

## Significant representative publications by themes

(As of 6/30/2025)

### Summary

- ✓ Over 700 peer reviewed publications
- ✓ Google Scholar: h-index = **157**, >92,000 citations
- ✓ Web of Science: h-index = **141**, >74,000 citations
- ✓ **50** publications in *Science*, *Nature*-branded journals, and *Proceedings of the National Academy of Sciences*
- ✓ **214** papers published in **Nature indexed journals**, including *Science* (4), *Nature Climate Change* (5), *Nature Geoscience* (1), *PNAS* (13), *Nature Communications* (16), *Ecology Letters* (2), *Cell* (1), *The ISME Journal* by Nature Publishing Group (57) (The top one journal in microbial ecology), *Environmental Science & Technology* (28), *Water Research* (15), and *Geochimica et Cosmochimica Acta* (2), and other prestigious journals, e.g., *Nature Microbiology* (4), *Nature Ecology and Evolution* (2), *Nature Food* (1), *Nature Plants* (1), *Nature Water* (1), *Nature Reviews Microbiology* (2), *Microbiology and Molecular Biology Reviews* (1), *mBio* (25), *Global Change Biology* (20), *Microbiome* (12), and *Ecology* (1).

### Impacts

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|-----------|---|
| 2025      | <i>Research.com</i> <b>Best Scientist</b> , ranked at top # <b>25</b> worldwide, and # <b>12</b> in US in the field of <b>Ecology &amp; Evolution</b> , at top # <b>38</b> worldwide, and # <b>20</b> in US in the field of <b>Microbiology</b> ( <a href="https://research.com/">https://research.com/</a> ).  |
| 2021      | Among the 2021 Reuters List of World's Top 1000 Climate Scientists (#445)   |
| 2019-2025 | Among world's most highly cited researchers (top 0.1%) across all science & engineering fields among 10.2 million scientists based on Elsevier's <i>Scopus</i> in 2024 ( <a href="https://elsevier.digitalcommonsdata.com/datasets/btchxktzyw/7">https://elsevier.digitalcommonsdata.com/datasets/btchxktzyw/7</a> ).   |
| 2018-2024 | Top 0.1% global highly cited researcher in <b>both</b> fields of <b>Microbiology</b> , and <b>Environment &amp; Ecology</b> based on the numbers of top 1% highly cited publications by Web of Science. A total of 6,626 scholars across 21 research fields were recognized in 2024, only 216 ( <b>3%</b> ) being recognized in more than two fields). ( <a href="https://hcr.clarivate.com/">https://hcr.clarivate.com/</a> ). |

### A. Experimental genomic technologies

1. Shi, Z.; H. Yin, J.D. Van Nostrand, J.W. Voordeckers, Q. Tu, Y. Deng, M. Yuan, A. Zhou, P. Zhang, N. Xiao, D. Ning, Z. He, L. Wu, and **J.-Z. Zhou**. 2019. Functional gene array-based ultra-sensitive and quantitative detection of microbial populations in complex communities. *mSystems* 4: e00296-19. doi.org/10.1128/mSystems.00296-19.

The rapid advancement of metagenomic technologies, including microarrays, has significantly enhanced our understanding of complex microbial systems. However, designing a microarray that is representative, specific, sensitive, and quantitative remains challenging due to the constant discovery of novel microbial sequences. The newly developed GeoChip

5.0 is the most comprehensive functional microarray available, designed for studying microbial communities in biogeochemistry, ecology, environmental sciences, and human health. It has been validated through computational and experimental assays, demonstrating high specificity, sensitivity, and quantitative accuracy. Application of GeoChip 5.0 to contaminated groundwater samples provided novel insights into the effects of environmental contaminants on microbial communities.

2. **Zhou, J.-Z.**, Y.H. Jiang, Y. Deng, Z. Shi, B.-Y. Zhou, K. Xue, L. Wu, Z. He, and Y. Yang. 2013. *Random Sampling Process Leads to Overestimation of  $\beta$ -Diversity of Microbial Communities. mBio 4: e00324-13 (doi:10.1128/mBio.00324-13).*

Although large-scale metagenome sequencing technology has revolutionized microbial ecology, it suffers from several inherent drawbacks, including high sequencing errors and lower reproducibility, which could greatly overestimate microbial biodiversity. Based on general sampling theory, this study demonstrates mathematically that the low reproducibility problem inherent in high throughput sequencing-based detection technology is associated with the artifacts of random sampling processes. This finding has important implications for examining microbial biodiversity to address both basic theoretical and applied management questions. Since most ecological studies involve random sampling, the conclusions should also be applicable to other ecological studies in general.

