

Negative Linear or Unimodal: Why Forest Soil Fungal Latitudinal Diversity Differs across China

[Wenchen Song](https://orcid.org/0000-0002-7046-7488)a,b

AMERICAN SOCIETY FOR MICROBIOLOGY

aKey Laboratory of Ecology and Environment in Minority Areas (Minzu University of China), National Ethnic Affairs Commission, Beijing, China bCollege of Life and Environmental Sciences, Minzu University of China, Beijing, China

ABSTRACT To identify the reasons for the inconsistency in patterns of latitudinal gradients of forest soil fungal biodiversity in China, a reanalysis of data was performed. Causes are linked to the different environments of continents and islands and the inconsistency between different classification standards. The following three suggestions are made for future studies: sites on the mainland and islands should be distinguished in these types of studies, the Shannon index should be used to represent fungal diversity instead of operational taxonomic unit (OTU) richness, and using the diversity of higher taxa (such as family level) instead of OTU level represents a potential proxy for species-level diversity.

Microbiology
Spectrum

IMPORTANCE Latitudinal gradients of forest soil fungal biodiversity in China have been previously investigated; however, the results of these studies were inconsistent. In the present study, I reanalyzed the data from these studies on all forest types in China and showed that the differences in forest soil fungal latitudinal diversity were caused by the different environments of continents and islands, as well as by the inconsistency between different classification standards. Accordingly, three suggestions were outlined for future studies on this and similar topics. This study makes a significant contribution to the literature because these findings can be used to improve our understanding of the forest soil fungal latitudinal diversity and as a basis for future studies.

KEYWORDS forest, soil fungal diversity, fungal latitudinal diversity, fungi in China

Latitudinal gradients of forest soil fungal biodiversity have attracted considerable interest from ecologists [\(1\)](#page-2-0). China covers a vast territory with a large latitudinal gradient from tropical to boreal forests. It is a key area in fungal ecogeography. Until recently, there have been six studies on the variation in fungal biodiversity of forest soils across latitudinal gradients in sites of all forest types in China [\(Table 1](#page-1-0)). However, the latitudinal patterns observed in these studies are different. Some studies suggest that soil fungi in forest ecosystems follow a similar universal latitudinal trend, as latitudinal changes in temperature are often associated with variations in plant productivity and biodiversity and, thus, may support a higher abundance of soil fungi [\(2](#page-2-1)–[5\)](#page-2-2). The strongest evidence supporting these studies is that soil fungal richness is negatively correlated across latitudinal gradients globally [\(6](#page-2-3)). However, other studies disagree with this view because they found a unimodal trend, with fungal diversity peaking around 40°N in China [\(7](#page-3-0)[–](#page-3-1)[9](#page-3-2)) and in the range of 20°N to 50°N in the northern hemisphere [\(6,](#page-2-3) [7](#page-3-0)). The reason for this is that soil fungal diversity is strongly affected by community structure, soil nutrients, and plant-soil interactions, and the combination of these factors results in a unimodal pattern of forest soil fungal latitudinal diversity [\(7](#page-3-0)[–](#page-3-1)[9\)](#page-3-2). Why are these results different? Here, I attempt to answer this question.

It is noteworthy that all studies in which negative linear patterns were observed had stations on Hainan Island [\(Table 1](#page-1-0)) [\(3](#page-2-4)[–](#page-2-5)[5,](#page-2-2) [7](#page-3-0)[–](#page-3-1)[9](#page-3-2)). If the data collected on Hainan Island were deleted, the trends would change into a unimodal trend owing to the high fungal richness on Hainan Island [\(Fig. 1A](#page-1-1) to [C](#page-1-1)). In fact, the environments of continents and islands at the same latitude are quite different, as is the forest soil. Nonmetric multidimensional Editor Erik F. Y. Hom, University of Mississippi Copyright © 2023 Song. This is an openaccess article distributed under the terms of the [Creative Commons Attribution 4.0](https://creativecommons.org/licenses/by/4.0/) [International license](https://creativecommons.org/licenses/by/4.0/).

