



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

Kailiang Yu¹, Johan van den Hoogen¹, Zhiqiang Wang², Colin Averill¹, Devin Routh¹, Gabriel R. Smith^{3,1}, Rebecca E. Drenovsky⁴, Kate M. Scow⁵, Fei Mo⁶, Mark P Waldrop⁷, Yuanhe Yang^{8,9}, Weize Tang^{9,10},

Franciska T. De Vries¹¹, Richard D. Bardgett¹², Peter Manning¹³, Felipe Bastida¹⁴, Sara G. Baer¹⁵, Elizabeth M. Bach¹⁶, Carlos García¹⁴, Qingkui Wang¹⁷, Linna Ma⁸, Baodong Chen^{18,9}, Xianjing He¹⁹, Sven Teurlincx²⁰, Amber Heijboer^{21,22}, James A. Bradley^{23,24}, Thomas W Crowther¹

Corresponding author: Kailiang Yu (kai86liang@gmail.com); Thomas W Crowther (tom.crowther@usys.ethz.ch)

10 ¹Institute of Integrative Biology, ETH Zürich, Zürich, Switzerland

²Institute for Advanced Study, Chengdu University, Chengdu, China

³Department of Biology, Stanford University, California, USA

⁴Biology Department, John Carroll University, Ohio, USA

⁵Department of Land, Air and Water Resources, University of California, Davis, California, USA

15 ⁶College of Agronomy, Northwest A&F University, Shaanxi, PR China

⁷U.S. Geological Survey. Geology, Minerals, Energy, and Geophysics Science Center. Menlo Park, California, USA
⁸State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, China

⁹University of Chinese Academy of Sciences, Beijing, China

20 ¹⁰Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

¹¹Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, the Netherlands

¹²Department of Earth and Environmental Sciences, University of Manchester, Oxford Road, Manchester, UK

¹³Senckenberg Biodiversity and Climate Research Centre, Frankfurt, Germany

25 14CEBAS-CSIC. Department of Soil and Water Conservation. Campus Universitario de Espinardo, Murcia, Spain.

¹⁵Kansas Biological Survey and Department of Ecology & Evolutionary Biology, University of Kansas, Lawrence, Kansas, USA
¹⁶The Nature Conservancy, Nachusa Grasslands, Franklin Grove, IL, USA

¹⁷Huitong Experimental Station of Forest Ecology, CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Shenyang, PR China

30 ¹⁸State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Beijing, China

¹⁹Key Laboratory of the Three Gorges Reservoir Region's Eco-Environment, Ministry of Education, Chongqing University, Chongqing, China

²⁰Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, Netherlands

35 ²¹Biometris, Wageningen University & Research, Wageningen, Netherlands

²²Ecology and Biodiversity Group, Department of Biology, Institute of Environmental Biology, Utrecht University, Padualaan, Netherlands



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²³School of Geography, Queen Mary University of London, London, E1 4NS, UK

²⁴Interface Geochemistry, GFZ German Research Centre for Geosciences, Potsdam, Germany

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 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 in the top soil surface (>3000 distinct observations of soil fungal and bacterial abundance) to generate the first quantitative and spatially high resolution (1km) 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. Raw datasets and global maps generated in this study are available at

1. Introduction

https://doi.org/10.6084/m9.figshare.19556419 (Yu, 2022).

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 CO₂ 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; Strickland and Rousk, 2010). However, until now, the relative importance of these different environmental drivers remains relatively unclear at global scale,



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and the biogeography of these major functional groups (fungi *vs.* bacteria) has only been demonstrated at local and regional scales. A recent analysis suggested that the relative soil bacterial abundance is high in tropical latitudes and decreases in abundance towards the high-latitude boreal regions, where fungi tend to dominate (Bahram et al., 2018). Translating these broad-scale trends into quantitative, spatially explicit information will be necessary if we intend to represent regional variations in soil community functioning (Wieder et al., 2013, 2015), or predict future changes in terrestrial carbon and nutrient cycling.

