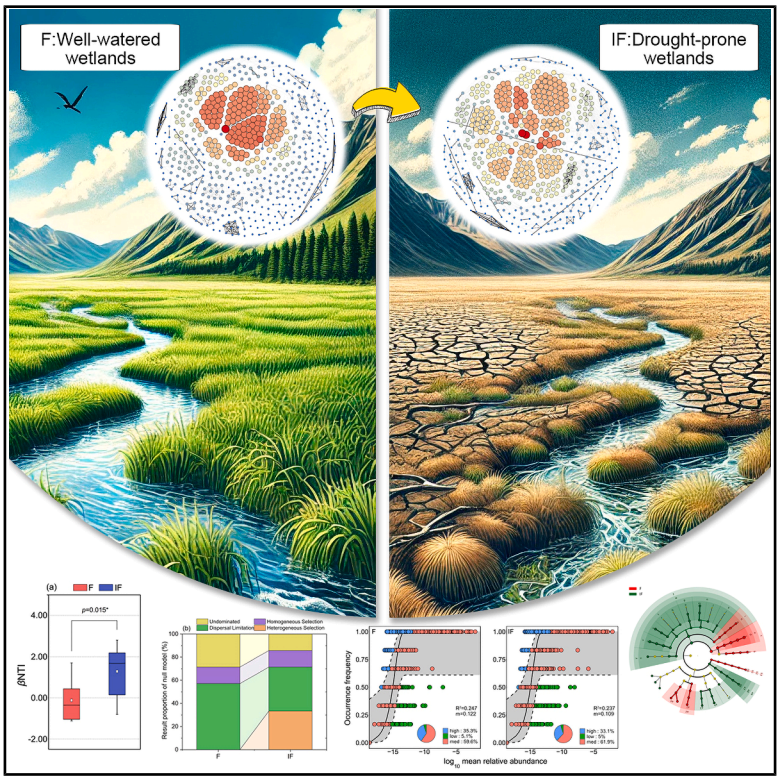
iScience

Article

Microbial community diversity and assembly processes in the aridification of wetlands on the Qinghai-Tibet Plateau

Graphical abstract



Authors

Kang Di, Chen Yuanyuan, Feng Shishi, Liu Qianmin, Zou Shuzhen

Correspondence

kangyuyao@foxmail.com

In brief

Environmental science; Aquatic science; Microbiology; Aquatic biology

Highlights

- Wetland drying reorganizes microbial phyla without affecting α diversity
- Wetland drying increases the sensitivity of bacterial β diversity to environmental distances
- Aridification boosts microbial network modularity and complexity
- Community assembly shifts from neutral to partially deterministic processes

Di et al., 2025, iScience *28*, 112494
May 16, 2025
https://doi.org/10.1016/j.isci.2025.112494

CellPress

iScience

CellPress
OPEN ACCESS

Article

Microbial community diversity and assembly processes in the aridification of wetlands on the Qinghai-Tibet Plateau

Kang Di,[1,2,3,*] Chen Yuanyuan,[1] Feng Shishi,[1] Liu Qianmin,[1] and Zou Shuzhen[1,2]
[1]Key Laboratory of Southwest China Wildlife Resources Conservation (Ministry of Education), China West Normal University, Nanchong 637009, China
[2]Key Laboratory of Environmental Science and Biodiversity Conservation (Sichuan Province), China West Normal University, Nanchong 637009, China
[3]Lead contact
*Correspondence: kangyuyao@foxmail.com
https://doi.org/10.1016/j.isci.2025.112494

SUMMARY

This study investigates soil microbial community dynamics in high-altitude wetlands on the Qinghai-Tibet Plateau under drought conditions. It compares the composition, structure, and assembly mechanisms of microbial communities in water-rich and water-deficient wetlands. The results show that while α diversity remains stable after aridification, the community undergoes significant phylum reorganization. Aridification leads to increased sensitivity in the β diversity of archaea and bacteria to environmental and geographic factors, while fungal β diversity remains unchanged. Co-occurrence network analysis reveals a more complex and denser microbial network in aridified wetlands. Hub microbial groups are found only in bacteria and fungi, and their richness decreases after aridification. The study suggests a shift from a neutral to a partially deterministic assembly process, marked by reduced dispersal limitations and stronger heterogeneous selections. These findings contribute to understanding microbial community evolution in response to global environmental changes.

INTRODUCTION

Microorganisms are essential components of soil systems forming the foundation for important ecological functions such as water and nutrient storage, purification, and biogeochemical cycling.[1–3] Research has shown that the composition, diversity, and community assembly of soil microorganisms are sensitive to changes in external environmental conditions and serve as critical indicators for predicting soil functional evolution following environmental changes.[1,4,5] Wetlands are among the ecosystems with the highest service capacities, benefiting from their active water–soil material exchange processes that are heavily influenced by microbial activity.[3,5,6] In recent years, amid global climate warming, many wetlands have faced drought and water scarcity issues, resulting in severe degradation of their soil ecological functions.[7,8] This impact is more pronounced in high-altitude areas than in low-altitude regions. For example, climate warming causing a rise in the snow line at higher elevations directly leads to inadequate water storage, thereby causing soil aridification in wetlands.[3,9]

The composition of soil microbial communities is essential for soil to fulfill its ecological functions. Changes in key environmental factors not only directly alter the composition, structure, and function of soil microbial communities but also influence how microbial communities respond to other environmental variables.[10–12] Studies indicate that increased soil moisture promotes anaerobic bacterial growth, whereas drought conditions favor aerobic and facultative anaerobic bacteria.[13] For example, in moist soils, Actinobacteria, Acidobacteria, and Bacillus are more abundant, whereas in arid soils, Actinobacteria are more abundant.[3,14] These shifts are likely due to changes in soil temperature, pH, salinity, or redox potential caused by drought,[14–16] which prompt adaptive changes in soil microbial community assembly patterns.

The general process of community assembly can be divided into ecological niche processes and neutral processes. Ecological niche processes are generally believed to involve both homogeneous and heterogeneous selections. Homogeneous selection in the assembly of soil microbial communities is often associated with the filtering effects of specific combinations of environmental factors, whereas heterogeneous selection is linked to the limited availability of environmental resources and biological interactions.[12,16] On the other hand, neutral processes are governed by microbial dispersal, random extinction, and drift.[17,18] According to current ecological theories, both ecological niche processes and neutral processes coexist in the assembly of soil microbial communities.[12,18] However, the relative importance of these two processes varies under different circumstances, such as differing intensities, durations, and frequencies of drought. In fragile highland habitats, droughts can

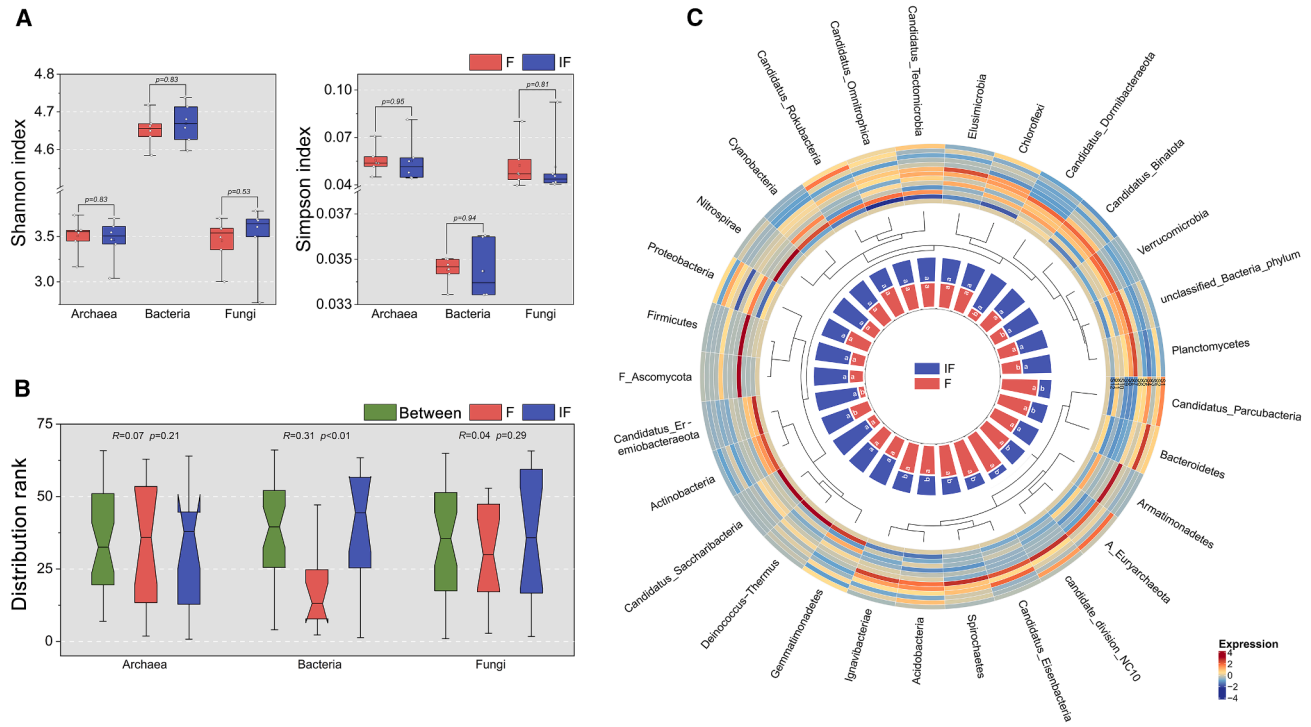


Figure 1. α diversity and community composition of soil microorganisms under wetland drought

