1 **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 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) 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.

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;

91   Strickland and Rousk, 2010). However, until now, the relative importance of these different

92   environmental drivers remains relatively unclear at global scale, and the biogeography of these

93   major functional groups (fungi *vs*. bacteria) has only been demonstrated at local and regional

94   scales. A recent analysis suggested that the relative soil bacterial abundance is high in tropical

95   latitudes and decreases in abundance towards the high-latitude boreal regions, where fungi tend

96   to dominate (Bahram et al., 2018). Translating these broad-scale trends into quantitative,

97   spatially explicit information will be necessary if we intend to represent regional variations in

98   soil community functioning (Wieder et al., 2013, 2015), or predict future changes in terrestrial

99   carbon and nutrient cycling.

100   Some progress was made in the quantitative and spatially explicit understanding of global

101   biogeographic patterns of fungal and bacterial biomass and their biomass ratio. By synthesizing

102   phospholipid-derived fatty acids data from 1323 locations across the globe, and extrapolating

103   linear relationships with environmental factors, a recent study generate the global maps of fungal

104   and bacterial biomass and their biomass ratio at the resolution of 0.5 degree for top soil (0-30

105   cm) (He et al., 2020). This approach provided the support for the broad-scale latitudinal trends,

106   with high fungal dominance in high-latitude regions. Yet to date, there are three crucial

107   knowledge gaps to be addressed. First, we still lack a high resolution evaluation of the spatial

108   patterns and regional contingencies in fungal:bacterial ratios, which would allow representation

109   of microbial-mediated mechanisms that operate within and/or across ecosystems at fine scales

110   (Frindte et al., 2019; Zhu et al., 2017). Second, the response of soil microbial community

111   composition across environmental gradients are expected to be non-linear, with strong interactive

112   effects of different environmental characteristics that give rise to thresholds that diverge from the

113   global latitudinal trends (Sengupta et al., 2021; Wang et al., 2018; Waring et al., 2013). This

114   non-linear linkage of soil microbial communities with environmental resource gradient has not

115   been assessed, while it has fundamental implications on ecosystem functions and management

116   solutions (Sengupta et al., 2021; Wang et al., 2018). Third, there are distinct difference of soil

117   nutrients, soil microbial community and the associated biogeochemical processes across soil

118   depths, i.e., from top surface soil (i.e., 0-10 cm) to top subsurface soil (i.e., 0-30 cm) (Lavahun et

119   al., 1996; Yue et al., 2015). A continental-scale empirical study further showed that strong

120   positive associations among soil microbial community, fertility and plant productivity are limited

121   to the top surface soil (Delgado-Baquerizo et al., 2017), thus highlighting its potential dominant

122   role regulated by top surface soil microbial communities on ecosystem functions and the

123   research needs of generating a global spatially explicit understanding of soil fungi and bacteria in

124   top surface soil.

125   Here, we present a global analysis of total and relative abundance of soil fungi and bacteria

126   in soil surfaces (defined as top 10-15 cm) informed from over 3000 spatially distinct surface soil

127   observations from phospholipid-derived fatty acids (PLFA) (Fig. 1a). The use of PLFA data

128   provides an opportunity to provide quantitative insights into the abundances of the major

129   functional groups. We conducted the analysis on the abundances in view of the uncertainty in

130   conversion factors used to convert abundance derived from PLFA to biomass (Frostegård et al.,

131   2011; Klamer and Bååth, 2004). We used machine learning to link the variation in soil fungi and

132   bacteria abundances to global variation in 95 climate, vegetation, and soil variables. This allowed

133   us to 1) explore the environmental drivers of fungal and bacterial dominance, defined as fungal

134   proportion - fungi/(fungi + bacteria), where values closer to 1 indicate a higher fungal dominance

135   and values closer to zero indicate a greater bacterial dominance (see Methods); 2) examine the

136   non-linear response or pattern of fungal proportion across environmental gradients, i.e., mean

137 annual temperature-MAT and net primary productivity-NPP. Based on the observed

138 relationships (by accounting for the non-linearity), we generated a quantitative spatially-explicit

139 global map (1 km^2) of fungal proportion, and assessed how soil fungal and bacterial dominance

140 varies with key climate, soil, vegetation and geographic drivers.

141 **2. Material and methods**

142 **2.1. Data acquisition of soil microbe composition**

143 We compiled data of abundance of soil fungi and bacteria and fungal proportion, defined as

144 fungi/(fungi + bacteria). We focused on phospholipid-derived fatty acids (PLFA) and the data

145 derived from PLFA reported the balance between fungal and bacterial PLFAs (Frostegård et al.,

146 2011) can provide a valuable estimation of the comparative dominance of both functional groups.

