

**Title page****Title:** Temperature thresholds drive the global distribution of soil fungal decomposers**Running title:** Biogeography of soil fungal decomposers**Authors:** Youzhi Feng<sup>1\*</sup>, Jianwei Zhang<sup>1</sup>, Miguel Berdugo<sup>2,3</sup>, Emilio Guirado<sup>4</sup>, Carlos A. Guerra<sup>5,6</sup>, Eleonora Egidi<sup>7,8</sup>, Juntao Wang<sup>7,8,9</sup>, Brajesh K. Singh<sup>7,8</sup>, Manuel Delgado-Baquerizo<sup>10\*</sup>**ORCID:**Youzhi Feng: <https://orcid.org/0000-0002-8519-841X>Jianwei Zhang: <https://orcid.org/0000-0002-6390-335X>Miguel Berdugo: <https://orcid.org/0000-0003-1053-8907>Emilio Guirado: <https://orcid.org/0000-0001-5348-7391>Carlos A. Guerra: <https://orcid.org/0000-0003-4917-2105>Eleonora Egidi: <https://orcid.org/0000-0002-1211-2355>Juntao Wang: <https://orcid.org/0000-0002-1822-2176>Brajesh K. Singh: <https://orcid.org/0000-0003-4413-4185>Manuel Delgado-Baquerizo: <https://orcid.org/0000-0002-6499-576X>**Affiliations:**<sup>1</sup>State Key Laboratory of Soil and Sustainable Agriculture, Institute of Soil Science, Chinese Academy of Sciences, 260000, Nanjing, China<sup>2</sup>Instituto Multidisciplinar para el Estudio del Medio “Ramón Margalef,” Universidad de Alicante, 03690 San Vicente del Raspeig, Alicante, Spain<sup>3</sup>Institut de Biologia Evolutiva (UPF-CSIC), 08003 Barcelona, Spain<sup>4</sup> Instituto Multidisciplinar para el Estudio del Medio “Ramón Margalef,” Universidad de Alicante, 03690 San Vicente del Raspeig, Alicante, Spain<sup>5</sup>German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany<sup>6</sup>Institute of Biology, Martin-Luther University Halle-Wittenberg, Halle (Saale), Germany<sup>7</sup>Global Centre for Land-Based Innovation, Western Sydney University, Penrith, New South Wales, Australia<sup>8</sup>Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales, Australia<sup>9</sup>State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental

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## Abstract

Unraveling the biogeographic pattern of soil fungal decomposers along temperature gradients – in a smooth linearity or an abrupt jump – can help us connect the global carbon cycle to global warming. Through a standardized global field survey, we identify the existence of temperature thresholds that control the global distribution of soil fungal decomposers, leading to abrupt reductions in their proportion (i.e. the relative abundance in fungal community) immediately after crossing particular air and soil temperature thresholds. For example, small increases over the mean annual temperature threshold of  $\sim 9^{\circ}\text{C}$  result in abrupt reductions in their proportion, paralleling a similar temperature threshold for soil carbon content. We further find that the proportion of soil fungal decomposers is more sensitive to temperature increases under arid conditions. Given the positive correlation between the global distributions of fungal decomposers and soil heterotrophic respiration, the reported temperature-driven abrupt reductions in fungal decomposers could further suppress their driven soil decomposition processes and reduce carbon fluxes from soils to the atmosphere with implications for climate change feedback. This work not only advances the current knowledge on the global distribution of soil fungal decomposers, but also highlights that small changes in temperature around certain thresholds can lead to potential unexpected consequences in global carbon cycling under projected climate change.

**Keywords:** Fungal decomposers, Biogeography, Biodiversity, Global change, Soil decomposition

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## Introduction

Fungi constitute the most important soil decomposers on the planet, and they play a fundamental role in global carbon cycling (Boddy, 2016; Treseder & Lennon, 2015). These organisms secrete a powerful cocktail of enzymes to degrade complex organic compounds (e.g., lignocellulose, chitin and soil organic matter). Hence, they also regulate important carbon fluxes from soils to the atmosphere (Baldrian & Valaskova, 2008; Crowther et al., 2012). It is well known that soil fungi are highly sensitive to temperature increases (Guo et al., 2018; Romero-Olivares et al., 2017). For example, the soil fungal diversity is higher at high latitudes (Větrovský et al., 2019). Not surprisingly, temperature is a major regulator of soil decomposition processes and heterotrophic respiration worldwide (Allison et al., 2010; Karhu et al., 2014; Walker et al., 2018). A recent report found that the soil heterotrophic respiration is not linearly correlated with air/soil temperatures. Instead, there are temperature thresholds that drive soil respiration (Johnston et al., 2021). The non-linear relationship indicates a drastic transition (e.g., in magnitude and sometimes even in direction), for example, of spatial changing pattern when the determined ecosystem properties (e.g., soil microbes) respond to changing environmental conditions (Berdugo et al., 2020; Johnston et al., 2021). Such a drastic transition challenges the applicability of a linear model in predicting responses and feedback of soil carbon stocks to global change (Sulman et al., 2018). In spite of the importance of soil fungal decomposers in global carbon cycling and carbon fluxes from soil to the atmosphere, it remains virtually unknown whether the responses of soil fungal decomposer abundances to temperature increases are linear or non-linear.

