Global Change Biology

WILEY

Global Change Biology

RESEARCH ARTICLE OPEN ACCESS

Global Distribution and Future Projections of Functional Groups Within Extremotolerant Soil Fungi

Claudia Coleine[1] | Federico Biagioli[2,3] | Tadeo Sáez-Sandino[4] | Leho Tedersoo[5] | Claudio Donati[6] | Miriam Muñoz-Rojas[1] | Lucia Muggia[7] | Manuel Delgado-Baquerizo[1]

[1]Laboratorio de Biodiversidad y Funcionamiento Ecosistémico, Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS), Consejo Superior de Investigaciones Científicas, Seville, Spain | [2]Department of Ecological and Biological Sciences, University of Tuscia, Viterbo, Italy | [3]Polo d'Innovazione di Genomica, Genetica e Biologia SRL, Terni, Italy | [4]Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia | [5]Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia | [6]Research and Innovation Centre, Fondazione Edmund Mach, San Michele all'Adige, Italy | [7]Department of Life Sciences, University of Trieste, Trieste, Italy

Correspondence: Claudia Coleine (claudia.coleine@irnas.csic.es) | Lucia Muggia (lmuggia@units.it)

Received: 5 May 2026 | **Revised:** 6 July 2026 | **Accepted:** 7 July 2026

Keywords: black fungi | climate change | environmental plasticity | functional ecology | fungal biogeography | global soil mycobiome | ITS PacBio

ABSTRACT

Black fungi are often described as ubiquitous specialists of harsh environments (extremotolerant), yet how their ecological lifestyles vary across environmental gradients remains poorly understood. Here, we use a global soil dataset based on ITS PacBio sequencing to characterize over 51,000 black fungal phylotypes across major functional groups and ascomycete lineages, including Chaetothyriales and Capnodiales. We find that their global distribution is strongly structured by lifestyles and environmental filtering, especially from climate. Capnodiales dominate arid regions, whereas Chaetothyriales are associated with cold and montane environments. Functional strategies further explain global patterns, with rock-inhabiting fungi exhibiting the broadest niche breadth and highest environmental tolerance. We also revealed limited niche conservatism and widespread convergence in stress-tolerance traits, suggesting repeated evolutionary adaptation to extreme conditions. Climate projections further suggest a spatial reorganization of dominant taxa and functional groups under future scenarios, with stress-tolerant fungi tracking the expansion of arid environments while plant pathogens are predicted to persist in current core regions and expand into areas where they are presently marginal. These findings challenge simplified representations of extremotolerant fungi in Earth system models and indicate current approaches may misrepresent how soil microbial communities reorganize under climate change.

1 | Introduction

Melanized (black) fungi represent a distinctive, polyphyletic, functional group of microorganisms characterized by an exceptional capacity to persist under extreme and fluctuating environmental conditions (Coleine, Selbmann, et al. 2022, Coleine et al. 2026; Gostinčar et al. 2022; Liu et al. 2022). They recurrently colonize deserts, polar and alpine environments and anthropogenic substrates, tolerating intense ultraviolet radiation, desiccation, oligotrophy and temperature fluctuations (Zakharova et al. 2014; Gostinčar et al. 2012; Muggia, Coleine, et al. 2021; Prenafeta-Boldú et al. 2022). This ecological breadth reflects a suite of conserved physiological traits associated with stress tolerance, including constitutive melanization, resistance to desiccation and radiation, and metabolic efficiency under nutrient limitation (Coleine, Delgado-Baquerizo, et al. 2022; Tesei 2022). In addition, being oligotrophic organisms able to respond to stress by phenotypic plasticity (Gostinčar et al. 2009), depending on the environmental conditions, these fungi can shift between a yeast-like, filamentous, and meristematic (isodiametrical, resulting in a small surface/volume ratio) growth (Gostinčar et al. 2009).

Black fungi span multiple ascomycete lineages and contrasting lifestyles, including rock-inhabiting specialists (polyextremotolerant; Gostinčar et al. 2015), soil and litter saprotrophs, endophytes of plants and lichens, and pathogens (Gorbushina 2007; Blasi et al. 2015; Quan et al. 2021; Muggia, Quan, et al. 2021; Chang et al. 2022). Beyond their extremotolerance, black fungi contribute to key ecosystem processes such as organic matter turnover, mineral weathering (Kirtzel et al. 2017) and plant interactions influencing productivity and stress resilience, while also affecting human well-being as opportunistic pathogens and sources of bioactive compounds (de Hoog et al. 2000). However, we do not know how contrasting black fungi lifestyles and environment interact with each other in explaining the biogeography of these important organisms. This knowledge is key to better forecasting the future of black fungi lifestyles under global change scenarios, including diverse organisms such as pathogens and rock-inhabiting fungi.

Yet, despite being widely regarded as extremophiles, this view may oversimplify the ecological distribution of black fungi. Many taxa occur across diverse environments, suggesting that their extremotolerance may reflect not only specialization to harsh habitats but also broader ecological plasticity. Disentangling these alternatives is key to understanding whether black fungi are restricted to extremes or exhibit structured responses across environmental gradients. It remains unclear whether the apparent extremotolerance of these taxa reflects niche specialization, broad environmental plasticity, or convergent evolutionary responses. This limits our ability to predict how these organisms will respond to changing temperature, aridity, and vegetation structure, with potential consequences for ecosystem functioning and plant performance (Jackson et al. 2021; Rillig et al. 2023; Adomako et al. 2022; Gao et al. 2025). Yet, despite increasing remain across diverse environments, a global-scale understanding of how black fungal lineages and ecological strategies respond to environmental gradients remains lacking, particularly at the level of individual taxa (Baron et al. 2021; Coleine, Selbmann, et al. 2022; Coleine, Delgado-Baquerizo, et al. 2022, 2024; Zajc et al. 2022; Gostinčar and Gunde-Cimerman 2024).

Here, we integrate lifestyle classification, machine-learning approaches and phylogenetic comparative analyses to investigate the global diversity and environmental responses of black fungi across thousands of soil sites worldwide using long-read ITS PacBio data. By focusing on globally distributed soils, we establish a common framework to compare taxa and ecological strategies across biomes and environmental gradients. Soils act as integrative systems where climatic conditions, substrate properties, vegetation inputs and disturbance co-occur (Capra et al. 2015; Phillips et al. 2024), and where diverse black fungal lineages, including rock-inhabiting and plant-associated taxa, are consistently detected, suggesting that multiple strategies overlap within the same environmental matrix. This approach allows us to test whether ecological strategies typically associated with specialized niches translate into predictable responses at the global scale. We specifically assess whether black fungi exhibit high environmental tolerance and multidimensional plasticity, and whether these traits are weakly constrained by phylogeny. We further evaluate whether shifts in climate are more likely to reorganize black fungal communities according to ecological strategy rather than lineage identity. Accordingly, we test three hypotheses: (i) major black fungal lineages occupy distinct regions of climatic space driven by different environmental factors; (ii) ecological strategies predict environmental plasticity and tolerance more strongly than phylogenetic affiliation; and (iii) projected climate change will restructure black fungi and distributions primarily according to their lifestyles, with stress-tolerant groups tracking the expansion of arid and environmentally stressful habitats.

2 | Methods

2.1 | Global Soils Dataset

The dataset from the GSMc (Global Soil Mycobiome consortium; https://GSMc-fungi.github.io/) database (Tedersoo et al. 2021) was used to investigate the global distribution and diversity patterns of black fungal taxa across environmental gradients. This dataset was obtained by the PacBio long-read sequencing of ITS and 18S-V9 variable regions of topsoil (−0−5 cm depth) soil communities, covering 3200 different localities, across 108 countries in all continents and major natural biomes. A total of 51,401 phylotypes were identified as belonging to black fungal lineages, commonly referred to as black fungi. These included representatives from key orders known for their stress-tolerant ecologies, in particular *Botryosphaeriales*, *Capnodiales*, *Chaetothyriales*, *Dothideales*, *Lichenostigmatales*, and *Venturiales*. Taxonomic assignments were obtained from the UNITE database (Abarenkov et al. 2024), and only sequences affiliated with established black fungal groups were retained for further analysis (Table S1). To explore their ecological roles, each phylotype was assigned to a primary lifestyle based on available annotations from the FungalTraits database (Põlme et al. 2020). This resource integrates trait-based ecological information from the literature and culture studies to classify fungal taxa into ecologically meaningful categories. Based on these annotations, the phylotypes assigned to genera known to include melanized taxa within the orders mentioned above were functionally grouped into 15 categories, encompassing a wide range of life strategies. These included the specialists "rock-inhabiting", "soil saprotrophs", "wood saprotrophs", "plant pathogens", "foliar endophytes", "sooty molds", and various parasites ("animal," "protistan," "lichen," or "mycoparasitic"), as well as more generalist or poorly characterized groups such as "epiphytes", "dung saprotrophs", and "unspecified saprotrophs" (Table S1). Functional groups abundances were calculated by aggregating the read counts of all phylotypes assigned to a specific primary lifestyle based on FungalTraits annotations. This functional framework was used as the basis for all subsequent analyses, allowing us to assess how different ecological strategies mediate environmental filtering, trait evolution, and potential shifts under future climate scenarios.

