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Experimental evidence that microbial activity lowers the albedo of glaciers

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Abstract

Darkening of glacier and ice sheet surfaces is an important positive feedback to increasing global temperatures. Deposition of impurities on glaciers is primarily believed to reduce surface albedo, resulting in greater melt and mass loss. However, no study has yet included the effects of biological activity in albedo reduction models. Here, we provide the first experimental evidence that microbial activity can significantly decrease glacier surface albedo. Indeed, the addition of nutrients at ice meltwater concentrations to microbe-impurity mixtures resulted in extensive microbial organic carbon fixation and accumulation in Greenland Ice Sheet surface debris. Accumulated organic carbon, over the period of a melt season, darkened the glacial debris in our experiments from 31.1 % to 15.6 % surface reflectivity (used as an analogue for albedo in our calculations), generating a strongly absorbing surface. Our experiments are the first to quantify the microbially-induced potential melt increase for the Greenland Ice Sheet (up to an average of 17.3 ± 2.5 Gt yr^{-1} at present and up to ~85 Gt yr^{-1} by 2100, based on our first order calculations). Mass loss from glaciers will conceivably intensify through enhanced microbial activity, resulting from longer melt seasons and fertilisation from anthropogenic sources.

Introduction

Glacier surfaces melt primarily by the absorption of solar radiation, which depends on the surface albedo (Boggild *et al.*, 2010; Box *et al.*, 2012). Albedo is affected by the physical properties of snow and ice, such as the geometric pattern of the snow surface (Pirazzini, 2004), snow metamorphism (Nakamura *et al.*,

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2001), water content (Ryser *et al.*, 2013) and particulate impurities on the glacier surface (Paterson, 1994). Most studies assume that the accumulation of inorganic and organic particulates, such as anthropogenic and naturally occurring black carbon (Doherty *et al.*, 2013), volcanic ash and dust (Dumont *et al.*, 2014), are key drivers of the darkening and reduction of the ice albedo.

Recent research shows that there is high microbial activity on glacial surfaces (Anesio *et al.*, 2009), some associated with pigmented algae, which absorb significantly more light than local inorganic dust particles on the Greenland Ice Sheet (GrIS) (Lutz *et al.*, 2014). Furthermore, microbially-rich glacier surface debris (cryoconite) reduces the glacier surface (supraglacial) albedo (Takeuchi *et al.*, 2001). Cryoconite accumulates in water-filled holes on glacier surfaces, causing enhanced melting around the deposited sediment (Fountain *et al.*, 2004). These so-called cryoconite holes contain a substantial amount of organic matter (5–10 %; Takeuchi *et al.*, 2001), with values often >6 % organic carbon (OC) on GrIS (Stibal *et al.*, 2010). Microbial activity is believed to cause a further darkening of the already dark inorganic particulates in cryoconite debris by producing and/or transforming OC (Anesio *et al.*, 2009; Hodson *et al.*, 2010a). Microbes are thought to decompose more labile OC to form dark-coloured humic substances (Takeuchi *et al.*, 2001) and to produce extracellular polymeric substances (EPS) (Hodson *et al.*, 2010b). These glue-like compounds help cement organic and inorganic particles (including black carbon; Stibal *et al.*, 2012a) into granules, thereby increasing their residence time on glacier surfaces (Hodson *et al.*, 2010b; Langford *et al.*, 2010). This can lead to a significant decrease in supraglacial albedo, considering cryoconite debris covers 0.1–10 % of the ablation zone of glaciers in the Northern Hemisphere (Hodson *et al.*, 2007; Anesio *et al.*, 2009; Hodson *et al.*, 2010a).

