparing the similarity between samples. The ecosystem and continent origin was found to be significantly correlated with the pattern of black yeasts composition (*P* < 0.05; Supporting Information Fig. S3) as well as with UV light, Clay + Silt, PSEA, MAP, and Aridity Index, confirming findings from RF modelling (Supporting Information Table S2). On the other hand, no significant correlations were obtained between black yeasts phylogenetic composition and the microbiota composition and Soil C, Soil CN, Soil pH, and NDVI.

On average, the surveyed soils were dominated by a few black fungal genera (top 10% in relative abundance, and occurring in >50% of all sites), which include *Exophiala*, and *Cladophialophora* (*Herpotrichiellaceae*; class *Eurotiomycetes*) (Supporting Information Figs. S4 and S5a), which together accounted for more than 25% of the retrieved ITS sequences classified as black yeasts.

Some dominant genera are affiliated with the family *Cladosporiaceae* (*Cladosporium*; class *Dothideomycetes*), here represented mainly by the species *C. delicatum* (>80%). The family *Cladosporiaceae* includes constitutively melanized air-borne worldwide-distributed fungi, but are not accounted as black yeasts; here, we maintained this third most abundant melanized group in the subsequent analyses to compare and highlight differences in the effect of considered parameters on black yeasts and not black yeasts groups. *Cladophialophora* spp. were almost all unidentified (ca. 80%) while *C. bantiana*, *C. boppii*, *C. minutissima*, *C. potulentorum*, and *C. sciallae* were present in lower percentage (1.5%, 1.2%, 3.5%, 1%, and 1.6%, respectively). The genus *Exophiala* was dominated by *E. equina* (38%) followed by *E. nigra* (12%), *E. crusticola* (6%), *E. xenobiotica* (5.5%), *E. brunnea* (3.6), and *E. opportunistica* (3%).

On average, we found distinct proportions of the dominant genera across both ecosystems and continents (Supporting Information Fig. S5b,c) with the greatest relative abundance of black yeasts in dry grasslands and Africa, respectively. However, the relative abundance of the three dominant genera varied across biomes and ecosystems, particularly between black yeasts and not black yeasts groups. Notably, for example, we found higher proportions of *Cladosporium* in drylands (dry forests, dry grasslands) and cold grasslands compared with those in boreal and cold forests. Instead, higher proportions of *Eurotiomycetes* (*Exophiala* and *Cladophialophora* spp.) were found in temperate forests, and particularly dominating in Australia. The genus *Cladosporium* prevailed in North America, instead (Supporting Information Fig. S5d).

Subsequently, we sought to identify the major predictors of the distribution of dominant black yeasts genera worldwide using a combination of RF and correlation analysis. The results consistently indicated that MDR was the most important factor associated with the relative abundance of *Exophiala*, while the Aridity Index was a significant predictor of the relative abundance of *Cladosporium* (Supporting Information Figs. S6 and S7). The richness of *Cladophialophora* abundance was significantly correlated with multiple soil properties (i.e. soil P and soil pH), and net primary productivity (i.e. NPP; MODIS NDVI) attributes (Supporting Information Fig. S8). In addition, overall, the richness of the three dominant black fungal genera had significant associations with UV light and elevation (Supporting Information Fig. S9).

Discussion

This study presents the first assessment of the global distribution of soil black yeasts based on ITS high-throughput sequencing and reveals which genera are dominant worldwide. Our sampling campaign covered the nine most common terrestrial biomes of the world, surveyed across 235 sites from 6 continents, making the present global database one of the most inclusive for fungi (Egidi *et al*., 2019). Our results indicate that black yeasts can be relatively abundant in topsoils from natural ecosystems worldwide, representing almost 15% of the total ITS sequences retrieved from our database. In particular, they were largely dominated by *Eurotiomycetes*, a monophyletic group comprising two major subclasses (Eurotiomycetidae and Chaetothyriomycetidae) of very different ascomycetous fungi (Geiser *et al*., 2006). In contrast, *Dothideomycetes*, the most ubiquitous and diverse class in the fungal kingdom (Schoch *et al*., 2009) and its sister class *Arthoniomycetes*, which represents the largest taxonomic group of primarily lichenized fungi outside *Lecanoromycetes* (Schoch and Grube, 2015), were represented by a lower percentage of ITS sequences.