(A) α Diversity; (B) ANOSIM analysis of species composition differences; (C) Differential abundance of major microbial phylum (relative abundance >0.005%) under different moisture conditions. Abbreviations: F indicates water-rich wetland; IF indicates water-deficient or dry wetlands. Outer ring in sub-figure(c) heatmap colors indicate the relative abundance score of microbial phyla across various sites, where red represents high abundance and blue represents low. The middle ring denotes inter-site clustering trees. The inner ring represents the significance of differences in abundance of each phylum under different moisture conditions. The length of the bars indicates the relative abundance of each phylum, and the letters highlighted on the bars represent the t-test results.

cause dramatic fluctuations in the ecological functions of wetland soils, which are closely related to changes in soil microbial characteristics. However, the patterns of changes in the soil microbial community structure and community assembly after the aridification of highland wetlands remain unclear, which hinders the ability of humans to predict and respond to the risks of global change.

The Qinghai–Tibet Plateau, known as the "Roof of the World", is also referred to as the "Asian Water Tower" because of its vast wetlands that are highly important for the ecological security of Asia and the world as a whole. However, factors such as reduced rainfall and rising snow lines caused by climate change pose a threat of drought to these wetlands. This region provides an ideal location for studying the drying of wetland soils. Currently, the composition characteristics of water and grassland soil microbial communities in this region have been reported,[12,19,20] but the changes in community diversity patterns and assembly processes after wetland drying remain unclear. In this study, we focused on the taxonomic characteristics of wetland soil microorganisms and the process of community assembly. The main objectives of this study are: (1) To test the hypothesis that wetland drying on the Qinghai-Tibet Plateau leads to a reorganization of microbial phyla, with bacterial changes potentially being more significant than those in archaea and fungi; (2) to investigate the hypothesis that aridification enhances the modularity and complexity of soil microbial co-occurrence networks, resulting in a denser and more interconnected microbial community structure; and (3) to evaluate the hypothesis that wetland drying strengthens the deterministic process in the assembly of soil microbial communities. These hypotheses aim to provide a mechanistic understanding of how microbial communities in high-altitude wetlands adapt to drought conditions and offer insights into predicting ecosystem responses to global climate change. The conclusions of this study will contribute to a more scientific prediction of the risk of decreased ecosystem services caused by drought in wetlands.

RESULTS

Alpha diversity and community composition of microorganisms in aridified soils of wetlands

We performed PcoA analysis of the microbial composition of all sample sites, and the results revealed that the microbial composition was clustered on the basis of differences in moisture conditions (Figure S1). We studied the α diversity indices of soil archaea, bacteria, and fungi in a high-altitude wetland under conditions of abundance and scarcity of water (Figure 1A). The results indicated that the bacterial diversity was the highest, whereas archaeal and fungal diversity were relatively lower. Furthermore, the α diversity of soil microorganisms did not

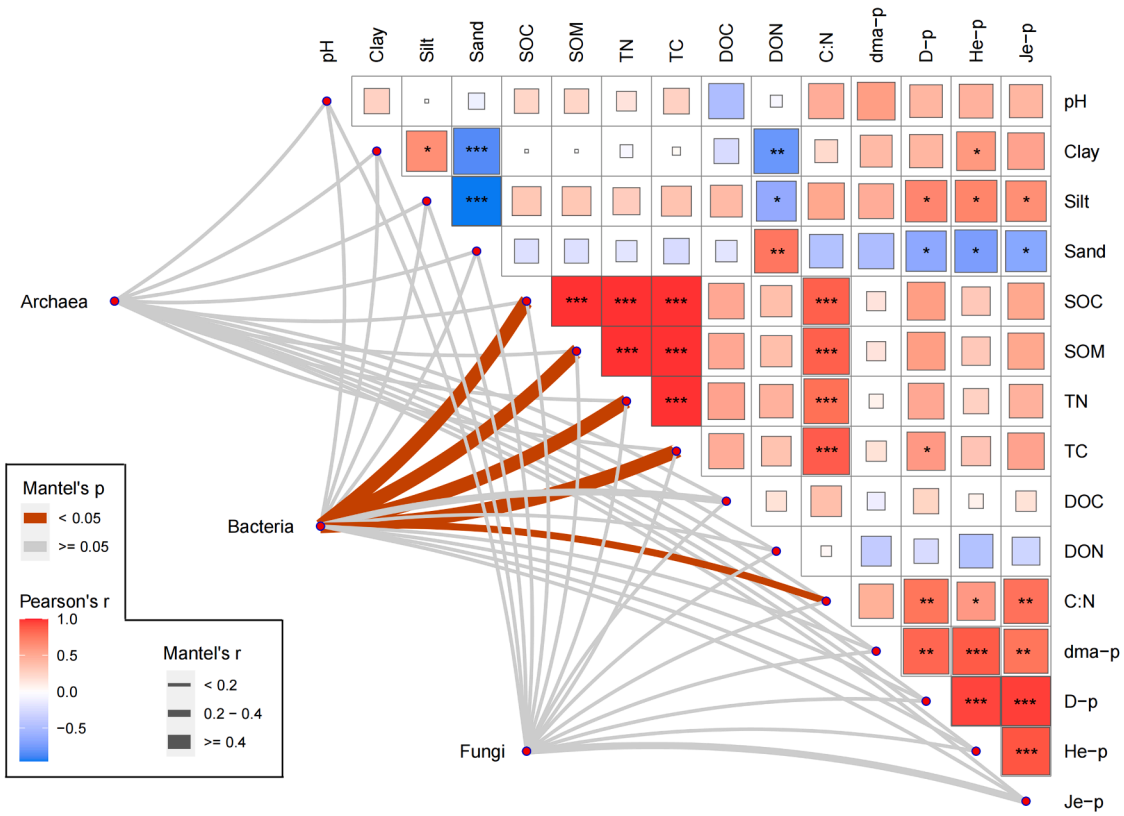


Figure 2. Relationship between wetland soil microorganisms and environmental factors

The legend shows the meaning of the main symbols in the figure. In addition, asterisks in the figure indicate the significance level of Pearson correlations, *: $p < 0.05$; **:$p < 0.01$; ***:$p < 0.001$.

significantly change during periods of dryness and drought in the wetland. Further investigation of 29 abundant phyla (relative abundance >0.005%) revealed significant differences in abundance between the two moisture conditions for 12 of these phyla. Notably, among the top ten most abundant microbial phyla, the abundances of Acidobacteria and Candidatus Eisenbacteria significantly increased after aridification, whereas those of Actinobacteria, Verrucomicrobia, and Planctomycetes decreased significantly. The average relative abundances of these genera across all the communities were 18.98%, 15.52%, 1.07%, 0.34%, and 0.23%, respectively (Figures 1C and S2). ANOSIM analysis was performed at the species level to assess the composition of the soil microorganisms, revealing significant differences in bacteria ($p < 0.01$) under different moisture conditions, whereas differences in archaea and fungi were not significant. In summary, the aridification of wetlands did not significantly affect the diversity of soil microorganisms, but it did lead to a significant change in the microbial composition, especially that of bacteria.

We studied the relationships between ancient archaea, bacteria, and fungi in alpine wetland soil and environmental factors (Figure 2). The Mantel test revealed that bacteria were significantly influenced by SOC, SOM, TN, and the C:N ratio, whereas archaea and fungi were not strongly influenced by any of the considered environmental factors.