Space-for-time substitution approaches can help fill this critical knowledge gap by revealing the global distribution and the ecology of soil fungal decomposers along temperature gradients. In this context, we posit that a temperature change – even if it is a very small one – that transitions from colder (e.g., continental and polar) to warmer (e.g., arid, tropical and temperate) ecosystems could result in abrupt non-linear decreases in the proportion of soil fungal decomposers in fungal community, leading to significant reductions in the soil CO<sub>2</sub> emission to the atmosphere. Indeed, non-linear associations have been found for soil fungi in response to aridity thresholds in global drylands (Berdugo et al., 2020; Groffman et al., 2006), but the influence of temperature on soil fungal decomposers at a global scale is far less studied. This knowledge is essential for a thorough understanding of the responses and feedback of soil fungal decomposers to global change (Frey et al., 2013; Walker et al., 2018).

Here, we conduct a global field survey (Egidi et al., 2019) including Internal Transcribed Spacer (ITS2, (Blaalid et al., 2013)) amplicon sequencing information for 235 natural ecosystems from six continents encompassing nine biomes (Fig. S1a) to investigate the responses of the proportion soil fungal decomposers to worldwide temperature increases. This global survey is fundamental to determine non-linear patterns in the proportion of soil fungal decomposers, as local and/or regional studies including narrow temperature conditions do not have sufficient data resolution to determine such patterns. Our global field survey includes a wide variety of vegetation, climates and soil types (Delgado-Baquerizo et al., 2020). This global survey was previously used to identify the major dominant fungal taxa in soils across the globe (Egidi et al., 2019). Here, the proportion (%) of soil fungal decomposers is determined using rarefied ITS zero-radius operational taxonomic units (zOTUs) (or phylotypes) tables (100% similarity), as the sum of relative abundances of all ITS sequences classified as soil fungal decomposers (i.e., sum of all ITS reads classified as soil fungal decomposers / all ITS reads x 100 at each soil sample). We classify fungal phylotype at the genus level into soil fungal decomposers with their primary lifestyle of saprotrophic mode using the most novel fungal-trait databases (Pölme et al., 2021). Fungal taxa with other and/or unclassified trophic modes are excluded from the downstream analyses (see Methods). In general, soil fungal decomposers represent 10.6% of all ITS sequences and 8.6% of phylotypes identified as fungi (Fig. S1b). Furthermore, we create the first global map of soil fungal decomposers. And then we correlate the proportion of soil fungal decomposers with soil heterotrophic respiration (Warner et al., 2019) using a global grid including >140000 locations.

## **Materials and Methods**

### **Identification of fungal decomposer phylotypes**

Details of sampling locations and collections have been reported and described previously (Egidi et al., 2019). In brief, we collected 235 soils samples in 18 countries, covering 9 biomes (temperate, tropical and dry forests; cold, boreal, temperate, tropical and arid grasslands and shrublands) across the globe (Fig. S1a), following a uniform sampling standard. Fungal communities were determined using the primer set FITS7/ITS4 (Ihrmark et al., 2012) targeting the Internal Transcribed Spacer (ITS) region 2 (Blaalid et al., 2013) on an Illumina MiSeq platform (PE 300) located in the Next Generation Genome Sequencing Facility of the University of Western Sydney (Australia). The detailed information on DNA extraction and PCR amplification

was presented previously (Egidi et al., 2019). All reads were quality filtered and dereplicated using the USEARCH pipeline (Edgar, 2010), with low-quality bases being end-trimmed before merging and expected error < 0.5 for merged reads (Egidi et al., 2019). Quality reads were clustered into zOTUs (or phylotypes) of the length of 180 bp at 100% similarity threshold using UNOISE2 (Edgar, 2016b). Phylotype identification was determined against the UNITE fungal database (V7.2, last accessed May 2020) (Abarenkov et al., 2010) using the SINTAX algorithm with a  $\geq 80\%$  probability threshold (Edgar, 2016a). The raw fungal data is publicly available in Figshare (<https://doi.org/10.6084/m9.figshare.5923876>).

We classified fungal phylotypes into fungal decomposers against FungalTraits database (according to commonly used category “Primary lifestyle”, last accessed February 2021) (Pöhlme et al., 2021) and calculated the proportion of phylotypes that matched a soil fungal decomposer (soil saprotrophic) trophic mode in all classified fungal phylotypes. Within 20,959 phylotypes belonging to the fungal kingdom (rarefaction to a sequence depth of 4,466), we identified 1,804 fungal decomposers with soil-trophic life style (namely soil saprotrophs). The proportion of soil fungal decomposers was then calculated using a rarefied (4,466 sequences/sample) ITS zOTU table (100% similarity), as the sum of the relative abundance (the proportion, %) of all ITS sequences classified as soil fungal decomposers (i.e., sum of all ITS reads classified as soil fungal decomposers / all ITS reads  $\times 100$  at each soil sample).

### **Identifying ecological preferences of soil fungal decomposers**

We used Random Forest analysis to identify environmental preferences of soil fungal decomposers across the globe. Our models included 15 environmental variables: climatic variables (mean annual temperature (MAT) and precipitation (MAP) and temperature and precipitation seasonality), elevation, net primary productivity (Normalized Difference Vegetation Index; NDVI index) and plant cover, soil properties (texture [% of clay + silt], soil pH, total C, N and P concentrations and C:N ratio) and dominant ecosystem types in our dataset (forests and grasslands). The coordinates of each site were recorded in situ with a portable GPS, and the ecosystem type (e.g., grassland and forest) of each location recorded when sampling. Climatic variables for all sampling locations were obtained from the Worldclim v2 database (~ 1 km resolution) ([www.worldclim.org](http://www.worldclim.org)) (Fick & Hijmans, 2017). NDVI data were obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) aboard NASA's Terra satellites (250 m resolution) (<http://neo.sci.gsfc.nasa.gov/>) and calculated the monthly averaged value between

sampling period (Delgado-Baquerizo et al., 2018). Plant cover was retrieved from Filipponi et al. (2018). Soil properties including soil texture (% of clay + silt), soil pH, concentrations of soil total C, N, P and soil C:N ratio were measured using standard laboratory methods (Delgado-Baquerizo et al., 2018). The proportion of soil fungal decomposers guild was log-transformed to increase normality. Ecosystem types were coded as categorical variables with two levels: 1 (a given ecosystem type) and 0 (remaining ecosystem types). This approach allowed us to compare the effect of a particular ecosystem type on the proportion of each phylotype compared with the average of the remaining ecosystem types. We included the most dominant ecosystem types in our models (e.g., forests and grasslands). These analyses were conducted using the *rfPermute* package (v2.1.81) (Archer, 2020) in R (v3.6.3) (Team, 2020).