2.2 | Environmental Variables Selection

The sample geographic coordinates provided within the GMSc metadata, were used to retrieve bioclimatic variables (i.e., elevation; slope; normalized difference vegetation index, NDVI;

mean annual temperature, MAT; temperature seasonality, TSEA; mean diurnal temperature range, MDR; mean annual precipitation, MAP; precipitation seasonality, PSEA) from Worldclim database ver. 2.0 (Fick and Hijmans 2017). Data on aridity index (AI) were calculated using the Global Aridity Index and Potential Evapotranspiration (ET0) Database (Zomer et al. 2022). Geographical information about elevation and slope was obtained from the Advanced Land Observation Satellite (ALOS, Hamazaki 1999). UV radiation (UV light), and plawere-cover was also included. The human impact (Human Influence Index; HI) was estimated by Sanderson et al. (2002). Other edaphic parameters such as pH, soil organic carbon (SOC), and sand percentage (Sand%), were included from SoilGrids v2.0 database (Poggio et al. 2021). Detailed information on the samples with their bioclimatic models can be found in Table S2.

2.3 | Statistical Analysis

No rarefaction was performed on the dataset. To account for uneven sequencing depth across samples while preventing the loss of biological information and rare taxa, the raw sequence were transformed into relative abundance prior to all downstream statistical and spatial analyses. To assess biogeographic and climatic patterns of black fungi, we used Spearman correlation and Redundancy (RDA) analysis to assess relationships between the relative abundance data of black fungi and the environmental metadata. To ensure the reliability of statistical inference in RDA analysis and species richness mapping, variance inflation factor (VIF) was calculated to check the multicollinearity among the evaluated environmental variables. Variables with VIF > 5 were discarded from the regression models. Further, for RDA analysis, the environmental variables were standardized (mean = 0, variance = 1), and "forward selection" was used to remove the non-significant predictors from the model. All tests applied were statistically validated by the Benjamini-Hochberg (FDR) *p*-value correction method. Analyses were performed using the R packages: "phyloseq" (McMurdie and Holmes 2013) and "microeco" (Liu et al. 2021).

2.4 | Phylogenetic Analyses

A multiple alignment of the filtered sequences was obtained using Mafft 7 (Katoh and Standley 2013) and a phylogenetic tree was inferred using FastTree 2.2 (Price et al. 2010). The resulting unrooted tree was subsequently rooted using midpoint rooting (von Hoyningen-Huene et al. 2019), and the tip labels were corrected by removing taxonomic strings added to the sequence IDs (such as _k__Fungi-p__... if present) by R, ensuring correct integration into downstream phylogenetic analyses.

To test evolutionary hypotheses of environmental specialization, we conducted a series of phylogenetic comparative analyses. First, a multi-dimensional environmental space was defined by performing a Principal Component Analysis (PCA) on a selected set of non-collinear bioclimatic, edaphic, and geographical variables. The first two principal components (PC1 and PC2) were selected as they explained the majority of environmental variance (Lu et al. 2023). For each phylotype, we quantified two key ecological traits. Environmental niche breadth was calculated as the sum of the standard deviations of a phylotype occurrences along the first two principal components (Segurado et al. 2011; Mod et al. 2020). This metric quantifies the overall dispersion of a species within the main environmental space, with higher values indicating a broader, more generalist niche. The distributions of these metrics were then compared across four key functional groups (i.e., litter saprotrophs, plant pathogens, rock-inhabiting, and soil saprotrophs) using a Kruskal-Wallis test, with post hoc pairwise comparisons performed using the Wilcoxon test with Benjamini-Hochberg FDR correction. To assess the degree of niche conservatism, we tested for a phylogenetic signal in both niche breadth and environmental tolerance using Blomberg's *K* statistic (Liu et al. 2015; Cruz-Nicolás et al. 2024).

2.5 | Present and Future Projections of the Distribution of Black Fungi

We used Random Forest regression (Breiman 2001) to predict the current global distribution of black fungi in global soils. Aridity and UV light were excluded due to collinearity with mean annual precipitation (MAP) and mean annual temperature (MAT), respectively, and TSEA was also removed prior to mapping. The final set of environmental predictors was implemented as raster layers using the *raster* package (Hijmans 2013). Predictive models were implemented using the *randomForest* package (Liaw and Wiener 2002) with 999 trees and 100 bootstrap replicates, a configuration that provides stable predictions while reducing overfitting. To assess the reliability of model predictions, we evaluated whether environmental conditions in the prediction space differed substantially from those represented in the training dataset. We therefore applied a Mahalanobis distance analysis to identify environmental outliers and generated a reliability mask highlighting areas where predictions were most robust. Grid cells exceeding the 0.95 quantile of the chi-square distribution (11 degrees of freedom; Mallavan et al. 2010) were excluded from visualization. Model performance was finally evaluated by comparing predicted and observed values following Piñeiro et al. (2008).

Future maps for 2050 were created using land-use projections and climate variables. First, we relied on the dataset provided by the Land-use Harmonized v2.0 project (http://luh.umd.edu/; Hurtt et al. 2011). Second, the climatic variables (MAT, MAP, MDR, and PSEA) were determined using the estimates provided by the MIROC6 global climate model (CMIP6 Landscape 2019). We employed four combined Shared Socioeconomic Pathway (SSP) and Representative Concentration Pathway (RCP) scenarios: SSP1-RCP2.6, SSP2-RCP4.5, SSP3-RCP7.0, and SSP5-RCP8.5. In this regard, SSP1 represents a sustainability scenario with low mitigation and adaptation challenges (characterized by low population growth and high economic growth). SSP2 and SSP3 present medium and high challenges respectively, where SSP3 reflects a fragmentation scenario with high population growth and low economic development. SSP5 assumes high mitigation challenges, featuring fossil fuel dependence with low population growth but high economic growth (Fricko et al. 2017). The RCP scenarios range from the lowest to the highest emission rates: RCP2.6 (+0.4°C to +1.6°C by 2050), RCP4.5, RCP7.0, and RCP8.5 (+1.4°C to +2.6°C by 2050) (see Meinshausen et al. 2011 for details).

3 | Results

3.1 | Taxonomic Turnover of Black Fungi Across Climate Zones

Community composition was dominated by Chaetothyriales (Eurotiomycetes) and Capnodiales (Dothideomycetes) orders, whose relative abundance varied markedly across climate regimes, followed by Venturiales (Dothideomycetes) (Figure 1A). Chaetothyriales were prevalent in montane and temperate environments, while Capnodiales dominated arid zones. Random Forest models identified climate zones as strong predictors of order-level abundance (Figure 1B). Botryosphaeriales (Dothideomycetes) were the most indicative order of tropical conditions, while Chaetothyriales showed the highest importance for montane climates. Venturiales were associated with continental zones, while Capnodiales and Lichenostigmatales (Arthoniomycetes) were more specific for arid regions.

Given their dominant abundance, the two orders Chaetothyriales and Capnodiales were selected for focused environmental modeling to assess the specific abiotic drivers influencing their distribution. For Chaetothyriales, relative abundance was primarily influenced by soil pH and soil organic carbon (SOC), with a secondary contribution from aridity index (AI), reflecting edaphic and xeric constraints. In contrast, Capnodiales showed a strong response to aridity and temperature (MAT) (Figure 1C).

Collectively, correlation analysis revealed that black fungal orders exhibit distinct environmental signatures (Figure 1D). For example, Chaetothyriales showed strong negative correlations with PET, plant cover, and temperature, whereas there were positive correlations with AI and elevation, consistent with