"We conducted an original laboratory experiment, the 'cryoconite casserole', to investigate the darkening of cryoconite debris as a result of OC accumulation driven by microbial activity. Greenlandic cryoconite debris (10 % natural cryoconite, mixed with 90 % cryoconite furnaced at 550 °C to remove all organic matter) was exposed to simulated Greenlandic summer conditions, in terms of temperature, lighting and nutrient availability (see Methodology in the Supplementary Information for full details). This cryoconite mixture simulated the early stages of cryoconite hole development, where the debris is mostly inorganic and it can become colonised by local microbial communities. Samples were kept either under 'light' (simulated daylight) or 'dark' (covered in aluminium foil) conditions. Three different water/nutrient applications were made: 1) blank, sterile water, 2) nitrogen (N) and phosphorous (P) additions and 3) N, P and organic carbon (C) additions. The nutrient additions simulated concentrations released from ice melt (Stibal *et al.*, 2012b; Telling *et al.*, 2012; Lawson *et al.*, 2014). All light and nutrient treatments had five replicates. Cryoconite casserole samples were analysed for their nutrient composition, surface reflection normal to the ice surface in the laboratory and chlorophyll *a* (chl*a*) concentration. The structure of the debris was observed with an optical and fluorescent microscope. Here, we present data collected at the end of one and three consecutive simulated summer seasons

(the latter was performed to confirm the results observed during the one simulated summer experiment). The reduction of surface reflection due to biological activity, derived from our results, was used as a proxy for a reduction in albedo in the regional climate model Modèle Atmosphérique Régional (MAR; Fettweis *et al.*, 2013) to project future microbially-mediated increases in GrIS melt (see Methodology, Supplementary Information).

Results and Discussion

Supraglacial Microbial Nutrient Production and Recycling. Substantial amounts of OC (~1.7 ± 0.5 mg OC/g of cryoconite) were produced and accumulated by microbes over the course of one simulated summer in 'light' conditions with NPC additions (Fig. 1a), compared to 'dark' and blank samples. OC concentrations quadrupled (~7.0 ± 0.9 mg OC/g of cryoconite) when the samples were exposed to three consecutive simulated summers (Fig. 1b). The total C addition was only 0.25 % of the final accumulated OC. Thus nearly all accumulated OC in this treatment originated from microbial C fixation/transformation.

'Light' treatments with NPC additions also generated the highest concentrations of particulate organic nitrogen (PON; 100.4 ± 26.7 µg PON/g cryoconite) and organic bound phosphorous (OP; 19.5 ± 6.4 µg OP/g cryoconite) (Table 1). By contrast, PON and OP were consumed in the dark NP treatments (6.6 ± 4.4 µg PON/g cryoconite and 22.0 ± 1.7 µg OP/g cryoconite, respectively, after one season). Additionally, the light samples with NPC additions had the biggest decrease in inorganic bound phosphorous (IP; 27.2 ± 5.4 µg IP/g cryoconite consumed), with respect to the starting IP concentrations. This is indicative of an uptake of P from the sediment, as a consequence of microbial fixation of OC. The concentrations of PON and OP increased 7-fold and 4-fold, respectively, for the same samples ('light' with NPC additions) after three simulated summers (Table 1).

