

Global diversity and ecological drivers of lichenised soil fungi

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Summary

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- Lichens play crucial roles in sustaining the functioning of terrestrial ecosystems; however, the diversity and ecological factors associated with lichenised soil fungi remain poorly understood.
- To address this knowledge gap, we used a global field survey including information on fungal sequences of topsoils from 235 terrestrial ecosystems.
- We identified 880 lichenised fungal phylotypes across nine biomes ranging from deserts to tropical forests. The diversity and proportion of lichenised soil fungi peaked in shrublands and dry grasslands. Aridity index, plant cover and soil pH were the most important factors associated with the distribution of lichenised soil fungi. Furthermore, we identified *Endocarpon*, *Verrucaria* and *Rinodina* as some of the most dominant lichenised genera across the globe, and they had similar environmental preferences to the lichenised fungal community. In addition, precipitation seasonality and mean diurnal temperature range were also important in predicting the proportion of these dominant genera. Using this information, we were able to create the first global maps of the richness and proportion of the dominant genera of lichenised fungi.
- This work provides new insight into the global distribution and ecological preferences of lichenised soil fungi, and supports their dominance in drylands across the globe.

Introduction

Lichenised fungi, those that live symbiotically with green algal and/or cyanobacterial partners, account for *c.* 20% of total fungi worldwide (Wang *et al.*, 2014). These organisms usually have slow growth rates, and occupy a range of terrestrial environments (Bowker *et al.*, 2016; Wang *et al.*, 2020). Most lichen symbiosis pursues similar lifestyles to those of plants as they can perform photosynthesis by autotrophic carbon dioxide fixation of symbiotic partners (Will-Wolf *et al.*, 2004). These lichens are also important components of biocrusts, where they play vital roles in mediating terrestrial ecosystem functions such as nutrient cycling, hydrology, habitat provision, soil stability and aggregation, and climate regulation (Rosentreter *et al.*, 2016; Asplund & Wardle, 2017; Moreno-Jiménez *et al.*, 2020). Previous studies had reported the distribution and ecology of lichenised soil fungi in some regions of the world (Will-Wolf *et al.*, 2004; Grube & Wedin, 2016; Chiva *et al.*, 2019); however, the major environmental factors associated with the global-scale distributions of these important organisms remain poorly known. Given their importance for structuring lichens and therefore moderating ecosystem functions and processes, a better understanding of

global distribution of lichenised soil fungi is required if we are to prioritise ecosystem-level conservation and management efforts.

Exploring ecological drivers of lichenised soil fungi is essential to improve our prediction of these important organisms, and therefore preserve their ecosystem functions. Regional studies have suggested that the diversity and distribution of lichenised soil fungi could be regulated by multiple ecological factors such as climate, topography, soil properties, and competition with vascular plants (Will-Wolf *et al.*, 2004; Bowker *et al.*, 2016; Sahu *et al.*, 2019). Temperature and precipitation are considered the key drivers that structure soil-inhabiting lichenised fungi (Alatalo *et al.*, 2017; Vančurová *et al.*, 2018; Větrovský *et al.*, 2019; Voříšková *et al.*, 2019). For example, the timing, frequency, and size of precipitation events had been shown to affect the diversity of lichenised fungi (Bowker *et al.*, 2016; Barnes *et al.*, 2018). These climate changes ultimately regulate moisture availability, which is particularly important for the development of lichen symbiosis (Bowker *et al.*, 2016; Ding & Eldridge, 2020). However, despite a general understanding of climate effects on lichenised soil fungi, we still have a poor understanding of how climate drives the distribution of these soil organisms at the large global scale.

Lichenised soil fungi are also known to be influenced by soil physical and chemical properties (Ochoa-Hueso *et al.*, 2011; Payette & Delwaide, 2018). Numerous studies have suggested the importance of soil texture, pH and nutrient availability in driving the distribution patterns of lichenised soil fungi at small or regional scales (Bowker *et al.*, 2006; Li *et al.*, 2017; Kubiak & Osyczka, 2020). For example, lichen communities are found widely in soils with pH ranging from neutral to alkaline. Conversely, lichens could influence underlying soil properties, which in turn feed back upon lichenised soil fungi (van Zuijlen *et al.*, 2020). In addition, adjacent vascular plants can also influence lichen symbiosis through their effects on soil properties and lichen development, and competition for resources (e.g. space and light) (Armstrong & Welch, 2007; O'Bryan *et al.*, 2009; Bowker *et al.*, 2016; Gauslaa *et al.*, 2020). Increasing plant litter cover could reduce light that reaches the soil surface and therefore the available lichen habitat (Bowker *et al.*, 2005). Together, these ecological factors may alter the spatial distribution of lichenised soil fungi, but the relative importance of these factors for their global occurrence has not been well explored.

