**The biogeography of relative abundance of soil fungi and bacteria in top surface soil**

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**Abstract.** Fungi and bacteria are the two dominant groups of soil microbial communities worldwide. By controlling the turnover of soil organic matter, these organisms directly regulate the cycling~~exchange~~ of carbon between the soil and the atmosphere. Fundamental differences in the physiology and life history of bacteria and fungi suggest that variation in the biogeography of soil fungal and bacterial relative abundance could drive striking differences in carbon decomposition and soil organic matter formation across different biomes. However, a lack of global and predictive information on the distribution of these organisms in terrestrial ecosystems has prevented the inclusion of soil fungal and bacterial relative abundance and the associated processes into global biogeochemical models. Here, we used a global scale dataset (>3000 distinct observations of soil fungal and bacterial abundance) in the top soil surface (up to 15 cm)~~(>3000 distinct observations of soil fungal and bacterial abundance)~~ to generate the first quantitative and spatially high resolution (1km$^2$) explicit map of soil fungal proportion, defined as fungi/fungi + bacteria, across terrestrial ecosystems. We reveal striking latitudinal trends where fungal dominance increases in cold and high latitude environments with large soil carbon stocks. There was strong non-linear response of fungal dominance to environmental gradient, i.e., mean annual temperature (MAT) and net primary productivity (NPP). Fungi and bacteria dominated in regions with low and high MAT and NPP, respectively, thus representing slow vs. fast soil energy channels, a concept with a long history in soil ecology. These high-resolution models provide the first steps towards representing the major soil microbial groups and their functional differences in global biogeochemical models to improve predictions of soil organic matter turnover under current and future climate scenarios.

~~Keywords:~~

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## 1. Introduction

Fungi and bacteria are the dominant members of soil microbial communities worldwide in terms of diversity, abundance and biomass (Bahram et al., 2018). Representing distinct kingdoms of life, bacteria and fungi systematically differ in a multitude of physiological and life-history traits with direct implications for global soil biogeochemical cycles (Waring et al., 2013; Wieder et al., 2015) including the decomposition of organic matter, which contributes to one of the largest fluxes of $CO_2$ on Earth (Glassman et al., 2018). Compared to bacteria, fungi generally have slower growth and turnover rates (Rousk and Bååth, 2007), greater carbon (C) to nutrient stoichiometry (Waring et al., 2013), greater capacity to degrade a wider and more recalcitrant range of substrates (Strickland and Rousk, 2010) and potentially higher C use efficiency (Soares and Rousk, 2019). For these reasons, a new generation of soil and ecosystem models have begun to explicitly represent these fundamentally distinct fast and slow cycling microbial groups, suggesting that spatially-explicit information about the relative abundance of fungal and bacteria in a region can dramatically improve the accuracy of global carbon cycling model predictions (Shi et al., 2018; Sulman et al., 2014; Wieder et al., 2013, 2015). Generating an understanding of the factors affecting the biogeography of the relative abundance of fungal and bacteria in soil, and its connection to global carbon cycle, would represent a breakthrough step forward in our general understanding of the natural history of soil microbial life.

Temperature, precipitation, soil pH and soil C:N have all been linked to the balance of fungi vs. bacteria within soil communities across different spatial scales (Bahram et al., 2018; Strickland and Rousk, 2010; Tedersoo et al., 2014). Relative to fungi, bacteria tend to dominate in locations with high soil nutrient contents or in frequently disturbed soils that limit the growth of fungal hyphae or make N more available (Fierer et al., 2009; Van Der Heijden et al., 2008;

92 Strickland and Rousk, 2010). However, until now, the relative importance of these different
93 environmental drivers remains relatively unclear at global scale, and the biogeography of these
94 major functional groups (fungi *vs*. bacteria) has only been demonstrated at local and regional
95 scales. A recent analysis suggested that the relative soil bacterial abundance is high in tropical
96 latitudes and decreases in abundance towards the high-latitude boreal regions, where fungi tend
97 to dominate (Bahram et al., 2018). Translating these broad-scale trends into quantitative,
98 spatially explicit information will be necessary if we intend to represent regional variations in
99 soil community functioning (Wieder et al., 2013, 2015), or predict future changes in terrestrial
100 carbon and nutrient cycling.