147 The data based on qPCR was not included because of difference in units with PLFA. With non-

148 significant difference using data of fungal proportion and fungi : bacteria ratio, we focused on and

149 reported the results on the fungal proportion rather than fungi : bacteria ratio because 1) The fungal

150 proportion is insensitive to whether fungi or bacteria are the numerator (i.e. bacterial proportion =

151 1 – fungal proportion), and 2) fungal proportion had more spread frequency distribution and thus

152 led to better machine learning predictions (Fig. S1). The data was compiled by a primary literature

153 review through Google Scholar, Web of Science (http://apps.webofknowledge.com) and China

154 National Knowledge Infrastructure Database (http://cnki.net) till 30 June, 2020 using the keywords

155 "fungi", "bacteria", "abundance", "PLFA". To be included in our data analysis, the study had to

156 at least have the following metadata: longitude and latitude, sampling date, sampling depth,

157 information on land use (agriculture, tree plantations, or natural sites), units and the methods used.

158 In total, this led to 319 references. We further used the following criteria to select eligible

159 references and datasets: (1) when the studies were manipulative experiments, we only included the

160   data from "control" plots (Chen et al., 2016). (2) we standardized our efforts by focusing on all

161   samples that were collected from the top surface soils ($\approx$ 0-10/15 cm) because this layer contains

162   greater biomass and has the majority of sample size. (3) we used the datasets based on reporting

163   abundance with units of nmol, umol, or mol% since the majority (>90%) of datasets reported

164   abundance. Thus, we exclude all datasets reporting biomass instead of abundance. (4) we excluded

165   observations located in sea since our study focuses on terrestrial ecosystems. (5) we only included

166   the datasets on soil samples derived from field experiments and thus excluded the datasets from

167   incubation experiments. (6) some datasets reported in original references as average across

168   sampling sites or sampling dates were included.

169   The criteria were carefully scrutinized by three independent researchers and this ultimately

170   led to 179 eligible references (see Supplementary references for PLFA) used for this study. In total,

171   we compiled a dataset of fungal proportion (n = 3224) at a global scale. The subset of data (n =

172   1795) with only natural ecosystems (Fig. S2a) were used to examine the potential role of land use

173   change (see Supplementary Methods). The results showed minimal difference of the two scenarios

174   of including all data and natural ecosystems. All data points falling within the same 30 arc-seconds

175   (~1-km^2) pixel were aggregated via an average. The aggregated data of fungal proportion (n = 946

176   for all data; n = 716 for natural ecosystems) were used to examine its environmental controls and

177   geospatial modelling in making the global map (Fig. 1a; Fig. S2a).

178   The spatial variations of fungi and bacteria ratio or fungal proportion across latitude could be

179   influenced by either changes (increases or decreases) in abundance of fungi or bacteria or both.

180   Thus, to better understand the biogeographic pattern of fungal and bacterial composition, we also

181   analysed the spatial patterns of abundance of fungi and bacteria by using the abundance data with

182   the same unit (nmol g^{-1} PLFA). In total, our data compiling led to a final subset of 2753, and 2759

183   samples which were used for further analyses of abundance of fungi and bacteria, respectively (Fig.

184   S3). As compared to the larger sample size of fungal proportion (n = 946 for all data), the data of

185   abundance of fungi (n = 646 for all data) and bacteria (n = 647 for all data) aggregated within the

186   30 arc-seconds (~1-km^2) pixel via an average were used for the analysis of their spatial trends

187   across vegetation biome, vegetation type and latitude (see Supplementary Methods).

188   **2.2. Geospatial modelling**

189   A stack (n = 95) of ecologically relevant, global map layers including soil physical, chemical and

190   nutrient properties, climate conditions, vegetative indices, radiation and topographic variables and

191   anthropogenic covariates (Supplementary Table 1) were used to derive the environmental factors

192   which could affect fungal proportion. All of these covariate map layers were standardized at 30

193   arc-seconds resolution ($\approx$1km^2 at the equator) (van den Hoogen et al., 2019). These covariates

194   were then derived based on the georeferenced coordinates of the soil samples aggregated at 30 arc-

195   seconds resolution.

