

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

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46

47 **Abstract.** Fungi and bacteria are the two dominant groups of soil microbial communities
48 worldwide. By controlling the turnover of soil organic matter, these organisms directly regulate
49 the cycling of carbon between the soil and the atmosphere. Fundamental differences in the
50 physiology and life history of bacteria and fungi suggest that variation in the biogeography of soil
51 fungal and bacterial relative abundance could drive striking differences in carbon decomposition
52 and soil organic matter formation across different biomes. However, a lack of global and predictive
53 information on the distribution of these organisms in terrestrial ecosystems has prevented the
54 inclusion of soil fungal and bacterial relative abundance and the associated processes into global
55 biogeochemical models. Here, we used a global scale dataset (>3000 distinct observations of soil
56 fungal and bacterial abundance) in the top soil surface (up to 15 cm) to generate the first
57 quantitative and spatially high resolution (1km²) explicit map of soil fungal proportion, defined as
58 fungi/fungi + bacteria, across terrestrial ecosystems. We reveal striking latitudinal trends where
59 fungal dominance increases in cold and high latitude environments with large soil carbon stocks.
60 There was strong non-linear response of fungal dominance to environmental gradient, i.e., mean
61 annual temperature (MAT) and net primary productivity (NPP). Fungi and bacteria dominated in
62 regions with low and high MAT and NPP, respectively, thus representing slow vs. fast soil energy
63 channels, a concept with a long history in soil ecology. These high-resolution models provide the
64 first steps towards representing the major soil microbial groups and their functional differences in
65 global biogeochemical models to improve predictions of soil organic matter turnover under current
66 and future climate scenarios. The code and data of machine learning is available at
67 <https://github.com/KailiangYu/Biogeography-of-soil-microbes.git> (Yu et al., 2022).

68

69 **1. Introduction**

70 Fungi and bacteria are the dominant members of soil microbial communities worldwide in terms
71 of diversity, abundance and biomass (Bahram et al., 2018). Representing distinct kingdoms of life,
72 bacteria and fungi systematically differ in a multitude of physiological and life-history traits with
73 direct implications for global soil biogeochemical cycles (Waring et al., 2013; Wieder et al., 2015)
74 including the decomposition of organic matter, which contributes to one of the largest fluxes of
75 CO₂ on Earth (Glassman et al., 2018). Compared to bacteria, fungi generally have slower growth
76 and turnover rates (Rousk and Bååth, 2007), greater carbon (C) to nutrient stoichiometry (Waring
77 et al., 2013), greater capacity to degrade a wider and more recalcitrant range of substrates
78 (Strickland and Rousk, 2010) and potentially higher C use efficiency (Soares and Rousk, 2019).
79 For these reasons, a new generation of soil and ecosystem models have begun to explicitly
80 represent these fundamentally distinct fast and slow cycling microbial groups, suggesting that
81 spatially-explicit information about the relative abundance of fungal and bacteria in a region can
82 dramatically improve the accuracy of global carbon cycling model predictions (Shi et al., 2018;
83 Sulman et al., 2014; Wieder et al., 2013, 2015). Generating an understanding of the factors
84 affecting the biogeography of the relative abundance of fungal and bacteria in soil, and its
85 connection to global carbon cycle, would represent a breakthrough step forward in our general
86 understanding of the natural history of soil microbial life.

87 Temperature, precipitation, soil pH and soil C:N have all been linked to the balance of fungi
88 vs. bacteria within soil communities across different spatial scales (Bahram et al., 2018;
89 Strickland and Rousk, 2010; Tedersoo et al., 2014). Relative to fungi, bacteria tend to dominate
90 in locations with high soil nutrient contents or in frequently disturbed soils that limit the growth
91 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