Our study aimed to explore the distributional patterns and ecological drivers of lichenised fungi in soil at a global scale. To achieve this aim, we used data from a global field survey of 235 natural ecosystems from nine biomes across six continents. The sampling sites included a wide range of vegetation, climate and soil types, and covered *c.* 73% of the environmental conditions found on Earth (Delgado-Baquerizo *et al.*, 2020). We expected to detect distinct patterns of lichenised soil fungal distribution, driven by various environmental parameters, across different biomes worldwide. To do this, we characterised the distribution of lichenised fungal diversity in the soil across the globe using internal transcribed spacer (ITS) amplicon sequencing. We then explored the relationship among diversity, relative abundance and environmental factors. Finally, we identified dominant genera across global soils and potential predictors of their distribution. The associations among lichenised soil fungi and ecological drivers allowed us to predict how their diversity and relative abundance might change, and therefore create global maps of their richness and the distribution of main genera.

Materials and Methods

Study areas and environmental conditions

We used a dataset from a global field survey (Egidi *et al.*, 2019) (<https://figshare.com/s/9772d31625426d907782>) to identify the distribution and ecological drivers of lichenised fungi 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 six continents and nine biomes (temperate, tropical and dry forests, cold, temperate, tropical and arid grasslands, shrubland and boreal forests). The selected sites represented a wide range of environmental gradients including climate, soil and vegetation types. For example, mean annual temperature and precipitation seasonality in these locations ranged from -11.4°C to 26.5°C and 7–127%,

respectively. Here we mainly targeted lichenised soil fungi from different biomes across the globe. Although lichens may not be present in every single soil samples, the species associated with lichenised fungi in the soil were analysed. The composite soil samples were comprised of 10–15 soil cores. Collected soils were homogenised and sieved through an ethanol-cleaned 2.0 mm sieves. One subsample was stored at -20°C for molecular analysis, and the rest of the soil was air dried for physicochemical analyses. Soil pH was measured with a pH meter in a 1 : 2.5 (w/w) soil : water mixture. Soil organic carbon (SOC) was measured according to the potassium dichromate oxidation method (Anderson & Ingram, 1993). Climate variables including mean annual temperature, precipitation seasonality and mean diurnal temperature range were collected from the WorldClim database (<https://www.worldclim.org>). The aridity index (precipitation/potential evapotranspiration) for each location was obtained from the Global Potential Evapotranspiration database (Zomer *et al.*, 2008), using interpolations from the WorldClim database. Lower values of aridity index indicated more hot/dry conditions, and higher values indicated cool/wet conditions. Plant cover (2001–2015) was obtained by remote sensing data from the Moderate Resolution Imaging Spectroradiometer at a *c.* 1 km resolution (Hijmans *et al.*, 2005).

Analyses of lichenised 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 (TCCTCCGCTTATTGATATGC) and an Illumina MiSeq platform (2×300 PE). The primers were modified with unique 8-bp Multiplex Identifier (MID) tags and adaptors. Bioinformatic processing was performed using a combination of USEARCH and UNOISE as previously described (Egidi *et al.*, 2019). Operational taxonomic units (OTUs) were partitioned at 97% similarity thresholds using UNOISE (Edgar, 2013). Fungal taxonomy was then annotated against the UNITE fungal database (v.7.2) and produced an OTU (phylotype) table (Kõljalg *et al.*, 2005). Lichenised fungal communities were identified based on the resulting OTU table using the FUNGuild database (<http://www.stbates.org/guilds/app.php>) (Nguyen *et al.*, 2016). We only included the lichenised fungal OTU (phylotype) with single trophic mode for downstream analyses, as the majority of mixed trophic modes (lichenised fungi and parasite) were unclassified. A complete list of the potential lichenised fungal phylotype in soils can be found in Table S1. The relative abundance of the lichenised fungi was calculated using the rarefied OTU table, as the sum of the relative abundance (%) of all the fungal sequences.

Statistical analyses

We used random forest models to identify those statistically significant ($P < 0.05$) predictors (Archer, 2016) of the richness of

lichenised fungi and the proportion of dominant genera across the globe. This approach enabled us to identify the importance of each predictor variable by evaluating the decrease in prediction accuracy as previously described (Delgado-Baquerizo *et al.*, 2018a,b). 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 lichenised fungal genera. Greater values of MSE% indicated a greater importance of variables. These analyses were conducted using the `RPERMUTE` package of the R statistical software (<http://cran.r-project.org/>). The variables included in the models were spatial (spatial dissimilarity and elevation), climate (mean annual temperature, aridity index, mean diurnal temperature range and precipitation seasonality), soil properties (pH, SOC and texture), and vegetation (ecosystem type and plant cover). 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). We also conducted Spearman correlation analyses to evaluate the associations between climate, vegetation, soil properties and the richness and relative abundance of the dominant lichenised fungal genera (top 10% in the relative abundance and occur in > 30% of all the surveyed locations). In parallel, we conducted a permutational multivariate analysis of variance to evaluate the effect of these environmental variables on the community structure of lichenised fungi using the `adonis2` function in the `VEGAN` package of R with 1000 permutations.