101 Some progress was made in the quantitative and spatially explicit understanding of global
102 biogeographic patterns of fungal and bacterial biomass and their biomass ratio. By synthesizing
103 phospholipid-derived fatty acids data from 1323 locations across the globe, and extrapolating
104 linear relationships with environmental factors, a recent study generate the global maps of fungal
105 and bacterial biomass and their biomass ratio at the resolution of 0.5 degree for top soil (0-30
106 cm) (He et al., 2020). This approach provided the support for the broad-scale latitudinal trends,
107 with high fungal dominance in high-latitude regions. Yet to date, there are three crucial
108 knowledge gaps to be addressed. First, we still lack a high resolution evaluation of the spatial
109 patterns and regional contingencies in fungal:bacterial ratios, which would allow representation
110 of microbial-mediated mechanisms that operate within and/or across ecosystems at fine scales
111 (Frindte et al., 2019; Zhu et al., 2017). Second, the response of soil microbial community
112 composition across environmental gradients are expected to be non-linear, with strong interactive
113 effects of different environmental characteristics that give rise to thresholds that diverge from the
114 global latitudinal trends (Sengupta et al., 2021; Wang et al., 2018; Waring et al., 2013). This

non-linear linkage of soil microbial communities with environmental resource gradient has not been assessed, while it has fundamental implications on ecosystem functions and management solutions (Sengupta et al., 2021; Wang et al., 2018). Third, there are distinct difference of soil nutrients, soil microbial community and the associated biogeochemical processes across soil depths, i.e., from top surface soil (i.e., 0-10 cm) to top subsurface soil (i.e., 0-30 cm) (Lavahun et al., 1996; Yue et al., 2015). A continental-scale empirical study further showed that strong positive associations among soil microbial community, fertility and plant productivity are limited to the top surface soil (Delgado-Baquerizo et al., 2017), thus highlighting its potential dominant role regulated by top surface soil microbial communities on ecosystem functions and the research needs of generating a global spatially explicit understanding of soil fungi and bacteria in top surface soil.

Here, we present a global analysis of total and relative abundance of soil fungi and bacteria in soil surfaces (defined as top 10-15 cm) informed from over 3000 spatially distinct surface soil observations from phospholipid-derived fatty acids (PLFA) (Fig. 1a). The use of PLFA data provides an opportunity to provide quantitative insights into the abundances of thethese major functional groups. We conducted the analysis on the abundances in view of the uncertainty in conversion factors used to convert abundance derived from PLFA to biomass (Frostegård et al., 2011; Klamer and Bååth, 2004). We used machine learning to link the variation in soil fungi and bacteria abundances to global variation in 95 climate, vegetation, and soil variables. This allowed us to 1) explore the environmental drivers of fungal and bacterial dominance, defined as fungal proportion - fungi/(fungi + bacteria), where values closer to 1 indicate a higher fungal dominance and values closer to zero indicate a greater bacterial dominance (see Methods); 2) examine the non-linear response or pattern of fungal proportion across environmental gradients, i.e., mean

annual temperature-MAT and net primary productivity-NPP. Based on the observed relationships (by accounting for the non-linearity), we generated a quantitative spatially-explicit global map (1 $km^2$) of fungal proportion, and assessed how soil fungal and bacterial dominance varies with key climate, soil, vegetation and geographic drivers.

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## 2. Material and methods

### 2.1. Data acquisition of soil microbe composition

We compiled data of abundance of soil fungi and bacteria and fungal proportion, defined as fungi/(fungi + bacteria). We focused on phospholipid-derived fatty acids (PLFA) and the data derived from PLFA reported the balance between fungal and bacterial PLFAs (Frostegård et al., 2011) can provide a valuable estimation of the comparative dominance of both functional groups. The data based on qPCR was not included because of difference in units with PLFA. With non-significant difference using data of fungal proportion and fungi : bacteria ratio, we focused on and reported the results on the fungal proportion rather than fungi : bacteria ratio because 1) The fungal proportion is insensitive to whether fungi or bacteria are the numerator (i.e. bacterial proportion = 1 – fungal proportion), and 2) fungal proportion had more spread frequency distribution and thus led to better machine learning predictions (Fig. S1). The data was compiled by a primary literature review through Google Scholar, Web of Science (http://apps.webofknowledge.com) and China National Knowledge Infrastructure Database (http://cnki.net) till 30 June, 2020 using the keywords "fungi", "bacteria", "abundance", "PLFA". To be included in our data analysis, the study had to at least have the following metadata: longitude and latitude, sampling date, sampling depth, information on land use (agriculture, tree plantations, or natural sites), units and the methods used. In total, this led to 319 references. We further used the following criteria to select eligible references and datasets: (1) when the studies were manipulative experiments, we only included the

data from "control" plots (Chen et al., 2016). (2) we standardized our efforts by focusing on all samples that were collected from the top surface soils (≈ 0-10/15 cm) because this layer contains greater biomass and has the majority of sample size. (3) we used the datasets based on reporting abundance with units of nmol, umol, or mol% since the majority (>90%) of datasets reported abundance. Thus, we exclude all datasets reporting biomass instead of abundance. (4) we excluded observations located in sea since our study focuses on terrestrial ecosystems. (5) we only included the datasets on soil samples derived from field experiments and thus excluded the datasets from incubation experiments. (6) some datasets reported in original references as average across sampling sites or sampling dates were included.