The amount of OC produced and accumulated in our experiments simulating glacial surfaces was disproportionate compared to the amounts of C, N and P added to the samples at ice meltwater concentrations. P concentrations were derived using the Redfield ratio C:N:P of 106:6:1 (Redfield, 1958), while keeping N and C concentrations within the range of concentrations detected in GrIS ice melt (Stibal *et al.*, 2012b; Telling *et al.*, 2012; Lawson *et al.*, 2014). Therefore, the experimental set-up provided a realistic scenario for the potential accumulation of organic matter at the surface of glaciers. Nevertheless, the ratio of the organic C:N:P fixed in this experiment was 93:5:1, over one simulated summer, and 90:9:1, over three simulated summers. These ratios are comparable to others reported in cold, high latitude regions (Stibal *et al.*, 2008; Martiny *et al.*, 2013). Cryoconite fertilisation with ambient nutrient conditions (NP and NPC additions) appears to produce a response of self-organisation: P mining out of sediment, autocatalytic N$_2$ fixation and significant OC fixation. The N$_2$ fixation was most probably performed by cyanobacteria species belonging to the *Nostocaceae* family, whose
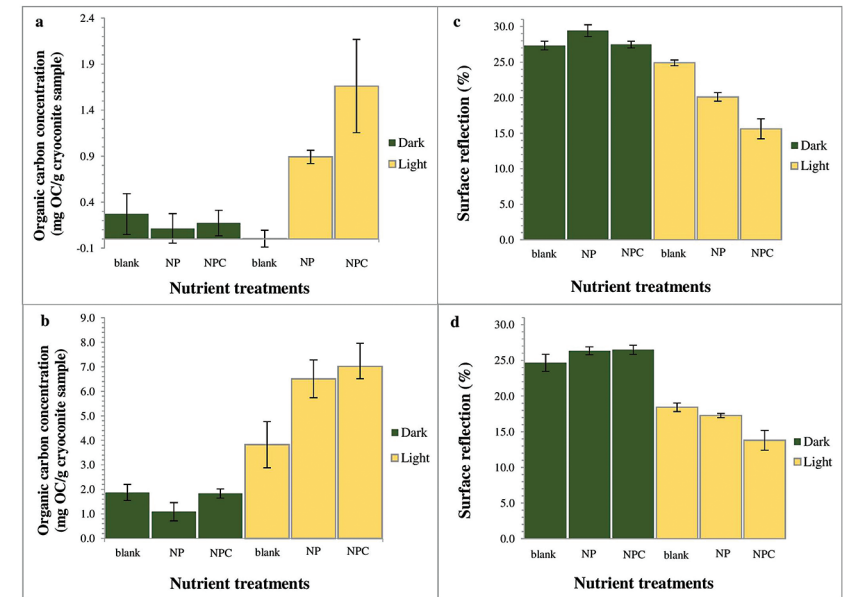
Figure 1 OC accumulated over **(a)** one simulated summer season and **(b)** over three simulated summer seasons. Surface reflection after **(c)** one simulated summer season and **(d)** three simulated summer seasons. 'Light' samples accumulated significantly more OC compared to 'dark' samples (two-way ANOVA p < 0.05 in (a) and p < 0.001 in (b)). This was accompanied by a decrease in cryoconite sediment reflectivity by ~15.5 percentage points, from a starting 31.1 %, for the 'light' with NPC treatment samples in (c) and a further 1.8 percentage points in (d). Two-way ANOVA analyses showed a significant difference in spectral reflection between 'light' and 'dark' samples (p < 0.001), nutrient conditions (p < 0.001) and the interaction of nutrient and light settings (p < 0.01). There was a significant difference (p < 0.001) between samples NPC and blanks, NCP and NP (p < 0.05) and NP and blanks (p < 0.05), using Turkey Post-hoc analyses in (c-d). Standard errors were calculated as 1σ (n = 5).

16S rRNA and N fixation functional genes have been found within Arctic and Antarctic cryoconite (Cameron *et al.*, 2012a,b). Phosphorous limitation was previously reported in glacial environments (Mindl *et al.*, 2007; Stibal *et al.*, 2009), while N limitation was shown to stimulate N$_2$ fixation on glaciers (Telling *et al.*, 2011). Supraglacial microbial activity can thus be a vital source of bioavailable nutrients for subglacial and downstream environments.

We hypothesise that adding C as bioavailable carbohydrate, at ambient concentrations, has a kinetic effect on the heterotrophic microbial community, speeding up the recycling of other organic matter. Dependence on labile OC additions demonstrates the importance of heterotrophic processes (recycling nutrients), acting in concert with autotrophic processes (fixing and accumulating OC), in the maintenance of self-organised supraglacial microbial communities. Blank and 'dark' samples receiving no nutrients initially showed no significant

Table 1   Concentrations of PON, OP, IP and chl*a* for each light and nutrient treatment, over one and three simulated summer seasons. The concentrations are the differences between the final and starting concentrations in each treatment. Significant differences (two-way ANOVA) are indicated between **(a)** 'light' and 'dark' samples, **(b)** nutrient treatments and **(c)** the interaction of nutrient and light settings.