Mapping the global distribution of lichenised fungi in soil

We used the prediction-oriented regression model `Cubist` to define the potential distribution of the richness and main genera of lichenised soil fungi across the globe, and these analyses were conducted using R package `CUBIST` (Kuhn *et al.*, 2016). The `Cubist` model uses a regression tree analysis to generate a set of hierarchical rules using information on environmental covariates from the 235 sampling locations. Covariates in our models included the 12 environmental parameters that were used in the analyses of random forest and correlations as described above. Global predictions of the distribution of lichenised fungal richness and the proportion of dominant genera were done on a 25 × 25 km resolution grid. Soil properties for this grid across the globe were obtained from Soil Grids (Hengl *et al.*, 2017). Global information on vegetation types in this study (grasslands and forests) was obtained using the `Globcover2009` map from the European Space Agency. Global climate parameters were obtained from the `WorldClim` database (www.worldclim.org) and NASA satellites (<https://neo.sci.gsfc.nasa.gov>).

Results

Diversity and distribution of lichenised soil fungi across the globe

Based on amplicon sequencing of ITS markers and subsequent functional predictions of obtained fungal OTUs, we identified a

total of 880 fungal phylotypes as lichenised soil fungi in our global survey. Almost all (99.8%) of lichenised fungi belonged to Ascomycota, with a few Basidiomycota. Lichenised fungal orders with the highest relative abundances included Verrucariales, followed by Caliciales and Teloschistales (Fig. 1a). We detected the presence of lichenised soil fungi at 95% of surveyed locations (Fig. 1b), with substantial variation in richness across the sites. Most locations had a small number of lichenised fungal phylotypes, but some exhibited high levels of richness. Furthermore, shrublands (mostly drylands) and dry grasslands had much greater richness and relative abundance compared with other biomes (Fig. 1c,d). Conversely, less diverse lichenised fungi were detected in the soil of cold forests or boreal forests. The distribution of lichenised fungi in soils differed markedly across continents (Figs S2, 3a,b), although the average proportion in the global soils was relatively low (2.21% of all the fungal sequences). Consistently, the highest richness and relative abundance were found in Africa.

Ecological factors associated with the global distribution of lichenised soil fungi

Our random forest analyses indicated that aridity index, soil pH and plant cover were the most important predictors of lichenised fungal richness, although other ecological factors such as spatial scale, ecosystem type and soil property, were also important (Fig. 2a). Furthermore, we found that the richness of lichenised soil fungi had significant environmental preferences. For example, richness was strongly negatively related to aridity index and plant cover, but positively related to soil pH (Fig. 2b). We also observed significant associations among the richness of lichenised fungi and other environmental parameters such as elevation, mean diurnal temperature range and ecosystem type (forests and grasslands) (Table S2). In particular, most of the ecological factors associated with the richness were also correlated with the relative abundance of the lichenised soil fungi. Moreover, we observed significant effects of environmental parameters on the community composition of lichenised soil fungi (Fig. S4), with aridity index and plant cover as the most important factors explaining variations.

Dominant genera of lichenised fungi in the soil

We identified *Endocarpon*, *Verrucaria* and *Rinodina* as the globally dominant lichenised fungal genera (top 10% in relative abundance, and occurring in > 33% of all sites) (Fig. 3a). These dominant genera were affiliated with the families Verrucariaceae and Physciaceae of Ascomycota, and comprised 27% of the total fungal sequences classified as lichenised fungi. We found distinct proportions of the dominant genera across both biomes and continents (Fig. 3b,c), with the greatest relative abundance in dry grassland and Africa, respectively. However, the relative abundance of the three dominant genera varied across biomes and continents (Fig. S5a,b). For example, we found higher proportions of *Endocarpon* and *Verrucaria* in drylands (dry forests, dry grasslands and shrublands) compared with those in boreal and