### **Evaluation of linear and non-linear responses to temperature attributes**

Additional temperature variables were obtained from the Worldclim v2 database ([www.worldclim.org](http://www.worldclim.org)) (Fick & Hijmans, 2017), including 8 more air temperature variables, such as mean diurnal/annual range (BIO2), maximum temperature of warmest month (BIO5), minimum temperature of coldest month (BIO6), as well as mean temperature of wettest (BIO8)/driest (BIO9)/warmest (BIO10)/coldest (BIO11) quarters. We also obtained soil temperature (land surface temperature) from <https://neo.gsfc.nasa.gov>, covering the period of study. Our choice of soil temperature was also positively and significantly correlated with a recent index of soil temperature (Lembrechts et al., 2021) ( $r = 0.89$ ;  $P < 0.001$ ;  $n = 235$ ). We fitted linear and non-linear (quadratic and general additive models [GAM] (Hastie, 2020)) regressions to the relationships between these temperature variables and the proportion of soil fungal decomposers as well as soil carbon content separately. Akaike information criterion (AIC) was used to decide the model that best fitted in each case (Figs. S2 and S3). This criterion penalizes model fit when more parameters (as used in non-linear regressions) are used, so that the most likely model has the lowest AIC value (Berdugo et al., 2020). In general, differences in AIC values higher than 2 indicate that the models are different (Berdugo et al., 2020). The linear model is the null hypothesis and assumes a gradual response of a given ecosystem attribute in response to increases in temperature. Quadratic and GAM models evidence a nonlinear but continuous trend throughout the temperature gradient. We chose quadratic to synthesize the simplest case of nonlinear trend, and GAM to summarize more complex trends (through smoothing parameters (Hastie, 2020)). We further applied likelihood ratio tests to compare the goodness of fit of nonlinear and linear models

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(Fig. S4) (Hothorn et al., 2020). A statistic P value less than 0.05 indicates that adding complexity to linear model (i.e., by adding more parameters) makes it significantly more accurate. Only when non-linear regressions were a better fit to the data, thresholds may be present. Therefore, we explored the presence of thresholds only when non-linear models were a better fit to the data by either segmented, step or stegmented regressions, which could detect the shift in the relationship in slope, intercept or slope + intercept, respectively. To obtain the variance associated to each threshold, we performed 1000 bootstrap samplings on each database, thus allowing us to find a set of 1000 plausible thresholds for each variable. To further test whether the thresholds identified significantly affected the slope and/or intercept of the fitted regressions, we bootstrapped linear regressions at both sides of each threshold for each variable. We then extracted the slope and the predicted value of the variable evaluated before and after the threshold and compared them using a Mann-Whitney U test. In all cases, we found significant differences in at least one of these two parameters (Figs. S5 and S6). We used the *chngpt* (v2021.5-12) (Fong et al., 2020) and *gam* (v1.20) (Hastie, 2020) packages in R to fit segmented/step/stegmented and GAM regressions, respectively.

### **Mapping the global distribution of soil fungal decomposers**

To predict the extent of the global distribution of soil fungal decomposers, we conducted a Random Forest regression analysis (Lahouar & Slama, 2015) using the variables (elevation, MAT, precipitation seasonality, MAP, temperature seasonality, clay and silt content, soil pH, soil nitrogen, soil carbon, plant cover, normalized difference vegetation index, forest (0/1) and grassland (0/1); presence/absent of these ecosystems in a given plot from the MCD12Q1 V6 product derived from the IGBP classification (Loveland et al., 1999) were used) and 235 locations with the proportions of soil fungal decomposer data. This model was built by finding the set of covariate combinations that most robustly predict the training samples with 9999 trees and 999 repetitions. To assess the accuracy of the predictions calculated from the random forest-based model, we calculated how much the parameter space of the predictors differed from the original dataset. We used the Mahalanobis distance of any multidimensional point of the fourteen dimensions given by the exogenous variables to the center of the known distribution that we have previously calculated and the distance of any multidimensional point to the convex hull formed by the 235 locations that were used in the model. Subsequently, we used outlier identification to mask our results and provide more reliable predictions at the 0.9 quantiles of the chi-square distribution



with fourteen degrees of freedom to which each location belongs (Mallavan et al., 2010). The modeling approach was then validated by returning the predicted values (x-axis) vs. the observed values (y-axis), following Piñeiro et al. (2008). Finally, we correlated our global map for the proportion of soil decomposers with the global map of soil heterotrophic respiration in Warner et al. (2019) using a global grid including >140000 locations.

### Statistical analysis

Differences in the relative abundance of soil fungal decomposer phylotypes and in their relative abundances among continents and ecosystems were evaluated with one-way ANOVA followed by post-hoc Tukey's HSD tests. Differences of  $P<0.1$ ,  $P<0.05$  and  $P<0.01$  were respectively considered statistically marginally significant, significant and highly significant.