The criteria were carefully scrutinized by three independent researchers and this ultimately led to 179 eligible references (see Supplementary references for PLFA) used for this study. In total, we compiled a dataset of fungal proportion (n = 3224) at a global scale. The subset of data (n = 1795) with only natural ecosystems (Fig. S2a) were used to examine the potential role of land use change (see Supplementary Methods). The results showed minimal difference of the two scenarios of including all data and natural ecosystems. All data points falling within the same 30 arc-seconds (~1-$km^2$) pixel were aggregated via an average. The aggregated data of fungal proportion (n = 946 for all data; n = 716 for natural ecosystems) were used to examine its environmental controls and geospatial modelling in making the global map (Fig. 1a; Fig. S2a).

The spatial variations of fungi and bacteria ratio or fungal proportion across latitude could be influenced by either changes (increases or decreases) in abundance of fungi or bacteria or both. Thus, to better understand the biogeographic pattern of fungal and bacterial composition, we also analysed the spatial patterns of abundance of fungi and bacteria by using the abundance data with the same unit (nmol $g^{-1}$ PLFA). In total, our data compiling led to a final subset of 2753, and 2759

samples which were used for further analyses of abundance of fungi and bacteria, respectively (Fig. S3). As compared to the larger sample size of fungal proportion (n = 946 for all data), the data of abundance of fungi (n = 646 for all data) and bacteria (n = 647 for all data) aggregated within the 30 arc-seconds (~1-km$^2$) pixel via an average were used for the analysis of their spatial trends across vegetation biome, vegetation type and latitude (see Supplementary Methods).

**2.2. Geospatial modelling**

A stack (n = 95) of ecologically relevant, global map layers including soil physical, chemical and nutrient properties, climate conditions, vegetative indices, radiation and topographic variables and anthropogenic covariates (Supplementary Table 1) were used to derive the environmental factors which could affect fungal proportion. All of these covariate map layers were standardized at 30 arc-seconds resolution (≈1km$^2$ at the equator) (van den Hoogen et al., 2019). These covariates were then derived based on the georeferenced coordinates of the soil samples aggregated at 30 arc-seconds resolution.

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We used the Random Forest machine learning algorithm (see Supplementary Methods) with the derived 95 covariates to extrapolate these relationships between fungal proportion and environmental conditions across the globe and generate the first spatially-explicit, quantitative map of fungal proportion at a global scale. The strength of prediction was evaluated using k-fold cross validation (with k = 10) and the best model having high coefficient of determination and low standard deviation in the mean cross-validation were used to generate the global map of fungal proportion. The standard error sharply decreased with increasing sample size across all vegetation biomes and the analysis showed that an efficient prediction required a large sample size (n > 500) (Fig. S4). To evaluate the sensitivity, we also generate the uncertainty (standard deviation as a fraction of the mean predicted value) map of fungal proportion by using a stratified bootstrapping

procedure (van den Hoogen et al., 2019). The stratification category was the sampled biomes of each point feature (fungal proportion) with the total number collection of fungal proportion points to avoid biases. In total, 100 bootstrap iterations were used, thus generating 100 global maps of fungal proportion used to quantify statistically robust 95% confidence intervals per pixel.

### 2.3. Environmental drivers and statistic analysis

To examine the environmental controls of soil microbial composition at a global scale, we chose the top drivers (Chen et al., 2016; Drenovsky et al., 2010a; de Vries et al., 2012) which include soil properties, climate conditions, vegetation index and human activities (see Supplementary Methods). These variables were examined to avoid multicollinearity using a matrix of pairwise correlations to remove any variable with high correlations (R>0.7) with other predictor variables (Anderegg et al., 2013). Random Forest machine learning algorithm was then used to determine variable importance for each variable(Breiman, 2001). Mean decrease in accuracy (%IncMSE) and mean decrease gini (IncNodePurity) were reported and the variables with greater values of %IncMSE and IncNodePurity are more important in influencing fungal proportion. Partial functions of most important variables (MAT and NPP) were plotted using forestFloor package to examine their influences on fungal proportion.

## 3. Code and data availability of machine learning

The code and data of machine learning is available at https://github.com/KailiangYu/Biogeography-of-soil-microbes.git.