196   We used the Random Forest machine learning algorithm (see Supplementary Methods) with

197   the derived 95 covariates to extrapolate these relationships between fungal proportion and

198   environmental conditions across the globe and generate the first spatially-explicit, quantitative

199   map of fungal proportion at a global scale. The strength of prediction was evaluated using k-fold

200   cross validation (with k = 10) and the best model having high coefficient of determination and low

201   standard deviation in the mean cross-validation were used to generate the global map of fungal

202   proportion. The standard error sharply decreased with increasing sample size across all vegetation

203   biomes and the analysis showed that an efficient prediction required a large sample size (n > 500)

204   (Fig. S4). To evaluate the sensitivity, we also generate the uncertainty (standard deviation as a

205   fraction of the mean predicted value) map of fungal proportion by using a stratified bootstrapping

206 procedure (van den Hoogen et al., 2019). The stratification category was the sampled biomes of

207 each point feature (fungal proportion) with the total number collection of fungal proportion points

208 to avoid biases. In total, 100 bootstrap iterations were used, thus generating 100 global maps of

209 fungal proportion used to quantify statistically robust 95% confidence intervals per pixel.

210 **2.3. Environmental drivers and statistic analysis**

211 To examine the environmental controls of soil microbial composition at a global scale, we chose

212 the top drivers (Chen et al., 2016; Drenovsky et al., 2010a; de Vries et al., 2012) which include

213 soil properties, climate conditions, vegetation index and human activities (see Supplementary

214 Methods). These variables were examined to avoid multicollinearity using a matrix of pairwise

215 correlations to remove any variable with high correlations (R>0.7) with other predictor variables

216 (Anderegg et al., 2013). Random Forest machine learning algorithm was then used to determine

217 variable importance for each variable(Breiman, 2001). Mean decrease in accuracy (%IncMSE)

218 and mean decrease gini (IncNodePurity) were reported and the variables with greater values

219 of %IncMSE and IncNodePurity are more important in influencing fungal proportion. Partial

220 functions of most important variables (MAT and NPP) were plotted using forestFloor package to

221 examine their influences on fungal proportion.

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

223 The code and data of machine learning is available at

224 https://github.com/KailiangYu/Biogeography-of-soil-microbes.git.

225 **4. Results and discussion**

226 **4.1. Raw data patterns of fungal proportion**

227 Globally, we observed greater than 10-fold variation in soil fungal proportion across all sites,

228 ranging from 0.01 to 0.6 (Fig. 1b). At a global scale, we found clear latitudinal trends, with the

229 abundance of both fungi and bacteria increasing in high-latitude regions. Yet, the abundance of

230 fungi increased with latitude at a greater rate than the abundance of bacteria (Fig. S5), resulting in

231 a higher proportion of fungi in the cold, high-latitude regions. These latitudinal trends lend support

232 to the general global patterns detected in a previous broad-scale analysis (Bahram et al., 2018) and

233 in a recent meta-data analysis (He et al., 2020). As such, the highest fungal dominance was

234 observed in tundra and boreal forest ecosystems (mean ± 1SE: 0.23 ± 0.02; Fig. 1b). In addition,

235 high elevation and cold grasslands (i.e., Montane grasslands) with large soil organic C (SOC)

236 content generally harbor higher proportion of fungi, relative to bacteria (Fig. 1b).

237 Within similar climates, soil fungal and bacterial abundance as well as fungal proportion

238 was greatest in ecosystems harboring woody vegetation compared to grasslands and managed

239 (agricultural) ecosystems (Fig. S6). This finding is consistent with the idea that ecosystems

240 dominated by woody plants generate lignified, more recalcitrant and nutrient poor soil C inputs

241 that characteristically favor fungal dominance (Fierer et al., 2009; Strickland and Rousk, 2010),

242 and have a biomass stoichiometry better suited to low nutrient environments (Waring et al., 2013).

243 But we stress that this link of belowground soil microbial composition (fungi vs bacteria) with

244 aboveground plant community composition (woody plants vs grasses) can be complex, non-linear

245 and even divergent, as demonstrated by the non-existence of woody plants in grasslands and

246 scarcity of grasses in forests but with well mixed fungi vs bacteria abundances. This raises the

247 curiosity whether the interactions, associations or couplings of belowground soil microbial

248 composition vs aboveground plant community composition are stronger in ecosystems where

249 woody plants and grasses interact or coexist (i.e., savannas) (Yu and D'Odorico, 2015). It also

250 remains unclear how this coupling could improve our understanding of ecosystem carbon cycling

251 and other services.

252   Management of agricultural ecosystems often disrupts soil fungal networks (i.e. tillage,

253   frequent dry/wet cycles due to irrigation, machine operations, etc.), which decreases the abundance

254   of fungi relative to bacteria in agricultural soils (Fig. S6) (Drenovsky et al., 2010b; Jangid et al.,

255   2011; Waldrop et al., 2017). A central concern in agricultural ecosystems is the tradeoff of

256   increased food production to feed the increasing population vs the decreased soil carbon storage

257   to accelerate the global climate change (Sanderman et al., 2017). This study showed the higher

258   bacterial abundance relative to fungal abundance in soils of agricultural lands where soil carbon

259   storge is low; this corresponds with the global trends of bacterial dominance in low latitude where

260   soil carbon storage is low. These results suggest the potential strong but complex interactions and

261   feedbacks of soil microbial composition and soil functions (i.e., soil carbon storge) (Bardgett et

262   al., 2008), while the mechanistic links need further studies.