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

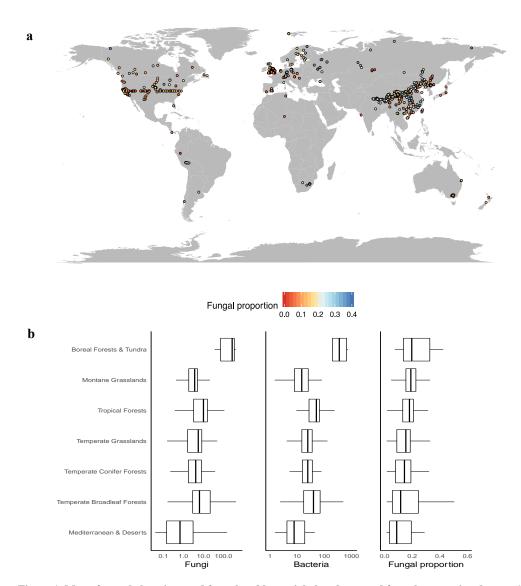


Figure 1. Map of sample locations and fungal and bacterial abundance and fungal proportion data. **a**, Sampling sites. A total of 3224 samples were collected and aggregated into 943 1-km2 pixels that were used for geospatial modelling. **b**, The median and interquartile range of abundance of fungi and bacteria and fungal proportion across vegetation biomes. Tundra and boreal forest, Mediterranean and desert have low sample sizes (<25) and thus were combined.

2. Material and methods

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120 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



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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 (\sim 1-km²) 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 (\sim 1-km²) 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 (\approx 1km 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

Raw datasets and global maps generated in this study are available at https://doi.org/10.6084/m9.figshare.19556419. The code 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 \pm 1SE: 0.23 \pm 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 grassland and managed (agricultural) ecosystems (Fig. S6). This finding is consistent



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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, nonlinear 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.

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

4.2. Drivers of fungal proportion

Globally, the fungal proportion in soil can be predicted by few primary environmental drivers (Fig. 2; Fig. S7). Specifically, mean annual temperature (MAT) and primary productivity (NPP) were strong determinants of fungal dominance. The responses of fungal proportion to both MAT and NPP were strongly non-linear, with warmer, more productive regions of the world (i.e. tropical forest biomes) showing lower dominance of fungi compared to colder, less productive ecosystems (i.e. boreal forest and tundra biomes, Fig. 3; Fig. S8). This pattern is consistent with the idea that fungi and bacteria represent slow vs. fast soil energy channels, respectively (Crowther et al., 2019; Malik et al., 2016), a concept with a long history in soil ecology (Moore et al., 2003; Moore and William Hunt, 1988). This finding is important because it could potentially link the belowground slow – fungi vs fast – bacteria energy channels with aboveground plant slow growth rates – woody plants vs fast growth rates – grasses, while the linkage could be complex, non-linear or even divergent. The fast vs slow concept or spectrum have fundamentally improved the understandings and predictions of land carbon storage across resource gradient or under global change. The faster growth could be typically trade off with higher mortality or heterotrophic respiration with resource enriched conditions (Jiang et al., 2020; Terrer et al., 2021; Yu et al., 2019), thus constraining land carbon storage. This raises the question of how the belowground fast vs slow energy channels and the aboveground fast vs slow growth spectrum could be potentially linked or integrated to assess land carbon storage.



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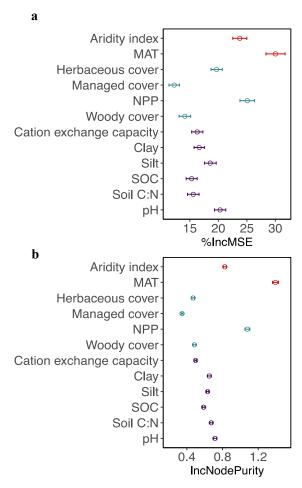


Figure 2. Mean decrease in accuracy (%IncMSE, mean and SD, a) and mean decrease gini (IncNodePurity, mean and SD, b) estimated from 1000 simulations of random forests. This is used to evaluate the importance of top environmental drivers on proportion of fungi derived from 'all' dataset.