## 4. Results and discussion

### 4.1. Raw data patterns of fungal proportion

Globally, we observed greater than 10-fold variation in soil fungal proportion across all sites, ranging from 0.01 to 0.6 (Fig. 1b). At a global scale, we found clear latitudinal trends, with the

abundance of both fungi and bacteria increasing in high-latitude regions. Yet, the abundance of fungi increased with latitude at a greater rate than the abundance of bacteria (Fig. S5), resulting in a higher proportion of fungi in the cold, high-latitude regions. These latitudinal trends lend support to the general global patterns detected in a previous broad-scale analysis (Bahram et al., 2018) and in a recent meta-data analysis (He et al., 2020). As such, the highest fungal dominance was observed in tundra and boreal forest ecosystems (mean ± 1SE: 0.23 ± 0.02; Fig. 1b). In addition, high elevation and cold grasslands (i.e., Montane grasslands) with large soil organic C (SOC) content generally harbor higher proportion of fungi, relative to bacteria (Fig. 1b).

Within similar climates, soil fungal and bacterial abundance as well as fungal proportion was greatest in ecosystems harboring woody vegetation compared to grasslands and managed (agricultural) ecosystems (Fig. S6). This finding is consistent with the idea that ecosystems dominated by woody plants generate lignified, more recalcitrant and nutrient poor soil C inputs that characteristically favor fungal dominance (Fierer et al., 2009; Strickland and Rousk, 2010), and have a biomass stoichiometry better suited to low nutrient environments (Waring et al., 2013). But we stress that this link of belowground soil microbial composition (fungi vs bacteria) with aboveground plant community composition (woody plants vs grasses) can be complex, non-linear and even divergent, as demonstrated by the non-existence of woody plants in grasslands and scarcity of grasses in forests but with well mixed fungi vs bacteria abundances. This raises the curiosity whether the interactions, associations or couplings of belowground soil microbial composition vs aboveground plant community composition are stronger in ecosystems where woody plants and grasses interact or coexist (i.e., savannas) (Yu and D'Odorico, 2015). It also remains unclear how this coupling could improve our understanding of ecosystem carbon cycling and other services.

253 Management of agricultural ecosystems often disrupts soil fungal networks (i.e. tillage,
254 frequent dry/wet cycles due to irrigation, machine operations, etc.), which decreases the abundance
255 of fungi relative to bacteria in agricultural soils (Fig. S6) (Drenovsky et al., 2010b; Jangid et al.,
256 2011; Waldrop et al., 2017). A central concern in agricultural ecosystems is the tradeoff of
257 increased food production to feed the increasing population vs the decreased soil carbon storage
258 to accelerate the global climate change (Sanderman et al., 2017). This study showed the higher
259 bacterial abundance relative to fungal abundance in soils of agricultural lands where soil carbon
260 storge is low; this corresponds with the global trends of bacterial dominance in low latitude where
261 soil carbon storage is low. These results suggest the potential strong but complex interactions and
262 feedbacks of soil microbial composition and soil functions (i.e., soil carbon storge) (Bardgett et
263 al., 2008), while the mechanistic links need further studies.

264 **4.2. Drivers of fungal proportion**

265 Globally, the fungal proportion in soil can be predicted by few primary environmental drivers (Fig.
266 2; Fig. S7). Specifically, mean annual temperature (MAT) and primary productivity (NPP) were
267 strong determinants of fungal dominance. The responses of fungal proportion to both MAT and
268 NPP were strongly non-linear, with warmer, more productive regions of the world (i.e. tropical
269 forest biomes) showing lower dominance of fungi as compared to colder, less productive
270 ecosystems (i.e. boreal forest and tundra biomes, Fig. 3; Fig. S8). This pattern is consistent with
271 the idea that fungi and bacteria represent slow vs. fast soil energy channels, respectively (Crowther
272 et al., 2019; Malik et al., 2016), a concept with a long history in soil ecology (Moore et al., 2003;
273 Moore and William Hunt, 1988). This finding is important because it could potentially link the
274 belowground slow – fungi vs fast – bacteria energy channels with aboveground plant slow growth
275 rates – woody plants vs fast growth rates – grasses, while the linkage could be complex, non-linear

276 or even divergent. The fast vs slow concept or spectrum have fundamentally improved the
277 understandings and predictions of land carbon storage across resource gradient or under global
278 change. The faster growth could be typically trade off with higher mortality or heterotrophic
279 respiration with resource (i.e., $CO_2$) enriched conditions (Jiang et al., 2020; Terrer et al., 2021; Yu
280 et al., 2019), thus constraining land carbon storage. This raises the question of how the
281 belowground fast vs slow energy channels and the aboveground fast vs slow growth spectrum
282 could be potentially linked or integrated to assess land carbon storage.

