

## 12 significant representative publications

(As of 3/17/2020)

Numerous papers have been published with total citations of >31,000, H-index, **93** based on Web of Science; Google Scholar Citations >42,000, H-index, **108** based on Google Scholar; (a) 2018, 2019 Global highly cited researcher in Cross-field based on numbers of top 1% highly cited publications by Web of Science. <https://hcr.clarivate.com/>; (b) World's most cited researcher (>99.8% percentile) of ~7 millions scientists across all science and engineering fields (176 subfields of 22 fields) by a composite metric based on the Scopus database from Elsevier (<https://doi.org/10.1371/journal.pbio.3000384>). (c) Most highly cited researcher (H-index > 100) according to their Google Scholar Citations A total of **135** papers published in Nature indexed journals, such as *Science* (4), *Nature Climate Change* (3), *PNAS* (10), *Nature Communication* (4), *Ecology Letters* (2), *The ISME Journal* by Nature Publishing Group (45) (The top one journal in microbial ecology), *Environmental Science & Technology* (22), *Water Research* (10), and *Geochimica et Cosmochimica Acta* (2), and other prestigious journals, e.g., *Nature Ecology and Evolution* (2), *Nature Microbiology* (1), *Nature Review in Microbiology* (2), *Nature Plants* (1), *Microbiology and Molecular Biology Reviews* (1), *mBio* (16), *Ecology* (1), and *Global Change Biology* (9).

1. 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.

Microorganisms in wastewater treatment plants (WWTPs) are essential for water purification to protect public and environmental health. However, their diversity and the underlying mechanisms are poorly understood. To this end, a global water microbiome consortium (GWMC) was established across more than 70 research groups from 23 countries. Using a systematic global-sampling effort, the 16S rRNA gene sequences from ~1,200 activated sludge samples from 269 WWTPs in 23 countries on 6 continents were analyzed to address theoretical questions, such as species abundance distributions, extent of global microbial diversity, global core bacterial community, latitudinal diversity pattern, scale-dependent distance-decay patterns, structure-functions relationships, and community assembly mechanisms. This is the first comprehensive global scale study to address various theoretical questions in engineered systems. Our results demonstrated extremely high microbiome diversity of global wastewater treatment plants, with a small global core strongly linked to system's performance. Unexpectedly, global microbial turnover is largely driven by stochastic processes. The findings of this study highlight how little we know of the world's microbiome, even in one of the most common and well-controlled systems in the built environment, and have important implications for microbial ecology and wastewater treatment processes.

2. 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.

Determining temporal scaling of biodiversity, typically described as species time relationships (STRs), in the face of global climate change is a central issue in ecology, because it is fundamental to biodiversity preservation and ecosystem management. However, whether and how climate change affects microbial STRs remains unclear, mainly due to the scarcity of long-term experimental data. This study examined STRs and phylogenetic time relationships (PTRs) of soil bacteria and fungi in a long-term multifactor global change experiment with warming, half precipitation, double precipitation and clipping (annual plant biomass removal). By examining the temporal scaling of soil bacteria and fungi across different treatments, this study provides explicit evidence that STRs exist for bacteria and fungi, and their lineages. This is the first study showing that soil microbes exhibit strong PTRs, with the overall rates significantly lower than STRs. This is also the first time to demonstrate that warming played a predominant role in accelerating both taxonomic and phylogenetic temporal scaling rates of soil microbial communities. The results on warming-enhanced temporal scaling of microbial biodiversity imply that the strategies of soil biodiversity preservation and ecosystem managements may require adjustments in a warmer world.

3. 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

Understanding the succession, adaptations and mechanisms of biological communities in response to environmental changes, especially anthropogenic changes, is a central issue in ecology and for society. However, very little is known about whether and how climate warming affects the succession of ecological communities, and their underlying mechanisms. This study is the **first** to demonstrate that warming played an important role in accelerating temporal succession towards higher divergence, stochastic processes played dominant roles in controlling the responses of soil microbial communities to climate warming, and experimental warming, acting as a filtering factor, reduced stochasticity as time proceeds. 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 due to warming-driven selection.

4. 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.

The northern permafrost stores more than 30% of the global soil organic C, which is a wildcard that could alter the future trajectory of climate change. How microorganisms respond to

warming (speed, direction, magnitudes) is critical to determine the fates of permafrost C and the feedbacks of the permafrost ecosystems to climate warming. Although a laboratory study indicated that microbial communities can respond to temperature increase rapidly, evidence from **field experiments** remains scarce. Using integrated metagenomic technologies, particularly GeoChip, this study reported a rapid response of the tundra microbial communities to experimental warming after only 1.5 years of warming. This is the **first** comprehensive field study demonstrating the *in situ* **vulnerability** of tundra soil C to climate warming and the importance of microbial communities in mediating such vulnerability. The results presented in this study have important implications for future climate projection. This study was highlighted as a breakthrough in tundra ecosystem studies by *The Washington Post* (<http://wpo.st/O4GE1>), and it was also specifically highlighted by ASM in its *MICROBES* publication, and DOE OBER. This paper is ranked as the top 1% highly cited based on Web of Science.