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

126 Here, we present a global analysis of total and relative abundance of soil fungi and bacteria
127 in soil surfaces (defined as top 10-15 cm) informed from over 3000 spatially distinct surface soil
128 observations from phospholipid-derived fatty acids (PLFA) (Fig. 1a). The use of PLFA data
129 provides an opportunity to provide quantitative insights into the abundances of the major
130 functional groups. We conducted the analysis on the abundances in view of the uncertainty in
131 conversion factors used to convert abundance derived from PLFA to biomass (Frostegård et al.,
132 2011; Klamer and Bååth, 2004). We used machine learning to link the variation in soil fungi and
133 bacteria abundances to global variation in 95 climate, vegetation, and soil variables. This allowed
134 us to 1) explore the environmental drivers of fungal and bacterial dominance, defined as fungal
135 proportion - fungi/(fungi + bacteria), where values closer to 1 indicate a higher fungal dominance
136 and values closer to zero indicate a greater bacterial dominance (see Methods); 2) examine the
137 non-linear response or pattern of fungal proportion across environmental gradients, i.e., mean

138 annual temperature-MAT and net primary productivity-NPP. Based on the observed
139 relationships (by accounting for the non-linearity), we generated a quantitative spatially-explicit
140 global map (1 km²) of fungal proportion, and assessed how soil fungal and bacterial dominance
141 varies with key climate, soil, vegetation and geographic drivers.

142 **2. Material and methods**

143 **2.1. Data acquisition of soil microbe composition**

144 We compiled data of abundance of soil fungi and bacteria and fungal proportion, defined as
145 fungi/(fungi + bacteria). We focused on phospholipid-derived fatty acids (PLFA) and the data
146 derived from PLFA reported the balance between fungal and bacterial PLFAs (Frostegård et al.,
147 2011) can provide a valuable estimation of the comparative dominance of both functional groups.
148 The data based on qPCR was not included because of difference in units with PLFA. With non-
149 significant difference using data of fungal proportion and fungi : bacteria ratio, we focused on and
150 reported the results on the fungal proportion rather than fungi : bacteria ratio because 1) The fungal
151 proportion is insensitive to whether fungi or bacteria are the numerator (i.e. bacterial proportion =
152 1 – fungal proportion), and 2) fungal proportion had more spread frequency distribution and thus
153 led to better machine learning predictions (Fig. S1). The data was compiled by a primary literature
154 review through Google Scholar, Web of Science (<http://apps.webofknowledge.com>) and China
155 National Knowledge Infrastructure Database (<http://cnki.net>) till 30 June, 2020 using the keywords
156 “fungi”, “bacteria”, “abundance”, “PLFA”. To be included in our data analysis, the study had to
157 at least have the following metadata: longitude and latitude, sampling date, sampling depth,
158 information on land use (agriculture, tree plantations, or natural sites), units and the methods used.
159 In total, this led to 319 references. We further used the following criteria to select eligible
160 references and datasets: (1) when the studies were manipulative experiments, we only included the

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

170 The criteria were carefully scrutinized by three independent researchers and this ultimately
171 led to 179 eligible references (see Supplementary references for PLFA) used for this study. In total,
172 we compiled a dataset of fungal proportion ($n = 3224$) at a global scale. The subset of data ($n =$
173 1795) with only natural ecosystems (Fig. S2a) were used to examine the potential role of land use
174 change (see Supplementary Methods). The results showed minimal difference of the two scenarios
175 of including all data and natural ecosystems. All data points falling within the same 30 arc-seconds
176 ($\sim 1\text{-km}^2$) pixel were aggregated via an average. The aggregated data of fungal proportion ($n = 946$
177 for all data; $n = 716$ for natural ecosystems) were used to examine its environmental controls and
178 geospatial modelling in making the global map (Fig. 1a; Fig. S2a).

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

184 samples which were used for further analyses of abundance of fungi and bacteria, respectively (Fig.
185 S3). As compared to the larger sample size of fungal proportion (n = 946 for all data), the data of
186 abundance of fungi (n = 646 for all data) and bacteria (n = 647 for all data) aggregated within the
187 30 arc-seconds ($\sim 1\text{-km}^2$) pixel via an average were used for the analysis of their spatial trends
188 across vegetation biome, vegetation type and latitude (see Supplementary Methods).