283 Temperature can affect soil microbial composition in complex ways, via directly
284 physiology or via indirectly soil substrate (Romero-Olivares et al., 2017). Previous studies have
285 shown the non-linear response of soil fungal and bacterial ratio to soil substrate (Waring et al.,
286 2013). The non-linear trends of the temperature sensitivity (Q10) of soil organic C decomposition,
287 as regulated by soil fungal and bacterial ratio, were also found along latitude (Wang et al., 2018).
288 Other environmental variables such as soil C to nitrogen ratio (C:N) have previously been found
289 to be important drivers in influencing fungal proportion within local and regional scale analyses
290 (Fierer et al., 2009; Waring et al., 2013). Our results suggest a more complicated relationship
291 between fungal proportion and the soil C:N. In the low range of soil C:N values, fungal proportion
292 decreased with soil C:N (Fig. S9a), suggesting the likely role of site-specific differences (i.e.,
293 climate or plant community) in out-weighting the influence of N availability (Soares and Rousk,
294 2019). Aside from these ecosystems, we observed a positive relationship between fungal
295 proportion and soil C:N at a global scale, consistent with previous work at local and regional scales
296 (Strickland and Rousk, 2010; Waring et al., 2013). Additionally, pH has been thought as a critical
297 driver of microbial diversity and biomass in soils. At local scales, previous studies reported either
298 no relationship, a negative correlation or convex curve between fungal and bacterial ratio and soil

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pH (Rousk et al., 2009, 2010; de Vries et al., 2012). Our global scale analysis suggests a convex relationship between fungal proportion and soil pH, with fungi dominating only within a narrow pH range (<5-6) (Fig. S9b).

**4.3. Biogeographic pattern from the machine learning model**

Across all samples, the machine learning model was able to predict the variation in fungal and bacterial dominance with high predictive accuracy ($R^2$ = 0.43/0.35 in 10-fold cross validation; $R^2$ = 0.92/0.91 in final model; Fig. S10a-b). By extrapolating these relationships across terrestrial ecosystems, we could identify clear global trends in fungal dominance. Despite these general global scale patterns of increase in fungi dominance with latitude, our models also revealed regional contingencies that diverge from the global trends (Fig. 4a; Fig. S11a). For instance, Northeastern Europe is dominated by woody vegetation and exhibits high fungal proportion, while the United Kingdom and northern Kazakhstan have much lower fungal proportion despite being at comparable latitude, likely because these areas are dominated by herbaceous vegetation with lower lignin content than in woody tissues. Tibetan alpine grasslands are at comparatively much lower latitude but have high values of fungal proportion in part due to very high SOC stocks and cold temperatures. Model predictions of fungal proportion had high uncertainty in dry regions (i.e., Northern and Southern Africa, Australia, Western USA, eastern Mongolia) (Fig. 4b; Fig. S11b), presumably because of the low sample size in drylands and/or complex response of fungi and bacteria to water availability (Fierer et al., 2009; Strickland and Rousk, 2010). Indeed, our datasets are mostly concentrated to US, Europe and East Asia, thus highlighting the data gaps at tropical and boreal biomes. Even for the temperate biome, there were data gaps in west Australia and central Asia. Because of the unbalanced sample distribution, we also used a bootstrapping strategy (100 iterations) by randomly sampling 90% data with replacement. The results showed

the similar spatial patterns of fungal proportion (Fig. S12a) and uncertainty (Fig. S12b) as the scenario of using full dataset without bootstrapping.

Our study differs from a previous study (He et al., 2020) in several aspects including sample size (n > 3000), spatial resolution (1km$^2$), consideration of non-linearity (through random forest analysis), soil depth (soil surface 0-10/15 cm). We also note that our analysis sticks to the original data of abundance derived from PLFA instead of converting abundance to biomass. Conversion of abundance to biomass needs the conversion factor, which has large uncertainty (Frostegård et al., 2011; Klamer and Bååth, 2004). Our high resolution map would allow representation of microbial-mediated mechanisms at fine scales to link with ecosystem functions. For instance, the significant functional differences between fungi and bacterial mean that the relative dominance of fungi *vs*. bacteria is likely to influence a wide range of ecosystem functions such as C use efficiency (CUE) of the decomposer community (Six et al., 2006; Soares and Rousk, 2019) and enzymatic activity in soil N vs P acquisition (Caldwell, 2005; Crowther et al., 2019). At fine, local or even regional scales, these relationships between soil microbial composition and ecosystem functions could only be well identified using fine scale maps of soil microbial composition.