We also identified major orders and families of black yeasts in soils at a global scale. Members of *Chaetothyriales* were found as the most abundant. This order comprise species with disparate ecologies, possessing a high degree of versatile extreme-tolerance (Quan *et al*., 2020), including aquatic, rock-inhabiting, ant-associated, and mycoparasitic life-styles, as well as species that tolerate toxic compounds. Some *Chaetothyriales* lineages are also particularly known through the black yeasts and filamentous relatives that cause opportunistic infections in humans (Teixeira *et al*., 2017). Within this order, the family *Herpotrichiellaceae* was predominant in this study, representing almost half of the sequences classified as black yeasts. This family harbours a vast diversity of polyphyletic asexual morphs, which include both saprobic species on plant debris and clinically important species such as opportunistic taxa that cause a wide array of clinical syndromes in cold- and warm-blooded vertebrates (Crous *et al*., 2007; Seyedmousavi *et al*., 2013). The potential pathogenicity of a species is partly determined by its natural ecological niche (de Hoog, 1993). Dothideaceous black yeasts are xerotolerant rather than pathogenic; herpotrichiellaceous fungi, instead, likely have high competitive ability and are found in rather special niches as secondary saprophytes. Man-made environments can provide an alternative habitat for species in this family having opportunistic potentialities, promoting the selection of virulent strains (Zalar *et al*., 2011); yet, since opportunists are generally incapable of the host-to-host transmission and lack specialized virulence traits, opportunistic infections should be seen as an evolutionary dead end and unlikely to lead to true pathogenicity (Gostinčar *et al*., 2018).

Other families, are here less represented; *Trichomeriaceae*, which includes epiphytic (Chomnunti *et al*., 2012) as well as rock-inhabiting species (Isola *et al*., 2016), and *Epibryaceae* that encompasses mainly fungi occurring in lithic and soil habitats or on vascular plants (Gueidan *et al*., 2014), were barely found. The order *Capnodiales* and its families (i.e. *Teratosphaeriaceae*, and *Extremaceae*) have been globally found at low abundance in this study. *Capnodiales*, encompassing morphologically and ecologically diverse fungi with different lifestyles and modes of nutrition, represents the second largest order in *Dothideomycetes*, including saprobes, plant and human pathogens, mycoparasites, lichenized, epi-, ecto- and endophytes and, most importantly, some species that have evolved and adapted to thrive on bare naked rock surfaces (namely rock-inhabiting fungi, RIF). In particular, for their ability to thrive in harshest conditions such as drought, temperature and pH extremes, excessive radiation, and oligotrophy, RIF are accounted as the most resistant eukaryotic organisms known to date (Coleine and Selbmann, 2021). The most stunning endurance is displayed by *C. antarcticus*, isolated from the McMurdo Dry Valleys of Antarctic desert, which still survived after exposure to high doses of space-relevant gamma (6 Co; up to 117.07 kGy) that is almost 30 000 times that of human cells and 5000 times that of *Escherichia coli*, treated with deuteron (2H; up to 1500 Gy), and sparsely ionizing (X-rays up to 300 Gy) radiation (Onofri *et al*., 2020). The presence of these potentially highly resistant but scarcely competitive black yeasts in soils worldwide may be due to a random transportation by air circulation; once reached the ground their physiological characteristics may allow them to persist, even if at low occurrence, and eventually multiply and propagate under conditions that could inhibit the growth of more competitive but less resistant species; for instance, we found that UV light, positively correlate with both richness and relative abundance of black yeasts.