Beta diversity and geographic analysis of soil microorganisms

The relationships among archaea, bacteria, and fungi in plateau wetland soil and their environmental characteristics were investigated on the basis of Bray–Curtis distance (Figure 3). The results indicate that after wetland aridification, the β diversity of archaea was significantly influenced by the environmental distance ($p < 0.01$), altitude distance ($p < 0.01$), and geographic distance ($p < 0.01$). Similarly, the β diversity of bacteria was also significantly impacted by the environmental distance ($p < 0.01$), altitude distance ($p < 0.01$), and geographic distance ($p < 0.05$). However, the β diversity of fungi did not significantly change in response to the environment, altitude, or geographic distance following wetland aridification. These findings suggest that the diversity patterns of archaea and bacteria in plateau wetland soil are more sensitive to changes in moisture.

Patterns of change in microbial co-occurrence networks in aridified wetland soils

Under the two moisture conditions, species with a relative abundance greater than 0.01% were selected to construct a co-occurrence network of all the microorganisms, and the topological characteristics of the network nodes and edges were calculated (Figures 4A and 4B). The results revealed a total of

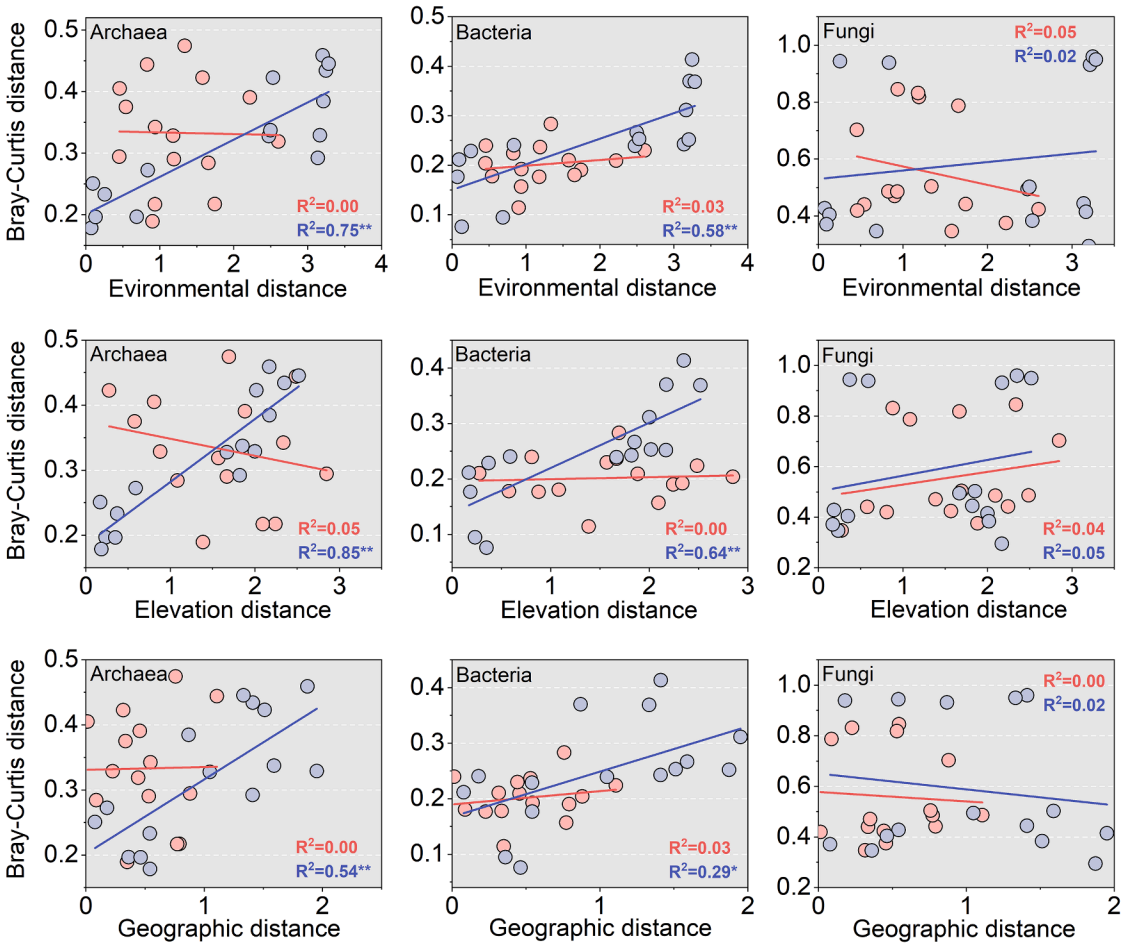


Figure 3. Relationship between soil microbial β-diversity and environmental characteristics based on Bray-Curtis distance analysis

Red color in the figure indicates water-rich wetlands and blue color indicates water-deficient or dry wetlands; asterisks indicate the significance level of the linear fitness, *: $p < 0.05$; **:$p < 0.01$.

582 nodes and 23,174 edges in the network analysis of the water-rich wetland (Figure 5A), whereas the water-deficient wetland had 584 nodes and 29,113 edges (Figure 4B). The results from the network analysis indicate that in the rich-water wetland, the networks for archaea, bacteria, and fungi had 58, 489, and 35 nodes, respectively, and 182,17139, and 88 edges, respectively. In aridified wetlands, the networks for archaea, bacteria, and fungi had 55, 489, and 40 nodes, respectively, and 163, 21863, and 112 edges, respectively. For all microbes included in the study, the average path length in the rich-water wetland was 2.573, which decreased to 2.446 in the aridified wetland, a reduction of approximately 4.93%. When different types of microorganisms were considered separately, the average path lengths for archaea and bacteria decreased by 7.18% and 7.14%, whereas those for fungi increased by 28.49%. Overall, after aridification, the microbial networks presented denser nodes and shorter average network path distances, indicating closer relationships among them.

We used the degree to express the topological characteristics of the network (Figure 4C), and the results indicate that after wetland aridification, there was a significant increase in the distribution of bacteria ($p < 0.001$) and fungi ($p < 0.05$). We defined the top 10% rank of degree and closeness centrality as hub taxa. We found that in rich-water wetland soil, there were 47 top hub taxa for bacteria, whereas in aridified wetland soil, the number decreased to 22. In the rich-water wetland soil, there was 1 top hub taxa for fungi, whereas none were found in the aridified wetland. No top hub taxa were found for archaea under any moisture conditions.

Wetland aridification microbial community assembly patterns

In this study, null models and Sloan neutral models were used to investigate the assembly process of soil microbial communities along environmental gradients. On the basis of the null model results, random processes ($|\beta NTI| < 2$) dominated the assembly process of microbial communities in well-watered wetland soils (Figure 6A). After wetland aridification, while microbial community assembly remained driven primarily by random processes, the βNTI significantly increased ($p < 0.05$), indicating that some