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**4.4. Implications and limitations of this study**

It is generally accepted that the soil microbiome exerts major control over soil processes, and in turn ecosystem functioning, and by extension the global biogeochemical cycles (Bahram et al., 2018; Crowther et al., 2019; Van Der Heijden et al., 2008; Jenny, 1941). Fungi and bacteria represent most of the diversity of life on Earth (Bardgett and van der Putten, 2014; Locey and Lennon, 2016). Yet, inclusion of fungal and bacterial abundance into quantitative ecosystem and Earth system models has been hindered by the paucity of information about organisms at

appropriate spatial scales. Here, we impose a global top-down constraint on the broad composition of soil microbial life. By doing so, we hope to empower microbial, ecosystem and Earth-system scientists to consider how this broad constraint on the soil biodiversity may inform and transform how we understand terrestrial ecosystem functioning. As we develop a spatially-explicit understanding of the global soil community, we will be able to better parameterize and benchmark our predictions about the rate and efficiency of carbon turnover in soil and the feedbacks to ongoing climate change.

Despite of the progress made in this study, here we clarify two limitations on this study. First, our study highlights the data gaps in fungal proportion prediction in low latitude – tropical biome and high latitude – boreal biome (i.e., boreal forests and tundra). Tropical vs boreal biomes are hotpots or debated regions with their relative capacity and capability to sequestrate atmospheric $CO_2$ and mitigate climate change in an increasingly changing climate (Schimel et al., 2015; Tagesson et al., 2020). ~~;~~ T~~t~~hey are also regions with striking differences of soil microbial composition (fungal proportion), plant communities and soil carbon storge, thus suggesting their potentially strong interactions and feedbacks in these regions (Bardgett et al., 2008). Boreal biome contains large amount of soil organic carbon which could be sensitive to global change (i.e., warming), whereby soil microbial community (i.e., total biomass or the relative abundance of of soil fungi and bacteria) could play an essential role. Second, microbial biomass (C) is more relevant to be linked with soil carbon cycling and carbon stock in term of their own contribution by living carbon pools and the impacts of its microbial necromass (Liang et al., 2019), while the conversion factor of converting abundance into biomass across space is currently not available. To mechanistically and explicitly incorporate soil microbial composition into biogeochemical models, the biogeographic patterns of abundance or biomass of each major

group (fungi vs bacteria), the relative ratio within fungi (i.e., saprotrophic fungi, arbuscular mycorrhiza fungi vs ectomycorrhizal fungi) and/or bacteria (i.e., gram positive bacteria vs gram negative bacteria) would also be critical in view of their striking functional difference (Averill et al., 2014; Crowther et al., 2019). These knowledge gaps highlight the urgent research needs in these new research endeavors with the increasing availability of datasets.

## 5. Conclusions

This study used a global scale dataset (>3000 distinct observations of soil fungal and bacterial abundance) in the top soil surface (up to 15 cm) ~~(>3000 distinct observations of soil fungal and bacterial abundance)~~ to generate the first quantitative and spatially high resolution (1 $km^2$) explicit maps of soil fungal and bacterial relative abundance across global terrestrial ecosystems. Our machine learning approach (random forest) enabled us to link the variation in fungal proportion to global variation in climate, soil, vegetation and other environmental drivers, whilst accounting for the interactions and non-linearities among them. We found the striking latitudinal trends where fungal dominance increases in cold and high latitude environments with large soil carbon stocks. The fungal proportion in soil can be predicted by few primary environmental drivers – temperature and NPP with strong non-linear effects of temperature and NPP. We demonstrated that fungi and bacteria represent slow vs fast energy channels, whereby they dominate in regions of low MAT and NPP vs high MAT and NPP, respectively. Overall, our spatially-explicit model would enable us to explicitly represent the different contributions of fast - bacterial vs. slow – fungal energy channels in spatially-explicit biogeochemical models, with the potential to enhance the accuracy of soil carbon turnover and carbon storge predictions. We further highlight the data gaps in tropical and boreal regions and needs of future research endeavors in generating high resolution

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biogeographic patterns of biomass of each major microbial group, the relative biomass ratios across and within major microbial groups.