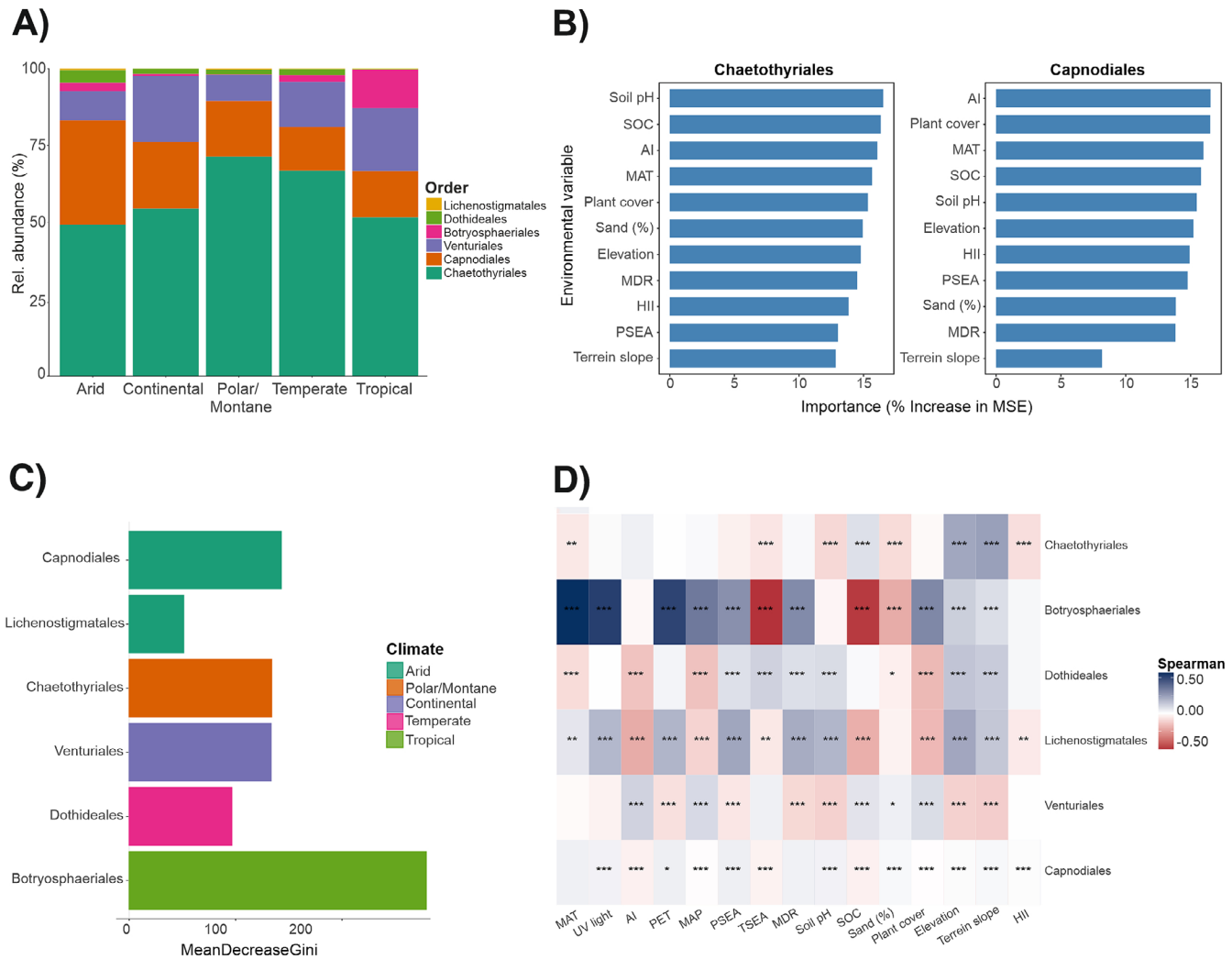

FIGURE 1 | Taxonomic turnover of black fungal orders across climate zones and their environmental associations. (A) Relative abundance of the fungal orders within melanized Ascomycota across five major climatic zones; (B) Random Forest model assessing the discriminatory power of each order in classifying climate categories, based on mean decrease in Gini index; (C) Variable importance from Random Forest regressions predicting the abundance of *Chaetothyriales* and *Capnodiales*; (D) Spearman rank correlations between order-level relative abundance and 15 abiotic variables. Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$); color scale reflects direction and strength of correlation; the color scale reflects the direction and strength of correlations, with blue indicating positive and red negative correlation. AI, aridity index; HII, human influence index; MAP, mean annual precipitation; MAT, mean annual temperature; MDR, mean diurnal range; PET, potential evapotranspiration; Plant, plant coverage; PSEA, precipitation seasonality; SOC, soil organic carbon; TSEA, temperature seasonality; UV light, ultraviolet radiation.

their occurrence in high-elevation and low-productivity environments. Botryosphaeriales, in contrast, were positively correlated with SOC and soil pH, reflecting their tendency to occur in organic-rich environments. Capnodiales exhibited almost no correlation (neither positive nor negative) with both abiotic and topographic variables.

3.2 | Climatic Partitioning and Environmental Associations of Dominant Black Fungal Genera

To refine our understanding of taxonomic turnover and environmental filtering at finer resolution, we analyzed the 20 most abundant melanized fungal genera across global climate zones. Genus-level distributions revealed distinct biogeographic patterns (Figure 2A). For instance, *Cladophialophora* (Chaetothyriales) was abundant across all biomes, whereas *Exophiala* (Chaetothyriales) was most prevalent in continental regions, *Knufia* (Chaetothyriales) in arid environments, and *Capronia* (Chaetothyriales) in montane habitats. Phylogenetic trees of the three most diverse genera (*Cladophialophora*, *Exophiala*, and *Cladosporium*) showed that phylotypes associated with different climatic zones were distributed across the phylogeny, highlighting the broad evolutionary diversity represented within each genus (Figures S1–S3).

Furthermore, we used RF classification to identify the taxa most predictive of climate categories (Figure 2B). *Cladosporium* (Dothideomycetes), *Cladophialophora* (Chaetothyriales), *Cercospora* (Dothideomycetes), and *Knufia* showed the highest variable importance. In particular, *Cladophialophora* was most strongly associated with temperate environments, *Knufia* with arid regions, and *Cladosporium* with continental climates. Spearman correlation analyses further supported these patterns by revealing distinct environmental preferences among genera (Figure 2C). For example, *Exophiala* showed negative correlations with UV radiation, aridity, and temperature (MAT), but positive associations with the Human Influence Index (HII). *Cladosporium* also showed positive associations with HII, whereas *Ochroconis* (Dothideomycetes) was positively correlated with aridity, temperature, and UV radiation.

3.3 | Functional Composition and Environmental Drivers of Black Fungal Lifestyles

To assess how ecological strategies shape melanized fungal community structure across climates, we classified all black fungal taxa into functional lifestyle categories. The relative abundance of these lifestyle groups varied substantially across climatic regions (Figure 3A,B). Soil saprotrophs and plant pathogens were consistently dominant in most biomes, together accounting for more than 50% of the taxa. Notably, soil saprotrophs peaked in montane and temperate zones, whereas plant pathogens were more represented in continental and tropical regions. Other prominent groups included litter saprotrophs, wood saprotrophs, and rock-inhabiting fungi, each showing distinct distributional patterns, with rock-inhabiting fungi particularly abundant in arid and montane environments. Foliar endophytes emerged mainly in tropical environments, as indeed these fungi are highly associated with plants and trees in the Tropics. Less abundant categories (e.g., mycoparasites, protistan parasites) contributed minimally to climate-based differentiation.

Spearman correlation analysis between lifestyle group abundance and 15 environmental variables (Figure 3C) revealed numerous significant associations. Soil saprotrophs were positively correlated with soil organic carbon, plant cover, and precipitation (MAP) and negatively correlated with soil pH and the Human Influence Index. Rock-inhabiting fungi showed positive associations with UV radiation, temperature, and elevation and negative correlations with HII, SOC, and sand content. Plant pathogens were positively correlated with temperature, SOC, and soil pH and negatively correlated with aridity and UV radiation. Several other categories, including animal-associated fungi and endophytes, showed more complex or variable correlations across environmental predictors.

3.4 | Ecological Strategies and Environmental Plasticity Across Black Fungi

To evaluate variation in diverse lifestyles across black fungi, we compare lifestyles with respect to their environmental plasticity and tolerance. Environmental niche breadth, reflecting the range of environmental conditions occupied across multiple gradients, differed significantly among functional supergroups (Figure 4A; Kruskal–Wallis, $p = 3.6 \times 10^{-14}$). Rock-inhabiting fungi exhibited the highest niche breadth values and showed significantly higher environmental tolerance, as measured by the range along the first principal component (PC1) summarizing abiotic gradients (Figure 4B; Kruskal–Wallis, $p = 3.3 \times 10^{-10}$). Importantly, both niche breadth and tolerance showed no detectable phylogenetic signal (Blomberg's $K \approx 0$; breadth: $K = 1.29 \times 10^{-5}$, $p = 0.653$; tolerance: $K = 1.06 \times 10^{-5}$, $p = 0.706$), indicating that these traits are evolutionarily labile and not conserved across lineages.

3.5 | Projected Shifts in Dominant Taxa and Functional Groups Under Climate Change

Model projections revealed striking, yet contrasting, distributional shifts for major black fungal lineages under future climate scenarios (Figure 5). We modeled the spatial niche projections of Capnodiales and Chaetothyriales under present and future scenarios. Present-day maps reveal that Capnodiales dominate arid and semi-arid regions, with high predicted abundance across North Africa, the Atacama Desert (Chile), western North America (e.g., Utah and Arizona), central Australia, and the Chinese Taklamakan desert. In contrast, Chaetothyriales are more prevalent in northern temperate and cold regions, such as northern Europe, Canada, and high-altitude Asian zones. Future projections (based on SSP5-8.5 scenarios) show a marked expansion of Capnodiales, with increased abundance not only in current arid zones but also extending into mesic and northern regions, suggesting a potential range shift under warming conditions. Conversely, Chaetothyriales are predicted to decline in southern arid zones, including North Africa, western USA, and southern Asia, where Capnodiales currently thrive, while maintaining some presence in cooler and montane areas. These patterns are supported by model outputs: for Capnodiales, the variable with highest explanatory power was the aridity index