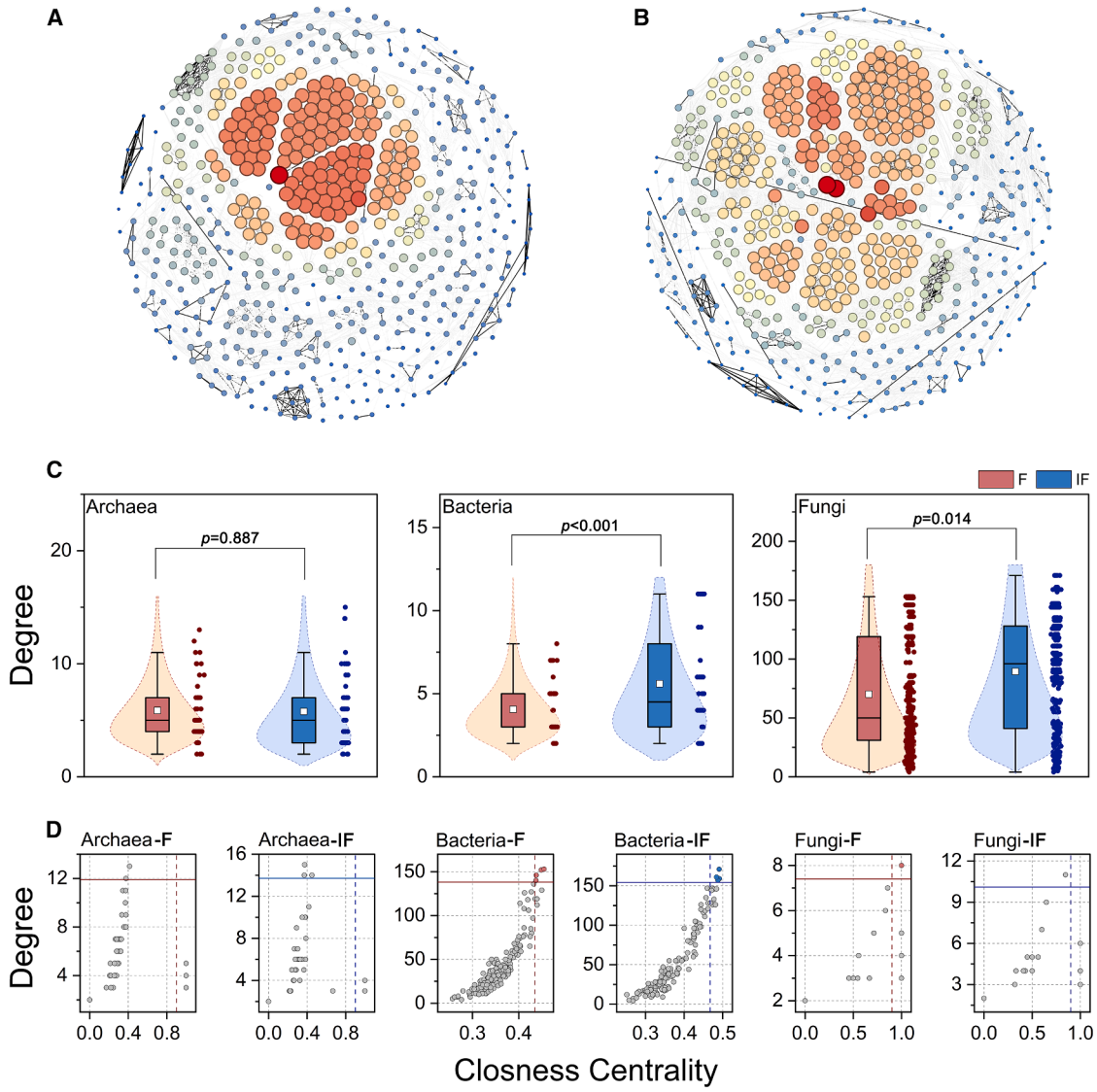


Figure 4. Co-occurrence network analysis

(A and B) (A) Soil microbial co-occurrence network in water-rich wetland; (B) Soil microbial co-occurrence network in water-deficient or dry wetlands; in the network diagram, circles represent nodes, the color of the circle represents the clustering features, and the size of the circle represents the node's high or low degree of degree value; the connecting lines represent the edges, and the darker the edges represent the higher their weights.

(C and D) (C) Node-level topological feature parameters; (D) hub taxa analysis.

site communities had transitioned to deterministic processes (Figure 5A). Further analysis via RC_{bray} null models revealed the proportional dominance of different community assembly drivers within the sites (Figure 5B). We found that after wetland aridification, undominated processes decreased from 28.57% to 14.29%, dispersal limitation processes decreased from 57.14% to 38.10%, heterogeneous selection processes increased from 0% to 33.33%, and homogeneous selection processes remained unchanged. The migration rate (m) estimated by the neutral model reflects the dispersal capacity of a species (Figure 5C). The migration rates for rich-water wetlands (0.122) and aridified wetlands (0.109) were both relatively low (Figure 6A).

DISCUSSION

In the context of global change, high-altitude wetlands, owing to their fragile ecological environment, are more sensitive to climate change than many low-altitude wetlands are and face greater ecological risks.[3,9] Studying plateau wetland degradation can provide scientific references for wetland degradation in more areas. Microbes are key to the ecological functions of wetland soil. Currently, research on plateau wetland soil microbes has been initiated, but the characteristics of soil microbial community diversity and community assembly mechanisms in plateau wetlands under arid conditions remain unclear. Therefore, this study aimed to explore these aspects.

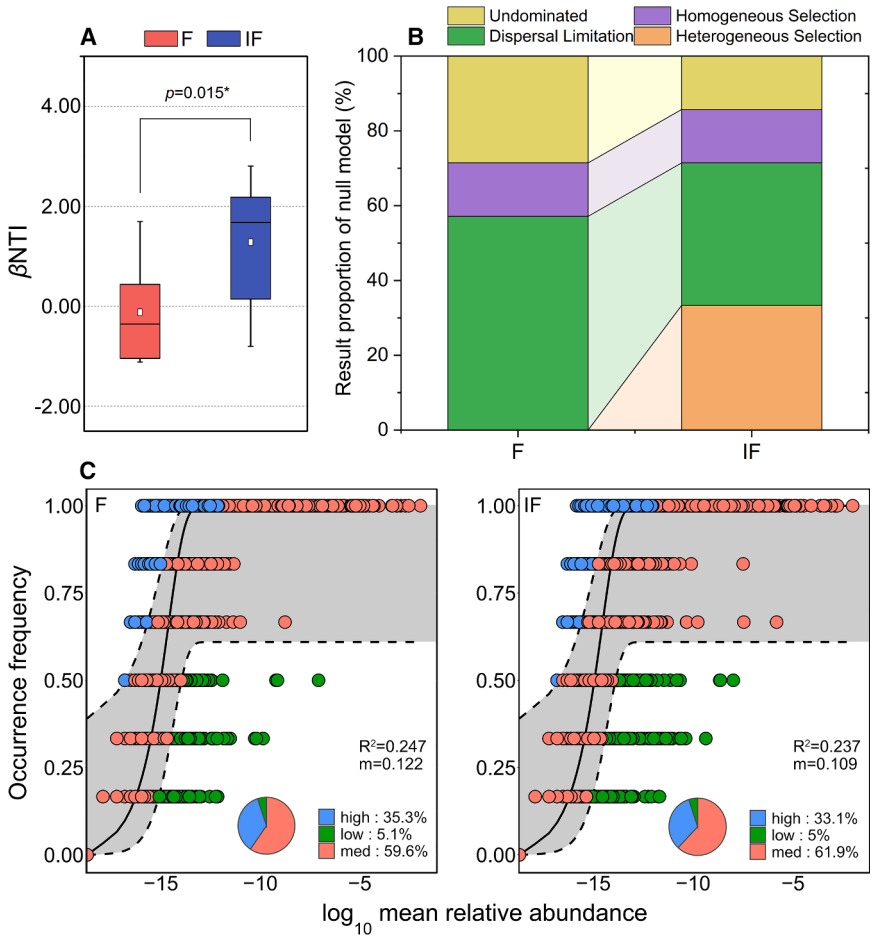


Figure 5. The assembly process of soil microbial communities in alpine wetlands

(A) Differentiality of βNTI under different moisture conditions; (B) Contribution of different ecological processes to the assembly of eukaryotic microbial communities; (C) Neutral community model. In the neutral model, blue and green circles represent species with occurrences higher or lower than predicted by the model; solid black line indicates best fitness with the neutral community model, while the dashed black line represents the 95% confidence interval. "m" represents the estimated migration rate, and "R^2" represents the goodness of fitness with the neutral community model. *: $p < 0.05$.

Microbial diversity and species composition of soils in aridized plateau wetlands

Owing to climate change, global drought is increasing and may have significant impacts on the structure and function of wetland microbes.[3,21,22] We observed that drought did not significantly alter the α diversity of the plateau wetland soil microbial communities. This differs from some previous research conclusions; for example, studies have reported that intensified drought in arid ecosystems can lead to a loss of soil microbial diversity.[23,24] However, there are varying conclusions for different ecosystems. For example, a study by Chen et al. explored fungal diversity in dry and wet season sediments in rivers and reported greater diversity in the dry season.[25] Similarly, Feng et al. studied soil microbes in secondary forests under changes in precipitation and reported that both increases and decreases in water sources had no impact on soil microbial α diversity.[26] In summary, the influence of water resources on soil microbes varies across different ecosystems and is very complex. Further detailed research is needed to clarify the underlying patterns and mechanisms involved.