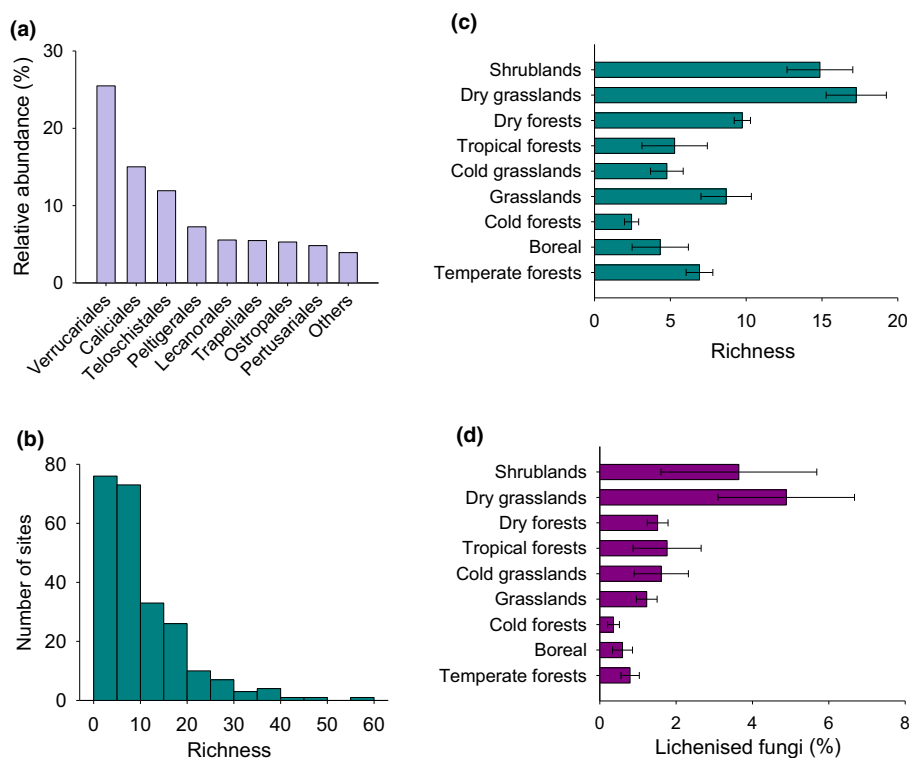


Fig. 1 Diversity and distribution of lichenised soil fungi. (a) Taxonomic information on the proportions (relative to total fungal sequences) of orders across all sites. (b) Distribution of the richness of total lichenised fungi from the 235 ecosystems surveyed. (c) Mean values (\pm SE) for the richness of lichenised fungi across nine biomes, including shrublands ($n = 15$), drylands ($n = 42$), dry forests ($n = 60$), tropical forests ($n = 7$), cold grasslands ($n = 22$), grasslands ($n = 41$), cold forests ($n = 18$), boreal ($n = 3$) and temperate forests ($n = 27$). (d) Mean values (\pm SE, with the same sample number as used for the richness calculation) for the relative abundance (relative to total fungal sequences) of lichenised fungi across different biomes.

cold forests. We then sought to identify the potential predictors of the distribution of dominant lichenised fungal taxa using a combination of random forest and correlation analysis. The results consistently indicated that pH was the most important factor associated with the relative abundance of *Verrucaria*, while seasonal precipitation was the only significant predictor of the relative abundance of *Rinodina* (Fig. S6a). There were no significant predictors of *Endocarpon* based on the random forest analysis; although their relative abundance was significantly correlated with multiple soil properties and climatic attributes (Fig. S6b). In addition, the relative abundance of the dominated lichenised genera had significant associations with aridity index, pH and plant cover (Fig. 4). This information allowed us to map the global distribution of the richness and proportion of dominant lichenised soil fungi (i.e. *Verrucaria* and *Endocarpon*) (Fig. 5). Our results were in accordance with results of those of our multivariate analyses, and identified drylands as the most important hotspots of lichenised fungal biodiversity.

Discussion

A large body of knowledge indicates that soil lichenised soil fungi play important roles in sustaining multiple terrestrial ecosystem functions (Bowker *et al.*, 2016; van Zuijlen *et al.*, 2020; Wang *et al.*, 2020), but the drivers of their global distribution are poorly known. Our study presents a novel assessment of the global distribution of lichenised soil fungi based on high-throughput sequencing of ITS markers. Our results indicated that aridity, soil pH and plant cover are the most important factors influencing their global distribution, allowing us to generate the first global

maps of the richness and of the dominant genera of lichenised fungi in soil. We therefore deciphered the major environmental factors at a global scale associated with distributions of lichenised soil fungi. Our identified environmental preferences and predicted maps pave the way for a greater understanding of the global diversity and major drivers of this important group of organisms on Earth.

Consistent with our current understanding of fungal community composition, lichenised soil fungi were dominated by Ascomycota, the most ubiquitous fungal taxa globally (Tedersoo *et al.*, 2014; Egidi *et al.*, 2019). In addition, we identified major orders and genera of lichenised fungi in soil at a global scale that could be key drivers of the ecosystem functions they sustain. Important, we characterised their distribution across different biomes and continents, and found that the global distribution of lichenised soil fungi was highly variable. Our results are in accordance with previous studies indicating the relatively high richness of lichenised fungi in Europe and Africa, but relatively low richness in South America (Will-Wolf *et al.*, 2004; Bowker *et al.*, 2016; Rodriguez-Caballero *et al.*, 2018). Disjunct global distribution patterns of lichenised soil fungi are likely to be related to distinct climatic characteristics across continents (Will-Wolf *et al.*, 2004; Tedersoo *et al.*, 2014; Alatalo *et al.*, 2017; Smith *et al.*, 2020). For example, Africa had relatively high annual mean temperature and aridity (i.e. low aridity index, Fig. S7), which may promote a more diverse lichen flora that generally prefers arid conditions or relies on nonrainfall inputs of moisture (dew) for survival (Lalley & Viles, 2008; Asplund & Wardle, 2017; Rodriguez-Caballero *et al.*, 2018). This is also supported by the strong negative associations between aridity index and the

Fig. 2 Environmental factors associated with the richness of lichenised fungi. (a) Random forest (RF) analyses identifying the importance of potential predictors of lichenised fungal richness. RF Importance = Increase in % mean square error. Coloured and white 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; SOC, soil organic carbon; TSEA, temperature seasonality. The aridity index, precipitation/potential evapotranspiration, and lower values of aridity index indicate higher aridity. (b) Relationships between main environmental predictors and the richness of lichenised fungi in soils across the globe. **, $P < 0.01$.