3. **Zhou, J.-Z.** \*, L.-Y. Wu\*, Y. Deng, X.-Y. Zhi, Y.-H. Jiang, Q.-C. Tu, J.-P. Xie, J. D. Van Nostrand, Z.-H. He, and Y.-F. Yang. 2011. *Reproducibility and Quantitation of Amplicon Sequencing-Based Detection. ISME J, 5:1303-1313. (Top 1% highly cited)*

Large-scale metagenome sequencing and associated genomic technologies have revolutionized the study of microbial communities, which allow scientists to address research questions that could not be approached previously. However, it is not clear whether metagenome sequencing-based detection is reproducible and quantitative. This study discovered that the amplicon sequencing-based detection has poor reproducibility and quantitative accuracy for analyzing complex microbial communities, and highlight the importance of random sampling processes in overestimating the  $\beta$ -diversity of the microbial community structure. The findings of this study are important for experimental design, statistical analysis, and data interpretation of high throughput metagenomics sequencing data to appropriately address biological questions.

4. He, Z., T. J. Gentry, C. W. Schadt, L. Wu, J. Liebich, S. C. Chong, W.M. Wu, B. Gu, P. Jardine, C. Criddle, and **J.Z. Zhou**. 2007. *GeoChip: A comprehensive microarray for investigating biogeochemical, ecological, and environmental processes. The ISME Journal, 1: 67-77 (One of the 5 top-cited articles in the first 10 years of ISME J, #1 microbial ecology journal).*

Due to the vast diversity and as-yet uncultivated status of many species, rapid detection, characterization and quantification of microorganisms under natural settings are extremely difficult, and linking community structure to function - a central goal in ecology, is even more difficult. To this end, this study developed a revolutionary high-throughput technology (GeoChip) for dissecting microbial community functional structure, which was highlighted in the NRC's report in the *New Science of Metagenomics* and in the roadmap for NSF's NEON. In addition, it

won an R&D 100 Award in 2009 as one of 100 most innovative scientific and technological breakthroughs. GeoChip-based detection is highly sensitive, quantitative and reproducible. It has been widely used to address questions relevant to ecological theories, climate change, bioremediation, bioenergy, biogeochemistry, agriculture, environmental engineering, and human health.

5. **Zhou, J.-Z.**, M. A. Bruns, and J. M. Tiedje. 1996. DNA recovery from soils of diverse composition. *Appl. Environ. Microbiol.* 62: 316-322.

Although rapid development of molecular biology in the 1990s has presented a great opportunity for microbial ecology, one of the biggest bottlenecks was recovering high-quality DNA from environmental samples. This pioneering study presented a robust and efficient method to isolate high quality of DNA from a variety of soils. It has been highly influential and widely used by other scientists in molecular ecology as evidenced of >**4000** citations (GS). It is among the **12** most cited papers in Applied and Environmental Microbiology (a leading microbiology journal) based on statistics from 2008 to 2020. Because it recovers high molecular weight DNA from soils with high yields and purity, this method laid a **foundation** for the widely used metagenomics and other molecular microbial ecology studies in the coming decades.

## **B. Computational genomic technologies**

6. Xiao, N., A. Zhou, M. L. Kempher, B. Y. Zhou, Z. Jason Shi, M. Yuan, X. Guo, L. Wu, D. Ning, M. K. Firestone, and **J.-Z. Zhou**. 2022. Disentangling Direct from Indirect Relationships in Association Networks. *Proc. Nat. Acad. Sci.*, 119 No. 2 e2109995119, <https://doi.org/10.1073/pnas.2109995119>. (top 1% highly cited)

Quantitatively disentangling direct and indirect relationships in complex networks remains a formidable task in science and engineering. By tackling several mathematical challenges, this study provides a conceptual framework for disentangling direct and indirect relationships in association networks. The applications of iDIRECT (Inference of Direct and Indirect Relationships with Effective Copula-based Transitivity) to synthetic, gene expression, and microbial community data demonstrate that it is a powerful, robust, and reliable tool for network inference. As a general approach, iDIRECT has great advantages for complex network studies across diverse disciplines in science and engineering, and allows scientists to address research questions that could not be approached previously.

7. Guo, X., Q. Gao, M. Yuan, G. Wang, X. Zhou, J. Feng, Z. Shi, L. Hale, L. Wu L, A. Zhou, R. Tian R, F. Liu, B. Wu, L. Chen, C. Jung, S. Niu, D. Li, X. Xu, L. Jiang, A. Escalas, L. Wu, Z. He, J.D. Van Nostrand, D. Ning, X. Liu, Y. Yang, E.A.G. Schuur, K.T. Konstantinidis, J. R. Cole, C. R. Penton, Y. Luo, J.M. Tiedje, and **J.-Z. Zhou**. 2020. Gene-informed decomposition model predicts lower soil carbon loss due to persistent microbial adaptation to warming. *Nature Communications*. 11, 4897. doi:10.1038/s41467-020-18706-z.