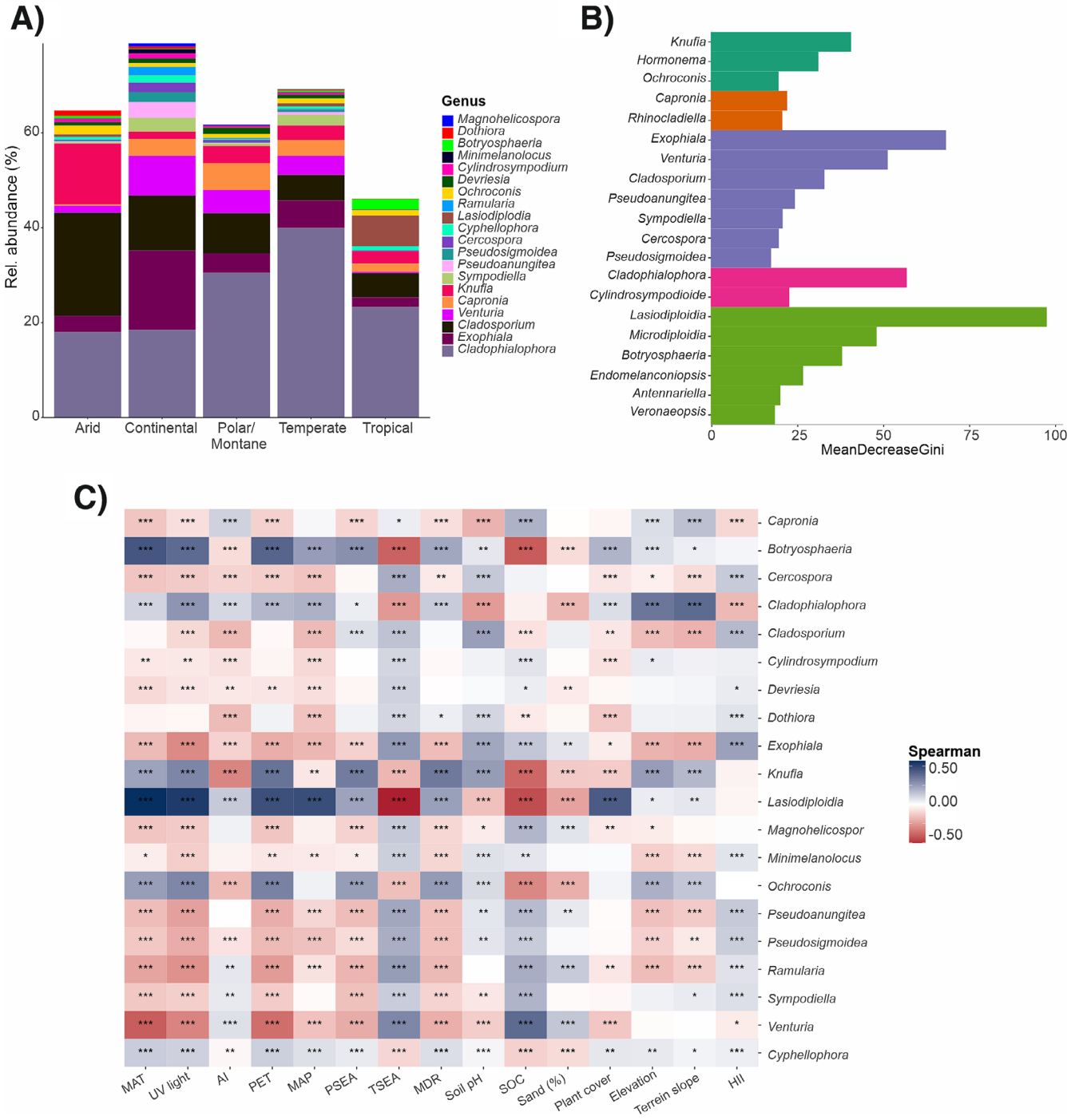

FIGURE 2 | Genus-level patterns of relative abundance, climatic specificity, and environmental associations in black fungi. (A) Relative abundance of the 20 most prevalent black fungal genera across five major climate zones; (B) Variable importance of fungal genera for predicting climate zone based on Random Forest classification (mean decrease in Gini index); (C) Spearman correlations between the relative abundance of the 20 most prevalent black fungal genera and 15 environmental variables. Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$); color scale reflects direction and strength of correlation, with blue indicating positive and red negative correlation. AI, aridity index; HII, human influence index; MAP, mean annual precipitation; MAT, mean annual temperature; MDR, mean diurnal range; PET, potential evapotranspiration; Plant, plant coverage; PSEA, precipitation seasonality; SOC, soil organic carbon; TSEA, temperature seasonality; UV light, ultraviolet radiation.

(explaining 16.11% of variance), while Chaetothyriales were most influenced by elevation (20.75% of variance explained).

At the functional group level, distinct spatial patterns emerge between current and projected distributions, reflecting lifestyles and environmental filtering (Figure 5, Figures S4 and S5; Table S3). Rock-inhabiting fungi consistently maintain high predicted presence under both present and future scenarios (Min: 0.073; Max: 0.740), with distributions stable across arid, high-elevation environments. This group exhibits a notable shift in distribution showing a reduction in current hotspots (e.g., North Africa, western U.S., and parts of central Asia) and an expansion

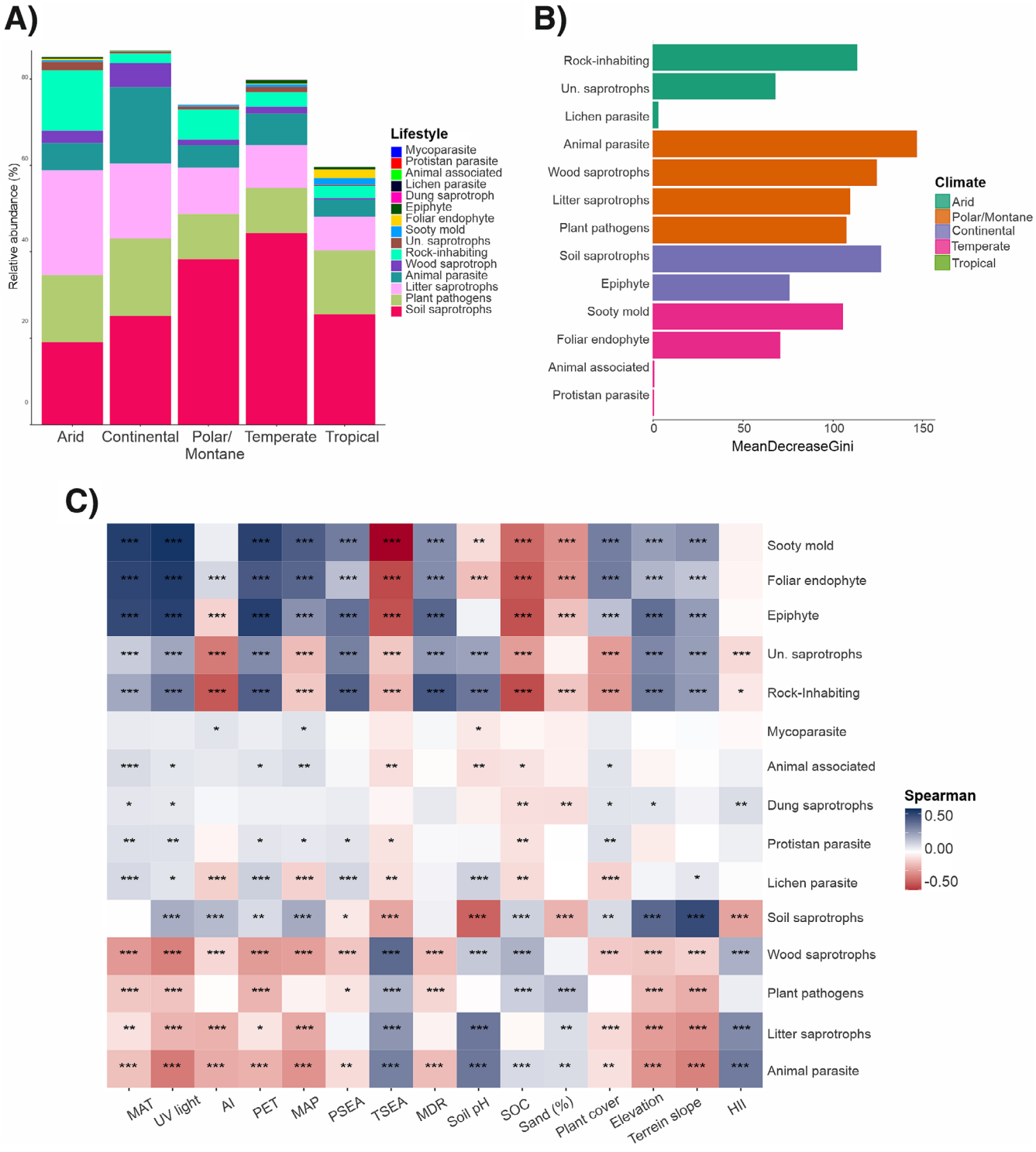

FIGURE 3 | Functional group composition of black fungi and their environmental filtering across climates. (A) Relative abundance of black fungi grouped by functional lifestyle across climatic zones; (B) Random Forest classification showing lifestyle groups most predictive of climate categories (based on mean decrease in Gini index); (C) Spearman rank correlations between lifestyle-level abundance and environmental variables. Asterisks indicate significance (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$); color scale reflects direction and strength of correlation, with blue indicating positive and red negative correlation. AI, aridity index; HII, human influence index; MAP, mean annual precipitation; MAT, mean annual temperature; MDR, mean diurnal range; PET, potential evapotranspiration; Plant, plant coverage; PSEA, precipitation seasonality; SOC, soil organic carbon; TSEA, temperature seasonality; UV light, ultraviolet radiation.

into new regions under future conditions. Soil saprotrophs currently display moderate presence values (0.038–0.564), primarily concentrated in vegetated temperate and continental zones. However, future projections suggest a contraction in these areas, particularly in semi-arid regions undergoing desertification, alongside a potential expansion into desert and subtropical