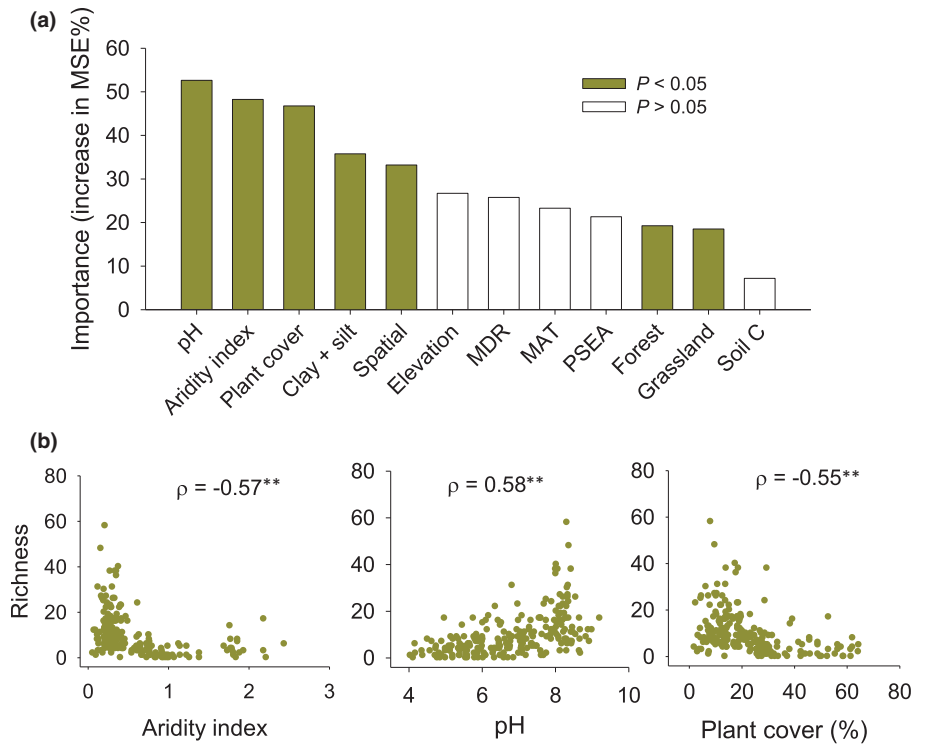
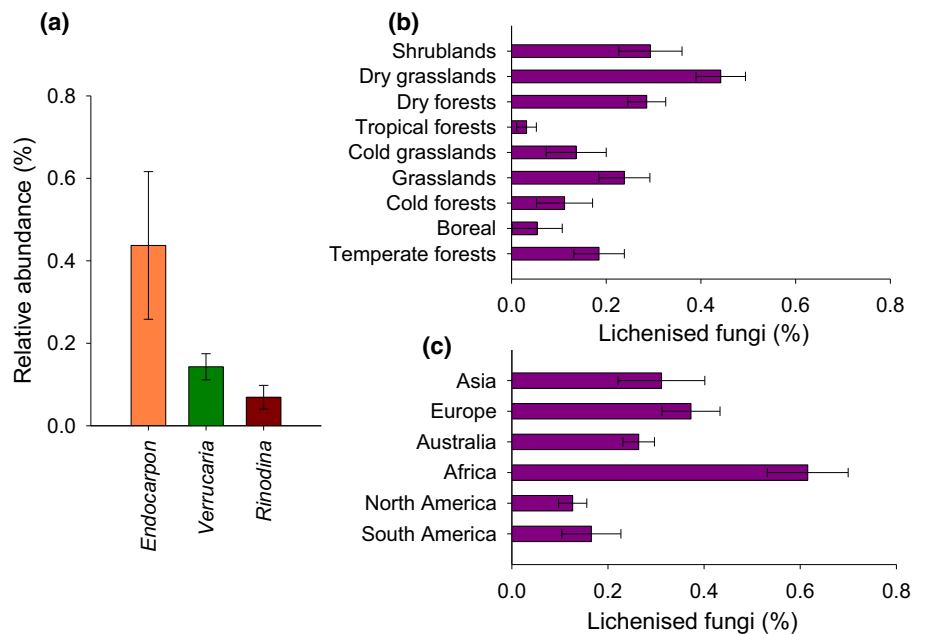


Fig. 3 Relative abundance (% of all the fungal sequences) of dominant lichenised fungal genera. (a) Mean values (\pm SE) for the relative abundance of the dominant lichenised fungal genera in the soil from global 235 sites. (b) Mean values (\pm SE) for the relative abundance of the dominant genera across different biomes. (c) Mean values (\pm SE) for the relative abundance of the dominant genera across continents including Africa ($n = 18$), Europe ($n = 31$), Asia ($n = 10$), Australia ($n = 85$), North America ($n = 77$) and South America ($n = 14$).