### Results

Global ITS amplicon analyses indicate that soil fungal decomposers are widely distributed across all sampling locations (Figs. 1a and S1a), and further highlight that the higher proportions of soil fungal decomposers can be found in high latitude continents (Global ANOVA,  $F_{(5, 229)} = 1.83$ ,  $P=0.08$ ) and/or cold ecosystems ( $F_{(8, 226)} = 5.85$ ,  $P<0.001$ ) (Fig. 1b). *Endogonomycetes* and *Taphrinomycetes* phylotypes are found to be the dominant soil fungal decomposers in our survey ( $F_{(15, 1410)} = 10.97$ ,  $P<0.001$ ) (Fig. 1c).

Using the Machine-learning Random Forest algorithm, MAT is identified as a fundamental driver of the proportion of soil fungal decomposers in terrestrial ecosystems worldwide (Fig. 2a). As expected, MAT does not stand alone as the single driver of the proportion of soil fungal decomposers. Other key environmental factors such as soil carbon (a surrogate of organic matter) and key edaphic properties (i.e., pH and % of Clay+Silt) are also identified as important factors influencing the proportion of soil fungal decomposers (for example, *Leotiomycetes* and *Tremellomycetes*) (Figs. 2a and S7). Given that we are able to efficiently predict the distribution of soil fungal decomposers, we use Random Forest to create the first global map of soil fungal decomposers worldwide (at 10 km resolution;  $R^2=0.696$ ,  $P<0.001$ ; Fig. 2b). Moreover, we find that the proportion of soil fungal decomposers is highly and positively correlated with global soil heterotrophic respiration reported by Warner et al. (2019) (Pearson's  $r=0.40$ ,  $P<0.001$ , Fig. 2c).

Further non-linear regression analyses reveal that there are several temperature thresholds associated with the global distributions of soil fungal decomposers and topsoil carbon content.

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Specifically, when air temperature crosses a  $\sim 8.86^{\circ}\text{C}$  temperature threshold, we find the abrupt reduction in the proportion of soil fungal decomposers at a global scale (Figs. 3 and S5). Subsequently, the proportion of soil fungal decomposers decreases sharply (namely with the higher slope) when soil temperature is higher than the threshold of  $\sim 22.41^{\circ}\text{C}$ , or the max temperature of warmest month is over  $\sim 27.97^{\circ}\text{C}$  (Fig. 3). Consistently, non-logged transformed data exhibit similar temperature thresholds for soil fungal decomposers (Fig. S8). Such divergent temperature-dependent patterns are largely consistent with other temperature attributes (e.g., mean temperature of warmest and coldest quarters) (Fig. 4). In addition, the temperature threshold value of mean temperature driest quarter is  $\sim 7.91^{\circ}\text{C}$ , smaller than MAT threshold of  $\sim 8.86^{\circ}\text{C}$  (Fig. 4). For topsoil carbon, we find similar temperature thresholds influencing their amount worldwide, such as  $\sim 7.31^{\circ}\text{C}$  for MAT,  $\sim 24.42^{\circ}\text{C}$  for soil temperature and  $\sim 31.43^{\circ}\text{C}$  for max temperature of warmest month (Figs. 3 and S6). Namely, abrupt decreases in topsoil carbon content occur when these temperatures transit.

## Discussion

Our study provides new insights on the importance of temperature as a driver of the proportion of soil fungal decomposers (Fig. 2a), showing that temperature thresholds control the global distribution of fungal decomposers. Our findings add to previous independent studies highlighting the importance of temperature as a driver of fungal communities (Tedersoo et al., 2014; Větrovský et al., 2019) and decomposition processes (Ayres et al., 2009; Glassman et al., 2018). Here, we further draw the first global map of soil fungal decomposers (Fig. 2b) and infer their ecological functions, by associating their proportion with soil heterotrophic respiration (Fig. 2c). This map shows that soil fungal decomposers thrive in colder and wetter soils with relatively high soil carbon contents. We also show that soil heterotrophic respiration is positively and significantly correlated with the proportion of soil fungal decomposers (Fig. 2c), which is in line with the fact that soil fungal decomposers are one group of major drivers of soil heterotrophic respiration (Boddy, 2016; Treseder & Lennon, 2015). Even so, an important portion of variation in soil respiration could not be explained by soil fungal decomposers. This is not totally unexpected, as our study did not include other important groups of soil dwelling organisms, such as bacteria, protists and invertebrates, which are also in charge of soil respiration. However, we would like to highlight that this result agrees with other reports on the high soil carbon content (Crowther et al., 2019) and high proportion of ectomycorrhizal fungi (Clemmensen et al., 2013) in high latitudes.

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All these ecosystem properties mentioned above highly correlate to soil respiration. Our findings suggest adding another important correlation factor – soil fungal decomposers – to the equation for us to better understand the soil respiration worldwide, and further support the robustness of our global map of soil fungal decomposers.