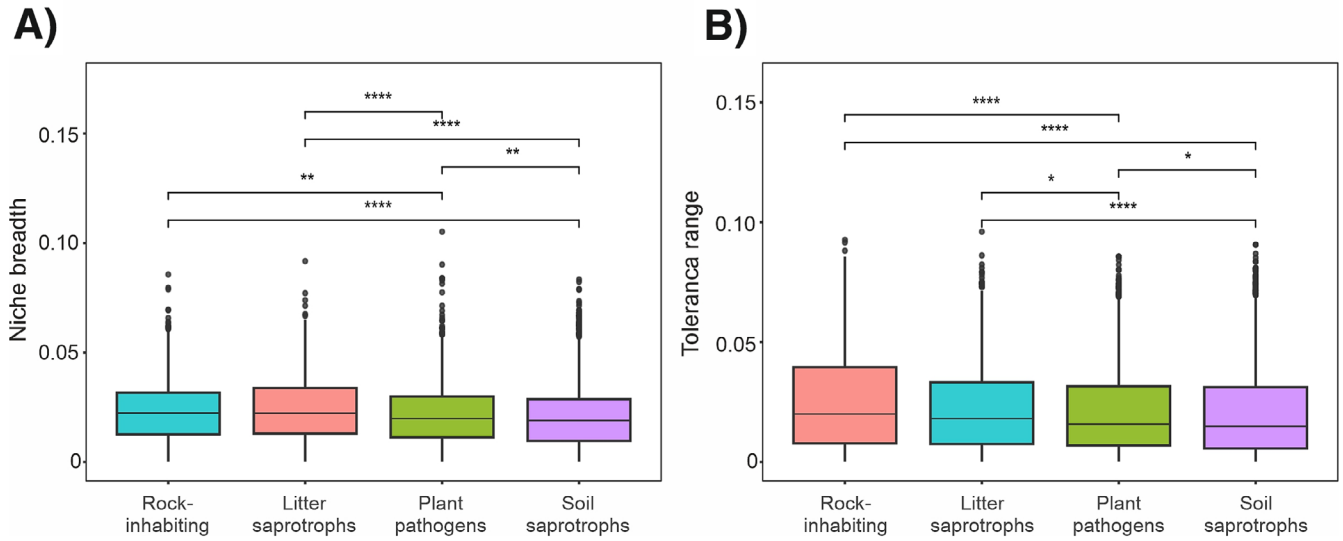

FIGURE 4 | Patterns of environmental plasticity and tolerance across black fungi functional groups and phylogeny. (A) Environmental niche breadth (based on the variance of normalized environmental scores across axes) (Kruskal–Wallis $p = 3.6e^{-14}$); (B) Tolerance range along the first principal component (PC1), used as a proxy for environmental tolerance (Kruskal–Wallis $p = 3.3e^{-10}$).

zones. Future projections indicate that plant pathogens will continue to persist in these core regions but also expand into areas where they are now only sporadically present, such as parts of South America and Europe. Similarly, litter saprotrophs (0.018–0.648) are currently most concentrated in North Africa and South Asia.

4 | Discussion

Our results indicate that black fungi lifestyle provides a stronger and more consistent predictor of environmental responses than taxonomic identity on the global scale. We further demonstrate clear climatic partitioning among dominant lineages and show that ecological strategy predicts environmental responses more strongly than phylogenetic identity. Together, these findings indicate that trait-mediated environmental filtering plays a central role in shaping the global distribution of melanized fungal communities.

4.1 | Environmental Filtering Shapes Black Fungi Distribution

At the taxonomic level, our analyses reveal clear climatic differentiation between major lineages. Capnodiales dominate arid regions and respond strongly to aridity and temperature, consistent with their ability to persist across both xeric and vegetated habitats (Ruibal et al. 2009; Sterflinger et al. 2012; Velez et al. 2016). In contrast, Chaetothyriales are more prevalent in cooler and montane environments and are primarily structured by edaphic factors such as soil pH and organic carbon (Narisawa et al. 2007; Männistö et al. 2018). Other orders further reflect this deterministic partitioning: Botryosphaeriales are indicative of tropical climates (Slippers et al. 2017), whereas Venturiales were most frequently detected in continental regions, and Lichenostigmatales are characteristic of arid environments (Muggia et al. 2016; Muggia, Quan, et al. 2021). These patterns are consistent with strong environmental filtering shaping black fungal communities across global soils.

At finer taxonomic resolution, genus-level patterns reveal substantial ecological divergence even among closely related taxa. *Cladosporium*, one of the most ubiquitous fungal genera worldwide, was particularly abundant in arid and continental climates (Pereira et al. 2022; Razak and Abass 2023). In contrast, genera such as *Cladophialophora* and *Knufia* were strongly associated with temperate and arid environments, respectively. Random Forest models identified both genera as key predictors of these climatic categories, suggesting specialization toward xeric and complex habitats. Notably, *Knufia* is frequently reported from lithic substrates including natural rock surfaces and stone monuments (Erdmann et al. 2022; Mihalyi et al. 2025), although it is also known to occur in soils (Gałązka et al. 2020; Wang et al. 2024). The strong association with arid soils observed here is consistent with its preference for habitats characterized by low water availability and other environmental stresses. *Exophiala* showed negative associations with UV radiation and aridity index, and positive correlations with soil pH, soil organic carbon, and the Human Influence Index. This pattern is consistent with the frequent detection of *Exophiala* species in anthropogenic and urban environments, where organic substrates and human-associated niches can favor their persistence (Blasi et al. 2015, 2016).

4.2 | Ecological Lifestyles Predict the Ecological Responses of Black Fungi

Grouping taxa according to their ecological lifestyle further clarifies these assembly patterns. Functional categories showed strong discriminatory power in climate classification models, indicating that lifestyle-mediated traits strongly influence environmental persistence. While lifestyle assignments simplify complex ecological roles, they provide a useful framework to capture broad functional differences across taxa. Soil

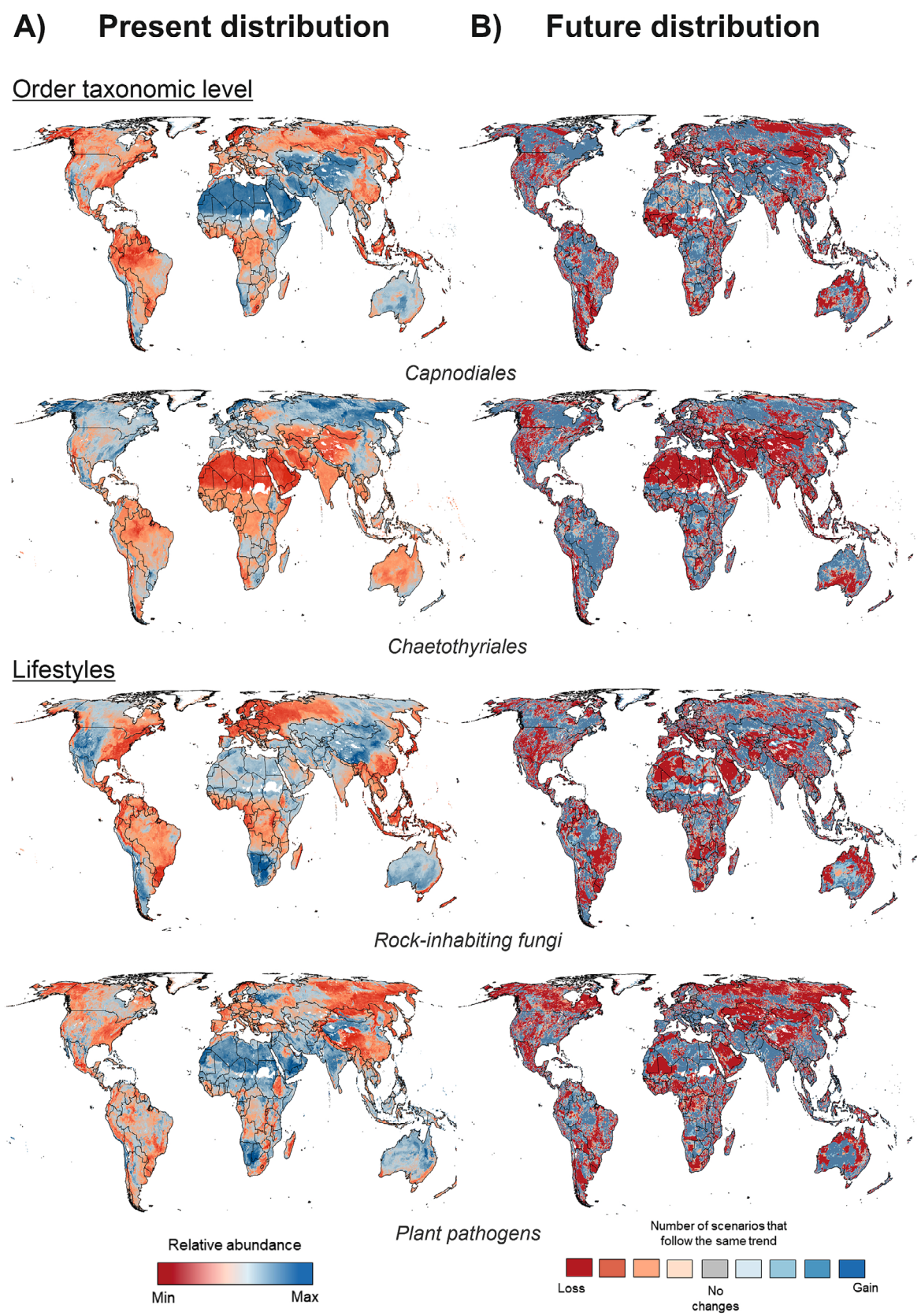

FIGURE 5 | Predicted global distribution of selected black fungi groups under current and future climate scenarios. Maps show modeled presence probabilities for Capnodiales, Chaetothyriales and for rock-inhabiting and soil saprotrophs, derived from environmental niche modeling. Present (left) and future (right, 2050, RCP 8.5) distributions are shown using a blue-to-red gradient, where blue indicates high probability of presence and red indicates low probability.

saprotrophs were associated with soil pH, Human Influence index and precipitation, reflecting resource-driven assembly in productive ecosystems (Rousk and Bååth 2011; Carteron et al. 2021). Such environments likely promote faster microbial turnover and competitive interactions, favoring taxa adapted to exploit transient organic resources (Nielsen and Ball 2015). Plant pathogens were positively associated with aridity, temperature and UV radiation, and negatively correlated with soil organic carbon. This pattern suggests that many melanized pathogenic taxa are adapted to stressful and exposed environments, where melanization and other protective traits are known to enhance the survival of propagules under high radiation, desiccation and thermal variability (Silva et al. 2022).