One grand challenge in ecology is to integrate microbial omics information into ecosystem models to inform large scale ecosystem sciences. With highly integrated experimental and computational

technologies, this is the **first** report demonstrating the feasibility of incorporating microbial functional gene information into soil ecosystem models for improving model predictability. Modeling simulation also revealed persistently warming-induced lower temperature sensitivity of microbial respiration - a critical source of uncertainty in projecting future climate and carbon cycle feedbacks. The results imply that the warming-induced potential positive feedback of soil microbial respiration may be less than previously predicted if such microbially mediated dampening effects occur across different spatial and temporal scales.

8. Ning, D., M. Yuan, L. Wu, Y. Zhang, X. Guo, X. Zhou, Y. Yang, A. P. Arkin, M. K. Firestone, and J.-Z. Zhou. 2020. A quantitative framework reveals ecological drivers of grassland soil microbial community assembly in response to warming. *Nature Communication*, 11:4717. (Highlighted by DOE, <https://www.energy.gov/science/ber/articles/new-approach-helps-determine-how-much-microbial-community-composition-driven>) (**top 1% highly cited**)

Selection, dispersal, diversification, and drift are considered major ecological processes controlling community assembly, but quantifying their contribution to the assembly of ecological communities is extremely difficult. The developed framework to quantitatively infer community assembly mechanisms by phylogenetic bin-based null model analysis (iCAMP) has high precision, sensitivity, specificity, and accuracy. Application of iCAMP to grassland soil microbial communities demonstrates that warming increases homogeneous selection, which has important implications for predicting and mitigating the ecological consequences of climate warming. The developed general framework is useful for not only microbial ecology, but also plant and animal ecology.

9. Ning, D. Y. Deng, J. M. Tiedje, and J.-Z. Zhou. 2019. A General Framework for Quantitatively Assessing Ecological Stochasticity. *Proc. Nat. Acad. Sci.*, 116: 16893-16898. (**top 1% highly cited**)

An ecological community is a dynamic and complex system controlled by various scale-dependent deterministic and stochastic forces. This makes quantifying their relative importance a great challenge. A general mathematical framework was developed to quantify ecological stochasticity with 50% as the boundary for stochasticity evaluation. Applying it to estimate stochasticity controlling the responses of groundwater microbial communities to organic carbon injection demonstrated that this new framework is highly robust and reliable. This study also provides general guidance for the appropriate use of null model-based approaches for examining microbial community assembly processes. These guidelines should also be applicable to plant and animal communities.

10. Zhou, J.-Z., Y. Deng, F. Luo, Z. He, and Y.F. Yang. 2011. Phylogenetic Molecular Ecological Network of Soil Microbial Communities in Response to Elevated CO<sub>2</sub>. *mBio*, 2(4): doi:10.1128/mBio.00122-11. (**Top 1% highly cited**)

Elucidating network interactions and their responses to environmental changes is important but challenging in microbial ecology. This study described a novel random matrix theory (RMT)-based conceptual framework for **unambiguously** identifying interaction networks, and for discerning **keystone** populations, a formidable task in microbial ecology. This is also the **first**

publication to document that network interactions among different phylogenetic and functional populations in soil microbial communities were substantially altered by elevated CO<sub>2</sub> in a long-term climate change experiment, which has important implications in assessing the responses of ecosystems to climate change. This framework will allow microbiologists to address research questions previously unapproachable by focusing on network interactions beyond parts list of species.

### C. Environmental remediation

1. Zhu, C., L. Wu, D. Ning, R. Tian, S. Gao, B. Zhang, J. Zhao, Y. Zhang, N. Xiao, Y. Wang, M. R. Brown, Q. Tu, Global Water Microbiome Consortium, F. Ju, G. F. Wells, J. Guo, Z. He, P. H. Nielsen, A. Wang, Y. Zhang, T. Chen, Q. He, C. S. Criddle, M. Wagner, J. M. Tiedje, T. P. Curtis, X. Wen, Y. Yang, L. Alvarez-Cohen, D. A. Stahl, P. J. J. Alvarez, B. E. Rittmann, and **J.-Z. Zhou**. 2025. *Global Diversity and Distribution of Antibiotic Resistance Genes in Human Wastewater Treatment Systems. Nature Communications*, 16: 4006; doi.org/10.1038/s41467-025-59019-3.

Antibiotic resistance poses a major health threat, with wastewater treatment plants (WWTPs) serving as key ARG reservoirs. By analyzing 226 activated sludge samples from 142 WWTPs across six continents, this study identified a core set of 20 ARGs present in all plants. While ARG abundance remained consistent globally, compositions varied across continents and differed significantly from human gut and ocean resistomes. ARG profiles strongly correlated with bacterial taxonomy, with Chloroflexi, Acidobacteria, and Deltaproteobacteria as major carriers. Most of the recovered genomes contained mobile ARGs, which are shaped primarily by stochastic processes, while abiotic factors played a smaller yet significant role. These findings provide important insights for mitigating ARG dissemination in municipal wastewater systems.