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

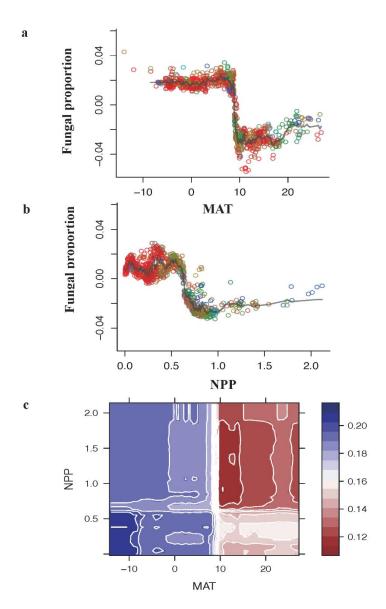


Figure 3. Fungal proportion is primarily associated with climate- mean annual temperature (MAT) and net primary

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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4.3. Biogeographic pattern from the machine learning model

255 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 260 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 265 drylands and/or complex response of fungi and bacteria to water availability (Fierer et al., 2009; Strickland and Rousk, 2010). 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), 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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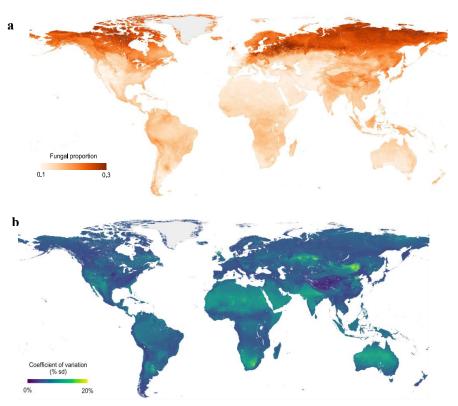


Figure 4. Global map of fungal proportion (a) and bootstrapped (100 iterations) coefficient of variation (b) at the 30 arcsec (approximately 1 km) pixel scale. Bootstrapped coefficient of variation is standard deviation divided by the mean predicted value as a measure of prediction accuracy. Sampling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

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. Tropical vs boreal biomes are hotpots or debated regions with their relative capacity and capability to sequestrate atmospheric CO₂ and mitigate climate change in an increasingly changing climate (Schimel et al., 2015; Tagesson et al., 2020); they are also regions with striking differences of soil microbial composition (fungal proportion), plant communities and soil carbon storge, thus suggesting their potential strong interactions and



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feedbacks in these regions (Bardgett et al., 2008). 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, arbu scular 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 in the top soil surface (>3000 distinct observations of soil fungal and bacterial abundance) to generate the first quantitative and spatially high resolution (1 km) 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 regions and needs of future research endeavors in generating high resolution biogeographic patterns of biomass of each major microbial group, the relative biomass ratios across and within major microbial groups.

Data availability

Raw datasets, R code, and global maps generated in this study are available at 10.6084/m9.figshare.19556419 (Yu et al., 2022). **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.

Competing interests

The authors declare that they have no conflict of interest.

References

Anderegg, L. D. L., Anderegg, W. R. L., Abatzoglou, J., Hausladen, A. M. and Berry, J. A.: Drought characteristics' role in widespread aspen forest mortality across Colorado, USA, Glob. Chang. Biol., 19(5), 1526–1537, doi:10.1111/gcb.12146, 2013.