richness and relative abundance of lichenised soil fungi, based on our combined analyses of random forest and correlation (Fig. 2; Table S2). Strikingly, we observed extremely low diversity of lichenised soil fungi in humid areas (e.g. aridity index greater than 0.5), and this was consistent with the sporadic distribution of the dominant genera in areas of high rainfall. High aridity could limit the development of vascular plants, giving lichen symbiosis a competitive advantage over vascular plants, unlike the humid areas where lichens are unable to cope with high levels

of litter cover (Ding & Eldridge, 2020). Our observations were also consistent with the results of recent studies of the habitat preferences of dominant Ascomycota and cyanobacteria in drylands (Egidi *et al.*, 2019; Cano-Díaz *et al.*, 2020). Consequently, there were more diverse lichenised soil fungi and greater cover in drylands (shrublands and dry grasslands) compared with those in boreal forests. Arid and semiarid environments typically have a greater cover of bare soil, which provides opportunities for lichen colonisation and development. Furthermore, sparse plant cover

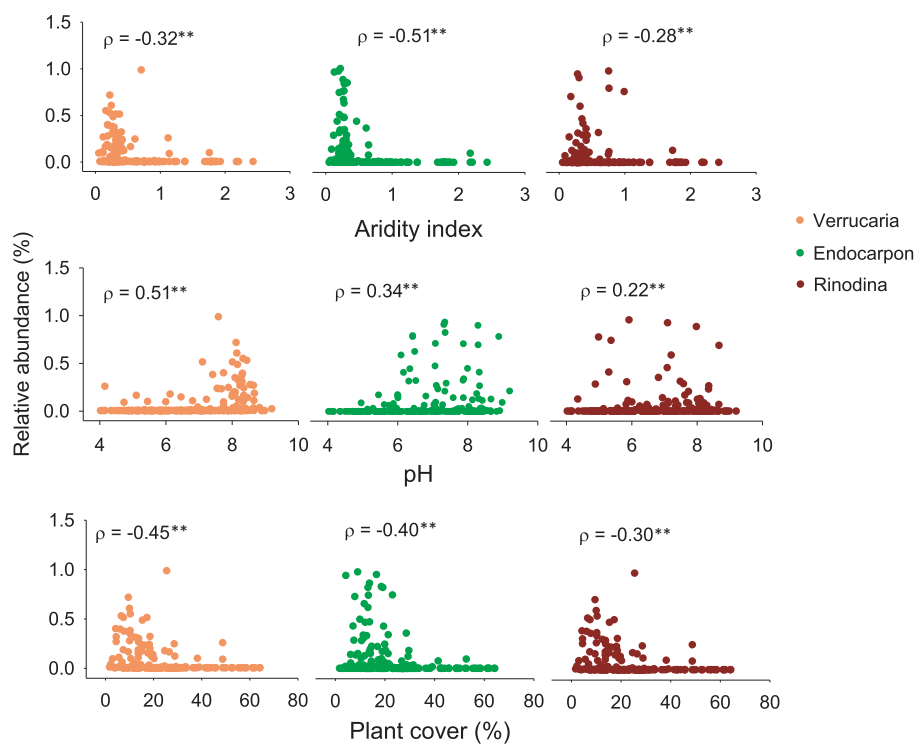


Fig. 4 Environmental preferences (aridity, pH, and plant cover) of dominant lichenised fungal genera in soil. Significant ($P < 0.05$) Spearman correlation coefficients are shown in the upper part of each panel. **, $P < 0.01$.

in drylands allows sites to receive more sunlight, which would probably support a lichenised fungal community through enhanced photosynthesis of their symbiotic partners (Sahu *et al.*, 2019). Finally, relatively less plant litter in arid environments would have a lower suppressive effect (e.g. reducing light exposure) on lichen functions such as respiration (Ding & Eldridge, 2020). Together, this evidence provides strong support for the notion that aridity plays a significant role in influencing the global distribution of lichenised soil fungi. We acknowledge, however, that alternate wetting and drying may also be important for lichen development (Rogers, 1971). As aridity is a measurement of temperature and precipitation patterns, changes in aridity, predicted by current global change models suggest that the distribution of lichenised soil fungi is likely to change over the next century. Given the relationship between aridity and vascular plant cover (Fig. S8), we might expect interactive effects on lichenised soil fungi due to a combination of altered climate and vascular plant vegetation.

Our combined analyses indicate an overriding importance of soil properties as global drivers of lichenised fungi. Of particular importance was soil pH, specifically high pH, which is probably the most important soil variable regulating their richness and relative abundance (Bowker *et al.*, 2016). Our results are consistent with numerous studies highlighting the crucial role of soil pH in regulating the geographic distribution of both biocrusts and soil microbial communities (Root & McCune, 2012; Tedersoo *et al.*, 2014; Bowker *et al.*, 2016; Fierer, 2017; Cano-Díaz *et al.*, 2020). This effect might be related to the physiology of lichenised fungi (Ochoa-Hueso *et al.*, 2011), although underlying mechanisms are yet to be fully explored. In addition, soil texture is an important predictor of global distribution of lichenised soil fungi, and

is consistent with the results of recent studies conducted at small spatial scales (Bowker *et al.*, 2016; Ding & Eldridge, 2020). However, soil carbon could play a relatively less important role in driving the distribution of lichenised soil fungi due to autotrophic photosynthesis of their symbiotic partners. These findings advance our understanding of the roles of soil properties in global distribution of lichenised soil fungi.