263   **4.2. Drivers of fungal proportion**

264   Globally, the fungal proportion in soil can be predicted by few primary environmental drivers (Fig.

265   2; Fig. S7). Specifically, mean annual temperature (MAT) and primary productivity (NPP) were

266   strong determinants of fungal dominance. The responses of fungal proportion to both MAT and

267   NPP were strongly non-linear, with warmer, more productive regions of the world (i.e. tropical

268   forest biomes) showing lower dominance of fungi as compared to colder, less productive

269   ecosystems (i.e. boreal forest and tundra biomes, Fig. 3; Fig. S8). This pattern is consistent with

270   the idea that fungi and bacteria represent slow vs. fast soil energy channels, respectively (Crowther

271   et al., 2019; Malik et al., 2016), a concept with a long history in soil ecology (Moore et al., 2003;

272   Moore and William Hunt, 1988). This finding is important because it could potentially link the

273   belowground slow – fungi vs fast – bacteria energy channels with aboveground plant slow growth

274   rates – woody plants vs fast growth rates – grasses, while the linkage could be complex, non-linear

275   or even divergent. The fast vs slow concept or spectrum have fundamentally improved the

276   understandings and predictions of land carbon storage across resource gradient or under global

277   change. The faster growth could be typically trade off with higher mortality or heterotrophic

278   respiration with resource (i.e., CO_2) enriched conditions (Jiang et al., 2020; Terrer et al., 2021; Yu

279   et al., 2019), thus constraining land carbon storage. This raises the question of how the

280   belowground fast vs slow energy channels and the aboveground fast vs slow growth spectrum

281   could be potentially linked or integrated to assess land carbon storage.

282   Temperature can affect soil microbial composition in complex ways, via directly

283   physiology or via indirectly soil substrate (Romero-Olivares et al., 2017). Previous studies have

284   shown the non-linear response of soil fungal and bacterial ratio to soil substrate (Waring et al.,

285   2013). The non-linear trends of the temperature sensitivity (Q10) of soil organic C decomposition,

286   as regulated by soil fungal and bacterial ratio, were also found along latitude (Wang et al., 2018).

287   Other environmental variables such as soil C to nitrogen ratio (C:N) have previously been found

288   to be important drivers in influencing fungal proportion within local and regional scale analyses

289   (Fierer et al., 2009; Waring et al., 2013). Our results suggest a more complicated relationship

290   between fungal proportion and the soil C:N. In the low range of soil C:N values, fungal proportion

291   decreased with soil C:N (Fig. S9a), suggesting the likely role of site-specific differences (i.e.,

292   climate or plant community) in out-weighting the influence of N availability (Soares and Rousk,

293   2019). Aside from these ecosystems, we observed a positive relationship between fungal

294   proportion and soil C:N at a global scale, consistent with previous work at local and regional scales

295   (Strickland and Rousk, 2010; Waring et al., 2013). Additionally, pH has been thought as a critical

296   driver of microbial diversity and biomass in soils. At local scales, previous studies reported either

297   no relationship, a negative correlation or convex curve between fungal and bacterial ratio and soil

298   pH (Rousk et al., 2009, 2010; de Vries et al., 2012). Our global scale analysis suggests a convex

299   relationship between fungal proportion and soil pH, with fungi dominating only within a narrow

300   pH range (<5-6) (Fig. S9b).

301   **4.3. Biogeographic pattern from the machine learning model**

302   Across all samples, the machine learning model was able to predict the variation in fungal and

303   bacterial dominance with high predictive accuracy (R^2 = 0.43/0.35 in 10-fold cross validation; R^2

304   = 0.92/0.91 in final model; Fig. S10a-b). By extrapolating these relationships across terrestrial

305   ecosystems, we could identify clear global trends in fungal dominance. Despite these general

306   global scale patterns of increase in fungi dominance with latitude, our models also revealed

307   regional contingencies that diverge from the global trends (Fig. 4a; Fig. S11a). For instance,

308   Northeastern Europe is dominated by woody vegetation and exhibits high fungal proportion, while

309   the United Kingdom and northern Kazakhstan have much lower fungal proportion despite being

310   at comparable latitude, likely because these areas are dominated by herbaceous vegetation with

311   lower lignin content than in woody tissues. Tibetan alpine grasslands are at comparatively much

312   lower latitude but have high values of fungal proportion in part due to very high SOC stocks and

313   cold temperatures. Model predictions of fungal proportion had high uncertainty in dry regions

314   (i.e., Northern and Southern Africa, Australia, Western USA, eastern Mongolia) (Fig. 4b; Fig.