Sample conditions		Light			Dark			Two-way ANOVA analysis:
		Sterile water	N and P additions	N, P and C additions	Sterile water	N and P additions	N, P and C additions	
One simulated summer season	PON concentration (µg PON/g cryoconite sample)	11.7 ± 3.8	32.6 ± 21.4	100.4 ± 26.7	-3.1 ± 6.0	-6.6 ± 4.4	-2.4 ± 10.2	a (p < 0.01)
	OP concentration (µg OC/g cryoconite sample)	-2.1 ± 9.6	13.4 ± 6.0	19.5 ± 6.4	-21.9 ± 1.8	-22 ± 1.7	-10 ± 7.1	a (p < 0.001) b (p < 0.05)
	IP concentration (µg OC/g cryoconite sample)	-3.9 ± 5.5	-22 ± 9.8	-27.2 ± 5.4	16.9 ± 8.5	23.6 ± 10.4	12.5 ± 2.4	a (p < 0.001)
	Chl*a* concentration (in µg of chl*a*/g of sample)	1.6 ± 0.2	3.1 ± 0.1	3.8 ± 0.2	1 ± 0.1	1.1 ± 0.1	1.1 ± 0.0	a (p < 0.001) b (p < 0.01) c (p < 0.01)
Three simulated summer seasons	PON concentration (µg PON/g cryoconite sample)	149.6 ± 31.7	253.4 ± 42.9	680.5 ± 51.1	51.2 ± 19.2	67.3 ± 14.2	61.4 ± 18.1	a (p < 0.001) b (p < 0.001) c (p < 0.001)
	OP concentration (µg OC/g cryoconite sample)	27.7 ± 8.9	35.6 ± 9.1	85.4 ± 13.6	15.2 ± 0.9	13.6 ± 1.4	16.3 ± 4.5	a (p < 0.001) b (p < 0.001) c (p < 0.01)
	IP concentration (µg OC/g cryoconite sample)	-35.6 ± 9.4	-46.7 ± 13.5	-97.7 ± 15.1	-21.8 ± 6.3	-24.1 ± 5.2	-19.6 ± 7.3	a (p < 0.001) b (p < 0.01) c (p < 0.01)
	Chl*a* concentration (in µg of chl*a*/g of sample)	1.5 ± 0.2	2.0 ± 0.0	4.0 ± 0.5	1.0 ± 0.1	1.1 ± 0.2	1.1 ± 0.0	a (p < 0.001) b (p < 0.001) c (p < 0.001)

OC accumulation. However, even these samples showed substantial amounts of OC accumulation after three simulated summer seasons. The blank samples may have simply needed a longer period of time for autotrophic processes to dominate in the microbial community. We postulate that chemolithotrophic activity is the likely explanation for the small OC accumulation in the dark samples.

Impacts of Microbial Activity on Glacial Ice Reflectivity and Calculated Melt Rates. There was a strong negative correlation between OC accumulation and surface reflection (Pearson's r = -0.897, p < 0.05). The accumulation of microbially-produced OC caused a significant reduction of ~15.5 percentage

points in the cryoconite's reflectivity in the 'light' with NPC treatment samples, from a starting 31.1 %, over the one simulated summer (Fig. 1c). It decreased by a further 1.8 percentage points after three simulated summers (Fig. 1d). This is most likely a result of the cryoconite material becoming darker through microbial OC production, accumulation and OC decomposition into dark-coloured humic substances. Microbial activity had the greatest effect in reducing the cryoconite material's surface reflectivity over the first simulated summer. Afterwards, the surface reflectivity of the cryoconite-organic material mixture probably approached a plateau, since further microbial activity and OC accumulation led to only a slight additional reduction in its surface reflectivity after three simulated summers. Additionally, there was a strong correlation between the chl*a* concentration and OC accumulation across all treatments (Table 1, Fig. 1) (Pearson's r = 0.934, p < 0.01). Cyanobacterial sediment granules only developed in 'light' samples with nutrient additions, after one simulated summer (Fig. 2), which also experienced a substantial decrease in reflectivity. Conversely, blank samples only contained sediment granules after three simulated summers. Furthermore, dark and round microbial cell clusters were predominant in the samples with cyanobacterial granule development. These were most likely colonies of cyanobacteria, such as *Oscillatoriales* and *Nostocales,* previously observed in Greenlandic cryoconite (Cameron *et al.*, 2012b; Stibal *et al.*, 2012b). They may have further contributed to the darkening of the samples' reflectivity. Similar cyanobacterial granules can be found in supraglacial cryoconite holes around the world under *in situ* conditions (Hodson *et al.*, 2010b; Langford *et al.*, 2010). The granules form partially by microbial EPS excretion (Hodson *et al.*, 2010b; Langford *et al.*, 2010), which we suggest enables more nutrient and particle retention within the cryoconite. Further OC fixation and transformation is, therefore, likely to occur in the cryoconite granules, ultimately leading to the darkening of glacial cryoconite sediment. Over longer periods of time, larger cryoconite aggregations will melt into the surface ice to form cryoconite holes, which are more stable environments for organic matter accumulation. However, in the short term, new cryoconite on glaciers undergoes an important decrease in albedo. The increase in anthropogenic NO_3^- deposition on glaciers (Lyons *et al.*, 1990; Duderstadt *et al.*, 2014) has been reported to reduce the microbial N limitation in cryoconite habitats (Telling *et al.*, 2011). Enhanced anthropogenic NO_3^- input will likely lead to a significant decrease in N_2 fixation, allowing more bio-energy to be available for C fixation. Consequently, we envisage that there would be a rise in OC production within cryoconite debris, causing considerable albedo reduction, and thus mass loss on glaciers and ice sheets covered in cryoconite.