Our study also indicated that the distribution of the lichenised fungi in soil was correlated with vegetation, although the mechanisms underpinning this relationship are likely to be complicated. The observed environmental preferences of lichenised soil fungi suggested the potential role of plant cover in regulating their richness and relative abundance. More diverse and abundant lichenised soil fungi mainly occurred in the sites with less than 30% plant cover (Figs 2, 4). These observations were consistent with previous studies highlighting the negative effects of plant canopies on soil lichens through changing microenvironments such as light, moisture and temperature (Bowker *et al.*, 2016). For example, increasing plant litter may reduce light exposure and suppress lichenised fungal metabolisms (e.g. photosynthesis and respiration) (Ding & Eldridge, 2020). However, recent studies have indicated that small amounts of litter may advantage lichenised fungi by buffering environmental stress (e.g. drought and heat) (Serpe *et al.*, 2013; Belnap *et al.*, 2016). Plant cover also plays roles in sustaining soil stability and fertility (Maestre, 2003; O'Bryan *et al.*, 2009; Bowker *et al.*, 2016) and, therefore, has positive effects on the development of lichenised symbiosis. Conversely, an extensive cover of lichen-forming biocrusts may benefit adjacent vascular plants by increasing the availability of runoff water and by reducing evaporation (Eldridge *et al.*, 2020). Consequently, the net effect of competition and facilitation is the

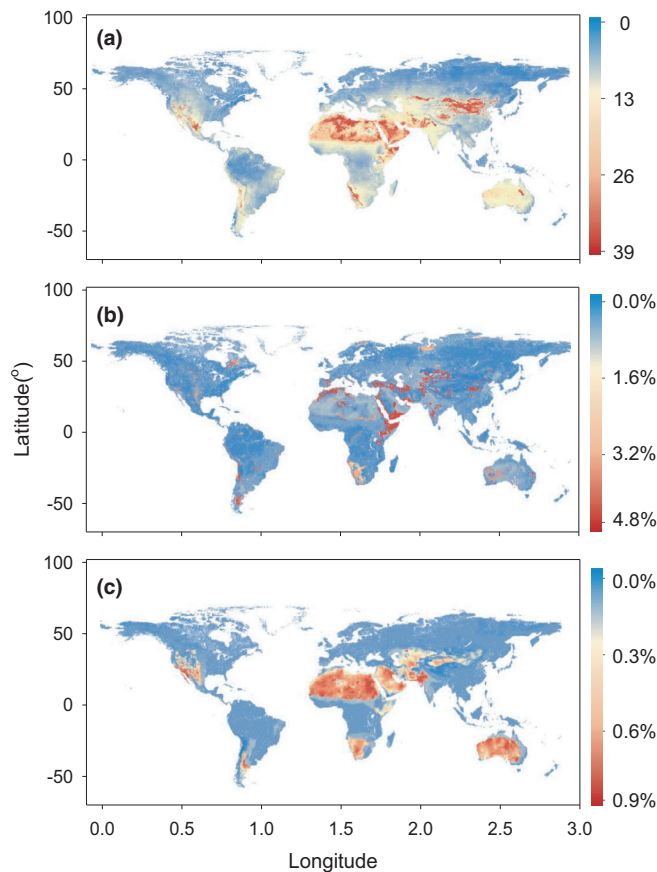


Fig. 5 Predicted global distribution of lichenised fungi in soil. The percentages of variation explained by the models are as follows. (a) Richness of lichenised fungi, $r = 0.43$; $P < 0.001$. (b) Relative abundance (% of all the fungal sequences) of *Verrucaria*, $r = 0.46$; $P < 0.001$. (c) Relative abundance (% of all the fungal sequences) of *Endocarpon*, $r = 0.30$; $P < 0.001$.

co-occurrence of lichen symbiosis and vascular plants. Competitive effects are important for structuring lichen communities at a global scale, as lichen symbiosis may confer a competitive advantage and promote stability (Rogers, 1971; Bowker *et al.*, 2016; van Zuijlen *et al.*, 2020; Veres *et al.*, 2020). However, drought conditions may favour lichen development over vascular plants in drylands and give greater tolerance by lichens to extreme dryness, light and temperature (Belnap, 2006; Ding & Eldridge, 2020). We also noted that plant cover was related to plant type, suggesting the important of ecosystem type (e.g. forests and grassland) for the occurrence of lichenised soil fungi, as observed in this study. Compared with grasslands and shrublands, there would be greater competition for light in forests, thereby negatively affecting lichenised fungi in soil.