315   S11b), presumably because of the low sample size in drylands and/or complex response of fungi

316   and bacteria to water availability (Fierer et al., 2009; Strickland and Rousk, 2010). Indeed,

317   our datasets are mostly concentrated to US, Europe and East Asia, thus highlighting the data gaps

318   at tropical and boreal biomes. Even for the temperate biome, there were data gaps in west Australia

319   and central Asia. Because of the unbalanced sample distribution, we also used a bootstrapping

320   strategy (100 iterations) by randomly sampling 90% data with replacement. The results showed

321   the similar spatial patterns of fungal proportion (Fig. S12a) and uncertainty (Fig. S12b) as the

322   scenario of using full dataset without bootstrapping.

323   Our study differs from a previous study (He et al., 2020) in several aspects including

324   sample size (n > 3000), spatial resolution (1km^2), consideration of non-linearity (through random

325   forest analysis), soil depth (soil surface 0-10/15 cm). We also note that our analysis sticks to the

326   original data of abundance derived from PLFA instead of converting abundance to biomass.

327   Conversion of abundance to biomass needs the conversion factor, which has large uncertainty

328   (Frostegård et al., 2011; Klamer and Bååth, 2004). Our high resolution map would allow

329   representation of microbial-mediated mechanisms at fine scales to link with ecosystem functions.

330   For instance, the significant functional differences between fungi and bacterial mean that the

331   relative dominance of fungi *vs*. bacteria is likely to influence a wide range of ecosystem

332   functions such as C use efficiency (CUE) of the decomposer community (Six et al., 2006; Soares

333   and Rousk, 2019) and enzymatic activity in soil N vs P acquisition (Caldwell, 2005; Crowther et

334   al., 2019). At fine, local or even regional scales, these relationships between soil microbial

335   composition and ecosystem functions could only be well identified using fine scale maps of soil

336   microbial composition.

337   **4.4. Implications and limitations of this study**

338   It is generally accepted that the soil microbiome exerts major control over soil processes, and in

339   turn ecosystem functioning, and by extension the global biogeochemical cycles (Bahram et al.,

340   2018; Crowther et al., 2019; Van Der Heijden et al., 2008; Jenny, 1941). Fungi and bacteria

341   represent most of the diversity of life on Earth (Bardgett and van der Putten, 2014; Locey and

342   Lennon, 2016). Yet, inclusion of fungal and bacterial abundance into quantitative ecosystem and

343   Earth system models has been hindered by the paucity of information about organisms at

344   appropriate spatial scales. Here, we impose a global top-down constraint on the broad composition

345   of soil microbial life. By doing so, we hope to empower microbial, ecosystem and Earth-system

346   scientists to consider how this broad constraint on the soil biodiversity may inform and transform

347   how we understand terrestrial ecosystem functioning. As we develop a spatially-explicit

348   understanding of the global soil community, we will be able to better parameterize and benchmark

349   our predictions about the rate and efficiency of carbon turnover in soil and the feedbacks to

350   ongoing climate change.

351   Despite of the progress made in this study, here we clarify two limitations on this study.

352   First, our study highlights the data gaps in fungal proportion prediction in low latitude – tropical

353   biome and high latitude – boreal biome (i.e., boreal forests and tundra). Tropical vs boreal

354   biomes are hotpots or debated regions with their relative capacity and capability to sequestrate

355   atmospheric CO_2 and mitigate climate change in an increasingly changing climate (Schimel et

356   al., 2015; Tagesson et al., 2020). They are also regions with striking differences of soil microbial

357   composition (fungal proportion), plant communities and soil carbon storge, thus suggesting their

358   potentially strong interactions and feedbacks in these regions (Bardgett et al., 2008). Boreal

359   biome contains large amount of soil organic carbon which could be sensitive to global change

360   (i.e., warming), whereby soil microbial community (i.e., total biomass or the relative abundance

361   of of soil fungi and bacteria) could play an essential role. Second, microbial biomass (C) is more

362   relevant to be linked with soil carbon cycling and carbon stock in term of their own contribution

363   by living carbon pools and the impacts of its microbial necromass (Liang et al., 2019), while the

364   conversion factor of converting abundance into biomass across space is currently not available.