5. **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

Climate warming is increasingly leading to dramatic changes in plant and animal biodiversity, but it remains unclear how temperature rising affects microbial biodiversity, particularly in terrestrial soils. In this study, we showed that taxonomic and phylogenetic diversity of soil bacteria, fungi, and nitrogen fixing bacteria all are better predicted by variation in environmental temperature rather than pH, which is consistent with metabolic theory of ecology (MTE). But, the rates of diversity turnover across global temperature gradients are substantially lower than that recorded for trees. These results indicate that the diversity of plant, and animal, and soil microbial communities will show differential responses to climate change. This study clearly demonstrate that the diversity of different microbial groups has significantly lower rates of turnover across temperature gradients than other major taxa, which has important implications for assessing the effects of human-caused changes in climate, land use, and other factors. This is the **first demonstration** that temperature plays a primary role in shaping microbial diversity in the forest soils, but it could operate in different ways between plants and microorganisms, and that MTE is applicable to microbial communities.

6. **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

Unraveling the rules that govern assembly and succession of biological communities is a central topic, but poorly understood, in ecology. It is generally believed that both deterministic and stochastic processes play important roles in shaping community composition and structure, but their relative importance remains elusive. To understand their relative importance in mediating microbial community assembly and succession, a novel framework comprised of four theoretical models was proposed and tested with a fluidic groundwater ecosystem after nutrient addition. This study showed that community assembly and succession were driven by a dynamic, time-dependent interaction of stochastic and deterministic processes, with

stochastic forces dominating. This is the **first** time to demonstrate that community succession responding to nutrient amendment is primarily controlled by stochastic processes, rather than deterministic processes as traditional ecological succession theory predicted. This is also the **first** demonstration showing 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 natural and managed ecosystems. The importance of this study is evidenced as Editor's Pick in PNAS and Genomeweb. This study was also highlighted by OBER (<http://genomicscience.energy.gov/program/berhighlights.cfm>) as OBER Research Highlights. It is listed as a highly cited publication (top 1%) in Web of Science. More recently, based on this study, a general null-model-based framework was further developed (*Proc. Nat. Acad. Sci.*, 116: 16893-16898), which provides an effective and robust tool to ecologists for quantitatively assessing ecological stochasticity.

7. **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 such as PCR-based-amplicon sequencing has revolutionized the studies of microbial communities, it suffers from several inherent drawbacks such as high sequencing errors, biases, poor quantitation, and very high technical variations, which could greatly overestimate microbial biodiversity. Based on general sampling theory, in this study, mathematical approaches were developed to predict and minimize the artifacts associated with random sampling processes. Along with a previous study in ISME Journal (ISME J, 5:1303, top 1% highly cited), our study was the **first** to document the low reproducibility problem of high throughput sequencing-based detection technology, discern the phenomenon of random sampling artifacts in comparing community diversity across different samples, and provide the first **explicit** evidence to demonstrate the importance of random sampling processes in estimating microbial  $\beta$ -diversity, which has not been adequately recognized and addressed in microbial ecology. As indicated by a mBio Editor as **Editor's Pick**, this study would make a fundamental contribution for designing and interpreting microbiome research because high throughput sequencing technologies have been widely used in microbial ecology. Since most ecological studies are involved in random sampling, the conclusions learned from this study should also be applicable to other ecological studies in general.

8. **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.

Although understanding the responses and adaptations of biological communities to environmental changes is critical in ecology, how microbial communities respond to environmental changes is poorly understood and controversial. Using integrated genomics technologies with isotope and ecosystem process analysis, 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 genes for degrading labile but not recalcitrant carbon, and (iii) enhancing nutrient-cycling processes. These results have fundamental implications for projecting future climate change. Currently, global climate models have ignored the importance of microbial communities in regulating carbon dynamics. However, this study indicated that ecological models must consider incorporating the dynamics of microbial communities for more accurate and reliable predictions. Furthermore, identification of coherent fingerprints to signature climate warming is of a great challenge. The results from this study also provide key signatures to identify positive or negative feedbacks of microbial communities to climate warming, which could then be incorporated for modeling prediction. In a word, these results represent groundbreaking discoveries in global change biology, and ranked by Faculty 1000 as the top 2% of the published articles in biology and medicine, and as a highly cited publication (top 1%) in Web of Science.

9. **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.