2. Ning, D., Y. Wang, Y. Fan, J. Wang, J.D. van Nostrand, L. Wu, P. Zhang, D.J. Curtis, R. Tian, L. Lui, T.C. Hazen, E.J. Alm, M.W. Field, F. Poole F, M.W.W. Adams, R. Chakraborty, D.A. Stahl, P.D. Adams, A.P. Arkin, Z. He, and **J.-Z. Zhou**. 2024. *Environmental stress mediates groundwater microbial community assembly. Nature Microbiology*, 9:490-501. doi.org/10.1038/s41564-023-01573-x. (**Top 0.1% highly cited hot paper**)

Community assembly is the study of the processes that shape the identity and abundance of species within ecological communities, yet the influences of environmental factors on community assembly remains elusive. A novel framework is developed to conceptualize the relationships between community assembly processes and environmental stresses, applying it to data from a highly contaminated former nuclear waste site—among the world's most heavy-metal polluted groundwaters. As predicted, the relative importance of stochastic assembly processes in shaping community structure decreased as stress increased. In contrast to dispersal limitation and 'drift', heterogeneous selection increased with stresses. These findings underscore the critical roles of microbial dispersal limitation and environmental heterogeneity in ecosystem restoration and management.

3. Wu, L. \*, D. Ning\*, B. Zhang\*, Y. Li, P. Zhang, X. Shan, Q. Zhang, M. Brown, Z. Li, J. D. Van Nostrand, F. Ling, N. Xiao, Y. Zhang, J. Vierheilig, G. F. Wells, Y. Yang, Y. Deng, Q. Tu, A. Wang, Global Water Microbiome Consortium†, Tong Zhang, Z. He, J. Keller, P. H. Nielsen, P. J. J. Alvarez, C. S. Criddle, M. Wagner, J. M. Tiedje, Q. He, T. P. Curtis, D. A. Stahl, L. Alvarez-Cohen, B. E. Rittmann, X. Wen, and **J.-Z. Zhou**. 2019. Global diversity and biogeography of bacterial communities in wastewater treatment plants. *Nature Microbiology*, 4:1183–1195. doi:10.1038/s41564-019-0426-5. (**top 1% highly cited**)

Microorganisms in wastewater treatment plants (WWTPs) are essential for water purification to protect public and environmental health, but their diversity and underlying mechanisms are poorly understood. With ~1200 samples from 269 WWTPs in 23 countries on 6 continents, the global water microbiome consortium (GWMC) revealed various interesting macroecological patterns in worldwide WWTPs. Although global WWTPs have extremely high microbiome diversity (1 billion phylotypes), a small global core, strongly linked to system performance, exists. Unexpectedly, global microbial turnover in these well-controlled engineered ecosystems is largely driven by stochastic, rather than deterministic, processes. These findings have important implications for microbiome manipulation for desired functions and as a model system for microbial ecology in general.

4. Hemme, C.L., S. J. Green, L. Rishishwar, O. Prakash, A. Pettenato, R. Chakraborty, A. M. Deutchbauer, J. D. Van Nostrand, L. Wu, Z. He, I. K. Jordan, T. C. Hazen, A. P. Arkin, J. E. Kostka, and **J.-Z. Zhou**. 2016. Lateral Gene Transfer in a Heavy Metal-Contaminated Groundwater Microbial Community. *mBio*, 7:e02234-15. doi:10.1128/mBio.02234-15.

Comparative genomics studies suggest that lateral gene transfer (LGT) is a major force driving microbial genome evolution, but its role in the evolution of microbial communities remains elusive. It is believed that LGT is critical in shaping microbial community structure, but its direct evidence and rates in extant **natural** microbial communities are still lacking. This study provides explicit evidence of LGT importance in driving the evolution of a groundwater microbial community in response to extreme heavy metal contamination. It appears that acquisition of genes critical for survival, growth, and reproduction via LGT is the most rapid and effective way to enable microbial communities to quickly adapt to abrupt harsh environmental stresses.

5. Hazen, T. C., E. Dubinsky, T. DeSantis, G. Andersen, Y. Piceno, N. Singh, J. Jansson, A. Probst, S. Borglin, J. Fortney, W. Stringfellow, M. Bill, M. Conrad, L. Tom, K. Chavarria, T. Alusi, R. Lamendella, D. Joyner, C. Spier, J. Baelum, M. Auer, M. Zemla, R. Chakraborty, E. Sonnenthal, P. D'haeseleer, H.-Y. Holman, S. Osman, Z.M. Lu, J. van Nostrand, Y. Deng, **J.-Z. Zhou**, and O. U. Mason. 2010. Deep-sea oil plume enriches Indigenous oil-degrading bacteria. *Science*, 330: 204-208. (**Top 1% highly cited**)

The environmental fate of the vast amount of oil from the Deepwater Horizon blowout - the worst environmental disaster in American history, are unknown owing to the depth and magnitude of this event. Primarily with the revolutionary GeoChip-based technology, this study revealed the existence of a variety of hydrocarbon-degrading genes/populations in the deep-sea environment, and strong linkages between particular hydrocarbon-degrading genes and hydrocarbon concentrations, indicating a great potential for *intrinsic* bioremediation of the oil plume, which has

been confirmed by many later studies. This study also provides a shining example on how GeoChip technology can be used in an integrated synergistic fashion to address complex emergent environmental problems, which is a cornerstone of basic science.