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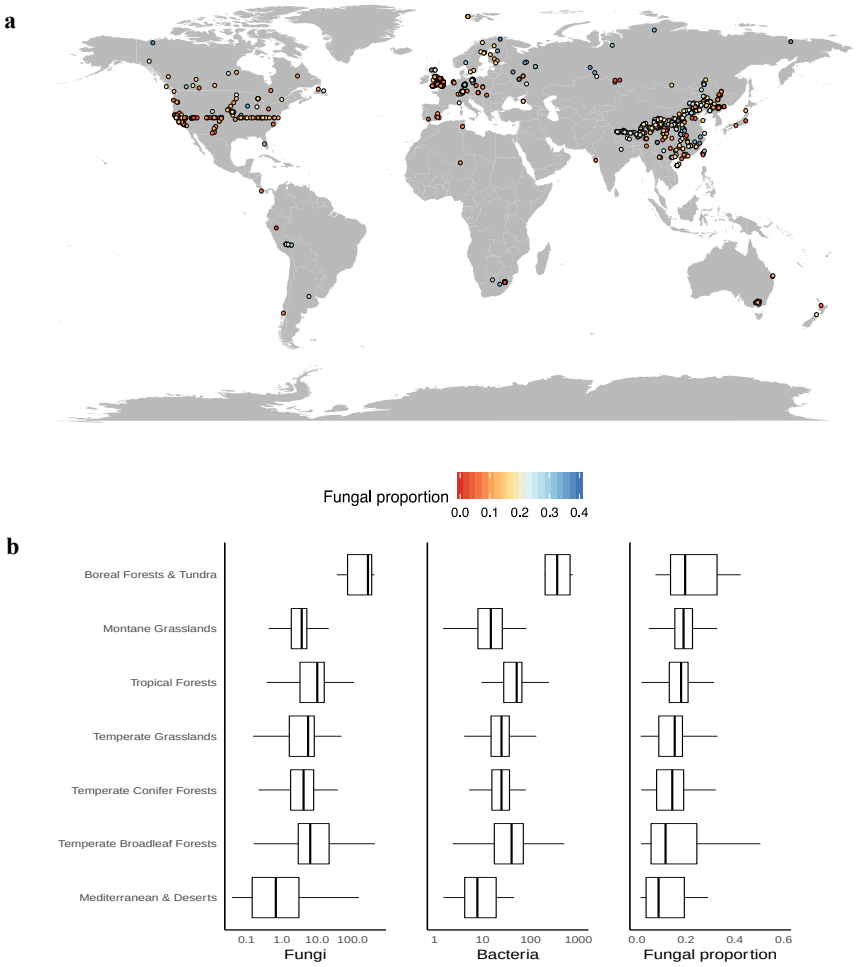


**Figure 1. Map of sample locations and fungal and bacterial abundance and fungal proportion data**. **a**, Sampling sites. A total of 3224 samples were collected and aggregated into 943 1-km$^2$ pixels that were used for geospatial modelling. **b,** The median and interquartile range of abundance of fungi and bacteria and fungal proportion across vegetation biomes. Tundra and boreal forest, Mediterranean and desert have low sample sizes (<25) and thus were combined.

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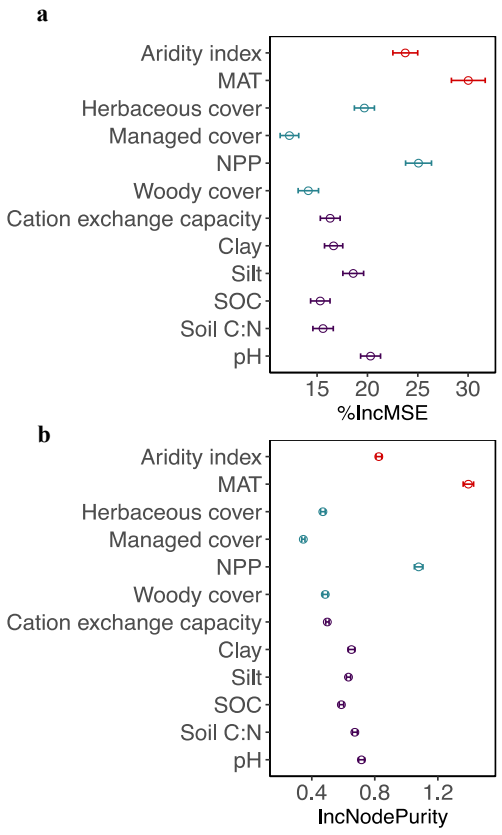
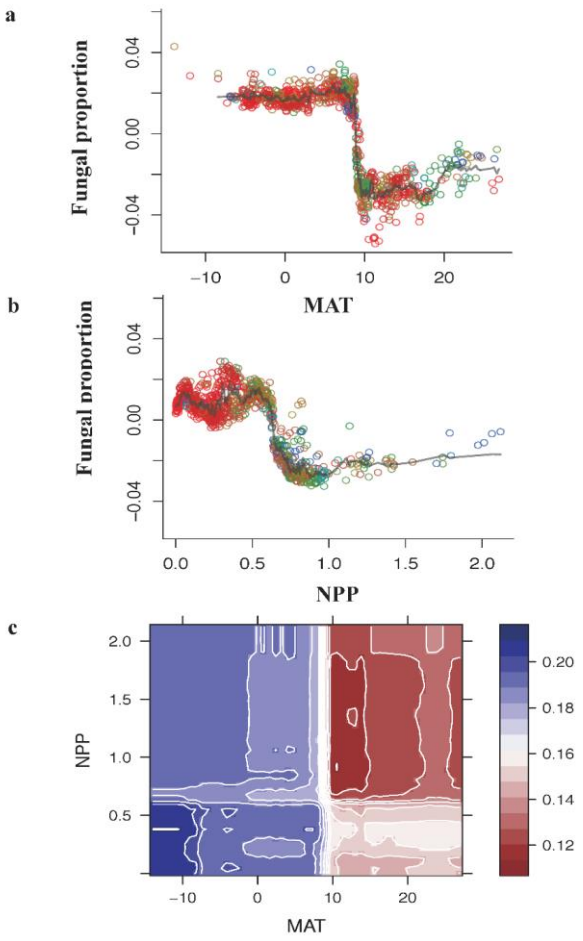



