COMMENTARY



Linkage between microbial shift and ecosystem functionality

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Funding information

Strategic Priority Research Program A (XDA20050104 and XDA1907304) and the Second Tibetan Plateau Scientific Expedition and Research (STEP) program (2019QZKK0304) of Chinese Academy of Sciences.

Microbial shifts induced by permafrost thaw have been reported previously (e.g. Yuan et al., 2018); however, their linkage to permafrost carbon (C) release remains elusive. Clearly, permafrost C-climate feedbacks are determined, or at least mediated, by not only how microbes respond to permafrost thaw, but also what microbial responses mean for ecosystem functionality. Chen et al., (2020) provide experimental evidence demonstrating that increases in microbial functional diversity and C decomposition gene abundances, rather than taxonomic shifts, are associated with permafrost C release upon permafrost thaw. This work represents a valuable step towards elucidating the ecological consequences of microbial shifts, thus detangling uncertainties in understanding and predicting permafrost C-climate feedback (Xue, Xie, et al., 2016).

As permafrost thaw is predicted to become more extensive under climate change (Chadburn et al., 2017), elucidating the linkage between microbial shifts and permafrost C release upon permafrost thaw is especially important for enhancing our understanding of global C cycling. With a storage of ~50% of global belowground C, permafrost thaw may trigger the greatest positive ecosystem feedback to climate change on our planet (Xue et al., 2016) due to accelerated microbial decomposition activities in soil organic matter, otherwise preserved by low temperature and water saturation. Although it has received less attention, the importance of microbial functional gene shifts, rather than taxonomic shifts, was highlighted by Chen et al., (2020). The well-established linkage between functional genes (reflecting genetic potential) and C release via laboratory incubation (reflecting field potential) is a good start that provides clues about the magnitude of in situ permafrost C release under permafrost thaw on the basis of microbial functional gene changes.

The study by Chen et al., (2020) was conducted on the Tibetan Plateau, which has the largest high-altitude permafrost and experiences approximately twice the warming effect as the global average. However, most current permafrost studies on global climate change have been conducted in high-latitude rather than high-altitude permafrost regions. High-altitude permafrost ecosystems on the Tibetan Plateau generally differ from high-latitude ecosystems in a number of ways (e.g. containing relatively ice-poor soils with lower soil organic matter), likely leading to distinct microbial communities that respond differently to permafrost thaw. Thus, investigations on high-altitude permafrost on the Tibetan Plateau are essential for understanding global C cycling, especially with regard to the vital role of the Tibetan Plateau in regulating the regional and even global climate.

Exploring the linkage between microbial shifts and ecological processes or ecosystem functionality is a central focus in microbial ecology. However, a few obstacles theoretically impede investigative attempts. A large gap exists between DNA-based information and biochemical processes. DNA-based technologies dominate current microbial ecology studies because of their relatively high repeatability compared to enzyme measurements, and the enhanced feasibility and ability to reflect cumulative effects compared to RNA-based technologies (Xue, Yuan, et al., 2016). However, DNA-based information is generally believed to not directly reflect the actual activity of active microbial populations. Greater abundances of certain functional genes would not necessarily represent increased gene expression and subsequent increased translation into the

This article is a Commentary on Chen et al, 27, 3218-3229.

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corresponding enzymes. There is even a gap between enzyme activities and in situ ecosystem process rates. It is challenging to quantify the relative contributions of individual enzymes involved in the same or various pathways, regardless of the complex interactions and mediating factors.

Moreover, asynchronization may exist in microbial shifts and changes in microbial functionality. It has been widely reported that plant structural composition shifts do not necessarily indicate ecosystem function changes, and usually occur with a hysteresis in functionality (e.g. Hao et al., 2020). Similarly, the taxonomic and functional attributes of the soil microbial community were uncoupled by Chen et al., (2020). Functional redundancy is commonly used to explain the asynchronization or discrepancy between taxonomic shifts in plant or microbial communities and their functionality. If multiple taxa involve the same or complementary functions, destruction or disturbances on the part of these taxa would not affect the corresponding ecosystem functions as a whole. This may explain why the taxonomic shift was not linked to biochemical processes in many cases. However, if functionality becomes redundant, there is no way to observe a clear linkage between changes in microbial functional diversity or C decomposition gene abundance with permafrost C release upon permafrost thaw. Therefore, we would prefer to express functional redundancy as 'function potential redundancy', reflecting a more precise meaning.

Despite these obstacles, the linkage between microbially functional gene changes and biochemical processes has been discovered for obligatory processes (e.g. methanogenic process; Jiang et al., 2010) or even non-obligatory processes such as permafrost C release (Chen et al., 2020). The abundance of certain functional genes in a microbial community as a whole may reflect the corresponding microbial activities, to a certain extent, in habitats where the microbial community has long been adapted to the local environment. The ontological kind of parsimony principle (Ockham's razor) assumes the 'simplicity of nature', which may explain this phenomenon, even though it might be refuted in some cases (Crisci, 1982). Currently, microbial functional gene analysis could possibly be performed on a large scale, while the measurement for in situ permafrost C release could not. Thus, the findings of Chen et al., (2020) inspire the possible adoption of microbial functional gene information as a proxy for field potential in Earth system models to predict future climate scenarios.

However, attention must be paid when extrapolating conclusions across various scales that are likely regulated by distinct laws (e.g. from molecular to ecosystem levels, or from laboratory incubation to in situ field dynamics). Permafrost thaw in the field is more complex than laboratory incubation, which supplies a constant temperature above 0°C in an optimally controlled condition, as stated by Chen et al., (2020). Freeze-thaw cycles may occur in the field and influence soil microbial communities in more complex ways. Other than biological processes, physical changes play critical roles in permafrost C release during freeze-thaw cycles. Thus, better simulation of these processes would be key for further enhancing our understanding of microbial responses and their ecological consequences.

For future perspective, non-linear linkages between microbial shifts and ecosystem functionality should be considered, and novel methods for elucidating their cause and effect would be needed to overcome the current bottleneck of research in microbial ecology. Ecosystems may have non-linear responses to permafrost thaw, or the relationship between microbial shifts and permafrost C release could be non-linear. If so, a more sophisticated methodology in experimental design (e.g. including a gradient of temperature increases in controlled experiments), more comprehensive data analyses (e.g. piecewise regression rather than correlation or linear regression) and increased sample size to enhance the representativeness of various conditions are necessary to fully quantify these non-linear responses or relationships and identify thresholds that are critical for modelling. More importantly, linkage or correlation represents a lack of cause and effect to a certain extent in most current microbial ecology studies. In future studies, we must pave the way for innovative, if not revolutionary, means to manipulate microbial communities (e.g. Zhang et al., 2019), which may entail more straightforward demonstrations of the consequences of microbial shifts.

ACKNOWLEDGEMENTS

This work is supported by the Strategic Priority Research Program A (XDA20050104 and XDA1907304) and the Second Tibetan Plateau Scientific Expedition and Research (STEP) program (2019QZKK0304) of the Chinese Academy of Sciences.

CONFLICT OF INTEREST

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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How to cite this article: Wang Y, Xue K. Linkage between microbial shift and ecosystem functionality. *Glob Change Biol.* 2021;27:3197–3199. https://doi.org/10.1111/gcb.15615