6. Hemme, C. L., Y. Deng, T. J. Gentry, M. W. Fields, L. Wu, Z. Fang, S. Barua, K. Barry, S. Green-Tringe, D. B. Watson, Z. He, T. C. Hazen, J. M. Tiedje, E. M. Rubin and **J.-Z. Zhou**. 2010. Metagenomic insights into evolution of a uranium-contaminated groundwater microbial community. *The ISME J*, 5: 660-672. (Highlighted by *The Scientist*, <http://www.the-scientist.com/blog/display/57342/>)

Understanding adaptation of biological communities to environmental change is a central issue in ecology and evolution. Lateral gene transfer (LGT), positive selection and gene duplication are the three main mechanisms driving adaptive evolution of microbial genomes and communities, but their relative importance is unclear. Metagenomic analysis of a stressed groundwater microbial community reveals that prolonged exposure to high concentrations of heavy metals has resulted in a massive decrease in species and metabolic diversity. This is the first community level metagenomic sequencing analysis to document the impacts of environmental contaminants on microbial communities, and to demonstrate the importance of LGT in the adaptation of a microbial community to anthropogenic environmental change.

7. Liu, Yongqing\*, **J.-Z. Zhou**\*, Marina Omelchenko, Alex Beliaev, Amudhan Venkateswaran, Julia Stair, Liyou Wu, Dorothea K. Thompson, Dong Xu, Igor B. Rogozin, Elena K. Gaidamakova, Min Zhai, Kira S. Makarova, Eugene V. Koonin, and Michael J. Daly. 2003. Transcriptome dynamics of *Deinococcus radiodurans* recovering from ionizing radiation. *Proc. Nat. Acad. Sci*, 100: 4191-4196. \*equal contribution. (Reviewed by *Jeremy S. Edwards* and *John R. Battista*. 2003. *TRENDS in Biotechnology*: 21: 381-382).

Ionizing radiation induces DNA double-stranded breaks, which are the most lethal form of DNA damage. Various bacteria such as *Deinococcus radiodurans* R1 can resist the extreme lethal effects of ionizing radiation. However, the molecular mechanisms underlying this phenotype remain poorly understood. This study reports on the whole genome wide regulation of *Deinococcus*'s response to the lethal effects of ionizing radiation. Results suggest that *Deinococcus* can efficiently recover from the radiation damage via complex metabolic network interactions and metabolic pathway switching to prevent additional genomic damage elicited by metabolism-induced free radicals. Numerous previously unsuspected gene candidates and mechanisms that underlie the exceptional radiation resistance were identified.

8. Liu, S., **J.-Z. Zhou**, C.-L. Zhang, D. R. Cole and T. J. Phelps. 1997. Thermophilic Fe(III)-reducing bacteria from the deep subsurface: The evolutionary implications. *Science* 277: 1106-1109.

While thermophilic dissimilatory iron-reducing bacteria are thought to have critical roles in the geochemistry and paleomagnetism of hot primitive planets, non-thermophilic dissimilatory Fe(III)-reducing microorganisms were found in similar environments. This study discovered a unique group of dissimilatory thermophilic metal-reducing and magnetite-producing bacteria in geologically isolated, millions-of-years-old deep subsurface (>860 m), suggesting that

thermophily may be an ancestral feature associated with Fe(III)-reduction. Molecular analyses revealed that these bacteria represent an unrecognized phylogenetic group of dissimilatory Fe(III)-reducing bacteria, which are the oldest (up to 200 million years) viable cultivated bacteria available, and should be valuable in studying life on early Earth and Mars.

#### **D. Theoretical ecology**

9. Guo, X. \*, X. Zhou \*, L. Hale \*, M. Yuan, D. Ning, J. Feng, Z. Shi, Z. Li, B. Feng, Q. Gao, L. Wu, W. Shi, A. Zhou, Y. Fu, L. Wu, Z. He, J. D. Van Nostrand, G. Qiu, X. Liu, Y. Luo, J. M. Tiedje, Y. Yang, and **J.-Z. Zhou**. 2019. Climate warming accelerates temporal scaling of grassland soil microbial biodiversity. *Nature Ecol & Evol*, **3**, 612–619.