We further characterized the distribution of black yeasts across different ecosystems and continents and found that their global distribution was variable. The black yeasts richness was particularly high in temperate (i.e. temperate forests) and dry (i.e. dry forests) biomes, suggesting that distinct patterns could be related to the specific climatic conditions across continents (Bowker *et al*., 2005; Rodriguez-Caballero *et al*., 2018; Liu *et al*., 2021). For instance, in our dataset, we found particularly high black yeasts richness in the Australian continent, which encompasses numerous drylands sampled sites.

Our combined analyses of machine learning RF modelling, Unifrac distance, and correlations suggested that, from the wide range of selected environmental factors included here, UV light, soil fine texture (i.e. Clay + Silt), and precipitation seasonality were the most important universal predictors of black yeasts phylogenetic composition and diversity both within and across the three globally distributed biomes differing markedly in vegetation, climate and soil types. The importance of seasonality and fine soil texture in shaping the soil microbial community was recently demonstrated at global scale (Delgado-Baquerizo *et al*., 2016). In addition, soil texture is an important predictor in promoting soil fungal richness globally (Xia *et al*., 2020; Ding and Eldridge, 2020), which is consistent with the results of a recent study conducted on black yeasts from soils of Antarctic desert (Canini *et al*., 2021). On the other hand, high levels of UV light are known to reduce the abundance of several fungal lineages (Pfendler *et al*., 2019) as well as other microbial groups (e.g. bacteria) (Santos *et al*., 2012).

Remarkably, in our work, we found that UV light had an important capacity to predict and promote black yeasts distribution in dry environments. Such a relationship between UV light and black yeasts diversity has not been described previously for natural arid terrestrial ecosystems worldwide. We found increasing richness with higher UV light levels. In particular, there was evidence of a positive relationship between an increase in UV light from intermediate to high (i.e. from 0 to 14 when 0 means minimal UV exposure risk and 16 extreme risk) levels of intensity and higher black yeasts richness. Some black yeasts are, in fact, given the pivotal role of melanin, are exceptionally adapted to resist to high radiation environments such as deserts or mountains located at high elevation that are typically exposed to high UV radiation (Coleine *et al*., 2021). For examples, the black yeast *C. antarcticus* was proved to survive increasing UV-B (280–360 nm) irradiation (Selbmann *et al*., 2011) doses corresponding to over five to eight times the Antarctic terrestrial UV-B irradiance, which is substantially higher than elsewhere on Earth (50%–130% more UV radiation reaching the Earth's surface) (Madronich *et al*., 1998). As UV radiation greatly contributes to global warming (Bornman *et al*., 2015), it is now becoming urgent, in an era of rapid desertification and climate change, to understand connections between increasing levels of UV radiation and changes in species composition of soil microbial communities at a global scale with potential subsequent destabilization of ecosystem functioning.

In our work, soil pH was a poor predictor of the richness and relative abundance of the whole black yeasts community. This result is consistent with other global studies, which reported a significant correlation of pH and soil elements with a few particular fungal functional groups such as mycorrhizae (Tedersoo *et al*., 2012; Põlme *et al*., 2013) and a generally minor influence of edaphic characteristics on other fungi (Garcia *et al*., 2018; Egidi *et al*., 2019). Strikingly, no single variable could predict the distribution of black yeasts across

the three global biomes, but that specific influences are limited to particular biomes. For example, we found that the elevation and soil total nitrogen were the major predictors of black yeasts diversity in dry and continental biomes, respectively. Aridity index, instead, was a potential predictor in temperate biomes. As this index is a measurement of temperature and precipitation patterns, changes in aridity, predicted by current global change models (Berdugo *et al.*, 2020; Martínez-Valderrama *et al.*, 2020; Lian *et al.*, 2021), are expected to likely change the distribution of these organisms over the next century.