To gain deeper insights into the characteristics of soil microbial communities in aridified plateau wetlands, we investigated the community composition of soil microbes at both the phylum and species levels. The results revealed significant alterations in several important microbial phyla, with bacteria being the most affected. Similarly, at the species level, there were notable changes in bacterial species composition. Specifically, the abundances of Acidobacteria and Candidatus Eisenbacteria increased, whereas those of Actinobacteria, Verrucomicrobia, and Planctomycetes decreased. Acidobacteria and Candidatus Eisenbacteria are generally considered to be involved in the decomposition and mineralization of soil organic matter, such as cellulose, lignin, and hemicellulose, indicating that an increase in their abundance may signify an increase in soil carbon release in the region.[3,27] In addition, some microorganisms in the Acidobacteria phylum are able to participate in N, P, and S metabolism, and some microorganisms in the Candidatus Eisenbacteria are similarly able to participate in sulfate metabolism; thus, increases in Acidobacteria and Candidatus Eisenbacteria may also affect pH in wetland soils by altering the concentrations of acid radicals and particles.[28,29] Moreover, the phylum Actinobacteria is also associated with soil carbon decomposition, including various bacteria, such as Edaphobacter and Telmatobacter.[30,31]

Actinobacteria are also linked to nitrogen fixation; for example, genera such as Rhizobium can influence soil nitrogen productivity, which is beneficial for plant growth.[32,33] Planctomycetes also play a crucial role in soil nitrogen cycling; these microorganisms mineralize nitrogen under anaerobic conditions, thus preventing wetland eutrophication.[34] To further validate the above inferences, we explored the relationships between archaeal, bacterial, fungal, and environmental factors on the basis of phylum-level data. The results indicated significant associations between bacteria and soil carbon and nitrogen, whereas archaea and fungi were significantly related to environmental factors. These conclusions suggest that although there was no substantial change in the community α diversity in the aridified plateau wetlands, a reorganization of microbial communities occurred.

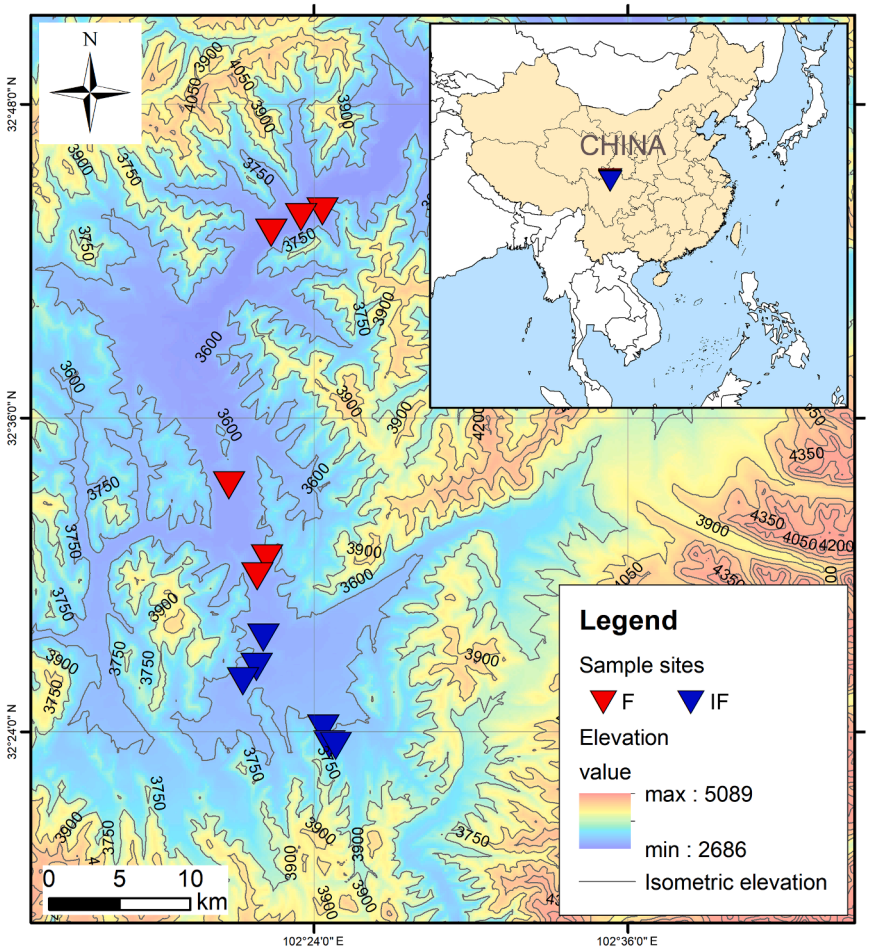


Figure 6. Location of sample sites
Well-watered wetlands (F) and 6 sites in water-deficient or drought-prone wetlands (IF).

After aridification of the plateau wetlands, the β diversity of archaea and bacteria became more sensitive to environmental distance, elevation distance, and geographical distance, whereas that of fungi did not significantly change. This suggests that the diversity patterns of archaea and bacteria in plateau wetland soil are more sensitive to moisture changes.[12]

Soil microbial co-occurrence networks in aridized plateau wetlands

The patterns of interaction among microorganisms are linked to species interactions, such as competition or coexistence.[15,21] Previous research has shown that modularity is positively associated with community stability, potentially limiting the impact within its own module by constraining the number of biological taxa.[12,35] A highly modular network comprises multiple relatively independent and internally connected modules (or subnetworks, subcommunities), each potentially representing a specific ecological function, environmental adaptation, or interacting microbial community.[36]

In our study, the modularity of aridified wetlands increased, suggesting potential diversification of microbial ecological functions following wetland aridification. Research indicates that increased community differentiation may lead to intensified competition between different modules, thereby reducing community stability.[37,38] Conversely, other studies suggest that an increase in modularity could signify more functional groups, leading to heightened stability and resilience in the community.[35]

Our study also demonstrated that the microbial network structure in aridified wetland soil was more complex and compact than that in normal wetland soil (characterized by a decreased average path distance) and presented a greater co-occurrence frequency of microbial taxa (higher degree). One hypothesis suggests that within compact communities, microorganisms have greater connectivity, enhancing microbial interactions.[24] Given this context, it is easier for a functional group of microorganisms to compensate for environmental pressure through interactions with other linked functional groups, thereby improving community stability.[16,24,35] Another hypothesis suggests that environmental stress or increased diversity might lead to a more compact microbial community network structure.[39,40] The characteristics exhibited by the network structure and community features in our study align more closely with the latter hypothesis. However, there is currently no definitive method to accurately quantify the proportion of effects from various hypotheses, warranting future research for confirmation.

Research has demonstrated that hub taxa occupy crucial topological positions within a network and contribute to maintaining the structure of microbial communities. The loss of hub taxa can lead to network instability or even collapse.[12,35] In this study, hub taxa were observed only within bacteria and fungi, and their numbers decreased after aridification occurred. Typically, a reduction in the number of hub taxa signifies a decrease in community stability, possibly due to changes in community composition or even the loss of key species.[41]

The results in Section 3.1 indicate significant changes in the abundance and species composition of several high-abundance phyla of soil microbes following wetland aridification, which might be a direct cause of decreased community stability.[42] Previous studies have suggested that in addition to fluctuations in community structure, a weakening of interspecies relationships may also result in a decrease in the number of hub taxa.[43] However, in this study, following aridification, the number of network nodes significantly increased while the average path distance

decreased, without indicating any signs of weakened interspecies relationships.

Patterns of soil microbial community assembly in aridized plateau wetlands

The results of this study suggest that aridification is a significant factor influencing the construction of soil microbial communities in highland wetlands. In our study, the βNTI of arid wetlands significantly increased compared with that of water-rich wetlands, indicating a shift in community assembly processes from randomness toward greater determinism. Further analysis of community βRCbray revealed that the dispersal limitation process decreased according to null models, while homogeneous selection showed no significant change and heterogeneous selection significantly increased. This could be due to wetland aridification leading to a shift from relatively uniform to more complex environmental factors, resulting in diverse environments that exert heterogeneous selection pressures on microorganisms.[44,45] Other studies have also suggested that after wetland aridification, soil microbial communities transition from predominantly anaerobic and facultative anaerobic microbes to coexisting anaerobic, facultative anaerobic, and aerobic microbes, potentially increasing heterogeneous selection processes.[46,47] These findings are consistent with our study, indicating that wetland aridification leads to a more deterministic community assembly process, especially regarding heterogeneous selection processes.