Whether and how climate change affects microbial species time relationships (STRs), and phylogenetic time relationships (PTRs) remains unclear, mainly due to the scarcity of long-term experimental data. By examining STRs and PTRs of soil bacteria and fungi in a long-term multifactor experiment with warming, clipping, half precipitation, and double precipitation, this is the first study demonstrating that soil microbes exhibit strong PTRs with the overall rates significantly lower than STRs, and warming played a predominant role in accelerating their temporal scaling rates. These findings on warming-enhanced temporal scaling imply that soil biodiversity preservation and ecosystem management strategies may require adjustments in a warmer world.

10. **Zhou, J.-Z.**, Y. Deng, L. Shen, C. Wen, Q. Yan, D. Ning, Y. Qin, K. Xue, L. Wu, Z. He, J. W. Voordeckers, J. van Nostrand, V. Buzzard, S. T. Michaletz, B. J. Enquist, M. D. Weiser, M. Kaspari, R. Waide, Y. Yang, and J. H. Brown. 2016. Temperature mediates continental-scale diversity of microbes in forest soils. *Nature Communication*, **7**, Article number: 12083, doi:10.1038/ncomms12083. (**Top 1% highly cited**)

Metabolic theory of ecology (MTE) predicts that rising temperature would have dramatic effects on biodiversity. Despite intensive studies in macroecology, how temperature rising affects microbial biodiversity remains elusive. This is the **first** demonstration that temperature plays a primary role in shaping the continental biodiversity of bacteria, fungi and nitrogen fixing bacteria in forest soils, but with substantial lower turnover rates than recorded for trees, and that MTE is applicable to microbial communities as a general fundamental ecological theory. These findings have important implications for understanding and predicting the ecological consequences of human-caused changes in climate, land use, and other factors.

11. **Zhou, J.-Z.**, Y. Deng, P. Zhang, K. Xue, Y. Liang, J. D. Van Nostrand, Y. Yang, Z. He, L. Wu, D. A. Stahl, T. C. Hazen, J. M Tiedje, and A. P. Arkin. 2014. Stochasticity, Succession and Environmental Perturbations in a Fluidic Ecosystem. *Proc. Nat. Acad. Sci.*, **111**: E836-E845. (**Top 1% highly cited**)

Unraveling the rules that govern assembly and succession of biological communities is a central, but poorly understood, topic in ecology. With a newly developed theoretical framework, this is the



**first** time to demonstrate that the succession of groundwater microbial communities is primarily controlled by stochastic rather than deterministic processes as traditional ecological succession theory predicts, and that the drivers controlling biodiversity and community succession are dynamic rather than static. By identifying the mechanisms controlling microbial community assembly and succession, this study makes seminal contribution to the mechanistic understanding essential for a predictive microbial ecology of many systems ranging from microbiomes of humans and plants to natural and managed ecosystems.

12. **Zhou, J.-Z., W. Liu, Y. Deng, Y. Jiang, K. Xue, Z. He, J. D. Van Nostrand, L. Wu, Y. Yang, and A. Wang. 2013. Stochastic assembly leads to alternative communities with distinct functions. *mBio*, 4: e00584-12.**

Understanding how the extremely high diversity of microbial communities is generated and maintained is a central issue in microbial ecology. Although it is well documented that both deterministic and stochastic factors play important roles in shaping biodiversity, the connection between community assembly and ecosystem **functioning** remains elusive. Using many well-controlled replicate bioreactors and GeoChip technologies, this study provides the **first** empirical evidence for the dominant role of stochastic assembly in creating variations of microbial diversity and in influencing ecosystem functioning. These findings represent important contributions to the understanding of the mechanisms, especially the importance of stochastic processes, shaping microbial biodiversity and functions.

13. **Zhou, J.-Z., Sanghoon Kang, Christopher W. Schadt, and Charles T. Garten, Jr. 2008. Spatial Scaling of Functional Gene Diversity across Various Microbial Taxa. *Proc Nat. Acad. Sci.* 105: 7768-7773.**

Species-area relationship (SAR) is one of the principal generalizations demonstrated in plant and animal ecology, but unclear in microbial ecology. Using GeoChip-based metagenomic technologies, this is the **first** study to demonstrate that the forest soil microbial communities exhibit SARs at the **whole** community level across various functional and phylogenetic groups, with spatial turnover rates 2 to 3-fold lower than for plants and animals, which is most likely due to the unique biology of microorganisms. More importantly, this study provides strong evidence to support the general claim that SAR is a universal law in biology. These findings have important implications for biodiversity conservation, ecosystem restoration, environmental management, and climate change.