To detect and characterize the globally dominant soil black yeasts taxa, we selected those fungal phylotypes that were abundant (top 10% most common phylotypes sorted by their percentage of the total ITS rRNA reads), frequent (i.e. occurring in at least one third of the samples from a given biome), and had the highest habitat breadth (i.e. being dominant in at least one third of the sampled ecosystems). To the best of our knowledge, we reported for the first time the extensive dominance of a few phylotypes (*Exophiala* and *Cladophialophora*) from fungal communities across a broad range of soils and environmental conditions globally, highlighting their similar environmental preferences (i.e. UV light) to the total black yeasts community. The results of RF and correlation analysis revealed distinct predictors for the different dominant genera. For example, climate was important in predicting the relative abundance of *Exophiala* (mean diurnal temperature range and aridity, respectively), but not *Cladophialophora*; while arid conditions might favour some black yeasts taxa (Coleine *et al.*, 2021), high levels of hydration and moist conditions are known to promote their proliferation (Chowdhary *et al.*, 2015). Conversely, albeit soil pH should not be considered a potential predictor of total black yeasts diversity, we found that it was an important factor influencing *Cladophialophora*, suggesting that this genus might be sensitive to even small changes in chemical soil composition. Such differences in habitat preferences for dominant black yeasts confirm the importance of soil properties and climatic parameters in determining the composition and community assembly dynamics of fungi in soil (Bahram *et al.*, 2018). Notably, in addition to their saprobic life-styles, members of the genera *Exophiala* and *Cladophialophora* comprise several saprotrophic species on plant debris and species of important medical significance such as those frequently encountered in human infections, ranging from mild cutaneous lesions to fatal encephalitis opportunistic (Zeng *et al.*, 2007; Badali *et al.*, 2008). In particular, the presence of melanin and the ability to assimilate alkyl benzenes have been suggested to play an important role in opportunism and in evasion from the host defence (Najafzadeh *et al.*, 2013). We hypothesize that possessing disparate life-styles, ecologies and ability to colonize

multiple niches by these fungal lineages might be essential in defining habitat breadth, and consequently dominance, in terrestrial ecosystems. However, future soil surveys need to be performed to clarify the effects of environmental factors on the distribution of black yeasts, especially in the regions that are less well studied such as Russia, China and Africa.

Overall, our work paves the way for a deeper understanding of the global diversity and ecology of these exceptionally resistant organisms on terrestrial ecosystems. In particular, we underline the fact that precipitation seasonality, soil texture, and UV light play critical roles in driving their distribution at a global scale and may substantially modify the community under environmental changes. We also identified environmental preferences of the prevalence of dominant genera within and across three globally biomes. Besides, untangling the role, ecology, and distribution of stress-resistant microorganisms will be even more significant in the near future, as extreme ecosystems are continuously increasing in extension and prevalence due to global environmental changes and anthropogenic activities. This new knowledge will be of paramount importance to develop approaches and strategies aimed at preserving soil microbial diversity and functionality worldwide. Finally, by improving our understanding of the environmental factors that limit or promote occurrence of these stress-tolerant microorganisms in contrasting regions of Earth, our work may have also implications to disentangle how life may evolve and persist under extreme conditions of a warming and drying world and speculate the possibility of life in other planetary bodies, as for Mars or other habitable exoplanets.

Methods

Study areas and environmental conditions

We used a dataset from a global field survey (Egidi *et al.*, 2019) (https://figshare.com/s/9772d3162542 6d907782) to identify the distribution and ecological drivers of black yeasts in soils worldwide. Briefly, composite bulk soils (0–7.5 cm depth) under the dominant vegetation were collected from 235 sites (Supporting Information Fig. S1) located in 18 countries across nine ecosystems (temperate, tropical and dry forests, cold, tropical and arid grasslands, shrublands, and boreal forests) and six continents, excluding Antarctica. Locations were selected to provide a solid representation for most environmental conditions (e.g. climate, soil and vegetation types) found on Earth. For example, mean annual temperature and precipitation seasonality in these locations ranged from $-11.4°C$ to $26.5°C$ and 7%–127%, respectively. The composite soil samples consisted of

10–15 soil cores. Collected soils were homogenized and sieved through an ethanol-cleaned 2.0 mm sieve. One subsample was stored at $-20°C$ for molecular analysis, and the rest of the soil was air dried for physicochemical analyses. We measured soil texture (% of fine fractions: Clay + Silt), total organic carbon (soil C) (Anderson and Ingram, 1993), total nitrogen (soil N), and total phosphorus (soil P) concentrations as detailed in Maestre *et al*. (2012). Soil pH was measured with a pH metre in a 1:2.5 (w/w) soil : water mixture (Maestre *et al*., 2012).