Address correspondence to songw@muc.edu.cn. The author declares no conflict of interest. Received 1 July 2022 Accepted 31 January 2023 Published 22 February 2023

Reference	No. of sites	Diversity index	Latitudinal pattern	R^2	P value
8	10	Richness	Unimodal	0.764	< 0.05
		Shannon index	Unimodal	0.456	< 0.05
5	6	Richness	Negative linear	0.648	0.001
3	40	Richness	Negative linear	0.015	< 0.001
		Shannon index	Unimodal	0.179	< 0.001
		Simpson index	Negative linear	0.143	< 0.001
7	28	Richness	Unimodal	0.17	< 0.01
$\overline{4}$	26	Richness	Negative linear	0.22	< 0.001
9	33	Shannon index	Unimodal	0.625	< 0.001

TABLE 1 Results of six studies on the variation in fungal biodiversity of forest soils across latitudinal gradients in sites of all forest types across China^a

^aOnly significant results are listed.

scaling (NMDS) and principal-coordinate analysis (PCA) showed that the points on Hainan Island were more discrete than those on the other stations [\(3](#page-2-4)[–](#page-2-5)[5](#page-2-2)); this showed that the island environment different from the mainland affects the soil fungal community [\(10,](#page-3-3) [11](#page-3-4)). The soil P content of forests on Hainan Island is higher than that of the continental forests at the same latitude, and C, N, P, and their ratios exhibit large spatial variations on the island [\(12\)](#page-3-5). Nutrient-abundant soil improves microbial nutrition and the competitive advantage of fungi, thus increasing soil fungal richness [\(13,](#page-3-6) [14\)](#page-3-7). The diverse habitats with large spatial variations in soil nutrition were also found to be beneficial for soil fungal richness [\(15\)](#page-3-8). The higher fungal richness on Hainan Island increases the inclination of the trend line and decreases the fungal richness with increasing latitude.

The different categorizations may also result in different results of fungal latitudinal diversity in China. Currently, microbial diversity is mainly calculated using operational taxonomic units (OTUs) based on gene similarity because only a fraction of the global species pool is currently known [\(16](#page-3-9)). For this reason, the fungal diversity determined using different

FIG 1 Relationships between latitude and soil fungal richness. Based on data from references [3](#page-2-4) (A), [5](#page-2-2) (B), and [4](#page-2-5) (C). HN refers to samples from Hainan Island. Relationships between latitude and soil fungal Shannon index. Based on data from references [3](#page-2-4) (D), [5](#page-2-2) (E), and [4](#page-2-5) (F).

criteria shows different latitudinal patterns. In general, ACE and Chao1 richness are frequently used in microbiological studies. However, to study the theory of ecological geography, all six studies have adopted OTU richness or Shannon/Simpson diversity, which are more suitable for large-scale ecological research ([3](#page-2-4)–[9\)](#page-3-2). Notably, the studies that show unimodal patterns in the Shannon index also showed unimodal patterns in fungal richness [\(7](#page-3-0)[–](#page-3-1)[9](#page-3-2)); however, the studies that showed negative linear patterns in richness showed unimodal patterns in the Shannon index [\(Fig. 1D](#page-1-1) to [F\)](#page-1-1). In addition, the studies that showed negative linear patterns in richness also showed unimodal patterns in Pielou's evenness index, which can be used to measure the evenness of fungal communities (see Fig. S1 in the supplemental material). Since Shannon diversity is contributed to by both richness and evenness, OTU richness cannot reveal the role of evenness, which may lead to differences if evenness is ignored [\(17,](#page-3-10) [18](#page-3-11)). Furthermore, the family-OTU correlation of the Shannon index values is better than that of the richness values (Fig. S2). This correlation is similar to the family-species correlation of global terrestrial animal taxa, and it shows that the consistency of the Shannon index in different classification scales is better than the consistency of fungal richness [\(19\)](#page-3-12). The Shannon index is a function of entropy, which has thermodynamic significance; it can thus better reflect the thermal change caused by latitude ([20\)](#page-3-13). Therefore, the fungal latitudinal diversity pattern in China is similar according to the Shannon index but different according to fungal richness.

In conclusion, differences in the results of forest soil fungal latitudinal diversity are caused by the different environments of continents and islands, as well as by the inconsistency between different classification standards. Accordingly, I propose the following three suggestions for future studies of forest soil fungal latitudinal diversity: (i) sites on the mainland and sites on islands should be distinguished in these types of studies, (ii) the Shannon index should be used to represent fungal diversity instead of richness, and (iii) using the diversity of higher taxa (such as family level), instead of OTU level, represents a potential proxy for species-level diversity. Only in these ways can we better describe and understand the forest soil fungal latitudinal diversity in future studies.