14. **Zhou, J.-Z., B. C. Xia, D. S. Treves, T. L. Marsh, R. V. O'Neill, L.-Y. Wu, A. V. Palumbo and J. M. Tiedje. 2002. Spatial and resource factors influencing high soil microbial diversity. *Appl. Environ. Microbiol.* 68: 326-334.**

Although it is well known that microbial diversity is extremely high under natural environmental conditions, the underlying mechanisms remain elusive. This study reports **unusual** diversity patterns in microbial communities in surface soils, which are not typical in plant and animal communities. Further **mathematical** simulation indicated that spatial isolation was the key mechanism shaping microbial community structure. This was the **first** study to focus on the mechanisms that control microbial diversity and help explain why microbial diversity is so high

in soils. Further studies are focused on the mechanisms controlling community assembly, and factors (stochastic vs deterministic) shaping microbial community diversity and succession.

#### **E. Climate change biology**

15. Tao, X., Z. Yang, J. Feng, S. Jian, Y. Yang, C. Bates, C. G. Wang, X. Guo, D. Ning, M. Kemper, X. Liu, Y. Ouyang, S. Han, L. Wu, Y. Zeng, J. Kuang, Y. Zhang, X. Zhou, Z. Shi, W. Qin, J. Wang, M. K. Firestone, J. M. Tiedje, and **J.-Z. Zhou**. 2024. Experimental warming accelerates positive soil priming in a temperate grassland ecosystem. *Nature Communications*, 15:1178, [/doi.org/10.1038/s41467-024-45277-0](https://doi.org/10.1038/s41467-024-45277-0).

Soil priming, an effect of fresh plant-derived carbon (C) on native soil organic carbon decomposition, is a key feedback mechanism that could release large amounts of soil C into the atmosphere. This study first demonstrated that climate warming enhances positive soil priming in a temperate grassland ecosystem via altering active microbial functional community structure. This is also the first study to integrate both laboratory metagenomics data and field experimental data to calibrate ecosystem models and demonstrate their effectiveness in improving modeling performance. The findings of this study suggest that soil priming could play a significant role in terrestrial carbon cycle feedback processes and climate change.

16. Zhang, Y., D. Ning, L. Wu, M. M. Yuan, X. Zhou, X. Guo, Y. Hu, S. Jian, Z. Yang, S. Han, J. Feng, J. Kuang, C. R. Cornell, C. T. Bates, Y. Fan, J. P. Michael, Y. Ouyang, J. Guo, Z. Gao, Z. Shi, N. Xiao, Y. Fu, A. Zhou, L. Wu, X. Liu, Y. Yang, J. M. Tiedje, and **J.-Z. Zhou**. 2023. Experimental Warming Leads to Convergent Succession of Grassland Archaeal Community. *Nature Climate Change*, 13: 561–569. <https://doi.org/10.1038/s41558-023-01664-x>.

Despite its fundamental importance in ecology and evolution, little is known about how the Archaea domain responds to warming. Using integrated omics technologies (mainly, amplicon-sequencing, GeoChip), this is the first time to reveal that climate warming reduced grassland soil archaeal diversity, and altered their community functional structure, which had strong impacts on ecosystem functioning. In contrast to our previous observations on bacteria and fungi, experimental warming led to convergent succession of the soil archaeal communities, with stochastic processes of predominant roles. These results imply that, although the detrimental effects of biodiversity loss on ecosystems could be much severer, the soil archaeal community structure would be more predictable in a warmer world.

17. Wu, L., Y. Zhang, X. Guo, D. Ning, X. Zhou, J. Feng, M. M. Yuan, S. Liu, J. Guo, Z. Gao, J. Ma, J. Kuang, S. Jian, S. Han, Z. Yang, Y. Ouyang, Y. Fu, N. Xiao, X. Liu, L. Wu, A. Zhou, Y. Yang, J. M. Tiedje, and **J.-Z. Zhou**. 2022. Reduction of microbial diversity in grassland soil is driven by long-term climate warming. *Nature Microbiology*. 7, 1054–1062 [doi.org/10.1038/s41564-022-01147-3](https://doi.org/10.1038/s41564-022-01147-3). (**top 1% highly cited**)

The rapid loss of biodiversity due to human alternation of the global environment is threatening ecosystem functioning. Soil biodiversity is essential for maintaining the health of terrestrial systems, but how climate change affects soil microbial biodiversity remains elusive. By examining the temporal dynamics of microbial (i.e., bacterial, fungal, and protistan) diversity, this study

provides explicit evidences that climate warming decreases microbial diversity via the concomitant reductions in soil moisture, and the enhanced network interactions under warming. Also, microbial biodiversity has strong linkages with various ecosystem functional processes. These results imply that the detrimental effects of biodiversity loss could be more severe in a warmer world, making future ecosystems more vulnerable.