We also utilized a neutral model to investigate the mechanisms underlying the construction of soil microbial communities in aridified highland wetlands. The results indicated that following wetland aridification, the fitness of the neutral model (R^2) decreased, signifying reduced randomness in community assembly, which aligns closely with the findings from the null model analysis. The migration rate (m) represents the likelihood of microbial dispersal, and in our study, the difference in m values between aridified and normal wetland microbial communities was minimal, decreasing by only 2.5%. This may indicate that microbial dispersal was only moderately affected after wetland aridification.[12] Communities experiencing weaker environmental selection typically exhibit higher levels of dispersal limitation because environmental selection often leads to greater biological diversity, which in turn can increase microbial dispersal modes and pathways.[21,48]

Limitations of the study

This study offers valuable insights into the dynamics of soil microbial community structure and assembly in high-altitude wetlands under drought conditions. However, there are several limitations to consider. (1) The study was conducted on a specific geographic region (the Qinghai–Tibet Plateau), which may limit the generalizability of the findings to other wetland areas with different environmental conditions. (2) While the study investigates microbial community composition and structure, it does not explore the functional roles of these microbial groups, which could provide a more comprehensive understanding of their ecological roles under arid conditions. (3) The research primarily focuses on microbial diversity, but it lacks long-term temporal data to fully capture the ongoing dynamics and shifts in microbial communities over time in response to continued aridification. Future research could address these limitations by conducting similar studies in diverse wetland ecosystems to validate the generalizability of these findings. Additionally, future work should incorporate functional analysis of microbial communities to better understand how specific microbial groups contribute to ecosystem functions, especially under changing environmental conditions.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact Kang Di (kangdi@cwnu.edu.cn).

Materials availability

This study did not generate new unique reagents.

Data and code availability

- The metadata used in this study can be found at the following link: https://www.ncbi.nlm.nih.gov/bioproject?term=PRJNA987568&cmd=DetailsSearch.
- This paper does not report original code.
- Any additional information required to reanalyze the data reported in this article is available from the lead contact upon request.

ACKNOWLEDGMENTS

We are grateful for the financial support from the Sichuan Transportation Technology Project (2019-ZL-19), Natural Science Foundation of Sichuan Provence (2023NSFSC0143) and the National Natural Science Foundation of China (31800458). We are also grateful to the reviewers and editors for their valuable comments.

AUTHOR CONTRIBUTIONS

K.D., C.Y.Y., F.S.S., L.Q.M., and Z.S.Z. performed the experiments and analyzed the data. K.D. and Z.S.Z. provided key technical guidance and resources. K.D. designed the study. K.D. wrote the article. All authors discussed the results and commented on the article.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- METHOD DETAILS
  - Site selection
  - Field survey and sample collection
  - Determination of soil microbial genomes and identification of species
  - Measurement of soil indicators
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2025.112494.

Received: January 19, 2025
Revised: February 16, 2025
Accepted: April 16, 2025
Published: April 21, 2025

REFERENCES

1. Fernández-González, A.J., Villadas, P.J., Díaz-Peña, F., Notario-del-Pino, J., Lizano-Bastardín, Á., Fernández-López, M., and León-Barrios, M. (2024). Key microorganisms defining the microbial communities of an alpine legume-shrubland ecosystem on a volcanic island in natural and fire-affected soils. Plant Soil *498*, 651–670. https://doi.org/10.1007/s11104-023-06465-x.
2. Taborda, A., Frazão, T., Rodrigues, M.V., Fernández-Luengo, X., Sancho, F., Lucas, M.F., Frazão, C., Melo, E.P., Ventura, M.R., Masgrau, L., et al. (2023). Mechanistic insights into glycoside 3-oxidases involved in C-glycoside metabolism in soil microorganisms. Nat. Commun. *14*, 7289. https://doi.org/10.1038/s41467-023-42000-3.
3. Xiong, M., Jiang, W., Zou, S., Kang, D., and Yan, X. (2023). Microbial carbohydrate-active enzymes influence soil carbon by regulating the of plant- and fungal-derived biomass decomposition in plateau peat wetlands under differing water conditions. Front. Microbiol. *14*, 1266016. https://doi.org/10.3389/fmicb.2023.1266016.
4. Dadzie, F.A., Moles, A.T., Erickson, T.E., Machado de Lima, N., and Muñoz-Rojas, M. (2024). Inoculating native microorganisms improved soil function and altered the microbial composition of a degraded soil. Restor. Ecol. *32*, e14025. https://doi.org/10.1111/rec.14025.
5. Tveit, A., Schwacke, R., Svenning, M.M., and Urich, T. (2013). Organic carbon transformations in high-Arctic peat soils: key functions and microorganisms. Isme Journal *7*, 299–311. https://doi.org/10.1038/ismej.2012.99.
6. Yarwood, S.A. (2018). The role of wetland microorganisms in plant-litter decomposition and soil organic matter formation: a critical review. FEMS Microbiol. Ecol. *94*, fiy175. https://doi.org/10.1093/femsec/fiy175.
7. Lau, J.A., and Lennon, J.T. (2012). Rapid responses of soil microorganisms improve plant fitness in novel environments. Proc. Natl. Acad. Sci. USA *109*, 14058–14062. https://doi.org/10.1073/pnas.120231910.
8. Liu, F., Mo, X., Kong, W., and Song, Y. (2020). Soil bacterial diversity, structure, and function of in rhizosphere and non-rhizosphere soils in various habitats in the Yellow River Delta, China. Sci. Total Environ. *740*, 140144. https://doi.org/10.1016/j.scitotenv.2020.140144.
9. Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., Gao, Y., Zhu, D., Yang, G., Tian, J., et al. (2013). The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-Tibetan Plateau. Glob. Chang. Biol. *19*, 2940–2955. https://doi.org/10.1111/gcb.12277.
10. Dubey, M., Hadadi, N., Pelet, S., Carraro, N., Johnson, D.R., and van der Meer, J.R. (2021). Environmental connectivity controls diversity in soil microbial communities. Commun. Biol. *4*, 492. https://doi.org/10.1038/s42003-021-02023-2.
11. Tamminen, M., Spaak, J., Tlili, A., Eggen, R., Stamm, C., and Räsänen, K. (2022). Wastewater constituents impact biofilm microbial community in receiving streams. Sci. Total Environ. *807*, 151080. https://doi.org/10.1016/j.scitotenv.2021.151080.
12. Yang, Q., Zhang, P., Li, X., Yang, S., Chao, X., Liu, H., and Ba, S. (2023). Distribution patterns and community assembly processes of eukaryotic microorganisms along an altitudinal gradient in the middle reaches of the Yarlung Zangbo River. Water Res. *239*, 120047. https://doi.org/10.1016/j.watres.2023.120047.
13. Fenner, N., and Freeman, C. (2011). Drought-induced carbon loss in peatlands. Nat. Geosci. *4*, 895–900. https://doi.org/10.1038/NGEO1323.
14. Tripathi, B.M., Stegen, J.C., Kim, M., Dong, K., Adams, J.M., and Lee, Y.K. (2018). Soil pH mediates the balance between stochastic and deterministic assembly of bacteria. Isme Journal *12*, 1072–1083. https://doi.org/10.1038/s41396-018-0082-4.
15. Jiao, S., and Lu, Y. (2020). Soil pH and temperature regulate assembly processes of abundant and rare bacterial communities in agricultural ecosystems. Environ. Microbiol. *22*, 1052–1065. https://doi.org/10.1111/1462-2920.14815.
16. Li, W., Kuzyakov, Y., Zheng, Y., Li, P., Li, G., Liu, M., Alharbi, H.A., and Li, Z. (2022). Depth effects on bacterial community assembly processes in paddy soils. Soil Biol. Biochem. *165*, 108517. https://doi.org/10.1016/j.soilbio.2021.108517.
17. Chase, J.M., and Myers, J.A. (2011). Disentangling the importance of ecological niches from stochastic processes across scales. Philos. Trans. R. Soc. Lond. B Biol. Sci. *366*, 2351–2363. https://doi.org/10.1098/rstb.2011.0063.
18. Stegen, J.C., Lin, X., Fredrickson, J.K., and Konopka, A.E. (2015). Estimating and mapping ecological processes influencing microbial community assembly. Front. Microbiol. *6*, 370. https://doi.org/10.3389/fmicb.2015.00370.
19. Chen, X., Xue, D., Wang, Y., Qiu, Q., Wu, L., Wang, M., Liu, J., and Chen, H. (2023b). Variations in the archaeal community and associated methanogenesis in peat profiles of three typical peatland types in China. Environ. Microbiome *18*, 48. https://doi.org/10.1186/s40793-023-00503-y.
20. Li, H., Zhang, J., Tian, D., Liu, Y., and Dong, J. (2023). Nitrogen Significantly Affected N Cycling Functional Gene Abundances Compared with Phosphorus and Drought in an Alpine Meadow. Agronomy-Basel *13*, 1041. https://doi.org/10.3390/agronomy13041041.
21. Chen, W.D., Ren, K.X., Isabwe, A., Chen, H.H., Liu, M., and Yang, J. (2019). Stochastic processes shape microeukaryotic community assembly in a subtropical river across wet and dry seasons. Microbiome *7*, 148. https://doi.org/10.1186/s40168-019-0763-x.
22. Xie, G., Tang, X., Shao, K., Hu, Y., Liu, H., Martin, R.M., and Gao, G. (2020). Spatiotemporal patterns and environmental drivers of total and active bacterial abundances in Lake Taihu, China. Ecol. Indic. *114*, 106335. https://doi.org/10.1016/j.ecolind.2020.106335.
23. Jiao, S., Chu, H., Zhang, B., Wei, X., Chen, W., and Wei, G. (2022). Linking soil fungi to bacterial community assembly in arid ecosystems. iMeta *1*, e2. https://doi.org/10.1002/imt2.2.
24. Peng, Y., Xu, H., Shi, J., Wang, Z., Lv, J., Li, L., and Wang, X. (2024a). Soil microbial composition, diversity, and network stability in intercropping versus monoculture responded differently to drought. Agric. Ecosyst. Environ. *365*, 108915. https://doi.org/10.1016/j.agee.2024.108915.
25. Chen, X., Xu, G., Xiong, P., Peng, J., Fang, K., Wan, S., Wang, B., Gu, F., Li, J., and Xiong, H. (2023a). Dry and wet seasonal variations of the sediment fungal community composition in the semi-arid region of the Dali River, Northwest China. Environ. Sci. Pollut. Res. Int. *30*, 123694–123709. https://doi.org/10.1007/s11356-023-31042-1.
26. Feng, J., Ma, H., Wang, C., Gao, J., Zhai, C., Jiang, L., and Wan, S. (2024). Water rather than nitrogen availability predominantly modulates soil microbial beta-diversity and co-occurrence networks in a secondary forest. Sci. Total Environ. *907*, 167996. https://doi.org/10.1016/j.scitotenv.2023.167996.
27. Wang, K., Pan, R., Fei, H., Tong, Q., and Han, F. (2022). Changes in soil prokaryotic communities and nitrogen cycling functions along a groundwater table drawdown gradient in desert wetlands. Sci. Total Environ. *842*, 156868. https://doi.org/10.1016/j.scitotenv.2022.156868.
28. Jones, R.T., Robeson, M.S., Lauber, C.L., Hamady, M., Knight, R., and Fierer, N. (2009). A comprehensive survey of soil acidobacterial diversity using pyrosequencing and clone library analyses. ISME J. *3*, 442–453. https://doi.org/10.1038/ismej.2008.127.
29. Ward, N.L., Challacombe, J.F., Janssen, P.H., Henrissat, B., Coutinho, P.M., Wu, M., Xie, G., Haft, D.H., Sait, M., Badger, J., et al. (2009). Three Genomes from the Phylum Acidobacteria Provide Insight into the Lifestyles of These Microorganisms in Soils. Appl. Environ. Microbiol. *75*, 2046–2056. https://doi.org/10.1128/AEM.02294-08.