- Averill, C., Turner, B. L. and Finzi, A. C.: Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage, Nature, 505(7484), doi:10.1038/nature12901, 2014.
- Bahram, M., Hildebrand, F., Forslund, S. K., Anderson, J. L., Soudzilovskaia, N. A., Bodegom, P. M., Bengtsson-Palme, J., Anslan, S., Coelho, L. P., Harend, H., Huerta-Cepas, J., Medema, M. H., Maltz, M. R., Mundra, S., Olsson, P. A., Pent, M., Põlme, S., Sunagawa, S., Ryberg, M., Tedersoo, L. and Bork, P.: Structure and function of the global topsoil microbiome, Nature, 560(7717), 233–237, doi:10.1038/s41586-018-0386-6, 2018.
- Bardgett, R. D. and van der Putten, W. H.: Belowground biodiversity and ecosystem functioning., Nature, 515(7528), 505–11, doi:10.1038/nature13855, 2014.
 - Bardgett, R. D., Freeman, C. and Ostle, N. J.: Microbial contributions to climate change through carbon cycle feedbacks, ISME J., 2(8), doi:10.1038/ismej.2008.58, 2008.
 - Breiman, L.: Random forests, Mach. Learn., 45(1), 5-32, doi:10.1023/A:1010933404324, 2001.
 - Caldwell, B. A.: Enzyme activities as a component of soil biodiversity: A review, in Pedobiologia, vol. 49., 2005.
- 350 Chen, Y. L., Ding, J. Z., Peng, Y. F., Li, F., Yang, G. B., Liu, L., Qin, S. Q., Fang, K. and Yang, Y. H.: Patterns and drivers of soil microbial communities in Tibetan alpine and global terrestrial ecosystems, J. Biogeogr., 43(10), 2027–2039, doi:10.1111/jbi.12806, 2016.
 - Crowther, T. W., van den Hoogen, J., Wan, J., Mayes, M. A., Keiser, A. D., Mo, L., Averill, C. and Maynard, D. S.: The global soil community and its influence on biogeochemistry, Science (80-.)., doi:10.1126/science.aav0550, 2019.
- Delgado-Baquerizo, M., Powell, J. R., Hamonts, K., Reith, F., Mele, P., Brown, M. V., Dennis, P. G., Ferrari, B. C., Fitzgerald, A., Young, A., Singh, B. K. and Bissett, A.: Circular linkages between soil biodiversity, fertility and plant productivity are limited to topsoil at the continental scale, New Phytol., 215(3), doi:10.1111/nph.14634, 2017.
 - Drenovsky, R. E., Steenwerth, K. L., Jackson, L. E. and Scow, K. M.: Land use and climatic factors structure regional patterns in soil microbial communities, Glob. Ecol. Biogeogr., 19(1), 27–39, doi:10.1111/j.1466-8238.2009.00486.x, 2010a.
- Drenovsky, R. E., Steenwerth, K. L., Jackson, L. E. and Scow, K. M.: Land use and climatic factors structure regional patterns in soil microbial communities, Glob. Ecol. Biogeogr., doi:10.1111/j.1466-8238.2009.00486.x, 2010b.
 - Fierer, N., Strickland, M. S., Liptzin, D., Bradford, M. A. and Cleveland, C. C.: Global patterns in belowground communities, Ecol. Lett., 12(11), 1238–1249, doi:10.1111/j.1461-0248.2009.01360.x, 2009.
- Frindte, K., Pape, R., Werner, K., Löffler, J. and Knief, C.: Temperature and soil moisture control microbial community composition in an arctic–alpine ecosystem along elevational and micro-topographic gradients, ISME J., 13(8), doi:10.1038/s41396-019-0409-9, 2019.
 - Frostegård, Å., Tunlid, A. and Bååth, E.: Use and misuse of PLFA measurements in soils, Soil Biol. Biochem., doi:10.1016/j.soilbio.2010.11.021, 2011.
- Glassman, S. I., Weihe, C., Li, J., Albright, M. B. N., Looby, C. I., Martiny, A. C., Treseder, K. K., Allison, S. D. and Martiny, J.
 B. H.: Decomposition responses to climate depend on microbial community composition, Proc. Natl. Acad. Sci. U. S. A., doi:10.1073/pnas.1811269115, 2018.
 - He, L., Mazza Rodrigues, J. L., Soudzilovskaia, N. A., Barceló, M., Olsson, P. A., Song, C., Tedersoo, L., Yuan, F., Lipson, D. A. and Xu, X.: Global biogeography of fungal and bacterial biomass carbon in topsoil, Soil Biol. Biochem., 151, doi:10.1016/j.soilbio.2020.108024, 2020.
- Van Der Heijden, M. G. A., Bardgett, R. D. and Van Straalen, N. M.: The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems, Ecol. Lett., doi:10.1111/j.1461-0248.2007.01139.x, 2008.
 - van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D. A., de Goede, R. G. M., Adams, B. J.,