189 **2.2. Geospatial modelling**

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

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

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

211 **2.3. Environmental drivers and statistic analysis**

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

223 **3. Code and data availability of machine learning**

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

226 **4. Results and discussion**

227 **4.1. Raw data patterns of fungal proportion**

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

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

238 Within similar climates, soil fungal and bacterial abundance as well as fungal proportion
239 was greatest in ecosystems harboring woody vegetation compared to grasslands and managed
240 (agricultural) ecosystems (Fig. S6). This finding is consistent with the idea that ecosystems
241 dominated by woody plants generate lignified, more recalcitrant and nutrient poor soil C inputs
242 that characteristically favor fungal dominance (Fierer et al., 2009; Strickland and Rousk, 2010),
243 and have a biomass stoichiometry better suited to low nutrient environments (Waring et al., 2013).
244 But we stress that this link of belowground soil microbial composition (fungi vs bacteria) with
245 aboveground plant community composition (woody plants vs grasses) can be complex, non-linear
246 and even divergent, as demonstrated by the non-existence of woody plants in grasslands and
247 scarcity of grasses in forests but with well mixed fungi vs bacteria abundances. This raises the
248 curiosity whether the interactions, associations or couplings of belowground soil microbial
249 composition vs aboveground plant community composition are stronger in ecosystems where
250 woody plants and grasses interact or coexist (i.e., savannas) (Yu and D'Odorico, 2015). It also
251 remains unclear how this coupling could improve our understanding of ecosystem carbon cycling
252 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 storage 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 storage) (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., CO₂) 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

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

302 **4.3. Biogeographic pattern from the machine learning model**

303 Across all samples, the machine learning model was able to predict the variation in fungal and
304 bacterial dominance with high predictive accuracy ($R^2 = 0.43/0.35$ in 10-fold cross validation; R^2
305 $= 0.92/0.91$ in final model; Fig. S10a-b). By extrapolating these relationships across terrestrial
306 ecosystems, we could identify clear global trends in fungal dominance. Despite these general
307 global scale patterns of increase in fungi dominance with latitude, our models also revealed
308 regional contingencies that diverge from the global trends (Fig. 4a; Fig. S11a). For instance,
309 Northeastern Europe is dominated by woody vegetation and exhibits high fungal proportion, while
310 the United Kingdom and northern Kazakhstan have much lower fungal proportion despite being
311 at comparable latitude, likely because these areas are dominated by herbaceous vegetation with
312 lower lignin content than in woody tissues. Tibetan alpine grasslands are at comparatively much
313 lower latitude but have high values of fungal proportion in part due to very high SOC stocks and
314 cold temperatures. Model predictions of fungal proportion had high uncertainty in dry regions
315 (i.e., Northern and Southern Africa, Australia, Western USA, eastern Mongolia) (Fig. 4b; Fig.
316 S11b), presumably because of the low sample size in drylands and/or complex response of fungi
317 and bacteria to water availability (Fierer et al., 2009; Strickland and Rousk, 2010). Indeed,
318 our datasets are mostly concentrated to US, Europe and East Asia, thus highlighting the data gaps
319 at tropical and boreal biomes. Even for the temperate biome, there were data gaps in west Australia
320 and central Asia. Because of the unbalanced sample distribution, we also used a bootstrapping
321 strategy (100 iterations) by randomly sampling 90% data with replacement. The results showed

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

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

338 **4.4. Implications and limitations of this study**

339 It is generally accepted that the soil microbiome exerts major control over soil processes, and in
340 turn ecosystem functioning, and by extension the global biogeochemical cycles (Bahram et al.,
341 2018; Crowther et al., 2019; Van Der Heijden et al., 2008; Jenny, 1941). Fungi and bacteria
342 represent most of the diversity of life on Earth (Bardgett and van der Putten, 2014; Locey and
343 Lennon, 2016). Yet, inclusion of fungal and bacterial abundance into quantitative ecosystem and
344 Earth system models has been hindered by the paucity of information about organisms at