Data availability. The data have been published in references [3](#page-2-4) to [5](#page-2-2) and [7](#page-3-0) to [9.](#page-3-2)

SUPPLEMENTAL MATERIAL

Supplemental material is available online only. SUPPLEMENTAL FILE 1, PDF file, 0.2 MB.

ACKNOWLEDGMENTS

This study was sponsored by the Key Laboratory of Ecology and Environment in Minority Areas (Minzu University of China) and the National Ethnic Affairs Commission (10301-2021000302).

I declare no conflicts of interest.

W. Song developed the ideas and designed the experimental plans, performed the experiments, analyzed the data, and wrote the manuscript.

REFERENCES

- 1. Xu XF, Wang NN, Lipson D, Sinsabaugh R, Schimel J, He LY, Soudzilovskaia NA, Tedersoo L. 2020. Microbial macroecology: in search of mechanisms governing microbial biogeographic patterns. Global Ecol Biogeogr 29: 1870–1886. <https://doi.org/10.1111/geb.13162>.
- 2. Bahram M, Hildebrand F, Forslund SK, Anderson JL, Soudzilovskaia NA, Bodegom PM, Bengtsson-Palme J, Anslan S, Coelho LP, Harend H, Huerta-Cepas J, Medema MH, Maltz MR, Mundra S, Olsson PA, Pent M, Põlme S, Sunagawa S, Ryberg M, Tedersoo L, Bork P. 2018. Structure and function of the global topsoil microbiome. Nature 560:233–237. <https://doi.org/10.1038/s41586-018-0386-6>.
- 3. Hu Y, Veresoglou SD, Tedersoo L, Xu T, Ge T, Liu L, Chen Y, Hao Z, Su Y, Rillig MC, Chen BD. 2019. Contrasting latitudinal diversity and co-occurrence patterns of soil fungi and plants in forest ecosystems. Soil Biol Biochem 131: 100–110. [https://doi.org/10.1016/j.soilbio.2019.01.001.](https://doi.org/10.1016/j.soilbio.2019.01.001)
- 4. Liu S, Wang H, Tian P, Yao X, Sun H, Wang Q, Delgado-Baquerizo M. 2020. Decoupled diversity patterns in bacteria and fungi across continental forest

ecosystems. Soil Biol Biochem 144:107763. [https://doi.org/10.1016/j.soilbio.2020](https://doi.org/10.1016/j.soilbio.2020.107763) [.107763](https://doi.org/10.1016/j.soilbio.2020.107763).