365   To mechanistically and explicitly incorporate soil microbial composition into biogeochemical

366   models, the biogeographic patterns of abundance or biomass of each major group (fungi vs

367   bacteria), the relative ratio within fungi (i.e., saprotrophic fungi, arbuscular mycorrhiza fungi vs

368   ectomycorrhizal fungi) and/or bacteria (i.e., gram positive bacteria vs gram negative bacteria)

369   would also be critical in view of their striking functional difference (Averill et al., 2014;

370   Crowther et al., 2019). These knowledge gaps highlight the urgent research needs in these new

371   research endeavors with the increasing availability of datasets.

372   **5. Conclusions**

373   This study used a global scale dataset (>3000 distinct observations of soil fungal and bacterial

374   abundance) in the top soil surface (up to 15 cm) to generate the first quantitative and spatially high

375   resolution (1 km^2) explicit maps of soil fungal and bacterial relative abundance across global

376   terrestrial ecosystems. Our machine learning approach (random forest) enabled us to link the

377   variation in fungal proportion to global variation in climate, soil, vegetation and other

378   environmental drivers, whilst accounting for the interactions and non-linearities among them. We

379   found the striking latitudinal trends where fungal dominance increases in cold and high latitude

380   environments with large soil carbon stocks. The fungal proportion in soil can be predicted by few

381   primary environmental drivers – temperature and NPP with strong non-linear effects of

382   temperature and NPP. We demonstrated that fungi and bacteria represent slow vs fast energy

383   channels, whereby they dominate in regions of low MAT and NPP vs high MAT and NPP,

384   respectively. Overall, our spatially-explicit model would enable us to explicitly represent the

385   different contributions of fast - bacterial vs. slow – fungal energy channels in spatially-explicit

386   biogeochemical models, with the potential to enhance the accuracy of soil carbon turnover and

387   carbon storge predictions. We further highlight the data gaps in tropical and boreal regions and

388   needs of future research endeavors in generating high resolution biogeographic patterns of biomass

389 of each major microbial group, the relative biomass ratios across and within major microbial

390 groups.

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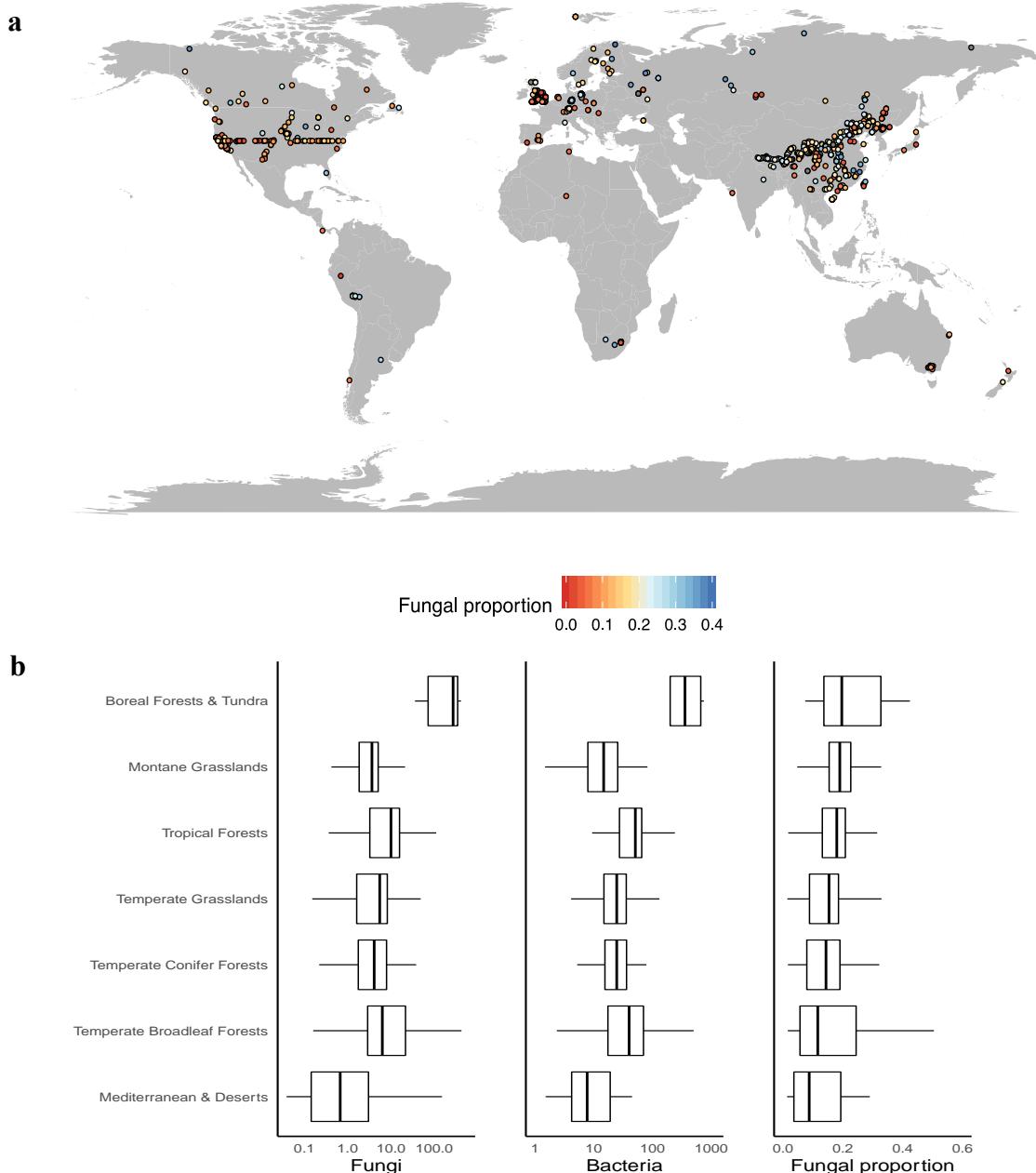
Figure 1. Map of sample locations and fungal and bacterial abundance and fungal

