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δ13C compositions of bacteriohopanetrol isomers reveal bacterial processes involved in the carbon cycle

Rachel Schwartz-Narbonne[1,2], Philippe Schaeffer[3], Sabine Lengger[4,5], Jerome Blewett[4], D. Martin Jones[1], Estelle Motsch[3], Alex Charlton[1], Andrew Crombie[6], Scott Hardy[2], Muhammad Farhan Ul Haquee[7,8], Mike S. M. Jetten[9], Deirdre Mikkelsen[10], Philippe Normand[11], Guylaine H. L. Nuijten[9], and Darci Rush[1,12]

[1]School of Natural and Environmental Sciences, Newcastle University, Newcastle upon Tyne, United Kingdom of Great Britain – England, Scotland, Wales
[2]Sheffield Hallam University, Biomolecular Sciences Research Center, Sheffield, United Kingdom of Great Britain – England, Scotland, Wales
[3]CNRS, Université de Strasbourg, Strasbourg, France
[4]Organic Geochemistry Unit, University of Bristol, Bristol, United Kingdom of Great Britain – England, Scotland, Wales
[5]Biogeochemistry Research Centre, University of Plymouth, Plymouth, United Kingdom of Great Britain – England, Scotland, Wales
[6]School of Biological Science, University of East Anglia, Norwich, United Kingdom of Great Britain – England, Scotland, Wales
[7]School of Environmental Sciences, University of East Anglia, Norwich, United Kingdom of Great Britain – England, Scotland, Wales
[8]School of Biological Sciences, University of the Punjab, Lahore, Pakistan
[9]Department of Microbiology, Radboud University, Nijmegen, the Netherlands
[10]School of Agriculture and Food Sciences, The University of Queensland, Brisbane Australia
[11]Ecologie Microbienne, Université de Lyon, Lyon, France
[12]Department of Marine Microbiology and Biogeochemistry, NIOZ Royal Netherlands Institute for Sea Research, Den Burg, the Netherlands

Bacteria play key roles in the carbon cycle. In many sediments and peatlands, methanotrophic bacteria consume a portion of released methane, reducing the emissions of this potent greenhouse gas. In marine oxygen minimum zones (OMZ) and other anoxic settings, anaerobic ammonium oxidizing (anammox) bacteria remove bioavailable nitrogen while performing chemoautotrophic carbon fixation. Methanotrophic and anammox bacteria synthesize a wide number of complex bacteriohopanepolyols (BHPs), comprising notably several stereoisomers of bacteriohopanetetrols (BHT), which are used as biomarker lipids. While BHT-17β(H), 21β(H), 22*R*, 32*R*, 33*R*, 34*S* (BHT-34*S*) is ubiquitous in the environment, its 34*R* stereoisomer (BHT-17β(H), 21β(H), 22*R*, 32*R*, 33*R*, 34*R*; BHT-34*R*) has only five known producers: the freshwater anammox genera '*Candidatus* Brocadia', the aerobic acidic peatland methanotroph *Methylocella palustris*, the nitrogen-fixing aerobic bacteria *Frankia* spp., and the aerobic acetic acid-producing bacteria *Acetobacter pasteurianus* and *Komagataeibacter xylinus*. BHT-*x*—another BHT isomer of unknown stereochemistry—has only one known producer, the marine anammox bacteria '*Candidatus* Scalindua' (Schwartz-Narbonne et al., 2020). The occurrence and extent of these

different carbon cycle processes can be assessed by measuring the concentrations of these BHT stereoisomers and changes in their $\delta^{13}C$ values (Hemingway et al., 2018; Lengger et al., 2019).However, the ^{13}C fractionation associated with the different carbon assimilation pathways of these bacteria has been minimally assessed, resulting in poorly constrained ranges in $\delta^{13}C$ values and difficulty in interpreting isotope results.

We used a gas chromatography-combustion-isotope ratio mass spectrometry (GC-C-IRMS) method to measure the $\delta^{13}C$ of BHT-34*S*, BHT34*R*, and BHT-*x* of cultured bacteria ('*Ca*. Scalindua', '*Ca*. Brocadia', *Methylocella tundrae*, *Frankia* spp., and *Komagataeibacter xylinus*). These $\delta^{13}C$ values were combined with bulk isotopic measurements of the bacterial biomass and $\delta^{13}C$ analyses of the bacterial growth substrates to establish carbon isotopic fractionation from substrate to biomass to BHT lipid. We demonstrated that bacteria using different metabolic pathways produced distinct fractionation factors between substrate and BHTs, which potentially allows for distinguishing BHT-34*R* produced by '*Ca*. Brocadia' and methanotrophs from other freshwater producers (e.g. in peatlands). Measurement of BHT-specific fractionation factors allowed us to better constrain the contribution of anammox bacteria to fixed carbon in OMZ. This work expands the application of BHT isomers to isotopically identify carbon cycle processes.

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