Machine-learning Random Forest algorithm is commonly used to identify non-linear patterns (Delgado-Baquerizo et al., 2020; Větrovský et al., 2019). Thus, the abovementioned results based on Random Forest algorithm provide us a benchmark to analyze the potential effects of temperature thresholds on the proportion of soil fungal decomposers across world. Non-linear models unambiguously indicate the existence of the temperature thresholds for the global distribution of soil fungal decomposers (Figs. 3 and S5). Specifically, the proportion of soil fungal decomposers abruptly decreases when MAT immediately transits  $\sim 8.86^{\circ}\text{C}$  (Fig. 3). Furthermore, our results indicate the existence of other important temperature thresholds associated with extreme values of soil and air temperatures (i.e.,  $\sim 22.41^{\circ}\text{C}$  and  $\sim 27.97^{\circ}\text{C}$ ) in driving the global distribution of soil fungal decomposers (Fig. 3). These abrupt transitions from cold to warmer ecosystems are a vivid proof that soil fungal decomposers can negatively respond to the increasing temperatures worldwide (Fig. 2b). Soil carbon content thresholds could provide a plausible mechanism for the abrupt reduction in the proportion of soil fungal decomposers in response to temperature increases. Soil carbon content is selected as a fundamental driver of the proportion of soil fungal decomposers in this study, followed immediately by MAT (Fig. 2a). And similar thresholds are found for soil carbon content ( $\sim 7.31^{\circ}\text{C}$  for MAT,  $\sim 24.42^{\circ}\text{C}$  for soil temperature and  $\sim 31.43^{\circ}\text{C}$  for max temperature of warmest month) (Figs. 3 and S6). The possible explanation is: as the temperature increases, the soil carbon content abruptly decreases, leading to a strong reduction of resources for decomposers. Consequently, an abrupt reduction in fungal decomposers in the soil system is followed. Here, our findings suggest that small changes in temperature at certain threshold could have great impacts on soil fungal decomposers and topsoil carbon storage worldwide. In addition, physiological features of microbe are also sensitive to temperature (Zhou et al., 2012). For example, the high temperature thresholds (i.e.,  $\sim 22.41^{\circ}\text{C}$  and  $\sim 27.97^{\circ}\text{C}$ ) fall into or around the  $25^{\circ}\text{C}$  to  $30^{\circ}\text{C}$  temperature range for the fungal decomposer optimal growth (Oghenekaro et al., 2015). Extracellular enzymes (e.g. cellulases) are also sensitive to high temperatures and their adaptation to temperature attributes should be considered (Sinsabaugh et al., 2008).

The strong correlation between temperature and precipitation thresholds could be further

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helpful in explaining the global distribution of soil fungal decomposers. For example, we find that small increases in mean temperature of the driest season over  $\sim 7.91^{\circ}\text{C}$  can result in drastic non-linear reductions in the proportion of soil fungal decomposers (Fig. 4). And this threshold value is smaller than MAT one ( $\sim 8.86^{\circ}\text{C}$ ) (Fig. 3). On the contrary, no correlation is found between the mean temperature of the wettest quarter and the proportion of soil fungal decomposers. When all of these findings are aggregated, we conclude that soil fungal decomposers are more sensitive to temperature increases under severely arid conditions (Větrovský et al., 2019). It is corroborated that the smallest proportion of soil fungal decomposers are observed in dry and hot regions (Fig. 1b), and the abrupt reductions in the proportion of soil fungal decomposers are observed in response to aridity increases (Berdugo et al., 2020). This work provides an indirect support to the report that the combination of elevated temperature and dry conditions can result in abrupt reductions in extracellular cellulolytic enzyme activities (A'Bear et al., 2014). Although the influence of aridity thresholds for soil microorganisms had been previously explored in global drylands (Berdugo et al., 2020), our analyses lead to the interlaced connection between global aridity conditions and temperature thresholds for soil fungal decomposers.

Such a biogeographic non-linear pattern can further give us the inference on the ecological change of soil fungal decomposers to global change, in spite of the limitation of space-for-time substitution approaches, such as dispersal limitation vs. ecological drift as well as the physiological adaptation of species (Bjorkman et al., 2018). The strong spatial temperature gradients combined with arid condition for soil fungal decomposers associated with relative abundances and ecosystem function infer the abrupt reductions of carbon cycling and negative feedback of soil  $\text{CO}_2$  flux driven by soil fungal decomposers when air temperature transits over  $\sim 9^{\circ}\text{C}$  and/or  $\sim 28^{\circ}\text{C}$ , especially in arid regions ( $\sim 8^{\circ}\text{C}$ ). To our knowledge, this is the first global-scale investigation of soil fungal decomposers identifying temperature thresholds driving their distribution and ecological adaptation, providing a better understanding of soil microbial potential responses and feedback to global change.

Our results align with previous studies, in encouraging in terms of collectively building the comprehensive understanding of temperature thresholds driving the global distribution of soil fungal decomposers. We would like to highlight, however, potential caveats to be considered and built upon in future investigations. First, the use of proportional compositional data vs. biomass of soil fungal decomposers due to current methodological limitations could influence ecological patterns. For example, the absolute abundance or biomass of microorganisms is more related to

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ecological functions they provide than their relative abundance in community (Bastida et al., 2021). Second, a considerable part of ITS sequences still has not been linked with fungal taxonomy (Tedersoo et al., 2014), as a consequence of current culturing and isolation limitations. For example, 43% of total reads in this study cannot be taxonomically classified at the genus level (by which to assign functional traits), which might underestimate the proportion of soil fungal decomposers in total fungal community. Finally, databases both used for taxonomic identification and linking fungal taxa to functional guilds are context dependent, which might result in the bias estimation and/or the underestimation on the conclusion in this global field survey. For instance, the geographic representation in UNITE database is strongly skewed toward Europe, North America, China and Japan (Koljalg et al., 2013). Fortunately, the latest trait database FungalTraits can mitigate some of these biases to the best extent possible, by representing the latest progress (re-annotated 10,210 fungal genera representing 92,623 fungal species at 1% dissimilarity threshold) in this effort, by combining the information from previous efforts such as most commonly used FunGuild (Nguyen et al., 2016) and new tool Fun<sup>Fun</sup> (Zanne et al., 2020) together with involvement of expert knowledge (Pöhlme et al., 2021).

