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Understanding diversity patterns in bacterioplankton communities from a sub-Antarctic peatland

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Summary

Bacterioplankton communities inhabiting peatlands have the potential to influence local ecosystem functions. However, most microbial ecology research in such wetlands has been done in ecosystems (mostly peat soils) of the Northern Hemisphere, and very little is known of the factors that drive bacterial community assembly in other regions of the world. In this study, we used high-throughput sequencing to analyse the structure of the bacterial communities in five pools located in a sub-Antarctic peat bog (Tierra del Fuego, Argentina), and tested for relationships between bacterial communities and environmental conditions. Bacterioplankton communities in peat bog pools were diverse and dominated by members of the *Proteobacteria*, *Actinobacteria*, *Bacteroidetes* and *Verrucomicrobia*. Community structure was largely explained by differences in hydrological connectivity, pH and nutrient status (ombrotrophic versus minerotrophic pools). Bacterioplankton communities in ombrotrophic pools showed phylogenetic clustering, suggesting a dominant role of deterministic processes in shaping these assemblages. These correlations between habitat characteristics and bacterial diversity patterns provide new insights into the factors regulating microbial populations in peatland ecosystems.

Introduction

Peatlands are ecosystems characterized by high acidity, low temperatures and low concentrations of mineral nutrients, in which the amount of carbon sequestered in net primary production, mainly by *Sphagnum* mosses, exceeds the amount of carbon lost by decomposition of organic matter by microorganisms (Dedysh, 2011). Thus, peatlands are acknowledged as an important sink for atmospheric CO_2, with carbon accumulation rates of 10–30 g C m^{-2} $year^{-1}$ and a global carbon pool of 200–450 Pg of carbon, which constitutes about 30% of the global soil C pool (Gorham, 1991). Decomposition of organic matter in deep anoxic peat layers generates methane (CH_4), which diffuses to the surface and is then partially emitted to the atmosphere, making peatlands a globally important source of methane (Basiliko *et al.*, 2013). Furthermore, in addition to their importance in the terrestrial carbon cycle, these ecosystems hold a key role in the global water balance, regulating the hydrological regime of rivers and represent one of the largest reservoirs of freshwater (Andersen *et al.*, 2013).

Microbial diversity research in peatlands has shown these habitats containing highly specific bacterial communities being dominated by members of the phyla *Acidobacteria*, *Proteobacteria*, *Bacteroidetes* and *Verrucomicrobia* (reviewed in Dedysh, 2011). In these ecosystems, bacterial communities have been found to vary along small-scale hydrological and chemical gradients. For instance, within a given peatland type, dissolved organic carbon (DOC) content (Lin *et al.*, 2012), as well as substrate quality and site wetness (Jaatinen *et al.*, 2007), have been proven to affect the composition of bacterial communities. Vegetation type also plays an important role in shaping bacterial communities in peatlands (Bragina *et al.*, 2012). However, an important limitation is that most of these researches have been done in a limited number of peatland ecosystems (i.e. peat soils), mainly situated in the Northern Hemisphere (see Andersen *et al.*, 2013). Therefore, more geographically and ecologically diverse samples (e.g. bog pools) are needed to elucidate the biogeographic patterns and environmental factors that shape the structure of bacterial communities in peatland ecosystems at different spatial scales.

Here we have investigated, for the first time, the bacterial diversity in five freshwater pools located along a 500 m transect in Rancho Hambre peat bog (Tierra del Fuego, Argentina). Pools are critical habitats for biodiversity in natural peatlands (Mazerolle *et al.*, 2006). Taking advantage of differences in hydrological connectivity, pool

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morphometry and minerotrophic versus ombrotrophic status (González Garraza *et al*., 2012), we addressed the following questions: (i) Does bacterial community composition vary within and between pools, and differ from that of northern peatlands?, (ii) Do variations in bacterial diversity reflect the underlying environmental conditions (Table S1)? and, if this is observed, (iii) Are bacterial communities from ombrotrophic (more acidic and hydrologically isolated) pools more phylogenetically clustered than those inhabiting minerotrophic pools (less acidic and interconnected)? Analysis of the degree of phylogenetic relatedness of taxa found within and between communities should provide insights into the processes that organize these communities (Webb *et al*., 2002). To answer these questions, we used high-throughput barcode amplicon pyrosequencing and a set of multivariate statistic tools.