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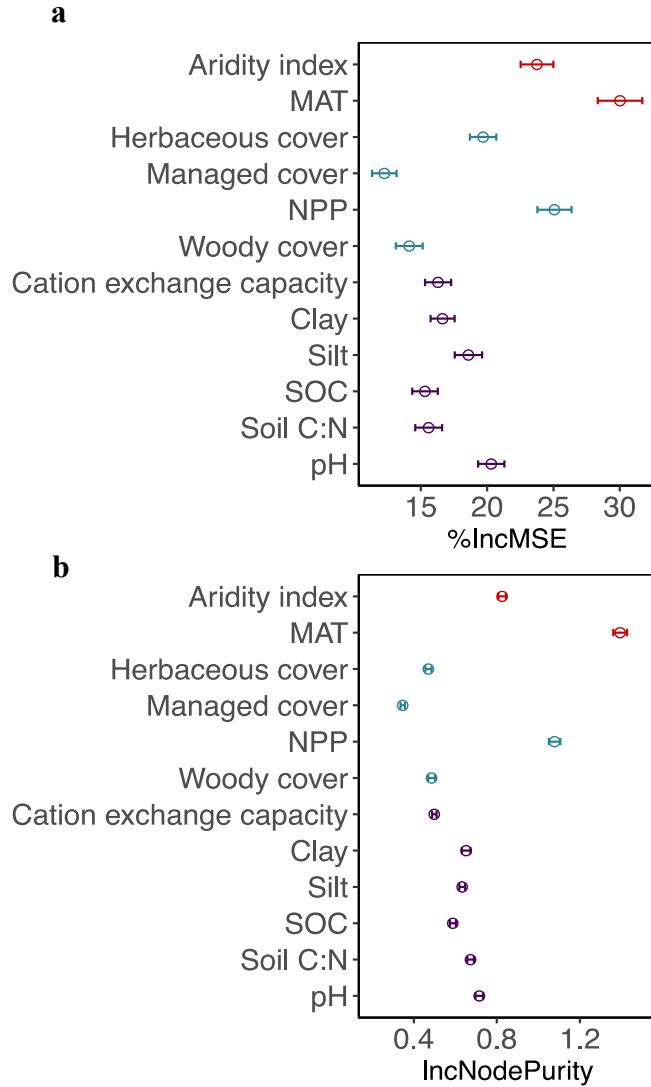
Figure 2. Mean decrease in accuracy (%IncMSE, mean and SD, a) and mean decrease gini (IncNodePurity, mean and SD, b) estimated from 1000 simulations of random forests. This is used to evaluate the importance of top environmental drivers on proportion of fungi derived from 'all' dataset.