## **Conclusion**

The findings from our global survey suggest that temperature thresholds drive the global distribution of soil fungal decomposers, with the higher proportions in cold ecosystems and mesic regions. Our results indicate the existence of two temperature thresholds driving the non-linear responses of soil fungal decomposers to mean annual temperature ( $\sim 8.86^{\circ}\text{C}$ ) and to maximum air temperature ( $\sim 27.97^{\circ}\text{C}$ ). Given the reported potential correlation between soil fungal decomposers and soil heterotrophic respiration, these findings are essential for understanding the soil-atmosphere climatic feedback. Simply put, soil fungal communities are much less dominated by fungal decomposers when these thresholds are crossed. We find a slightly lower temperature threshold ( $\sim 7.31^{\circ}\text{C}$ ) of topsoil carbon content, suggesting that the reduction in the proportion of soil fungal decomposers is most likely a result of the abrupt declines of available resources. Furthermore, there might be connections between temperature and aridity thresholds, which indicates that soil fungal decomposers are more sensitive to temperature increases under dry conditions and could allow us to better understand the distribution of soil fungal decomposers in drier environments. The declines of soil fungal decomposers potentially may have direct consequences on soil carbon storage and climate feedback when global climate becomes drier and

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hotter. Together, our findings not only present the global biogeographic patterns of soil fungal decomposers, but also unravel implications of fundamental temperature thresholds for understanding the potential responses and feedback of global carbon cycling to climate change.

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## **Author contributions**

M.D.-B., Y.Z.F. and J.W.Z. developed the ideas in this article. M.D.-B. and B.K.S. led the global survey. Y.Z.F., J.W.Z., M.D.-B., M.B., E.G., C.A.G. and E.E. analyzed the data. The manuscript was written by Y.Z.F. and M.D.-B. with contributions from all the co-authors.

## **Conflict of Interest**

Authors declare that there is no conflict of interest regarding the material discussed in the manuscript.

## **Data availability**

The raw reads are available at <https://figshare.com/s/9772d31625426d907782> (Doi: 10.6084/m9.figshare.5923876).

Metadata is available at <https://figshare.com/s/5005a0d4aa964c271165> (Doi: 10.6084/m9.figshare.18591488).

All other relevant data is available upon request.

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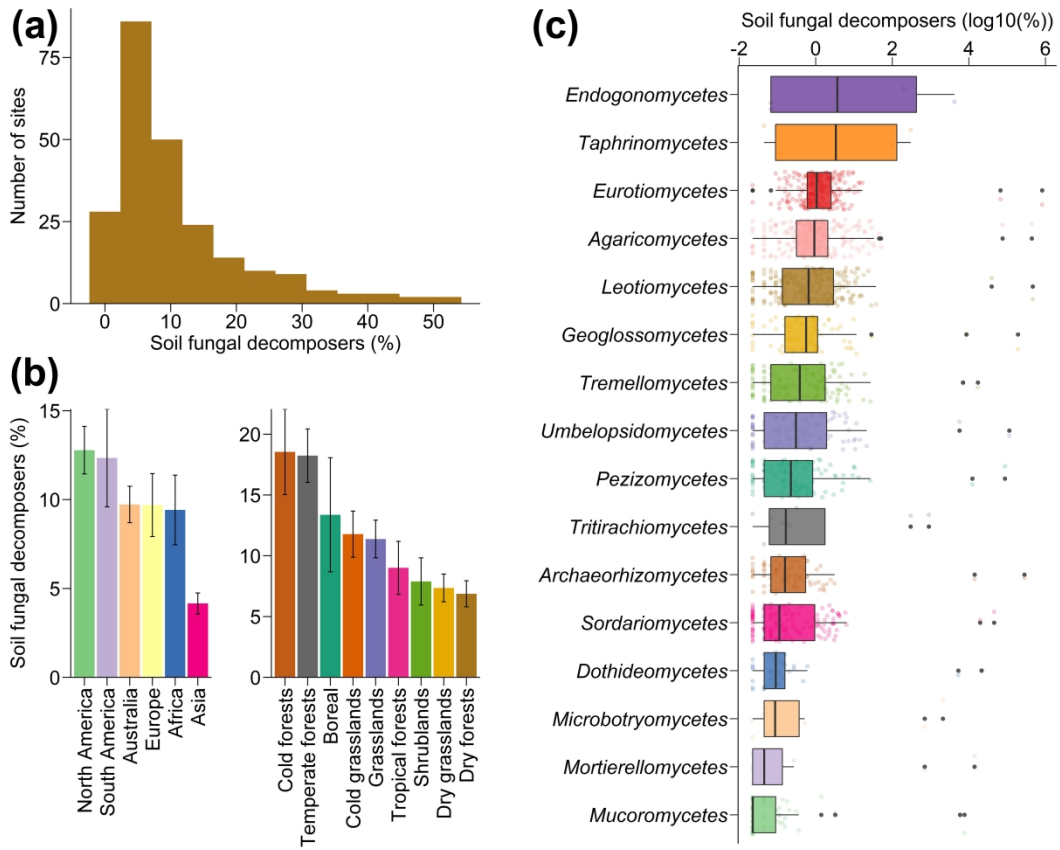
## Figure Legends

**Figure 1.** Distributions of soil fungal decomposers (the percentage of sequence reads affiliated with soil fungal decomposers in total classified fungi, %) across sampling units (a), as well as continents and ecosystems (b). The proportions of identified soil fungal decomposer phylotypes at the class level (c). There are the differences among continents (Global ANOVA,  $F_{(5, 229)} = 1.83$ ,  $P=0.08$ ), ecosystems ( $F_{(8, 226)} = 5.85$ ,  $P<0.001$ ) and phylotypes ( $F_{(15, 1410)} = 10.97$ ,  $P<0.001$ ).