Results and discussion

We have investigated bacterial diversity patterns in five pools from a sub-Antarctic peat bog located in Tierra del Fuego, Argentina (see Appendix S1). A total of 897 bacterial operational taxonomic units (OTUs, sequences binned at a 97% similarity cut-off) were identified in 30 225 sequences (2015 per sample, $n = 15$): an average of 109 ± 5 OTUs [mean $\pm$ standard error (SE)] per sample (Fig. S1). A collector's curve of the number of OTUs per sample revealed that additional bacterial taxa are likely to appear with every additional sample (Fig. S2). The total size of the bacterial OTU pool was estimated to be 1764 ± 111 OTUs (mean $\pm$ SE of Chao1 estimator of total OTU pool richness). Minerotrophic (less acidic) pools (RH1, RH4) typically had higher bacterial diversity than ombrotrophic (more acidic) pools (Fig. S1), although differences were statistically significant only for Shannon and inverse Simpson indices (paired *t*-test, $P < 0.05$), which agrees with previous results from other peatland environments (Opelt *et al*., 2007; Peltoniemi *et al*., 2009; Lin *et al*., 2012).

Thirteen phyla were detected across all samples (Fig. S3), of which *Proteobacteria* (51% of all sequences), *Actinobacteria* (22%), *Bacteroidetes* (15%) and *Verrucomicrobia* (7%) where the most abundant, constituting 95% of the sequences. These four phyla have been shown to be widely distributed in *Sphagnum*-dominated wetlands (Juottonen *et al*., 2005; Dedysh *et al*., 2006; Morales *et al*., 2006; Hartman *et al*., 2008; Ausec *et al*., 2009; Kanokratana *et al*., 2011; Pankratov *et al*., 2011; Bragina *et al*., 2013), although their relative abundances appear to vary across ecosystems.

In contrast to those studies, although detected, we did not find members of the Acidobacteria to be important components of the freshwater bacterial communities, more likely because of large differences in habitat characteristics (peat soil versus water material). Indeed, bacterial communities were found to shift in composition along the landscape from peat communities dominated by *Acidobacteria* to freshwater communities dominated by *Actinobacteria* (Kulichevskaya *et al*., 2011). In spite of this striking difference, the overlap between peat soil and freshwater bacterial communities support previous findings obtained across soil, sediment, stream and lake habitats, which suggest that aquatic environments are strongly coupled to terrestrial ecosystems through hydrological networks (Crump *et al*., 2012, and references therein).

The vast majority of the taxa found were rare, with 72% of OTUs occurring in a single sample (Fig. S4). Nevertheless, common and abundant bacterial phylotypes were also detected. Ten bacterial OTUs belonged to two phyla that were present in 80% or more of the samples, representing 1.1% of the bacterial taxonomic diversity but 53% of sequences (Fig. 1). These phyla were *Proteobacteria* (38% of all sequences, mostly *Betaproteobacteria*) and *Actinobacteria* (12%). The most abundant individual OTUs that could be classified in the 'core microbiome' at the genus level were *Polynucleobacter* (11%, *Betaproteobacteria*) and *Novosphingobium* (3%, *Alphaproteobacteria*). Members of the genera *Mucilaginibacter* (*Bacteroidetes*), *Flavobacterium* (*Bacteroidetes*) and *Limnohabitans* (*Betaproteobacteria*) were also abundant (representing 7%, 3% and 1% of all sequences, respectively), but were found in a lower number of samples (Fig. 2).

Knowledge is scarce about the specific ecology of these microorganisms in peatland ecosystems. Many of the bacterial taxa identified are not available in pure culture, which hampers determination of their physiologies and consequently assessment of their functional roles in these environments. Nevertheless, bacterial strains affiliated to *Polynucleobacter*, namely *Polynucleobacter necessarius*, have been reported to occur as obligate endosymbionts of ciliates (subsp. *necessarius*) [commonly found in the Rancho Hambre water bodies (Quiroga *et al*., 2013)], and also as free living strains (subsp. *asymbioticus*). The complete genomic sequence of both subspecies has shown the inability of either living forms to exploit sugars as carbon or energy sources or to perform nitrification, denitrification or nitrogen fixation (Boscaro *et al*., 2013). Conversely, the free-living form can perform the assimilatory reduction of nitrate and assimilate sulphur and sulphate.

Members of the genus *Limnohabitans*, highly widespread in freshwater food webs, have been ascribed a prominent role in the transfer of DOC from both autochthonous and terrestrial sources to the top trophic levels (Kasalický *et al*., 2013; Šimek *et al*., 2013). Most