In contrast, rock-inhabiting fungi were strongly associated with aridity and negatively correlated with soil pH, indicating strong selection along physical stress gradients in exposed environments (Choe et al. 2018; Coleine et al. 2021). This pattern is consistent with observations from dryland ecosystems, where endolithic microbial communities often represent some of the last active biological systems persisting under extreme aridity and environmental stress (Coleine, Kurbessoian, et al. 2024). Their prevalence in such habitats is likely reflected ecological release from competition for organic substrates and a shift toward persistence on mineral surfaces. Yet, rock-inhabiting fungi displayed a high environmental niche breadth and the widest environmental tolerance. Rather than being restricted to a single climatic regime, these taxa appear capable of persisting across heterogeneous environments characterized by recurring physical stress. Traits frequently associated with rock-inhabiting fungi including melanization, desiccation resistance, metabolic efficiency under oligotrophic conditions and radiation tolerance, likely form a stress-adaptive syndrome that allows persistence under combinations of desiccation, irradiation and nutrient limitation (Gorbushina 2007; Coleine et al. 2020; Erdmann et al. 2022; Keller et al. 2025). Such trait integration may increase survival across multiple environmental filters and explain the broad environmental occupancy of these taxa. Substrate specialization therefore does not necessarily imply climatic restriction; instead, their extremotolerance may enhance environmental versatility across abiotic gradients (Gostinčar et al. 2009).

4.3 | The Future of Black Fungi

Climate projections further suggest that ongoing environmental change may drive substantial reorganization of black fungi. Capnodiales are predicted to expand from current arid regions into mesic and northern areas across Eurasia and North America, consistent with their association with aridity (Sterflinger et al. 2012; Coleine, Selbmann, et al. 2022). In contrast, Chaetothyriales are projected to decline in southern arid regions while persisting in cooler and high-elevation habitats. Rock-inhabiting fungi maintain high predicted suitability but shift spatially from current hyperarid hotspots toward emerging drylands and transitional ecosystems. Plant pathogens are predicted to persist in current core regions and expand into areas where they are presently marginal, including parts of South America and Europe, suggesting increased climatic suitability and potential host redistribution under warming scenarios. Such conditions may even favor host shifts and/or the expansion of their host selectivity breadth. This pattern is particularly relevant in the context of ongoing global dryland expansion, as climate change is projected to increase the extent of arid and semi-arid regions worldwide (Sun et al. 2023; Li et al. 2025). The redistribution of stress-tolerant fungal lineages may therefore parallel the geographic expansion of drylands, potentially reshaping microbial community composition in ecosystems undergoing progressive desertification.

5 | Conclusions

Overall, our results highlight that ecological function strongly influences both present and future distributions of black fungi. Stress-tolerant taxa are likely to increase in importance under expanding environmental stress, whereas taxa dependent on vegetation structure may undergo spatial reorganization as plant communities and moisture regimes shift. Such functional realignment could have cascading consequences for ecosystem processes including carbon turnover, mineral weathering, vegetation dynamics, and pathogen emergence. By integrating taxonomy, functional traits, and predictive modeling, our study provides a trait-based framework for understanding and forecasting the response of extremotolerant microbial communities to ongoing climate change. Because several melanized genera include opportunistic human and plant pathogens, climate-driven redistribution may alter exposure risks at the human–soil–plant interface. Shifts in the balance between stress-tolerant and host-associated taxa could affect ecosystem resilience and pathogen pressure in agricultural and urban systems, highlighting the relevance of these patterns within a One Health perspective. These findings challenge simplified representations of extremotolerant fungi in Earth system models and indicate current approaches may misrepresent how soil microbial communities reorganize under climate change.

Author Contributions

Tadeo Sáez-Sandino: methodology, validation, visualization, investigation, writing – review and editing, data curation, formal analysis, software. **Leho Tedersoo:** methodology, investigation, data curation, writing – review and editing. **Claudia Coleine:** conceptualization, investigation, methodology, validation, writing – original draft, writing – review and editing, data curation, supervision, resources. **Claudio Donati:** writing – review and editing, investigation. **Miriam Muñoz-Rojas:** investigation, writing – review and editing, validation. **Manuel Delgado-Baquerizo:** conceptualization, validation, investigation, writing – review and editing, supervision. **Federico Biagioli:** methodology, validation, visualization, writing – review and editing, data curation, investigation, formal analysis, software. **Lucia Muggia:** conceptualization, writing – review and editing, validation.

Acknowledgments

C.C. and M.M.-R. acknowledges support from the project PID2021-123097OA-I00 funded by MCIN/AEI/10.13039/501100011033 and by "ERDF A way of making Europe". M.D.-B. is supported by a project from the Spanish Ministry of Science and Innovation (PID2020-115813RA-I00), and a project of the Fondo Europeo de Desarrollo Regional (FEDER) and the Consejería de Transformación Económica, Industria, Conocimiento y Universidades of the Junta de Andalucía (FEDER Andalucía 2014-2020 Objetivo temático 01—Refuerzo de la

investigación, el desarrollo tecnológico y la innovación) associated with the research project P20_00879 (ANDABIOMA). T.S.-S. is supported by the Australian Research Council (DP230101448).

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The GSMc original dataset files including OTU-table, OTU-taxonomy and relative metadata are available from the PlutoF data repository (https://doi.org/10.15156/BIO/2263453).

Code availability: The data in this study were analyzed with publicly available tool packages in R and the figures were produced with R. The R code used in the analysis presented in this paper is available in Figshare (10.6084/m9.figshare.20004335).

References

Abarenkov, K., R. H. Nilsson, K. H. Larsson, et al. 2024. "The UNITE Database for Molecular Identification and Taxonomic Communication of Fungi and Other Eukaryotes: Sequences, Taxa and Classifications Reconsidered." *Nucleic Acids Research* 52, no. D1: D791–D797.

Adomako, M. O., S. Roiloa, and F. H. Yu. 2022. "Potential Roles of Soil Microorganisms in Regulating the Effect of Soil Nutrient Heterogeneity on Plant Performance." *Microorganisms* 10, no. 12: 2399.

Baron, N. C., F. C. Pagnocca, A. A. Otsuka, F. X. Prenafeta-Boldú, V. A. Vicente, and D. Attili de Angelis. 2021. "Black Fungi and Hydrocarbons: An Environmental Survey for Alkylbenzene Assimilation." *Microorganisms* 9, no. 5: 1008.

Blasi, B., C. Poyntner, T. Rudavsky, et al. 2016. "Pathogenic Yet Environmentally Friendly? Black Fungal Candidates for Bioremediation of Pollutants." *Geomicrobiology Journal* 33, no. 3–4: 308–317.

Blasi, B., H. Tafer, D. Tesei, and K. Sterflinger. 2015. "From Glacier to Sauna: RNA-Seq of the Human Pathogen Black Fungus Exophiala Dermatitidis Under Varying Temperature Conditions Exhibits Common and Novel Fungal Response." *PLoS One* 10, no. 6: e0127103.

Breiman, L. 2001. "Random Forests." *Machine Learning* 45: 5–32.

Capra, G. F., A. Ganga, E. Grilli, S. Vacca, and A. Buondonno. 2015. "A Review on Anthropogenic Soils From a Worldwide Perspective." *Journal of Soils and Sediments* 15, no. 7: 1602–1618.

Carteron, A., M. Beigas, S. Joly, B. L. Turner, and E. Laliberté. 2021. "Temperate Forests Dominated by Arbuscular or Ectomycorrhizal Fungi Are Characterized by Strong Shifts From Saprotrophic to Mycorrhizal Fungi With Increasing Soil Depth." *Microbial Ecology* 82, no. 2: 377–390.

Chang, R., W. Cao, Y. Wang, et al. 2022. "Melanodevriesia, a New Genus of Endolichenic Oleaginous Black Yeast Recovered From the Inner Mongolia Region of China." *Fungal Systematics and Evolution* 9, no. 1: 1–9.

Choe, Y. H., M. Kim, J. Woo, et al. 2018. "Comparing Rock-Inhabiting Microbial Communities in Different Rock Types From a High Arctic Polar Desert." *FEMS Microbiology Ecology* 94, no. 6: fiy070.