- Ahmad, W., Andriuzzi, W. S., Bardgett, R. D., Bonkowski, M., Campos-Herrera, R., Cares, J. E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S. R., Creamer, R., Mauro da Cunha Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.
- S., Gutiérrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A. A., Li, Q., Liang, W., Magilton, M., Marais, M., Martín, J. A. R., Matveeva, E., Mayad, E. H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T. A. D., Nielsen, U. N., Okada, H., Rius, J. E. P., Pan, K., Peneva, V., Pellissier, L., Carlos Pereira da Silva, J., Pitteloud, C., Powers, T. O., Powers, K., Quist, C. W., Rasmann, S., Moreno, S. S., Scheu, S., Setälä, H., Sushchuk, A., Tiunov, A. V., Trap, J., van der Putten, W., Vestergård, M., Villenave, C., Waeyenberge, L., Wall, D. H., Wilschut, R.,
- Wright, D. G., Yang, J. and Crowther, T. W.: Soil nematode abundance and functional group composition at a global scale, Nature, doi:10.1038/s41586-019-1418-6, 2019.
 - Jangid, K., Williams, M. A., Franzluebbers, A. J., Schmidt, T. M., Coleman, D. C. and Whitman, W. B.: Land-use history has a stronger impact on soil microbial community composition than aboveground vegetation and soil properties, Soil Biol. Biochem., 43(10), 2184–2193, doi:10.1016/j.soilbio.2011.06.022, 2011.
- 390 Jenny, H.: Factors of Soil Formation, Soil Sci., doi:10.1097/00010694-194111000-00009, 1941.
 - Jiang, M., Medlyn, B. E., Drake, J. E., Duursma, R. A., Anderson, I. C., Barton, C. V. M., Boer, M. M., Carrillo, Y., Castañeda-Gómez, L., Collins, L., Crous, K. Y., De Kauwe, M. G., dos Santos, B. M., Emmerson, K. M., Facey, S. L., Gherlenda, A. N., Gimeno, T. E., Hasegawa, S., Johnson, S. N., Kännaste, A., Macdonald, C. A., Mahmud, K., Moore, B. D., Nazaries, L., Neilson, E. H. J., Nielsen, U. N., Niinemets, Ü., Noh, N. J., Ochoa-Hueso, R., Pathare, V. S., Pendall, E., Pihlblad, J.,
- Piñeiro, J., Powell, J. R., Power, S. A., Reich, P. B., Renchon, A. A., Riegler, M., Rinnan, R., Rymer, P. D., Salomón, R. L., Singh, B. K., Smith, B., Tjoelker, M. G., Walker, J. K. M., Wujeska-Klause, A., Yang, J., Zaehle, S. and Ellsworth, D. S.: The fate of carbon in a mature forest under carbon dioxide enrichment, Nature, 580(7802), doi:10.1038/s41586-020-2128-9, 2020.
- Klamer, M. and Bååth, E.: Estimation of conversion factors for fungal biomass determination in compost using ergosterol and PLFA 18:2ω6,9, Soil Biol. Biochem., 36(1), doi:10.1016/j.soilbio.2003.08.019, 2004.
 - Lavahun, M. F. E., Joergensen, R. G. and Meyer, B.: Activity and biomass of soil microorganisms at different depths, Biol. Fertil. Soils, 23(1), doi:10.1007/BF00335816, 1996.
 - Liang, C., Amelung, W., Lehmann, J. and Kästner, M.: Quantitative assessment of microbial necromass contribution to soil organic matter, Glob. Chang. Biol., 25(11), doi:10.1111/gcb.14781, 2019.
- 405 Locey, K. J. and Lennon, J. T.: Scaling laws predict global microbial diversity, Proc. Natl. Acad. Sci. U. S. A., doi:10.1073/pnas.1521291113, 2016.
 - Malik, A. A., Chowdhury, S., Schlager, V., Oliver, A., Puissant, J., Vazquez, P. G. M., Jehmlich, N., von Bergen, M., Griffiths, R. I. and Gleixner, G.: Soil fungal: Bacterial ratios are linked to altered carbon cycling, Front. Microbiol., 7(AUG), doi:10.3389/fmicb.2016.01247, 2016.
- 410 Moore, J. C. and William Hunt, H.: Resource compartmentation and the stability of real ecosystems, Nature, doi:10.1038/333261a0, 1988.
 - Moore, J. C., McCann, K., Setälä, H. and De Ruiter, P. C.: Top-down is bottom-up: Does predation in the rhizosphere regulate aboveground dynamics?, Ecology, doi:10.1890/0012-9658(2003)084[0846:TIBDPI]2.0.CO;2, 2003.
 - Romero-Olivares, A. L., Allison, S. D. and Treseder, K. K.: Soil microbes and their response to experimental warming over time: A meta-analysis of field studies, Soil Biol. Biochem., doi:10.1016/j.soilbio.2016.12.026, 2017.
 - Rousk, J. and Bååth, E.: Fungal biomass production and turnover in soil estimated using the acetate-in-ergosterol technique, Soil Biol. Biochem., 39(8), 2173–2177, doi:10.1016/j.soilbio.2007.03.023, 2007.