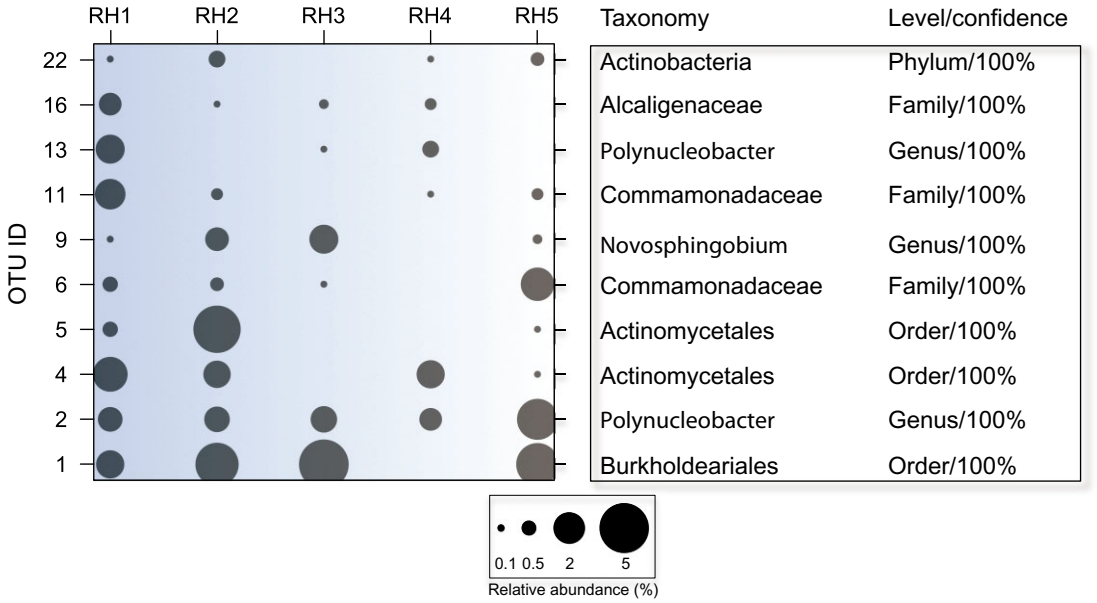

Fig. 1. Phylogenetic assignment and sequence distribution of 'core' OTUs (97% cut-off). Taxonomic assignments are the finest level that passed the Ribosomal Database Project classifier's (80% confidence threshold).

Bacteroidetes (i.e. *Flavobacterium* and *Mucilaginibacter*) have the ability to use a broad range of biopolymers, particularly polysaccharides and proteins (Thomas *et al*., 2011), and it has been proposed that a primary role for Flavobacteria is the conversion of high molecular weight (HMW) compounds into low molecular weight compounds (Teeling *et al*., 2012). Indeed, analysis of DOC quality in Rancho Hambre pools revealed the predominance of coloured, aromatic, HMW compounds (Quiroga *et al*., 2013), as found in other bog ecosystems (Hodgkins *et al*., 2014). Several *Novosphingobium* strains seem to have the capacity to degrade phenolic compounds from *Sphagnum*-derived litter (DeAngelis *et al*., 2013).

Interestingly, all OTUs belonging to *Limnohabitans* and *Flavobacterium* were found exclusively in minerotrophic pools (Fig. 2), which agrees with the fact that these genera strongly prefer non-acidic habitats (Šimek *et al*., 2010). In direct contrast, members of the *Mucilaginibacter*, which are reported to grow in a wide range of pH (Pankratov *et al*., 2007), were only found in ombrotrophic pools. Whether or not this lack of co-occurrence is due to biological interactions (e.g. competition or predation) or species-specific habitat associations deserves future investigation. All in all, the results suggest that there is a high degree of niche specialization among these taxa and that they play an important role for nutrient cycling in peatland limnetic ecosystems.

Bacterial communities in a given pool were highly similar and significantly different from those in other pools (Analysis of Similarity (ANOSIM) $R = 1$, $P < 0.001$). The inverse of Whittaker's β-diversity measure, in which mean within-pool diversity (α-diversity) is divided by overall regional diversity (γ-diversity), was close to 0 (Whittaker's $\beta^{-1} = 0.12$), indicating that between-pool diversity contributed more to total diversity than within-site diversity (Anderson *et al*., 2011). Variation in bacterial community structure was related to pH, ammonium, phosphate and total nitrogen. Based on Bray–Curtis dissimilarities, a permutational multivariate analysis of variance (PERMANOVA) found each of these four factors to be significant in structuring pool bacterial communities (PERMANOVA: $P < 0.01$; combined coefficient of determination $R^2 = 0.69$). pH explained most of the variation ($R^2 = 0.25$), followed by total N ($R^2 = 0.20$), ammonium ($R^2 = 0.14$) and phosphate ($R^2 = 0.10$). As pH can be considered a 'master variable' for the chemical state of aquatic ecosystems that influences and is influenced by other variables (Blodau, 2006), we cannot determine whether pH has a direct or indirect effect on these communities. Notwithstanding that the amount of community variation explained by each factor was conditional on the distance metric used, these four factors always remained significant (data not shown).