30. Grant, T., Sethuraman, A., Escobar, M.A., and Vourlitis, G.L. (2022). Chronic dry nitrogen inputs alter soil microbial community composition in Southern California semi-arid shrublands. Appl. Soil Ecol. *176*, 104496. https://doi.org/10.1016/j.apsoil.2022.104496.

31. Nemergut, D.R., Cleveland, C.C., Wieder, W.R., Washenberger, C.L., and Townsend, A.R. (2010). Plot-scale manipulations of organic matter inputs to soils correlate with shifts in microbial community composition in a lowland tropical rain forest. Soil Biol. Biochem. *42*, 2153–2160. https://doi.org/10.1016/j.soilbio.2010.08.011.

32. Amule FC, S.P., Rawat, A.K., and Mishra, U.S. (2018). Effect of actinobacterial, Rhizobium and plant growth promoting rhizobacteria consortium inoculation on rhizosphere soil properties in soybean in Jabalpur district of Madhya Pradesh. Int. J. Chem. Stud. *6*, 583–586.

33. Větrovský, T., Steffen, K.T., and Baldrian, P. (2014). Potential of Cometabolic Transformation of Polysaccharides and Lignin in Lignocellulose by Soil Actinobacteria. PLoS One *9*, 89108. https://doi.org/10.1371/journal.pone.0089108.

34. Jogler, C. (2014). The bacterial 'mitochondrium'. Mol. Microbiol. *94*, 751–755. https://doi.org/10.1111/mmi.12814.

35. Zhong, Y., Sorensen, P.O., Zhu, G., Jia, X., Liu, J., Shangguan, Z., Wang, R., and Yan, W. (2022). Differential Microbial Assembly Processes and Co-Occurrence Networks in the Soil-root Continuum Along an Environmental Gradient. iMeta *1*, e18. https://doi.org/10.1002/imt2.18.

36. Widder, S., Besemer, K., Singer, G.A., Ceola, S., Bertuzzo, E., Quince, C., Sloan, W.T., Rinaldo, A., and Battin, T.J. (2014). Fluvial network organization imprints on microbial co-occurrence networks. Proc. Natl. Acad. Sci. USA *111*, 12799–12804. https://doi.org/10.1073/pnas.1411723111.

37. Coyte, K.Z., Schluter, J., and Foster, K.R. (2015). The ecology of the microbiome: Networks, competition, and stability. Science *350*, 663–666. https://doi.org/10.1126/science.aad2602.

38. Zhang, S., Liu, J., Zhao, H., Li, Q., Zhang, H., and Zhao, M. (2024). *Flaveria bidentis* invasion modifies soil physicochemical properties and increases microorganism community diversity. J. Soils Sediments *24*, 2437–2448. https://doi.org/10.1007/s11368-024-03810-0.

39. Arboleda-Baena, C., Freilich, M., Pareja, C.B., Logares, R., De la Iglesia, R., and Navarrete, S.A. (2024). Microbial community and network responses across strong environmental gradients: How do they compare with macroorganisms? FEMS Microbiol. Ecol. *100*, fiae017.

40. Wu, X., Zhou, Q., Zeng, H., and Hu, X. (2024). Lake microbiome composition determines community adaptability to warming perturbations. Ecol. Process. *13*, 33. https://doi.org/10.1186/s13717-024-00516-6.

41. Toju, H., Tanabe, A.S., and Sato, H. (2018). Network hubs in root-associated fungal metacommunities. Microbiome *6*, 116. https://doi.org/10.1186/s40168-018-0497-1.

42. Zavarzin, G.A. (1992). Biodiversity and Stability of Microbe Community. Zh. Obshch. Biol. *53*, 394–406.

43. McGrady-Steed, J., and Morin, P.J. (2000). Biodiversity, density compensation, and the dynamics of populations and functional groups. Ecology *81*, 361–373.

44. Gao, C., Montoya, L., Xu, L., Madera, M., Hollingsworth, J., Purdom, E., Singan, V., Vogel, J., Hutmacher, R.B., Dahlberg, J.A., et al. (2020). Fungal community assembly in drought-stressed sorghum shows stochasticity, selection, and universal ecological dynamics. Nat. Commun. *11*, 34. https://doi.org/10.1038/s41467-019-13913-9.

45. Guo, B., Zhang, H., Liu, Y., Chen, J., and Li, J. (2023). Drought-resistant trait of different crop genotypes determines assembly patterns of soil and phyllosphere microbial communities. Microbiol. Spectr. *11*, e0006823–23. https://doi.org/10.1128/spectrum.00068-23.

46. Jin, Q., Liu, H., Xu, X., Zhao, L., Chen, L., Chen, L., Shi, R., and Li, W. (2023). Emission dynamics of greenhouse gases regulated by fluctuation of water level in river-connected wetland. J. Environ. Manage. *329*, 117091. https://doi.org/10.1016/j.jenvman.2022.117091.

47. Kim, S.Y., Lee, S.H., Freeman, C., Fenner, N., and Kang, H. (2008). Comparative analysis of soil microbial communities and their responses to the short-term drought in bog, fen, and riparian wetlands. Soil Biol. Biochem. *40*, 2874–2880. https://doi.org/10.1016/j.soilbio.2008.08.004.

48. Stovícek, A., Kim, M., Or, D., and Gillor, O. (2017). Microbial community response to hydration-desiccation cycles in desert soil. Sci. Rep. *7*, 45735. https://doi.org/10.1038/srep45735.

49. Bastian, M., Heymann, S., and Jacomy, M. (2009). Gephi: an open source software for exploring and manipulating networks. Proc. Int. AAAI Conf. Weblogs Soc. Media *3*, 361–362. https://doi.org/10.1609/icwsm.v3i1.13937.