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

352 Despite of the progress made in this study, here we clarify two limitations on this study.
353 First, our study highlights the data gaps in fungal proportion prediction in low latitude – tropical
354 biome and high latitude – boreal biome (i.e., boreal forests and tundra). Tropical vs boreal
355 biomes are hotspots or debated regions with their relative capacity and capability to sequester
356 atmospheric CO₂ and mitigate climate change in an increasingly changing climate (Schimel et
357 al., 2015; Tagesson et al., 2020). They are also regions with striking differences of soil microbial
358 composition (fungal proportion), plant communities and soil carbon storage, thus suggesting their
359 potentially strong interactions and feedbacks in these regions (Bardgett et al., 2008). Boreal
360 biome contains large amount of soil organic carbon which could be sensitive to global change
361 (i.e., warming), whereby soil microbial community (i.e., total biomass or the relative abundance
362 of soil fungi and bacteria) could play an essential role. Second, microbial biomass (C) is more
363 relevant to be linked with soil carbon cycling and carbon stock in term of their own contribution
364 by living carbon pools and the impacts of its microbial necromass (Liang et al., 2019), while the
365 conversion factor of converting abundance into biomass across space is currently not available.
366 To mechanistically and explicitly incorporate soil microbial composition into biogeochemical
367 models, the biogeographic patterns of abundance or biomass of each major group (fungi vs

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

373 **5. Conclusions**

374 This study used a global scale dataset (>3000 distinct observations of soil fungal and bacterial
375 abundance) in the top soil surface (up to 15 cm) to generate the first quantitative and spatially high
376 resolution (1 km²) explicit maps of soil fungal and bacterial relative abundance across global
377 terrestrial ecosystems. Our machine learning approach (random forest) enabled us to link the
378 variation in fungal proportion to global variation in climate, soil, vegetation and other
379 environmental drivers, whilst accounting for the interactions and non-linearities among them. We
380 found the striking latitudinal trends where fungal dominance increases in cold and high latitude
381 environments with large soil carbon stocks. The fungal proportion in soil can be predicted by few
382 primary environmental drivers – temperature and NPP with strong non-linear effects of
383 temperature and NPP. We demonstrated that fungi and bacteria represent slow vs fast energy
384 channels, whereby they dominate in regions of low MAT and NPP vs high MAT and NPP,
385 respectively. Overall, our spatially-explicit model would enable us to explicitly represent the
386 different contributions of fast - bacterial vs. slow – fungal energy channels in spatially-explicit
387 biogeochemical models, with the potential to enhance the accuracy of soil carbon turnover and
388 carbon storage predictions. We further highlight the data gaps in tropical and boreal regions and
389 needs of future research endeavors in generating high resolution biogeographic patterns of biomass

390 of each major microbial group, the relative biomass ratios across and within major microbial
391 groups.