Coleine, C., F. Biagioli, T. Sáez-Sandino, et al. 2026. "Genomic and Ecological Flexibility Shape the Global Distribution of a Black Fungus." *Environmental Microbiology* 28: e70301.

Coleine, C., M. Delgado-Baquerizo, D. Albanese, et al. 2022. "Rocks Support a Distinctive and Consistent Mycobiome Across Contrasting Dry Regions of Earth." *FEMS Microbiology Ecology* 98, no. 3: fiac030.

Coleine, C., M. Delgado-Baquerizo, J. DiRuggiero, et al. 2024. "Dryland Microbiomes Reveal Community Adaptations to Desertification and Climate Change." *ISME Journal* 18, no. 1: wrae056.

Coleine, C., T. Kurbessoian, G. Calia, et al. 2024. "Class-Wide Genomic Tendency Throughout Specific Extremes in Black Fungi." *Fungal Diversity* 125, no. 1: 121–138.

Coleine, C., S. Masonjones, K. Sterflinger, S. Onofri, L. Selbmann, and J. E. Stajich. 2020. "Peculiar Genomic Traits in the Stress-Adapted Cryptoendolithic Antarctic Fungus Friedmanniomyces Endolithicus." *Fungal Biology* 124, no. 5: 458–467.

Coleine, C., L. Selbmann, B. K. Singh, and M. Delgado-Baquerizo. 2022. "The Poly-Extreme Tolerant Black Yeasts Are Prevalent Under High Ultraviolet Light and Climatic Seasonality Across Soils of Global Biomes." *Environmental Microbiology* 24, no. 4: 1988–1999.

Coleine, C., J. E. Stajich, A. de Los Ríos, and L. Selbmann. 2021. "Beyond the Extremes: Rocks as Ultimate Refuge for Fungi in Drylands." *Mycologia* 113, no. 1: 108–133.

Cruz-Nicolás, J., N. Martínez-Méndez, E. Aguirre-Planter, L. E. Eguiarte, and J. P. Jaramillo-Correa. 2024. "Niche Conservatism and Strong Phylogenetic Signals in Climate, Soil, and Morphological Variation of Neotropical Firs (Abies, Pinaceae)." *Journal of Systematics and Evolution* 62, no. 3: 368–383.

de Hoog, G. D., F. Queiroz-Telles, G. Haase, et al. 2000. "Black Fungi: Clinical and Pathogenic Approaches." *Medical Mycology* 38, no. suppl 1: 243–250.

Erdmann, E. A., S. Nitsche, A. A. Gorbushina, and J. Schumacher. 2022. "Genetic Engineering of the Rock Inhabitant Knufia Petricola Provides Insight Into the Biology of Extremotolerant Black Fungi." *Frontiers in Fungal Biology* 3: 862429.

Fick, S. E., and R. J. Hijmans. 2017. "WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas." *International journal of climatology* 37, no. 12: 4302–4315.

Fricko, O., P. Havlik, J. Rogelj, et al. 2017. "The Marker Quantification of the Shared Socioeconomic Pathway 2: A Middle-Of-The-Road Scenario for the 21st Century." *Global Environmental Change* 42: 251–267.

Gałązka, A., J. Grządziel, R. Gałązka, K. Gawryjołek, A. Ukalska-Jaruga, and B. Smreczak. 2020. "Fungal Community, Metabolic Diversity, and Glomalin-Related Soil Proteins (GRSP) Content in Soil Contaminated With Crude Oil After Long-Term Natural Bioremediation." *Frontiers in Microbiology* 11: 572314.

Gao, M., W. Hu, M. Li, M. Guo, and Y. Yang. 2025. "Response of Soil Basal Respiration Rates, Microbial Attributes, and Organic Matter Composition to Land-Use Change." *Soil Science Society of America Journal* 89, no. 2: e70052.

Gorbushina, A. A. 2007. "Life on the Rocks." *Environmental Microbiology* 9, no. 7: 1613–1631.

Gostinčar, C., M. Grube, S. De Hoog, P. Zalar, and N. Gunde-Cimerman. 2009. "Extremotolerance in Fungi: Evolution on the Edge." *FEMS Microbiology Ecology* 71, no. 1: 2–11.

Gostinčar, C., and N. Gunde-Cimerman. 2024. "Black Yeasts in Hypersaline Conditions." *Applied Microbiology and Biotechnology* 108, no. 1: 252.

Gostinčar, C., N. Gunde-Cimerman, and M. Grube. 2015. "Polyextremotolerance as the Fungal Answer to Changing Environments." In *Microbial Evolution Under Extreme Conditions*, edited by C. Bakermans, 185–208. De Gruyter.

Gostinčar, C., L. Muggia, and M. Grube. 2012. "Polyextremotolerant Black Fungi: Oligotrophism, Adaptive Potential, and a Link to Lichen Symbioses." *Frontiers in Microbiology* 3: 390.

Gostinčar, C., P. Zalar, and N. Gunde-Cimerman. 2022. "No Need for Speed: Slow Development of Fungi in Extreme Environments." *Fungal Biology Reviews* 39: 1–14.

Hamazaki, T. 1999. "Advanced Land Observation Satellite (ALOS). 5 Outline of ALOS Satellite System." *Journal of the Japan Society of Photogrammetry and Remote Sensing* 38: 25–26.

Hijmans, R. J., J. Van Etten, M. Mattiuzzi, et al. 2013. "Raster package in R. Version." https://mirrorssjtugsjtueducn/cran/web/packages/raster/rasterpdf.

Hurtt, G. C., L. P. Chini, S. Frolking, et al. 2011. "Harmonization of Land-Use Scenarios for the Period 1500–2100: 600 Years of Global Gridded Annual Land-Use Transitions, Wood Harvest, and Resulting Secondary Lands." *Climatic Change* 109: 117–161.

Jackson, M. C., S. Pawar, and G. Woodward. 2021. "The Temporal Dynamics of Multiple Stressor Effects: From Individuals to Ecosystems." *Trends in Ecology & Evolution* 36, no. 5: 402–410.

Katoh, K., and D. M. Standley. 2013. "MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability." *Molecular Biology and Evolution* 30, no. 4: 772–780.

Keller, V., A. Calchera, J. Otte, and I. Schmitt. 2025. "Genomic Features of Lichen-Associated Black Fungi." *IUBMB Life* 77, no. 1: e2934.

Kirtzel, J., D. Siegel, K. Krause, and E. Kothe. 2017. "Stone-Eating Fungi: Mechanisms in Bioweathering and the Potential Role of Laccases in Black Slate Degradation With the Basidiomycete Schizophyllum Commune." *Advances in Applied Microbiology* 99: 83–101.

Li, G., B. Yang, G. Wu, et al. 2025. "Increased Desertification Exposure in Dryland Areas." *Ecological Indicators* 179: 114264.

Liaw, A., and M. Wiener. 2002. "Classification and Regression by randomForest." *R News* 2, no. 3: 18–22.

Liu, B., R. Fu, B. Wu, X. Liu, and M. Xiang. 2022. "Rock-Inhabiting Fungi: Terminology, Diversity, Evolution and Adaptation Mechanisms." *Mycology* 13, no. 1: 1–31.

Liu, C., Y. Cui, X. Li, and M. Yao. 2021. "Microeco: An R Package for Data Mining in Microbial Community Ecology." *FEMS Microbiology Ecology* 97, no. 2: fiaa255.

Liu, H., Q. Xu, P. He, L. S. Santiago, K. Yang, and Q. Ye. 2015. "Strong Phylogenetic Signals and Phylogenetic Niche Conservatism in Ecophysiological Traits Across Divergent Lineages of Magnoliaceae." *Scientific Reports* 5, no. 1: 12246.

Lu, W. X., Z. Z. Wang, X. Y. Hu, and G. Y. Rao. 2023. "Echoes of the Past: Niche Evolution, Range Dynamics, and Their Coupling Shape the Distribution of Species in the Chrysanthemum Zawadskii Species Complex." *Frontiers in Ecology and Evolution* 11: 1250491.

Mallavan, B. P., B. Minasny, and A. B. McBratney. 2010. "Homosoil, a Methodology for Quantitative Extrapolation of Soil Information Across the Globe." In *Digital Soil Mapping: Bridging Research, Environmental Application, and Operation*, 137–150. Springer Netherlands.

Männistö, M., J. Vuosku, S. Stark, et al. 2018. "Bacterial and Fungal Communities in Boreal Forest Soil Are Insensitive to Changes in Snow Cover Conditions." *FEMS Microbiology Ecology* 94, no. 9: fiy123.

McMurdie, P. J., and S. Holmes. 2013. "Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data." *PLoS One* 8, no. 4: e61217.

Meinshausen, M., S. J. Smith, K. Calvin, et al. 2011. "The RCP greenhouse gas concentrations and their extensions from 1765 to 2300." *Climatic change* 109, no. 1: 213.

Mihalyi, S., C. Zimmermann, F. Quartinello, et al. 2025. "Life on the Rocks: Unexpected Enzyme Activity of the Extremophilic Black Fungus Knufia Chersonesos." *Frontiers in Bioengineering and Biotechnology* 13: 1720118.

Mod, H. K., D. Scherrer, V. Di Cola, et al. 2020. "Greater Topoclimatic Control of Above-Versus Below-Ground Communities." *Global Change Biology* 26, no. 12: 6715–6728.