Climate variables including mean annual temperature (MAT), precipitation seasonality (PSEA), and mean diurnal temperature range (MDR) were collected from the WorldClim database (https://www.worldclim.org), which has a 1 km resolution (Hijmans *et al*., 2005). The aridity index (precipitation/potential evapotranspiration) for each location was obtained from the Global Potential Evapotranspiration database (van Straaten Oliver and Bossio, 2006), using interpolations from the WorldClim database. Lower values of aridity index indicated more hot/dry conditions, and higher values indicated cool/wet conditions. We used the Aridity index rather than mean annual precipitation because aridity includes both mean annual precipitation and potential evapotranspiration and is therefore a better measure of the long-term water availability at each site.

We used the normalized difference vegetation index (NDVI) as our proxy for net plant primary productivity (NPP; Pettorelli *et al*., 2011). This index provides a global measure of the 'greenness' of vegetation across Earth's landscapes for a given composite period, and thus acts as a proxy of photosynthetic activity and large-scale vegetation distribution. NDVI data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA's Terra satellites (http://neo.sci.gsfc.nasa.gov/). We calculated the monthly average value for this variable between the periods of 2003 and 2015 ($\sim$ 10 km resolution), when all soil samplings were conducted. We also obtained information on annual ultraviolet index (UV index) from NASA's Aura satellite (https://neo.sci.gsfc.nasa.gov), which has a 50 km resolution. The UV index is a measure of the intensity of UV radiation ranging from 0 (minimal UV exposure risk) to 16 (extreme risk).

To avoid biases associated with having multiple laboratories analysing soils from different sites, all the samples were analysed at the Universidad Rey Juan Carlos (Spain).

Analyses of soil fungal community

Total microbial DNA was isolated from freeze-dried soil using the MoBio Power Soil DNA Isolation Kit (MoBio Laboratories, Carlsbad, CA, USA) according to the manufacturer's instructions. Soil fungal communities were analysed by targeting ITS region 2 using primers FITS7 (GTGARTCATCGAATCTTTG) and ITS4 (TCCTCCGC TTATTGATATGC) and an Illumina MiSeq platform (2 $\times$ 300 PE). The primers were modified with unique 8-bp Multiplex Identifier (MID) tags and adaptors. Bioinformatics processing was performed using a combination of Usearch and Unoise as previously described (Egidi *et al*., 2019). Briefly, all reads were quality filtered and dereplicated with the USEARCH pipeline, and low-quality bases were end-trimmed before merging. All the merged reads had an expected error <0.5; the quality-filtered reads were clustered into operational taxonomic units (OTUs) or phylotypes of the length of 180 bp, at 97% similarity thresholds using UPARSE (Edgar, 2013). Fungal taxonomy was then annotated against the UNITE (Abarenkov *et al*., 2010) fungal database (v.7.2), using the SINTAX algorithm with a ≥80% probability threshold, and produced an OTU (phylotype) table (Kõljalg *et al*., 2005).

As the main purpose of this study was to focus on black yeasts, ITS sequences belonging to this group (i.e. members of *Capnodiales*, *Venturiales*, and *Dothideales* in the class *Dothideomycetes*; members of *Chaetothyriales* in the class *Eurotiomycetes*; members of *Arthoniales* and *Lichenostigmatales* in the class *Arthoniomycetes*) were filtered and used for downstream analysis. These ITS sequences ($n = 2732$) were then searched against the GenBank repository using the BLAST function and ITS_RefSeq_Fungi database. The relative abundance of the black yeasts was then calculated using the rarefied OTU table, as the sum of the relative abundance (%) of all the fungal sequences.