We calculated the maximum microbially-mediated GrIS potential melt to be on average 17.3 ± 2.5 Gt yr^{-1}, using the observed 15.5 percentage point decrease in the debris surface reflection (see Methodology, Supplementary Information). This is about 5 % of the present day runoff (Bamber *et al.*, 2012). The estimate is based on a 10 % debris cover concentration, over the extent of GrIS that undergoes persistent melting (more than 1-10 days/yr). The uncertainty in additional melt includes contributions due to the albedo and debris cover, but not any uncertainty in future climate projections. It is, therefore, a first order estimate.
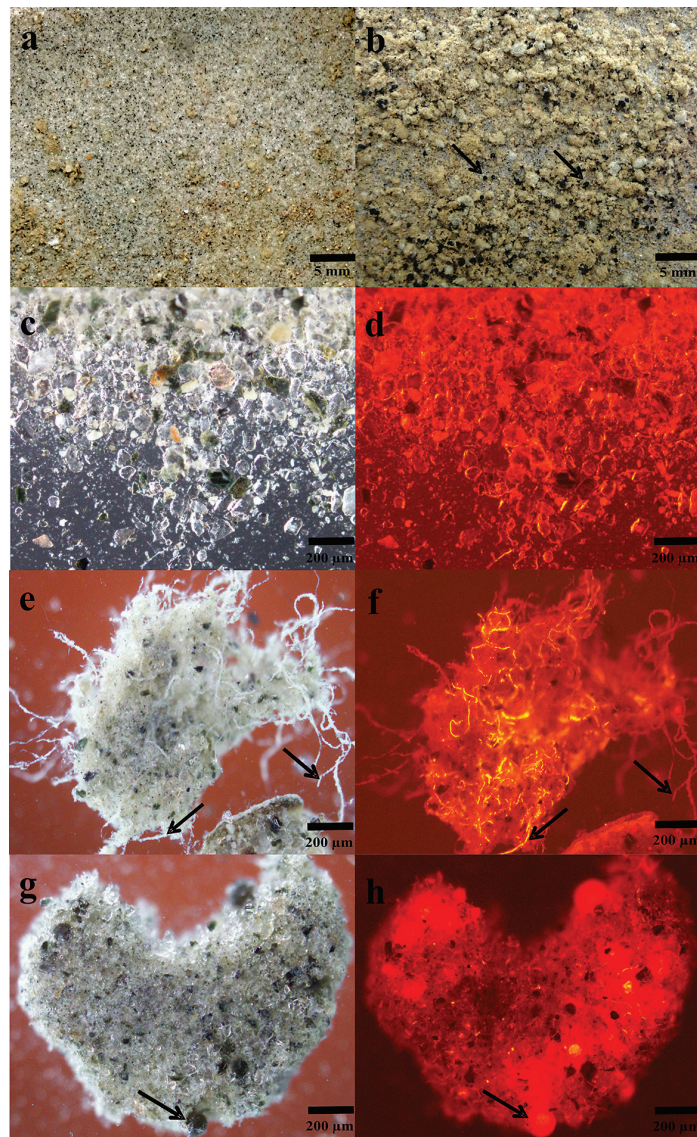
Figure 2   Microbial granule development in 'light' samples with nutrient additions. Images **(a-c)**, **(e)** and **(g)** were taken using optical microscopy. Autofluorescence microscopy was performed to visualise photosynthetic autotrophs in images **(d)**, **(f)** and **(h)**. The initial mixture of inorganic dust with 10 % natural cryoconite (a and c) developed into samples rich in granules and filamentous cyanobacteria (b, e-h). Examples of cyanobacterial filaments and colonies (resembling black spheres) are indicated by arrows in images (b), (e-h).