Muggia, L., C. Coleine, R. De Carolis, A. Cometto, and L. Selbmann. 2021. "Antarctolichenia Onofrii Gen. nov. sp. nov. From Antarctic Endolithic Communities Untangles the Evolution of Rock-Inhabiting and Lichenized Fungi in Arthoniomycetes." *Journal of Fungi* 7, no. 11: 935.

Muggia, L., A. Fleischhacker, T. Kopun, and M. Grube. 2016. "Extremotolerant Fungi From Alpine Rock Lichens and Their Phylogenetic Relationships." *Fungal Diversity* 76, no. 1: 119–142.

Muggia, L., Y. Quan, C. Gueidan, A. M. Al-Hatmi, M. Grube, and S. de Hoog. 2021. "Sequence Data From Isolated Lichen-Associated Melanized Fungi Enhance Delimitation of Two New Lineages Within Chaetothyriomycetidae." *Mycological Progress* 20: 911–927.

Narisawa, K., S. Hambleton, and R. S. Currah. 2007. "Heteroconium Chaetospira, a Dark Septate Root Endophyte Allied to the Herpotrichiellaceae (Chaetothyriales) Obtained From Some Forest Soil Samples in Canada Using Bait Plants." *Mycoscience* 48, no. 5: 274–281.

Nielsen, U. N., and B. A. Ball. 2015. "Impacts of Altered Precipitation Regimes on Soil Communities and Biogeochemistry in Arid and Semi-Arid Ecosystems." *Global Change Biology* 21, no. 4: 1407–1421.

Pereira, M. L., J. L. Carvalho, J. M. Lima, et al. 2022. "Richness of Cladosporium in a Tropical Bat Cave With the Description of Two New Species." *Mycological Progress* 21, no. 1: 345–357.

Phillips, H. R., E. K. Cameron, N. Eisenhauer, et al. 2024. "Global Changes and Their Environmental Stressors Have a Significant Impact on Soil Biodiversity—A Meta-Analysis." *iScience* 27, no. 9: 110540.

Piñeiro, G., S. Perelman, J. P. Guerschman, and J. M. Paruelo. 2008. "How to Evaluate Models: Observed vs. Predicted or Predicted vs. Observed?" *Ecological Modelling* 216, no. 3–4: 316–322.

Poggio, L., L. M. De Sousa, N. H. Batjes, et al. 2021. "SoilGrids 2.0: Producing Soil Information for the Globe With Quantified Spatial Uncertainty." *Soil* 7, no. 1: 217–240.

Põlme, S., K. Abarenkov, R. Henrik Nilsson, et al. 2020. "FungalTraits: A User-Friendly Traits Database of Fungi and Fungus-Like Stramenopiles." *Fungal Diversity* 105: 1–16.

Prenafeta-Boldú, F. X., C. Medina-Armijo, and D. Isola. 2022. "Black Fungi in the Built Environment—The Good, the Bad, and the Ugly." In *Viruses, Bacteria and Fungi in the Built Environment*, 65–99. Woodhead Publishing.

Price, M. N., P. S. Dehal, and A. P. Arkin. 2010. "FastTree 2–Approximately Maximum-Likelihood Trees for Large Alignments." *PLoS One* 5, no. 3: e9490.

Quan, Y., S. A. Ahmed, N. M. da Silva, et al. 2021. "Novel Black Yeast-Like Species in Chaetothyriales With Ant-Associated Life Styles." *Fungal Biology* 125, no. 4: 276–284.

Razak, N. J., and M. H. Abass. 2023. "First Report of *Cladosporium cladosporioides*, *C. oxysporum*, and *C. uredinicola* as Potential Pathogens on Tomato Shoots System in Iraq." *Applied Nanoscience* 13, no. 2: 1065–1072.

Rillig, M. C., M. G. Van der Heijden, M. Berdugo, et al. 2023. "Increasing the Number of Stressors Reduces Soil Ecosystem Services Worldwide." *Nature Climate Change* 13, no. 5: 478–483.

Rousk, J., and E. Bååth. 2011. "Growth of Saprotrophic Fungi and Bacteria in Soil." *FEMS Microbiology Ecology* 78, no. 1: 17–30.

Ruibal, C., C. Gueidan, L. Selbmann, et al. 2009. "Phylogeny of Rock-Inhabiting Fungi Related to Dothideomycetes." *Studies in Mycology* 64, no. 1: 123–133.

Sanderson, E. W., M. Jaiteh, M. Levy, K. Redford, A. Wannebo, and G. Woolmer. 2002. "The Human Footprint and the Last of the Wild." *Bioscience* 52: 891–904.

Segurado, P., J. M. Santos, D. Pont, et al. 2011. "Estimating Species Tolerance to Human Perturbation: Expert Judgment Versus Empirical Approaches." *Ecological Indicators* 11, no. 6: 1623–1635.

Silva, I., M. Alves, C. Malheiro, et al. 2022. "Short-Term Responses of Soil Microbial Communities to Changes in Air Temperature, Soil Moisture and UV Radiation." *Genes* 13, no. 5: 850.

Slippers, B., P. W. Crous, F. Jami, J. Z. Groenewald, and M. J. Wingfield. 2017. "Diversity in the Botryosphaeriales: Looking Back, Looking Forward." *Fungal Biology* 121, no. 4: 307–321.

Sterflinger, K., D. Tesei, and K. Zakharova. 2012. "Fungi in Hot and Cold Deserts With Particular Reference to Microcolonial Fungi." *Fungal Ecology* 5, no. 4: 453–462.

Sun, C., X. Feng, B. Fu, and S. Ma. 2023. "Desertification Vulnerability Under Accelerated Dryland Expansion." *Land Degradation & Development* 34, no. 7: 1991–2004.

Tedersoo, L., V. Mikryukov, S. Anslan, et al. 2021. "The Global Soil Mycobiome Consortium Dataset for Boosting Fungal Diversity Research." *Fungal Diversity* 111: 573–588.

Tesei, D. 2022. "Black Fungi Research: Out-of-This-World Implications." *Encyclopedia* 2, no. 1: 212–229.

Velez, P., J. Gasca-Pineda, E. Rosique-Gil, L. E. Eguiarte, L. Espinosa-Asuar, and V. Souza. 2016. "Microfungal Oasis in an Oligotrophic Desert: Diversity Patterns and Community Structure in Three Freshwater Systems of Cuatro Ciénegas, Mexico." *PeerJ* 4: e2064.

von Hoyningen-Huene, A. J. E., D. Schneider, D. Fussmann, A. Reimer, G. Arp, and R. Daniel. 2019. "Bacterial Succession Along a Sediment Porewater Gradient at Lake Neusiedl in Austria." *Scientific Data* 6, no. 1: 163.

Wang, S., Z. Xu, X. Tian, et al. 2024. "Profiling Mechanism of *Hippophae rhamnoides* Phytoremediation on Microecosystem of Rhizosphere Soil Surrounding a Magnetite Tailings Pond in North China." *Ecotoxicology and Environmental Safety* 286: 117167.

Zajc, J., A. Černoša, X. Sun, et al. 2022. "From Glaciers to Refrigerators: The Population Genomics and Biocontrol Potential of the Black Yeast Aureobasidium Subglaciale." *Microbiology Spectrum* 10, no. 4: e01455-22.

Zakharova, K., G. Marzban, J. P. de Vera, A. Lorek, and K. Sterflinger. 2014. "Protein Patterns of Black Fungi Under Simulated Mars-Like Conditions." *Scientific Reports* 4, no. 1: 5114.

Zomer, R. J., J. Xu, and A. Trabucco. 2022. "Version 3 of the Global Aridity Index and Potential Evapotranspiration Database." *Scientific Data* 9: 409.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Taxonomic classification and ecological lifestyle assignment of the black fungal phylotypes included in this study. **Table S2:** Metadata and environmental variables for the global soil samples used in this study. **Table S3:** Summary of Random Forest model performance and environmental predictors for the taxonomic and functional groups analyzed. **Figure S1:** Phylogenetic distribution of dominant climatic affiliations within the Cladophialophora genus. Tip colors indicate the dominant climate associated with each phylotype, defined as the climatic zone in which it reached its highest cumulative sequence abundance across all samples. Climatic categories include arid, continental, polar/montane, temperate and tropical environments. **Figure S2:** Phylogenetic distribution of dominant climatic affiliations within the Exophiala genus. Tip colors indicate the dominant climate associated with each phylotype, defined as the climatic zone in which it reached its highest cumulative sequence abundance across all samples. Climatic categories include arid, continental, polar/montane, temperate and tropical environments. **Figure S3:** Phylogenetic distribution of dominant climatic affiliations within the Cladosporium genus. Tip colors indicate the dominant climate associated with each phylotype, defined as the climatic zone in which it reached its highest cumulative sequence abundance across all samples. Climatic categories include arid, continental, polar/montane, temperate and tropical environments. **Figure S4:** Predicted global distribution of litter saprotrophs lifestyle under current and future climate scenarios. Maps show modeled presence probabilities derived from environmental niche modeling. Present (top) and future (bottom, 2050, RCP 8.5) distributions are shown using a blue-to-red gradient, where blue indicates high probability of presence and red indicates low probability. **Figure S5:** Predicted global distribution of soil saprotrophs lifestyle under current and future climate scenarios. Maps show modeled presence probabilities derived from environmental niche modeling. Present (top) and future (bottom, 2050, RCP 8.5) distributions are shown using a blue-to-red gradient, where blue indicates high probability of presence and red indicates low probability.