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- Rousk, J., Brookes, P. C. and Bååth, E.: Contrasting soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization, Appl. Environ. Microbiol., 75(6), 1589–1596, doi:10.1128/AEM.02775-08, 2009.
- Rousk, J., Bååth, E., Brookes, P. C., Lauber, C. L., Lozupone, C., Caporaso, J. G., Knight, R. and Fierer, N.: Soil bacterial and fungal communities across a pH gradient in an arable soil, ISME J., 4(10), 1340–1351, doi:10.1038/ismej.2010.58, 2010.
 - Sanderman, J., Hengl, T. and Fiske, G. J.: Soil carbon debt of 12,000 years of human land use, Proc. Natl. Acad. Sci. U. S. A., 114(36), doi:10.1073/pnas.1706103114, 2017.
 - Schimel, D., Stephens, B. B. and Fisher, J. B.: Effect of increasing CO2 on the terrestrial carbon cycle, Proc. Natl. Acad. Sci. U. S. A., doi:10.1073/pnas.1407302112, 2015.
 - Sengupta, A., Fansler, S. J., Chu, R. K., Danczak, R. E., Garayburu-Caruso, V. A., Renteria, L., Song, H. S., Toyoda, J., Wells, J. and Stegen, J. C.: Disturbance triggers non-linear microbe-environment feedbacks, Biogeosciences, 18(16), doi:10.5194/bg-18-4773-2021, 2021.
 - Shi, Z., Crowell, S., Luo, Y. and Moore, B.: Model structures amplify uncertainty in predicted soil carbon responses to climate change, Nat. Commun., doi:10.1038/s41467-018-04526-9, 2018.
 - Six, J., Frey, S. D., Thiet, R. K. and Batten, K. M.: Bacterial and Fungal Contributions to Carbon Sequestration in Agroecosystems, Soil Sci. Soc. Am. J., 70(2), 555, doi:10.2136/sssaj2004.0347, 2006.
 - Soares, M. and Rousk, J.: Microbial growth and carbon use efficiency in soil: Links to fungal-bacterial dominance, SOC-quality and stoichiometry, Soil Biol. Biochem., doi:10.1016/j.soilbio.2019.01.010, 2019.
- Strickland, M. S. and Rousk, J.: Considering fungal: Bacterial dominance in soils Methods, controls, and ecosystem implications, Soil Biol. Biochem., doi:10.1016/j.soilbio.2010.05.007, 2010.
 - Sulman, B. N., Phillips, R. P., Oishi, A. C., Shevliakova, E. and Pacala, S. W.: Microbe-driven turnover offsets mineral-mediated storage of soil carbon under elevated CO 2, Nat. Clim. Chang., doi:10.1038/nclimate2436, 2014.
- Tagesson, T., Schurgers, G., Horion, S., Ciais, P., Tian, F., Brandt, M., Ahlström, A., Wigneron, J. P., Ardö, J., Olin, S., Fan, L.,
 Wu, Z. and Fensholt, R.: Recent divergence in the contributions of tropical and boreal forests to the terrestrial carbon sink,
 Nat. Ecol. Evol., doi:10.1038/s41559-019-1090-0, 2020.
 - Tedersoo, L., Bahram, M., Põlme, S., Kõljalg, U., Yorou, N. S., Wijesundera, R., Ruiz, L. V., Vasco-Palacios, A. M., Thu, P. Q., Suija, A., Smith, M. E., Sharp, C., Saluveer, E., Saitta, A., Rosas, M., Riit, T., Ratkowsky, D., Pritsch, K., Põldmaa, K., Piepenbring, M., Phosri, C., Peterson, M., Parts, K., Pärtel, K., Otsing, E., Nouhra, E., Njouonkou, A. L., Nilsson, R. H.,
- Morgado, L. N., Mayor, J., May, T. W., Majuakim, L., Lodge, D. J., Lee, S., Larsson, K. H., Kohout, P., Hosaka, K., Hiiesalu, I., Henkel, T. W., Harend, H., Guo, L. D., Greslebin, A., Grelet, G., Geml, J., Gates, G., Dunstan, W., Dunk, C., Drenkhan, R., Dearnaley, J., De Kesel, A., Dang, T., Chen, X., Buegger, F., Brearley, F. Q., Bonito, G., Anslan, S., Abell, S. and Abarenkov, K.: Global diversity and geography of soil fungi, Science (80-.)., 346(6213), doi:10.1126/science.1256688, 2014.
- Terrer, C., Phillips, R. P., Hungate, B. A., Rosende, J., Pett-Ridge, J., Craig, M. E., van Groenigen, K. J., Keenan, T. F., Sulman, B. N., Stocker, B. D., Reich, P. B., Pellegrini, A. F. A., Pendall, E., Zhang, H., Evans, R. D., Carrillo, Y., Fisher, J. B., Van Sundert, K., Vicca, S. and Jackson, R. B.: A trade-off between plant and soil carbon storage under elevated CO2, Nature, 591(7851), doi:10.1038/s41586-021-03306-8, 2021.
- de Vries, F. T., Manning, P., Tallowin, J. R. B., Mortimer, S. R., Pilgrim, E. S., Harrison, K. A., Hobbs, P. J., Quirk, H., Shipley,
 B., Cornelissen, J. H. C., Kattge, J. and Bardgett, R. D.: Abiotic drivers and plant traits explain landscape-scale patterns in
 soil microbial communities, Ecol. Lett., 15(11), 1230–1239, doi:10.1111/j.1461-0248.2012.01844.x, 2012.
 - Waldrop, M. P., Holloway, J. M., Smith, D. B., Goldhaber, M. B., Drenovsky, R. E., Scow, K. M., Dick, R., Howard, D., Wylie,