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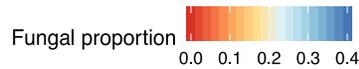
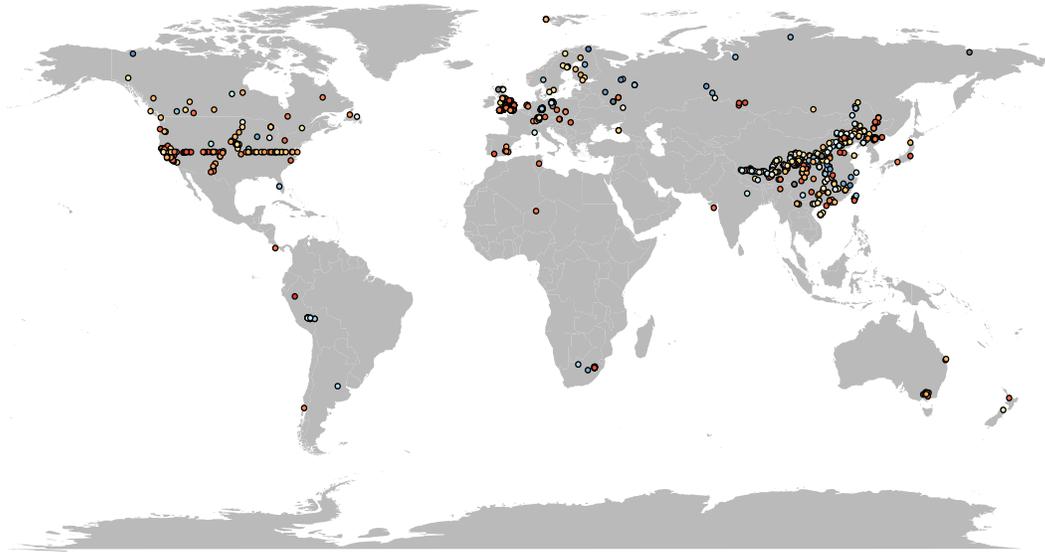
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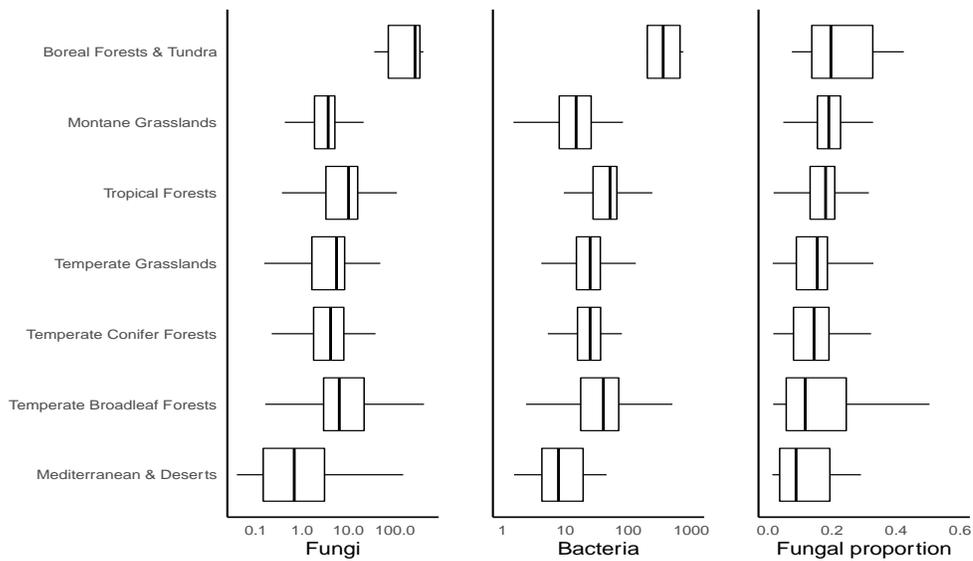
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a



b



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Figure 1. Map of sample locations and fungal and bacterial abundance and fungal

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proportion data. a, Sampling sites. A total of 3224 samples were collected and aggregated into

587

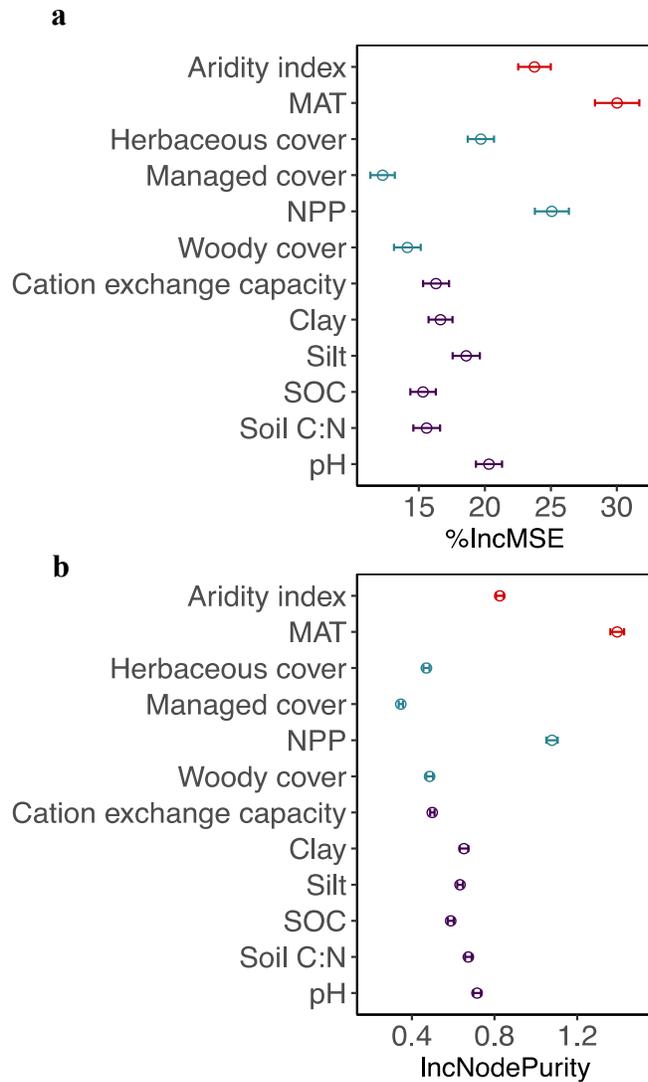
943 1-km² pixels that were used for geospatial modelling. **b**, The median and interquartile range