With the projected changing climate, the GrIS melt area is estimated to expand from the present day 31 % of the total ice sheet (Fig. 3a), to 65 % (Fig. 3b) and 92 % (Fig. 3c) by 2100. These projections are based on two representative greenhouse gas concentration pathways (RCP) 4.5 and 8.5. The former is associated with moderate increases in greenhouse gas concentrations, while the latter is closer to a 'business as usual' trajectory. The effect will be proportionally larger in small Alpine and Arctic valley glaciers, since the melt areas could cover up to 100 % of the glaciers by 2100 (see Methodology, Supplementary Information). The GrIS biologically-induced melt potential could therefore increase up to 42 and 85 Gt yr^{-1}, for RCP 4.5 and 8.5, respectively. These calculations assume no change in NO_3- concentrations and are, therefore, likely a conservative estimate. Furthermore, other ice surface organisms, such as algae (Yallop *et al.*, 2012; Lutz *et al.*, 2014), will likely significantly increase the overall biologically-induced melt potential calculated for cryoconite cyanobacteria in this study. The biological impact on albedo hence plays an important role in modulating mass loss from glacier surfaces and must be included in albedo models to capture adequately the evolving properties of glaciers in a changing climate. Additionally, it is postulated that the warming climate will likely extend melt seasons, leading to increases in biological activity and thus contributing further to the darkening of glaciers and ice sheets (Benning *et al.*, 2014).
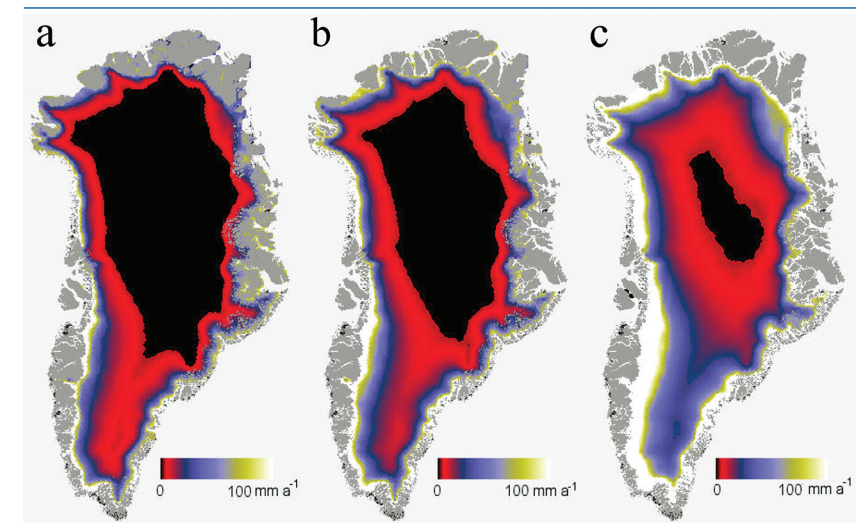

Figure 3   **(a)** Present biologically-induced GrIS potential increase in melt rate, in mm yr^{-1}. **(b)** and **(c)** Future biologically-induced GrIS potential increase in melt rate, in mm yr^{-1}. Melt days were derived for the period 2091-2100 for two different greenhouse gas trajectories, RCP4.5 **(b)** and RCP8.5 **(c)**.

In conclusion, this study provided for the first time a first-order estimate of the effect of microbial activity on glacial albedo and melt for the GrIS. This effect was significant enough to merit inclusion in albedo models for the GrIS and other glacial environments around the world. In future more elaborate models, other factors (such as the latitudinal variability in PAR; differences between surface reflection and albedo measurements, in the field and in the laboratory; and the influence of surface glacial flow and wind on microbial cryoconite communities) would need to be included to provide a more accurate upscaling of the calculations to the entire GrIS.

Acknowledgements

Author Contributions

M.M. and A.M.A designed the overall study. M.T. and N.T. were involved in advising the detail of the study design. J.B. performed the climate model simulations. M.M. performed the experiment, collected and processed the data, and wrote the paper. All authors discussed the results and commented on the manuscript.

Additional Information

Supplementary Information accompanies this letter at www.geochemicalper-spectivesletters.org/article1611

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