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One fundamental yet controversial question in network ecology is whether and how the complexity of ecological networks influences ecosystem stability, particularly under future climate change scenarios. By examining the temporal changes of grassland soil microbial communities in response to long-term experimental warming, this study provides the **first** evidence that climate warming enhances network complexity, which begets the stability of the networked microbial communities. The warming-enhanced network complexity and stability is also more tightly associated with microbial community functional structure and ecosystem functional processes. These results imply that preserving microbial interactions could be important to mitigate the detrimental effects of warming-induced biodiversity loss on ecosystem functions.

19. Gao, Q., G. Wang, K. Xue, Y. Yang, J. Xie, H. Yu, S. Bai, F. Liu, Z. He, D. Ning, S. Hobbie, P. Reich, and **J.-Z. Zhou**. 2021. *Stimulation of soil respiration by elevated CO<sub>2</sub> is enhanced under nitrogen limitation in a decade-long grassland study*. *Proc. Nat. Acad. Sci.*, doi.org/10.1073/pnas.2002780117.

Discerning the interactive effects of nitrogen (N) and CO<sub>2</sub> on soil respiration is critical to projecting future carbon-climate feedbacks. By examining the interactive effects of CO<sub>2</sub> and N enrichment in a decade-long experiment (BioCON), this study demonstrated that N limitation strengthened the stimulatory effects of elevated CO<sub>2</sub> on soil respiration, primarily via N mining during the decomposition of more recalcitrant organic compounds. This study also provides a novel strategy for integrating genomics information into ecosystem models for improving modeling predictions. Considering the worldwide N limitation in natural environments, the results imply that the heightened release of CO<sub>2</sub> back to the atmosphere from soil may be pervasive under conditions of persistent N limitation.

20. Guo, X., J. Feng, Z. Shi, X. Zhou, M. Yuan, X. Tao, L. Hale, T. Yuan, J. Wang, Y. Qin, A. Zhou, Y. Fu, L. Wu, Z. He, J. D. V. Nostrand, D. Ning, X. Liu, Y. Luo, J. M. Tiedje, Y. Yang, and **J.-Z. Zhou**. 2018. *Climate Warming Leads to Divergent Succession of Grassland Microbial Communities*. *Nature Climate Change*. 8:813-818, 10.1038/s41558-018-0254-2 (**Top 1% highly cited**)

Whether and how climate warming affects the succession of ecological communities and their underlying mechanisms remains elusive. This study is the **first** to demonstrate that warming played an important role in accelerating temporal succession of soil microbial communities towards

higher divergence. While stochastic processes play dominant roles in controlling microbial responses to warming, experimental warming reduces stochasticity as time proceeds by acting as a filtering factor. Our results imply that, although successional trajectories of microbial communities are difficult to predict under future climate change scenarios, their composition and structure are projected to be less variable because of warming-driven selection.

21. Xue, K., M. M. Yuan, Z. J. Shi, Y. Qin, Y. Deng, L. Cheng, L. Wu, Z. He, J. D. Van Nostrand, R. Bracho, S. Natali, E. A. G. Schuur, C. Luo, K. T. Konstantinidis, Q. Wang, J.R. Cole, J. M. Tiedje, Y. Luo, and **J.-Z. Zhou**. 2016. Tundra soil carbon is vulnerable to rapid microbial decomposition under climate warming. *Nature Climate Change*, 6: 595-600, doi:10.1038/nclimate2940. (**Top 1% highly cited**)

How microorganisms respond to warming is critical to determine the carbon-climate feedback of the northern permafrost which stores >30% of global soil C, a wildcard that could alter the future trajectory of climate change. Using integrated metagenomic technologies, particularly GeoChip, this study reported a rapid response of the tundra microbial communities to only 1.5 years of experimental warming, demonstrating the *in situ* **vulnerability** of tundra soil C and the importance of microbes in mediating such vulnerability. These findings have important implications for future climate projection. This study was highlighted as a breakthrough in tundra ecosystem studies by *The Washington Post*, ASM in *MICROBES*, and DOE OBER.

22. **Zhou, J.-Z.**, K. Xue, J.-P. Xie, Y. Deng, L.Y. Wu, X.L. Cheng, S.F. Fei, S.P. Deng, Z.-H. He, J.D. van Nostrand, and Y.Q. Luo. 2012. Microbial Mediation of Carbon Cycle Feedbacks to Climate Warming. *Nature Climate Change*, 2:106-110. (**Top 1% highly cited**)

Feedback between terrestrial carbon and climate warming is one of the major uncertainties in projecting future climate change, primarily owing to the poor understanding of microbial responses to climate warming. Using integrated genomics technologies, this study discovered that microorganisms play crucial roles in regulating soil carbon dynamics through three primary feedback mechanisms: (i) shifting microbial community composition, (ii) differentially stimulating functional genes for degrading labile but not recalcitrant carbon, and (iii) enhancing nutrient-cycling processes. These findings suggested that the microbial community functional structure determines whether microbially mediated feedbacks are positive or negative, which provides a mechanistic basis for future carbon–climate modelling.