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of abundance of fungi and bacteria and fungal proportion across vegetation biomes. Tundra and

589

boreal forest, Mediterranean and desert have low sample sizes (<25) and thus were combined.



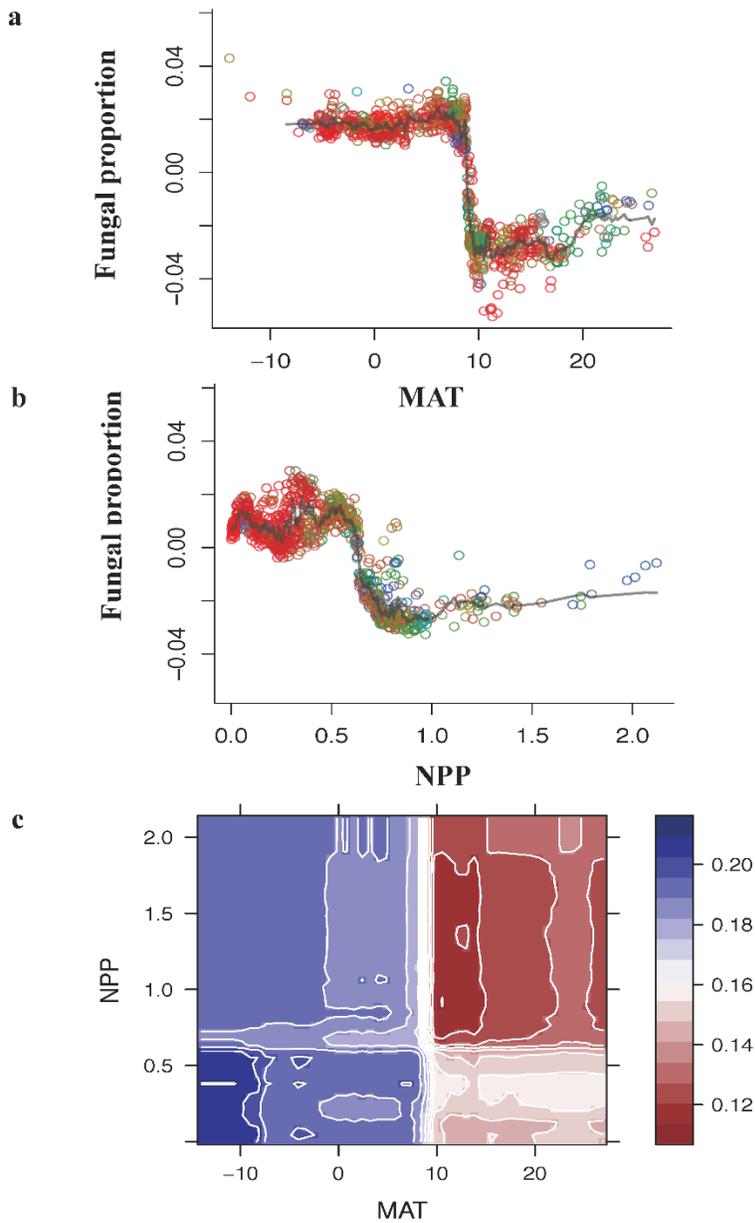
590

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

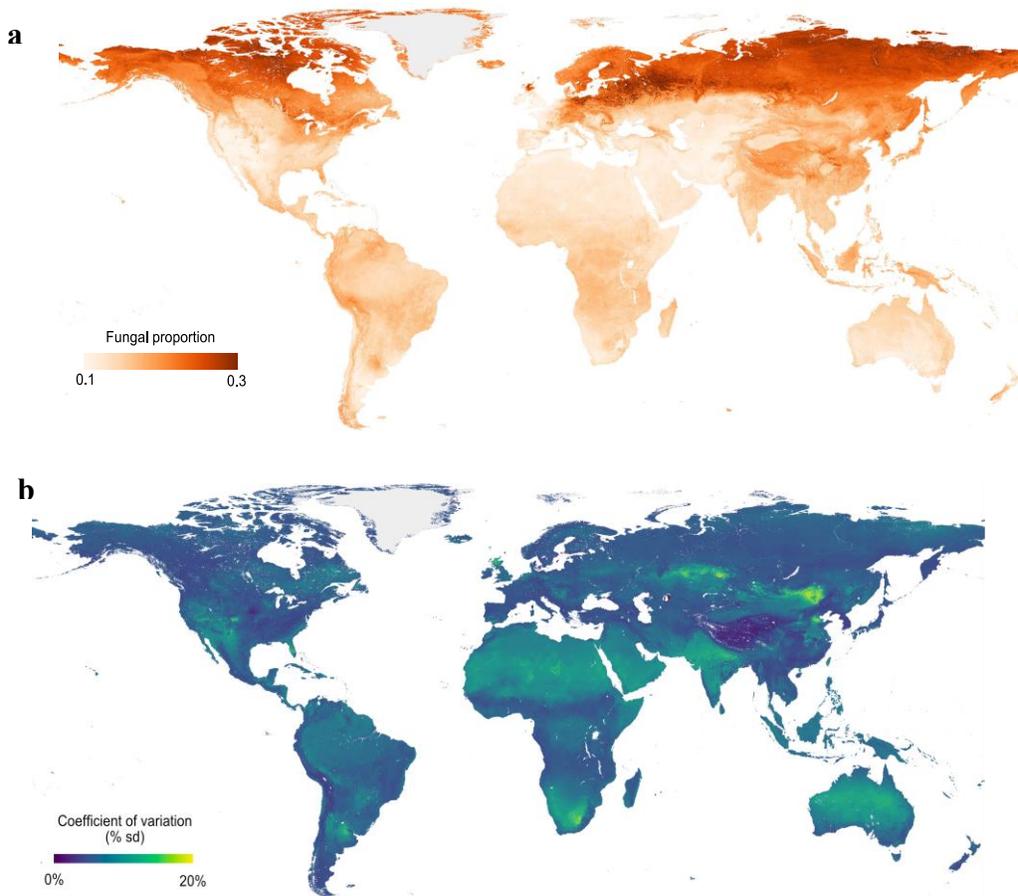
594 from ‘all’ dataset.



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.**

601



602
603
604 **Figure 4.** Global map of fungal proportion (a) and bootstrapped (100 iterations) coefficient
605 of variation (b) at the 30 arcsec (approximately 1 km²) pixel scale. Bootstrapped coefficient
606 of variation is standard deviation divided by the mean predicted value as a measure of prediction
607 accuracy. Sampling was stratified by biome.

608

609

610

611 Author contributions

612 KLY and TWC designed the project. KLY built the PLFA datasets with help from JVDH and

613 ZQW. KLY performed the analysis with inputs from DR and CA. KLY, CA, and TWC wrote the

614 paper with revisions from all other coauthors. GRS, RED, KMS, FM, MPW, YHY, FTDV,

615 RDB, PM, FB, SGB, EMB, CG, QKW, LM, BD C, XJH, WZT, ST, AH, JAB contributed to

616 PLFA datasets.

617