

## Significant representative publications

(As of 12/31/2022)

### Summary statistics of publications:

- Over 600 peer reviewed publications, h-index of **135**, >65,000 citations (GS); H-index of **117**, > 48,000 citations (Web of Sci), <https://scholar.google.com/citations?user=4ho6TVUAAAAJ&hl=en>
- **33** publications in Science, Nature-branded journals, and PNAS
- **164** papers published in **Nature indexed journals**, such as *Science* (4), *Nature Climate Change* (4), *PNAS* (12), *Nature Communication* (8), *Ecology Letters* (2), *The ISME Journal* by Nature Publishing Group (50) (The top one journal in microbial ecology), *Environmental Science & Technology* (24), *Water Research* (12), and *Geochimica et Cosmochimica Acta* (2), and other prestigious journals, e.g., *Nature Ecology and Evolution* (2), *Nature Microbiology* (2), *Nature Review in Microbiology* (2), *Nature Plants* (1), *Microbiology and Molecular Biology Reviews* (1), *mBio* (23), *Ecology* (1), and *Global Change Biology* (14).
- **Impacts:** Globally top 0.1% highly cited researcher by all three complementary metrics
  - ✓ World's most cited researcher (top 0.07% ) across all science & engineering fields among 9M scientists based on Elsevier's *Scopus* (<https://elsevier.digitalcommonsdata.com/datasets/btchxktzyw>).
  - ✓ Among the top 0.1% of the world's highly cited researchers (total of 6,938 scholars across 21 research fields) the field of Microbiology, and the field of Environment & Ecology, <https://clarivate.com/highly-cited-researchers/>
  - ✓ Most highly cited researcher (H-index > 100) according to their Google Scholar Citations (<http://www.webometrics.info/en/hlargerthan100>), (position at 2051; global total 5,882).
  - ✓ Among the 2021 Reuters List of World's Top 1000 Climate Scientists (<https://www.reuters.com/investigates/special-report/climate-change-scientists-list/>).

1. 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).

The rapid loss of biodiversity due to human alteration 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.

2. Xiao, N., A. Zhou, M. L. Kempfer, 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>.

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.

3. Yuan, M., X. Guo, L. Wu, Y. Zhang, N. Xiao, D. Ning, Z. Shi, X. Zhou, L. Wu, Y. Yang, J. M. Tiedje, and **J.-Z. Zhou**. 2021. Climate Warming Enhances Microbial Network Complexity and Stability. *Nature Climate Change*, 10.1038/s41558-021-00989-9. (Highlighted by DOE, <https://www.energy.gov/science/ber/articles/warming-soil-means-stronger-microbe-networks>) (Hot paper, Top 0.1% highly cited)

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.

4. 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.

5. 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. (**hot paper, top 0.1% 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.

6. 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.

7. 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

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.

8. 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.

9. **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.

10. **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.

11. **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.

12. 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.

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.

15. 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.

16. **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 ~ **3800** 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.