Statistical analyses

We used post hoc PERMANOVA analysis to compare the richness and relative abundance of black yeasts across ecosystems and continents. We also focused on those locations for which we had sufficient information to model the distribution of black yeasts diversity within different biomes. In particular, we focused on 223 locations across six continents (Supplementary Fig. S1) that included three major global biomes as reported by Delgado-Baquerizo and Eldridge (2019): (i) dry ($n = 102$), (ii) temperate ($n = 81$) and (iii) continental ($n = 40$) ecosystems. Together, these biomes cover more than 70% of terrestrial ecosystems on Earth (excluding Antarctica). The biome grouping used in this study is based on the Köppen climate classification (Kottek *et al*., 2006), one of the most widely used climate classification systems. We then conducted cross-biome analyses using the 235 locations included in the global

dataset, which also included tropical and polar ecosystems.

We used RF models to identify those statistically significant ($P < 0.05$) predictors of the richness of black yeasts and the proportion of dominant black fungal taxa across the globe. This approach enabled us to identify the importance of each predictor variable by evaluating the decrease in prediction accuracy. Increases in the percentage of mean squared error (MSE) were calculated to estimate the importance of factors contributing to the richness and relative abundance of the dominant black fungal genera. Greater values of MSE% indicated a greater importance of variables. These analyses were conducted using the rfPermute package of the R statistical software (http://cran.r-project.org/). The variables included in the models were spatial (elevation), environmental (UV light, mean annual temperature, aridity index, mean diurnal temperature range and precipitation seasonality), soil properties (pH, soil C, soil N, soil CN, soil P, and texture), and vegetation (ecosystem type and NDVI). The most common vegetation types (forests and grasslands) were included in the model as categorical variables with two levels: 1 (a given ecosystem type, that is forests or grasslands) and 0 (remaining ecosystem types). Shrublands were not available for all biomes and were not explicitly included in our analyses. These analyses were conducted, using the rfPermute package of the R statistical software (http://cran.r-project.org/). In addition, to exclude possible confounding effects due to spatial autocorrelation of environmental variables, we repeated the correlation analysis between the main environmental variables and black yeasts richness and relative abundance, while controlling for space (e.g. excluding latitude and longitude matrices in the RF modelling).

We also conducted Spearman correlation analyses to evaluate the associations between climate, vegetation, soil properties and the richness and relative abundance of the dominant black fungal genera (top 10% in the relative abundance and occur in >30% of all the surveyed locations). We used the Spearman rank correlations to measure the strength and direction of association between two ranked variables as they do not require normality of data, and linearity is not a strict assumption of these analyses. We used a false discovery rate approach to determine adjusted P values for all the correlations to control for spurious (false positives) correlations.

Further, to assess whether the phylogenetic and compositional differences of the black yeast populations found in different samples depict the environmental differences among samples, we calculated the weighted Unifrac distance among samples described according to the relative abundance of black yeasts 'phyloseq' v1.30.0 (McMurdie and Holmes, 2013) and 'vegan' v2.5–7 R packages. To assess the potential existence of a correlation among these phylogenetic distances and environmental factors we used PERMANOVA test with 999 permutation for pseudo F-distribution. The P values were Bonferroni corrected (FWER) for multiple testing. $P < 0.05$ was considered significant.

Data accessibility

The metadata associated with the global field survey are publicly available in Figshare (https://doi.org/10.6084/m9.figshare.11484747).

Authors' contributions

C.C. conceived and designed the study. M.D.-B. and B.K.S. put together the original global database. Statistical analyses and environmental modelling were done by C.C. The manuscript was written by C.C. with contributions from L.S., B.K.S., and M.D.-B. All authors have read and agreed to the published version of the manuscript.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1 Supporting information
Table S2 Supporting information
Figure S1 Supporting information