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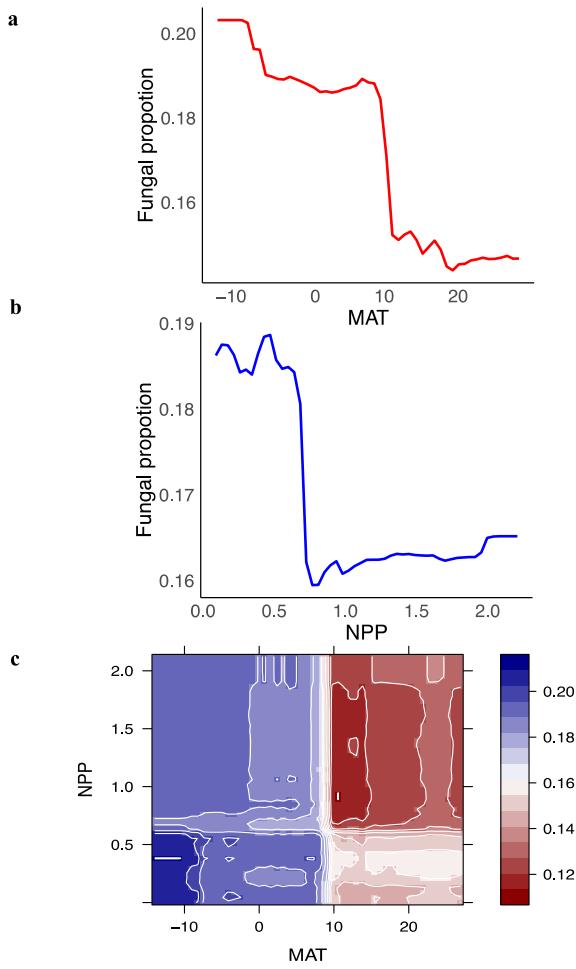
Figure 3. Fungal proportion is primarily associated with climate- mean annual

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

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

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

proportion.

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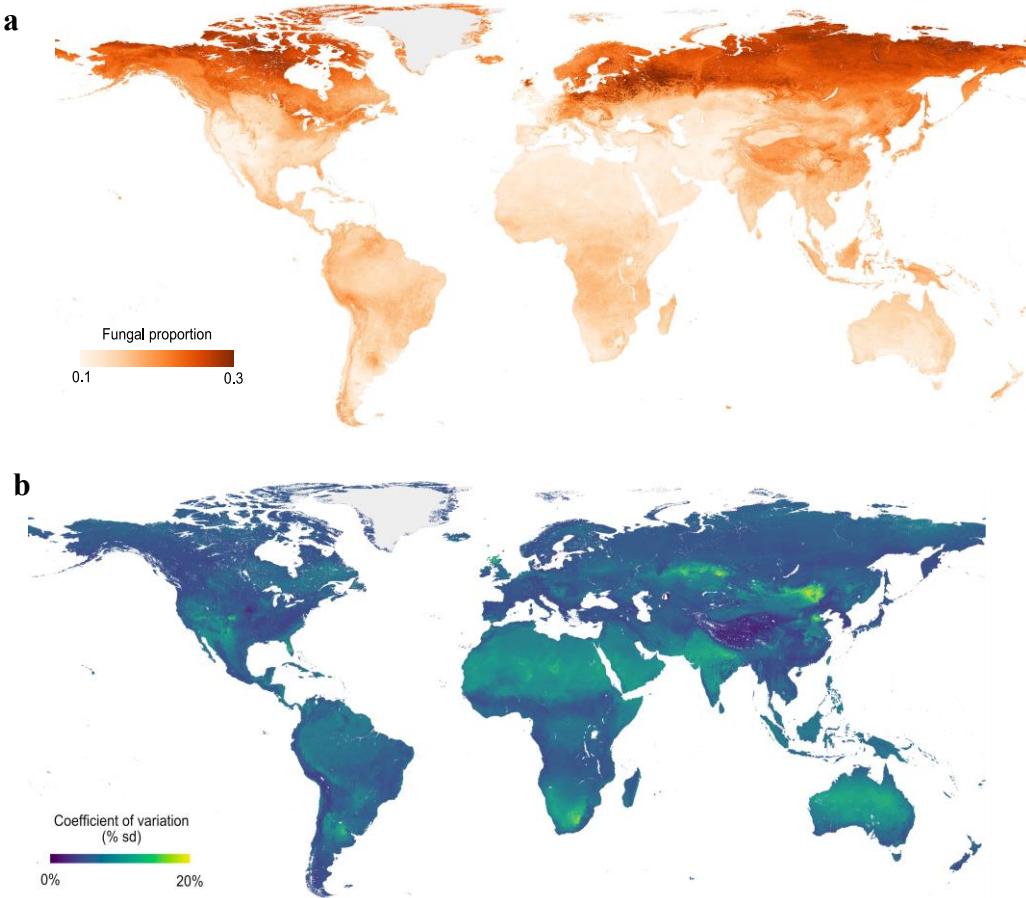
717 **Figure 4.** Global map of fungal proportion (a) and bootstrapped (100 iterations) coefficient

718 of variation (b) at the 30 arcsec (approximately 1 km^2) pixel scale. Bootstrapped coefficient

719 of variation is standard deviation divided by the mean predicted value as a measure of prediction

720 accuracy. Sampling was stratified by biome.

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727 Author contributions

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

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

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

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

732 PLFA datasets.

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