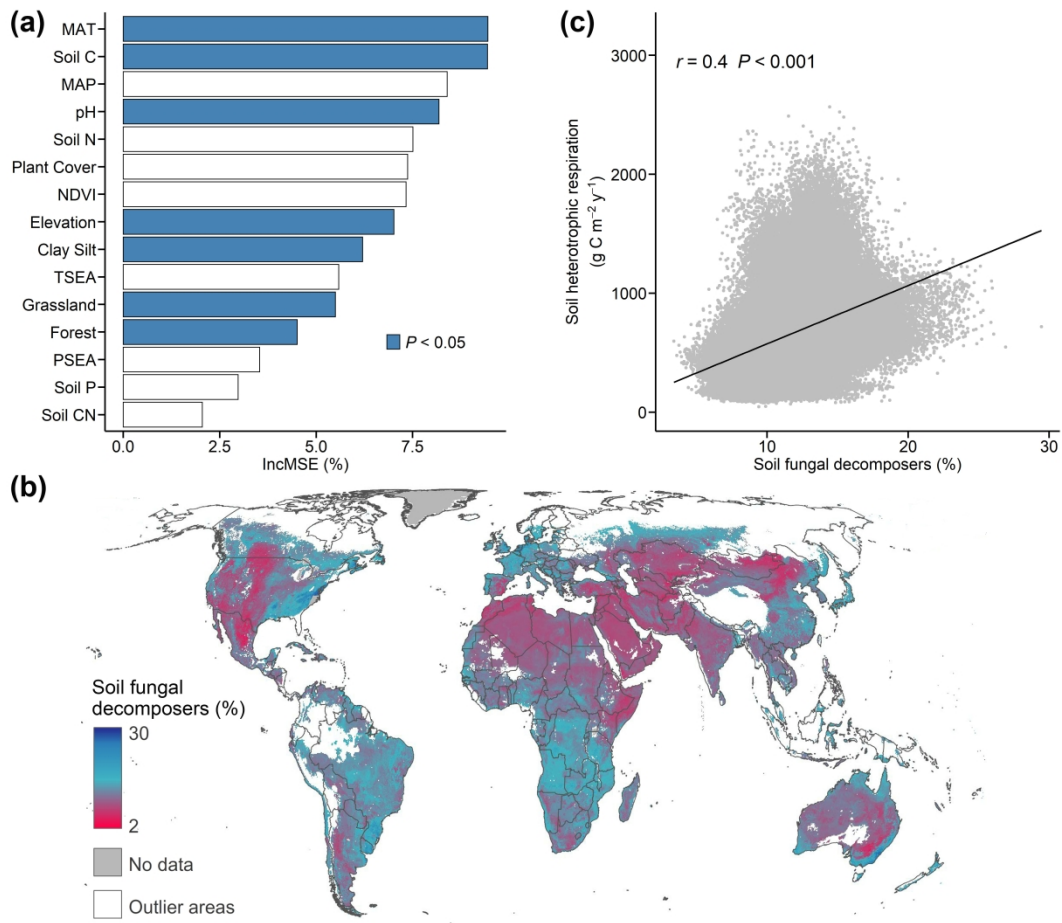
**Figure 2.** Ecological preferences of soil fungal decomposers across the globe. The importance of abiotic variables influencing the proportion of soil fungal decomposers identified by the Random Forest algorithm (a). %IncMSE indicates the increase of the mean squared error when given variable is randomly permuted, corresponding the importance of variables in the predicting the proportion of soil fungal decomposers. Blue bars indicate significant variables at the level of 0.05. Maps show the global distribution of soil fungal decomposers (b). Environmental outliers in this map represent environmental conditions which are underrepresented in our global survey, and therefore, are excluded from the map. These outliers are calculated based on the Mahalanobis multidimensional distance from the variability of climate, vegetation types and soil properties in our dataset vs. global distributions (using Chi-squared distribution). Outlayers = Mahalanobis quantil distribution  $>0.90$ . The relationship between the proportion of soil fungal decomposers and soil heterotrophic respiration (dataset (n=141,010) obtained from Warner et al. (2019)) (c).

**Figure 3.** Non-linear responses of the logged proportion of soil fungal decomposers and soil carbon content to mean annual temperature (MAT), soil temperature and max temperature of warmest month. Black dashed lines and blue solid lines represent the smoothed trend fitted by a generalized additive model (GAM) and the linear fits at both sides of each threshold, respectively. Inset numbers and the vertical dashed lines describe the temperature thresholds identified. Colors represent climatic conditions, including polar, continental, temperate, arid, and tropical zones.

**Figure 4.** Non-linear responses of the proportion of soil fungal decomposers to multiple temperature attributes. Black dashed lines and blue solid lines represent the smoothed trend fitted by a generalized additive model (GAM) and the linear fits at both sides of each threshold, respectively. Inset numbers and the vertical dashed lines describe the temperature thresholds identified.