In an ecosystem, various microorganisms interact with each other to form complicated networks. Elucidating such network interactions and their responses to environmental changes is an important topic in ecology, but is of a grand challenge in microbial ecology. Although high-throughput metagenomic technologies can rapidly produce a massive amount of data, one of the greatest difficulties is how to extract, analyze, synthesize, and transform such a vast amount of information into biological knowledge. This study described a novel random matrix theory (RMT)-based conceptual framework to analyze metagenomics data for **unambiguously** identifying interaction networks in microbial communities, and presents unique strategies to discern **keystone** populations, which is a formidable task in microbial ecology. Also, this study, along with a previous study (mBio, 1: e00169-10), is the **first** to document that the network interactions among different phylogenetic and functional populations in soil microbial communities were substantially changed by a global change factor such as an elevated CO<sub>2</sub> level, which could have important implications in assessing the responses of ecosystems to climate change. The novel framework developed in this study will allow microbiologists to address research questions unapproachable previously by focusing on network interactions (i.e. beyond the parts list).

10. **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.

Due to the vast diversity and as-yet uncultivated status, detection, characterization and quantification of microorganisms in natural settings are very challenging, and linking microbial biodiversity to ecosystem processes and functions is even more difficult. To meet these challenges, a revolutionary, high throughput technology (GeoChip) for addressing a central goal in microbial ecology --linking community structure to function. GeoChip was

highlighted in the NRC's report on the *New Science of Metagenomics* (2007), and in the roadmap for NSF's National Ecological Observatory Network (NEON, 2009), and won a R&D 100 Award in 2009 as one of 100 most innovative scientific and technological breakthroughs. Several generations of GeoChip (e.g. GeoChip 2.0 in 2007. *ISMZ J.* **1**:67-77, Among the 5 top-cited articles in *ISME J* in last 10 years; GeoChip 5.0 in 2019. *mSystems* **4**:e00296-19) were developed and used to analyze microbial communities from a variety of environments. As an example, in this study, GeoChip was used as the **primary** tool for assessing the shifts of microbial **functional** composition, structure and activities in response to oil spill of the deep-sea in the Gulf of Mexico --- which was described by President Barack Obama in a prime-time address as "the worst environmental disaster America has ever faced". GeoChip analysis revealed that a variety of hydrocarbon-degrading genes/populations exist in the deep-sea environment, and there were strong linkages between particular hydrocarbon-degrading genes and the hydrocarbon concentrations in the Deep Horizon oil. Primarily based on GeoChip results, along with other integrated analyses, this study convincingly concluded that the potential exists for *intrinsic* bioremediation of the oil plume in the deep-sea, which has been confirmed by many other studies. A subsequent publication with GeoChip data alone in *ISME J* (**6**: 451-460) was particularly highlighted by *Science for Environment Policy* of European Commission ([http://ec.europa.eu/environment/integration/research/research\\_alert\\_en.htm](http://ec.europa.eu/environment/integration/research/research_alert_en.htm)). This and many other studies clearly demonstrated that GeoChip is an excellent, unique high throughput technology for enabling comprehensive visualization of the functional structure of microbial communities and for establishing the relationships between biodiversity and ecosystem functioning - a central goal in microbial ecology. More importantly, this study provides a shining example on how GeoChip technology is used in an integrated synergistic fashion to address complex emergent environmental problems, which is a cornerstone of basic science.

11. **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.

Determining the spatial scaling of organisms and the underlying mechanisms shaping biotic communities is a central goal in community ecology. One of the most well documented spatial patterns in plant and animal communities is taxa-area relationship (TAR), which is one of the principal generalizations in ecology. TAR is fundamental to our understanding of the distribution of global biodiversity, but remains elusive in microbial communities. Using GeoChip-based metagenomic technologies, this is the **first** study to demonstrate that the forest soil microbial communities exhibit TARs at **whole** community level across various functional and phylogenetic groups, all with  $z$  values  $< 0.1$ . This study also revealed that the spatial turnover rates of microbial communities ( $z$  values,  $< 0.1$ ) are generally lower than those observed in plants and animals (with typical  $z$  values of 0.25), which are most likely due to the unique biology of microorganisms. More importantly, this study provides strong evidence to support the general claim that TAR is a universal law in biology. The results presented in these studies have important implications for biodiversity conservation, ecosystem restoration, environmental management, and climate change. The conclusions presented in this study are

supported by several of our more recent studies (Deng et al. 2018. *Environ. Microbiol.* In press; Liang et al. 2015. *mBio*, 6: e00240-15).

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

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 by citations of > **3300** times based on Google Scholar. It is among the **12** most cited papers in Applied and Environmental Microbiology (2008-2019 statistics). Because it recovers high molecular weight pure DNA from soils with high yields and purity, this method laid a **foundation** for the widely used metagenomics (by Jo Handelsman) and other molecular microbial ecology studies.