50. Gao, M., Xiong, C., Gao, C., Tsui, C.K.M., Wang, M.M., Zhou, X., Zhang, A.M., and Cai, L. (2021). Disease-induced changes in plant microbiome assembly and functional adaptation. Microbiome *9*, 187. https://doi.org/10.1186/s40168-021-01138-2.

51. Stegen, J.C., Lin, X., Fredrickson, J.K., Chen, X., Kennedy, D.W., Murray, C.J., Rockhold, M.L., and Konopka, A. (2013). Quantifying community assembly processes and identifying features that impose them. Isme Journal *7*, 2069–2079. https://doi.org/10.1038/ismej.2013.93.

52. R Core Team (2025). R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing). https://www.R-project.org/.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Metadata	NCBI	https://www.ncbi.nlm.nih.gov/bioproject?term=PRJNA987568&cmd=DetailsSearch
Software and algorithms		
Origin 2021	OriginLab Corporation, 2021	https://www.originlab.com/
Gephi[49]	Bastian M., Heymann S., and Jacomy M, 2009	Gephi: an open source software for exploring and manipulating networks. International AAAI Conference on Weblogs and Social Media. https://gephi.org/
R4.3.3	R Core Team, 2025	https://cloud.r-project.org/
SPSS 21	IBM Corp	https://www.ibm.com/products/spss-statistics
Hub taxa[50]	Gao et al., 2021	Disease-induced changes in plant microbiome assembly and functional adaptation. Microbiome 9(1), 187.
Bray–Curtis distances[18,51]	Stegen et al., 2013	Quantifying community assembly processes and identifying features that impose them. Isme Journal 7(11), 2079.

METHOD DETAILS

Site selection

The research site is located on the eastern edge of the Qinghai–Tibet Plateau (32.73° to 32.39°N, 102.34° to 102.41°E) (Figure S3), with an average elevation of 3,400-3,800 meters and a total area of approximately 36,970 square kilometers. The study area falls within the transitional zone of the plateau, which is characterized by a semihumid continental monsoon climate. The mean annual temperature (MAT) ranges from approximately 0.9 to 2.5°C, and the mean annual precipitation (MAP) ranges from approximately 518 to 800 millimeters. The climate has distinct growing and nongrowing seasons, with a short growing season (July-September) and a cold nongrowing season prevailing throughout the year. The wetlands on the eastern edge of the Qinghai–Tibet Plateau are typical high-altitude herbaceous and peat bogs in Asia, with well-developed ecosystems and abundant vegetation. They serve as important ecological barriers and water conservation areas for the upstream regions of the Yangtze and Yellow Rivers. The main rivers in the sampling area include the Baihe River, Suomo River, and Ake River, with average annual flow rates ranging from 50 to 100 cubic meters per second. The dominant vegetation in the wetlands includes *Carex alatauensis*, *Carex muliensis*, *Blysmus sinocompressus*, *Elymus nutans*, *Poa chalarantha* and *Cremanthodium brunneopilosum*.

Field survey and sample collection

Following the investigation, 12 sample sites with two distinct moisture conditions were selected: 6 sites in well-watered wetlands (F) and 6 sites in water-deficient or drought-prone wetlands (IF). To ensure that the two types of sample sites selected above represent long-term wetland moisture characteristics rather than temporary soil moisture characteristics, the sample sites were selected on the basis of localized moisture characteristics rather than being distributed in pairs over close distances, as wetland drought results from reduced surface runoff (Figure S3). Within each site, a 50 m × 50 m plot was established, and 10 random positions were chosen for sampling within each plot. During sampling, soil samples were collected from the top 10 cm after clearing visible vegetation and debris from the surface. Sampling in deep-water areas was avoided, and water was drained from shallow-water areas before sampling. The 10 individual samples were subsequently combined into composite soil samples after removal of fine roots and large plant debris. The composite samples were then stored at −40°C for further analysis and determination. The investigations and sample collection were completed in August 2022, and all experimental measurements were completed in 2023.

Determination of soil microbial genomes and identification of species

DNA extraction was performed via an E.Z.N.A. Soil DNA Kit (Omega, M5635-02, USA). The DNA was broken into fragments of approximately 500 bp via a Covaris 220. Then, PCR was performed with 2× Super Canace® II High-Fidelity Mix, primer mix

(p5/p7) and adaptor-ligated DNA. Finally, the PCR products were purified, and the library quality was assessed via a Qubit®4.0 fluorometer. Paired-end sequencing of the library was performed on a NovaSeq 6000 sequencer (Illumina, USA). Fastp (version 0.36) was used to evaluate the quality of the sequenced data. First, Megahit (version 1.2.9) was used to perform multisample mixed splicing to obtain preliminary spliced contig sequences. Then, Bowite2 (version 2.1.0) was used to map the clean reads back to the spliced results, and the unmapped reads were extracted and spliced again via SPAdes (version 3.13) to obtain low-abundance contigs. Prodigal (version 2.60) was used to predict the ORF of the splicing results, select genes with a length greater than or equal to 100 bp, and translate them into amino acid sequences. For the gene prediction results of each sample, CD-HIT (version 2.60) was used for redundancy to obtain a nonredundant gene set. Salmon (version 1.5.0) was used to construct a specific index of nonredundant gene sets, using a dual-phase algorithm and a method of constructing a bias model to accurately quantify the abundance of genes in each sample and calculate gene abundance on the basis of gene length information. DIAMOND (version 0.8.20) was used to compare the gene set with the NR database to obtain species annotation information. The screening conditions were as follows: E value<1e-5 and score>60.

Measurement of soil indicators

The soil pH was assessed via a pH monitor (Thermo Orion-868, MA, USA). Total nitrogen (TN) was quantified via the Kjeldahl method, which involves concentrated sulfuric acid and mixed catalyst decoction. Dissolved organic carbon (DOC) was extracted via an mK_2SO_4 solution and analyzed via a TOC-TN analyzer (Shimadzu, Kyoto, Japan). The total carbon (TC) and soil organic carbon (SOC) contents were determined via the external heating method with $K_2Cr_2O_7$. Dissolved organic nitrogen (DON) was computed as the disparity between soil soluble total nitrogen and soil inorganic nitrogen. The carbon-to-nitrogen ratio (C/N) was computed as the ratio of SOC to TN. The soil particle size distribution was determined via the hydrometer method, where ‘‘Clay’’ denotes soil particles with a size less than 0.002 mm, ‘‘Silt’’ denotes soil particles with a size less than 0.02 mm, and "Sand" denotes soil particles with a size greater than 0.2 mm.

QUANTIFICATION AND STATISTICAL ANALYSIS

In this study, we employed the Shannon index and Simpson index to quantify the α diversity of the soil microbial communities. At test was used to examine the differences in microbial α diversity and the abundance of major phyla under varying moisture conditions. Anosim analysis was conducted to assess the significant differences in bacteria, fungi, and archaea under distinct moisture conditions at the species level. Furthermore, a Mantel test was performed to analyze the relationships between bacteria, fungi, and archaea and environmental factors. We evaluated the β diversity of communities on the basis of Bray–Curtis distances in relation to environmental, elevation, and geographic distances. The elevation and geographic distance data were measured in m and km, respectively, and the data were normalized via the z score method prior to analysis. These calculations were carried out via the *vegan* package in R4.3.3(R Core Team, 2025[52]) and SPSS21 (IBM Corp). The significance test was performed using the T-test method. Significance levels are marked with asterisks throughout the article as follows, *: $p < 0.05$; **:$p < 0.01$; ***:$p < 0.001$.

To investigate the co-occurrence patterns, we computed multiple correlations on the basis of the species matrix, with an average relative abundance exceeding 0.01%. A symbiotic pattern was considered robust if the Pearson correlation coefficient was greater than 0.5 with a significance level of $p < 0.05$. In our network representation, nodes symbolize individual microbial genera, whereas edges denote paired relationships within the microbial community network, representing biologically or biochemically significant interactions. Visualization and calculation of node and edge quantities and degrees were performed via Gephi.[49] Hub taxa in each network were identified as the top 10% of nodes exhibiting the highest degree and closeness centrality.[50]

To quantify the contributions of key ecological processes to microbial community assembly, we used βNTI combined with Raup-Crick, which is based on Bray–Curtis distances.[18,51] Furthermore, Sloan’s neutral community model was employed to infer the contributions of random processes to microbial community assembly.[24] The fitness (R^2) of the neutral model was used to infer random processes, with ‘‘m’’ indicating estimated migration rates; higher ‘‘m’’ values suggest limited diffusion within the microbial community. Visualization was performed via the *ggplot2* package in R4.3.3 and Origin9.8 (OriginLab Corporation, 2021).