470

475



- B. and Grace, J. B.: The interacting roles of climate, soils, and plant production on soil microbial communities at a continental scale, Ecology, doi:10.1002/ecy.1883, 2017.
- Wang, Q., Liu, S. and Tian, P.: Carbon quality and soil microbial property control the latitudinal pattern in temperature sensitivity of soil microbial respiration across Chinese forest ecosystems, Glob. Chang. Biol., doi:10.1111/gcb.14105, 2018.
 - Waring, B. G., Averill, C. and Hawkes, C. V.: Differences in fungal and bacterial physiology alter soil carbon and nitrogen cycling: Insights from meta-analysis and theoretical models, Ecol. Lett., 16(7), 887–894, doi:10.1111/ele.12125, 2013.
 - Wieder, W. R., Bonan, G. B. and Allison, S. D.: Global soil carbon projections are improved by modelling microbial processes, Nat. Clim. Chang., 3(10), 909–912, doi:10.1038/nclimate1951, 2013.
 - Wieder, W. R., Allison, S. D., Davidson, E. A., Georgiou, K., Hararuk, O., He, Y., Hopkins, F., Luo, Y., Smith, M. J., Sulman, B., Todd-Brown, K., Wang, Y. P., Xia, J. and Xu, X.: Explicitly representing soil microbial processes in Earth system models, Global Biogeochem. Cycles, 29(10), 1782–1800, doi:10.1002/2015GB005188, 2015.
 - Yu, K. A global map of relative abundance of soil fungi and bacteria in top surface soil, doi: 10.6084/m9.figshare.19556419, 2022.
 - Yu, K. and D'Odorico, P.: Hydraulic lift as a determinant of tree-grass coexistence on savannas, New Phytol., 207(4), 1038–1051, doi:10.1111/nph.13431, 2015.
 - Yu, K., Smith, W. K., Trugman, A. T., Condit, R., Hubbell, S. P., Sardans, J., Peng, C., Zhu, K., Peñuelas, J., Cailleret, M., Levanic, T., Gessler, A., Schaub, M., Ferretti, M. and Anderegg, W. R. L.: Pervasive decreases in living vegetation carbon turnover time across forest climate zones, Proc. Natl. Acad. Sci. U. S. A., doi:10.1073/pnas.1821387116, 2019.
 - Yue, H., Wang, M., Wang, S., Gilbert, J. A., Sun, X., Wu, L., Lin, Q., Hu, Y., Li, X., He, Z., Zhou, J. and Yang, Y.: The microbe-mediated mechanisms affecting topsoil carbon stock in Tibetan grasslands, ISME J., 9(9), doi:10.1038/ismej.2015.19, 2015.
- Zhu, Q., Riley, W. J. and Tang, J.: A new theory of plant-microbe nutrient competition resolves inconsistencies between observations and model predictions, Ecol. Appl., 27(3), doi:10.1002/eap.1490, 2017.