590

591 **Figure 2. Mean decrease in accuracy (%IncMSE, mean and SD, a) and mean decrease gini**
592 **(IncNodePurity, mean and SD, b) estimated from 1000 simulations of random forests.** This
593 is used to evaluate the importance of top environmental drivers on proportion of fungi derived
594 from 'all' dataset.




595

596 **Figure 3. Fungal proportion is primarily associated with climate- mean annual**

597 **temperature (MAT) and net primary productivity (NPP). a**–**b**, Partial feature contributions

598 of primary environmental variables (**a**, MAT; **b**, NPP) to fungal proportion. **c**, Partial feature

599 contributions of primary environmental variable interactions (MAT vs NPP) to fungal

600 proportion.

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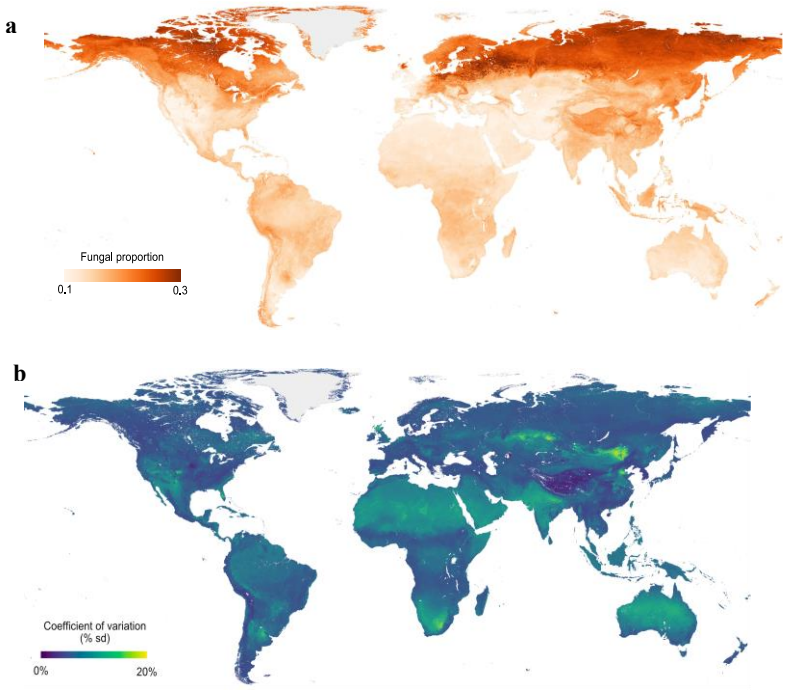


**Figure 4.** Global map of fungal proportion (a) and bootstrapped (100 iterations) coefficient of variation (b) at the 30 arcsec (approximately 1 $km^2$) pixel scale. Bootstrapped coefficient of variation is standard deviation divided by the mean predicted value as a measure of prediction accuracy. Sampling was stratified by biome.

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Author contributions

KLY and TWC designed the project. KLY built the PLFA datasets with help from JVDH and ZQW. KLY performed the analysis with inputs from DR and CA. KLY, CA, and TWC wrote the paper with revisions from all other coauthors. GRS, RED, KMS, FM, MPW, YHY, FTDV, RDB, PM, FB, SGB, EMB, CG, QKW, LM, BD C, XJH, WZT, ST, AH, JAB contributed to PLFA datasets.

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