- 5. Huang Y, Zhang X, Fu S, Zhang W. 2019. Environmental filtering drives local soil fungal beta diversity more than dispersal limitation in six forest types along a latitudinal gradient in eastern China. Forests 10:863. [https://](https://doi.org/10.3390/f10100863) doi.org/10.3390/f10100863.
- 6. Tedersoo L, Bahram M, Põlme S, Kõljalg U, Yorou NS, Wijesundera R, Villarreal Ruiz L, Vasco-Palacios AM, Thu PQ, Suija A, Smith ME, 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 AL, Nilsson RH, Morgado LN, Mayor J, May TW, Majuakim L, Lodge DJ, Lee SS, Larsson K-H, Kohout P, Hosaka K, Hiiesalu I, Henkel TW, Harend H, Guo L-d, Greslebin A, Grelet G, Geml J, Gates G, Dunstan W, Dunk C, Drenkhan R, Dearnaley J, De Kesel A, et al. 2014. Global diversity and geography of soil fungi. Science 346:1256688. [https://doi.org/10.1126/science.1256688.](https://doi.org/10.1126/science.1256688)
- 7. Wang P, Chen Y, Sun Y, Tan S, Zhang S, Wang Z, Zhou J, Zhang G, Shu W, Luo C, Kuang J. 2019. Distinct biogeography of different fungal guilds and their associations with plant species richness in forest ecosystems. Front Ecol Evol 7:216. [https://doi.org/10.3389/fevo.2019.00216.](https://doi.org/10.3389/fevo.2019.00216)
- 8. Shi LL, Mortimer PE, Ferry Slik JW, Zou XM, Xu J, Feng WT, Qiao L. 2014. Variation in forest soil fungal diversity along a latitudinal gradient. Fungal Divers 64:305–315. [https://doi.org/10.1007/s13225-013-0270-5.](https://doi.org/10.1007/s13225-013-0270-5)
- 9. Song W, Zhou Y. 2021. Linking leaf $\delta^{15}N$ and $\delta^{13}C$ with soil fungal biodiversity, ectomycorrhizal and plant pathogenic abundance in forest ecosystems of China. Catena 200:105176. [https://doi.org/10.1016/j.catena.2021.105176.](https://doi.org/10.1016/j.catena.2021.105176)
- 10. Tan H, Yu Y, Tang J, Liu T, Miao R, Huang Z, Martin FM, Peng W. 2021. Build your own mushroom soil: microbiota succession and nutritional accumulation in semi-synthetic substratum drive the fructification of a soil-saprotrophic morel. Front Microbiol 12:656656. [https://doi.org/10.3389/](https://doi.org/10.3389/fmicb.2021.656656) [fmicb.2021.656656](https://doi.org/10.3389/fmicb.2021.656656).
- 11. Zhu ZX, Nizamani MM, Harris AJ, Wang HF. 2021. Anthropogenic factors are stronger drivers of patterns of endemic plant diversity on Hainan Island of China than natural environmental factors. PLoS One 16:e0257575. [https://](https://doi.org/10.1371/journal.pone.0257575) [doi.org/10.1371/journal.pone.0257575.](https://doi.org/10.1371/journal.pone.0257575)
- 12. Hui DF, Yang XT, Deng Q, Liu Q, Wang X, Yang H, Ren H. 2021. Soil C:N:P stoichiometry in tropical forests on Hainan Island of China: spatial and vertical variations. Catena 201:105228. 2021 [https://doi.org/10.1016/j.catena](https://doi.org/10.1016/j.catena.2021.105228) [.2021.105228](https://doi.org/10.1016/j.catena.2021.105228).
- 13. Ma SH, Chen GP, Tian D, Du EZ, Xiao W, Jiang L, Zhou Z, Zhu JL, He HB, Zhu B, Fang JY. 2020. Effects of seven-year nitrogen and phosphorus additions on soil microbial community structures and residues in a tropical forest in Hainan Island, China. Geoderma 361:114034. [https://doi.org/10.1016/j.geoderma](https://doi.org/10.1016/j.geoderma.2019.114034) [.2019.114034](https://doi.org/10.1016/j.geoderma.2019.114034).
- 14. Zheng L, Song W. 2022. Phosphorus limitation of trees influences forest soil fungal diversity in China. Forests 13:223. <https://doi.org/10.3390/f13020223>.
- 15. Tecon R, Or D. 2017. Biophysical processes supporting the diversity of microbial life in soil. FEMS Microbiol Rev 41:599–623. [https://doi.org/10.1093/](https://doi.org/10.1093/femsre/fux039) [femsre/fux039.](https://doi.org/10.1093/femsre/fux039)
- 16. Balasundaram SV, Engh IB, Skrede I, Kauserud H. 2015. How many DNA markers are needed to reveal cryptic fungal species? Fungal Biol 119:940–945. <https://doi.org/10.1016/j.funbio.2015.07.006>.
- 17. Tan H, Liu T, Yu Y, Tang J, Jiang L, Martin FM, Peng W. 2021. Morel production related to soil microbial diversity and evenness. Microbiol Spectr 9:e00229-21. <https://doi.org/10.1128/Spectrum.00229-21>.
- 18. Tuomisto H. 2012. An updated consumer's guide to evenness and related indices. Oikos 121:1203–1218. <https://doi.org/10.1111/j.1600-0706.2011.19897.x>.
- 19. Zou Y, Werf W, Liu Y, Axmacher JC. 2020. Predictability of species diversity by family diversity across global terrestrial animal taxa. Global Ecol Biogeogr 29:629–644. <https://doi.org/10.1111/geb.13043>.
- 20. Altieri L, Cocchi D, Roli G. 2018. A new approach to spatial entropy measures. Environ Ecol Stat 25:95–110. <https://doi.org/10.1007/s10651-017-0383-1>.