Our work identified the major environmental factors associated with the richness and proportion of lichenised soil fungi at a global scale. This predictive knowledge allowed us to generate the first global atlas of the distribution of lichenised soil fungi worldwide. Our maps highlighted locations from Western America, Chile and Bolivia, Southern Spain, North and South Africa, China and Australia as major hotspots for the diversity of

lichenised soil fungi. All these locations have previously been highlighted as important regions supporting lichen communities (Will-Wolf *et al.*, 2004; Bowker *et al.*, 2016). However, a standardised global map highlighting the global distribution of these organisms has until now been unavailable. Our results suggested that the dominant lichenised fungal genera had similar ecological preferences as the whole lichenised fungal community across the globe. Consistently, aridity, soil pH and plant cover could be important factors associated with the global distribution of these dominant taxa. These results were in agreement with most previous studies suggesting that the dominant taxa parallel patterns of whole soil microbial communities (Delgado-Baquerizo *et al.*, 2018a,b). However, our results do not provide high-resolution information on the fine-scale distributions of lichenised soil fungi, which could be affected by factors not included in our analyses, such as microclimatic variations. More detailed information can be found in the map uncertainties (Fig. S9). Therefore, future work should identify more potential environmental factors associated with lichenised soil fungi worldwide.

The relative abundance of the dominant lichenised soil fungi sharply increased along elevated aridity (i.e. index lower than 0.5), which could be related to their physiological tolerance to harsh conditions. For example, *Endocarpon* was found to have genes involved in homothallic reproduction and drought tolerance based on the genomic analysis (Wang *et al.*, 2014), and *Verrucaria* can develop a strategy for overcoming extreme environments through its endolithic growth (Garvie *et al.*, 2008). However, the results of random forest analysis revealed distinct predictors for the different dominant genera. For example, pH is important in predicting the relative abundance of *Verrucaria* and *Endocarpon*, but not *Rinodina*. We found that precipitation seasonality is a potential predictor of *Rinodina*, suggesting that it is sensitive to changes in seasonal precipitation, similar to lichenised fungi in general (Bowker *et al.*, 2016; Veres *et al.*, 2020). While fluctuations in seasonal precipitation might favour some lichenised taxa (Lange, 1953; Rogers, 1971), high levels of hydration, particularly at high temperatures, are known to reduce photosynthetic levels of lichen symbiosis despite their high respiration (Rogers, 1971). Such knowledge advances our understanding of the ecological drivers of dominant lichenised fungi worldwide and, therefore, helps to improve our predictions and management of these organisms across the globe.

Our survey is based on topsoil samples from across the globe, which enabled us to characterise the diversity and community composition of lichenised soil components at a global scale. However, this study also has some limitations including the fact that we only measured the lichenised soil fungi or that we used FUNGuild to identify lichenised fungal taxa, which relied on well described taxa. Further analyses including new taxonomic information will expand our understanding of the classification through DNA marker sequencing. In addition, our results could not exclude free-living fungi in the soil, although lichenised fungi are obligate symbiotic associations with their partners (Abed *et al.*, 2013). We also noted that the results from statistically analyses may not reflect a real association of lichenised soil fungi with environmental parameters. Therefore, future work needs to be

done to clarify the effects of these factors on the distribution of lichenised soil fungi, especially in the regions that are less well studied such as Russia, China and Africa.

Collectively, our work provides novel insights into the global diversity and distribution of lichenised soil fungi. We identified environmental preferences of the richness and relative abundance of major taxa of lichenised fungi across the global, which allowed us to create the first global maps of their distribution. In particular, we underline the fact that aridity plays vital roles in driving the prevalence of lichenised soil fungi at a global scale. Consequently, projected global increases in aridity are likely to have profound effects on their distribution and ecosystem functions. These results also illustrate how environmental changes, including vegetation and soil properties, may substantially modify the community diversity and distribution of global lichenised soil fungi. Our work may have implications on improving the management of lichenised fungi by identifying specific biomes and locations where these taxa are an important component of the soil biodiversity.

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Author contributions

Y-RL and MD-B planned and designed the research. MD-B, JW, BKS and X-MZ performed experiments and analysed the data. The manuscript was written by Y-RL, DJE and MD-B with contributions from all co-authors.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Global survey including the 235 locations used in this study.

Fig. S2 Distribution of the relative abundance of total lichenised fungi in soils across the 235 ecosystems surveyed.

Fig. S3 Mean values for the richness and proportion of lichenised soil fungi across different continents globally.

Fig. S4 Canonical correspondence analysis between lichenised fungal community and environmental variables.

Fig. S5 Distribution for dominant lichenised fungal genera across nine biomes and continents.

Fig. S6 Associations between environmental factors and the proportion of lichenised soil fungi.

Fig. S7 Mean annual temperature and aridity index in the different continents.

Fig. S8 Relationship between aridity index and plant cover across the six continents.

Fig. S9 Map uncertainties for our global survey.

Table S1 A complete list of the potential lichenised fungal phylo-
types.

Table S2 Spearman correlation coefficients between environmen-
tal factors and the proportion of lichenised soil fungi.

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