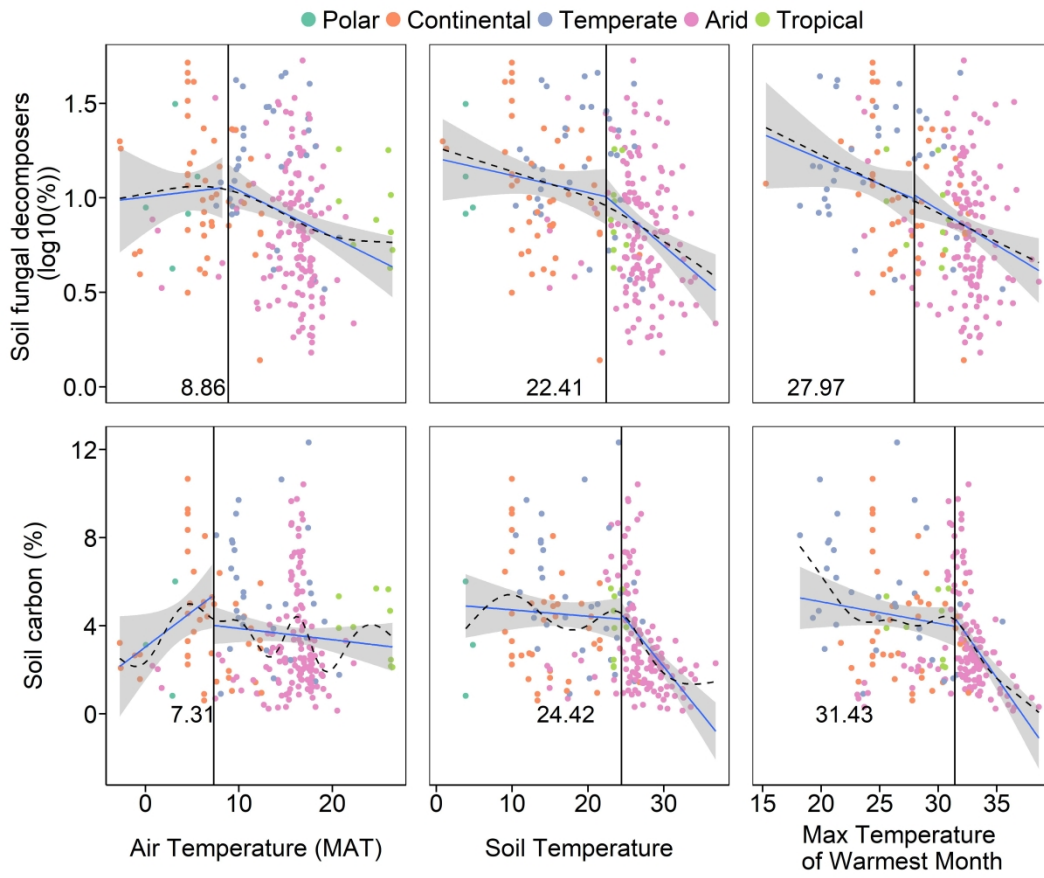


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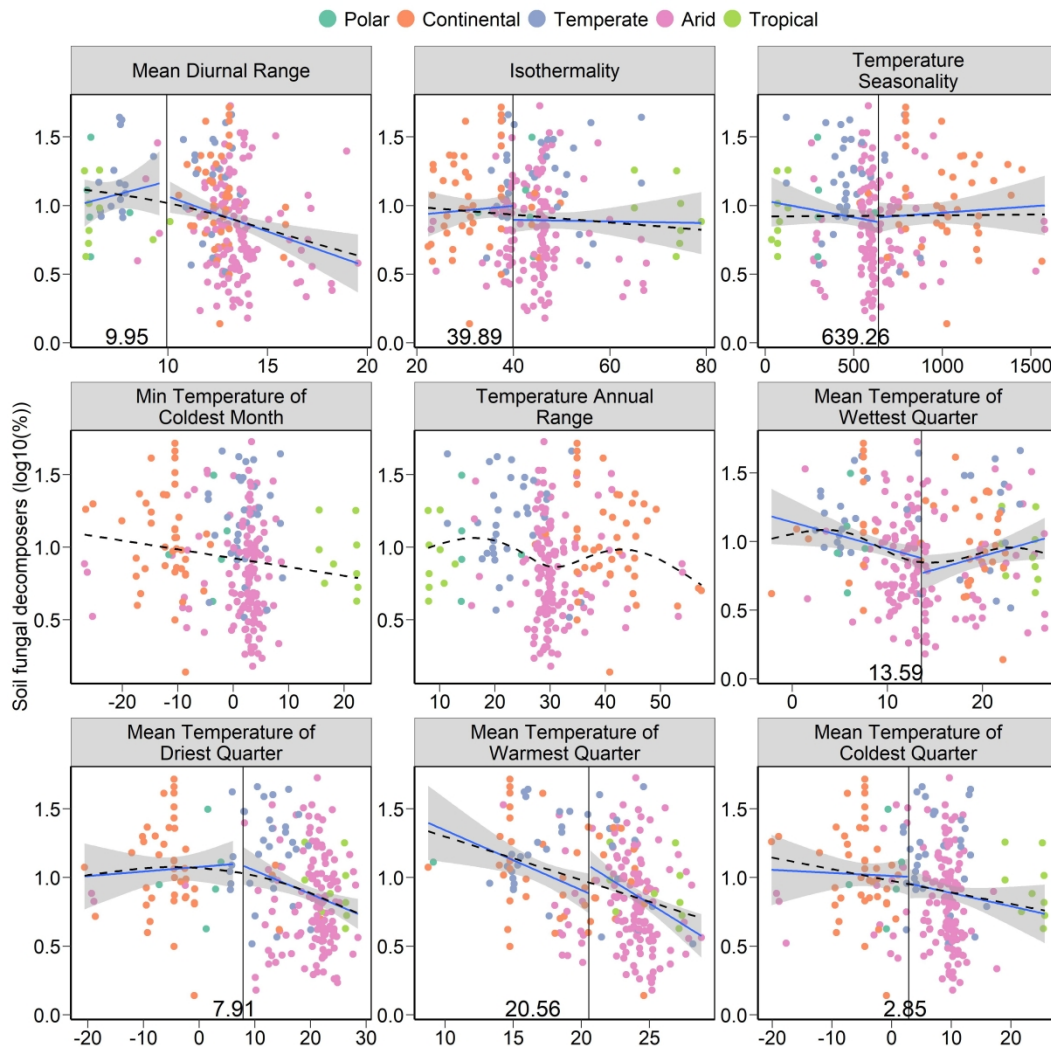


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