A non-metric multidimensional scaling plot confirmed the strong effect of these factors in the assembly of bacterial communities (Fig. 3), and grouped pools according to their trophic status, that is, minerotrophic (RH1 and RH4) versus ombrotrophic (RH2, RH3 and RH5), as described in González Garraza and colleagues (2012). When pH, ammonium, phosphate and total N were fitted to linear vectors in the ordination space, these vectors

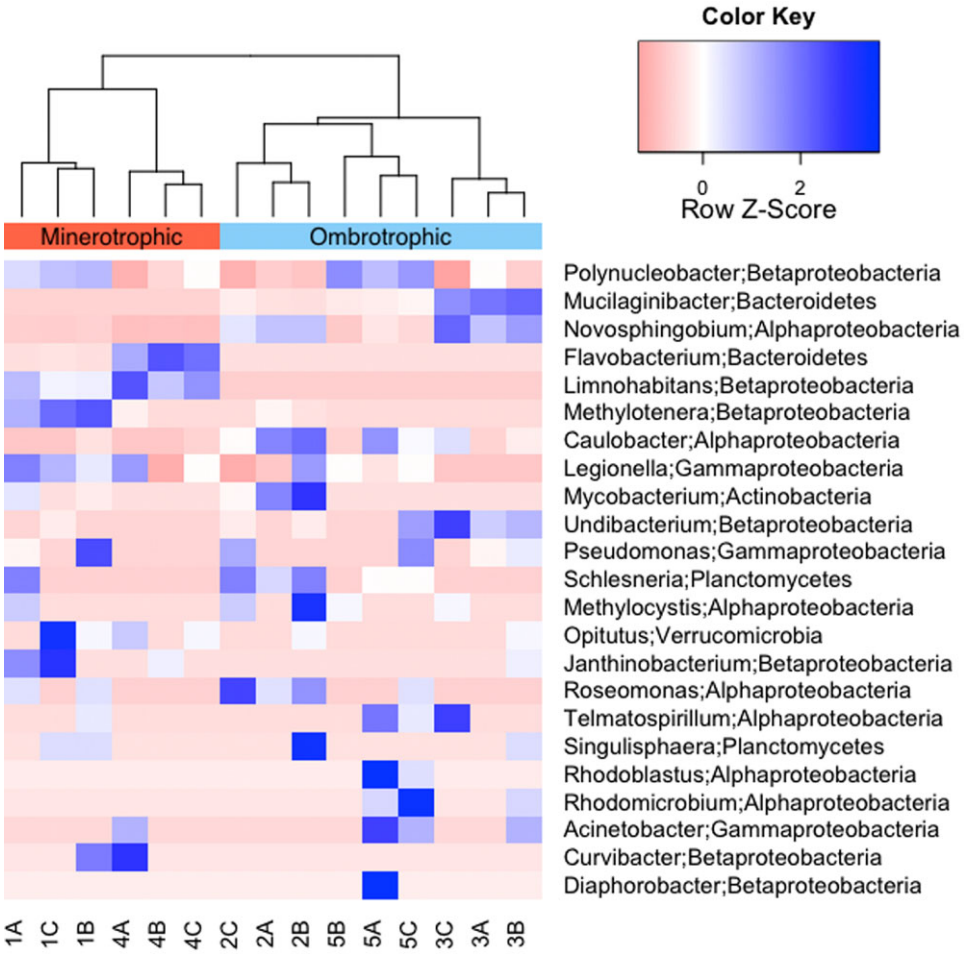

Fig. 2. Heatmap displaying the most abundant genera for ombrotrophic and minerotrophic samples. Pools are clustered based on the percent relative abundance of the 23 genus; phylum level classifications shown as rows in this figure. Each row was scaled so that the mean of each taxonomic group across samples was calculated and coloured by corresponding z-score of each cell.

were highly correlated with the placement of water pool centroids (pH: $r^2 = 0.60$, $P < 0.01$; ammonium: $r^2 = 0.79$, $P < 0.01$; phosphate: $r^2 = 0.95$, $P < 0.01$; total N: $r^2 = 0.78$, $P < 0.01$). Strong relationships between pH, nutrient concentrations and bacterial community composition have been observed in other wetlands (Hartman *et al*., 2008), and suggest environmental filtering (Wang *et al*., 2013). Indeed, environmental filtering seems to shape bacterial communities in some ombrotrophic pools (i.e. RH3 and RH5) (Fig. 4), as we were able to detect phylogenetic clustering using ecological null models (Kembel, 2009). The link between bacterial phylogenetic clustering and ombrotrophic status (SES.MPD = -3.1 ± 0.1, SES.MNTD = -1.6 ± 0.1; both $P < 0.05$) indicates that the prevailing conditions of these pools act as a stronger ecological filter compared with those of minerotrophic pools (SES.MPD = 0.5 ± 0.2, SES.MNTD = -0.6 ± 0.2; both $P > 0.05$). Habitat filtering has also been proposed as the major mechanism explaining bacterial community assembly in a peaty acidic soil (Felske *et al*., 1998).

Ombrotrophic environments are hydrologically isolated from the surrounding landscape and characterized by acidic pH and low nutrient values (Wheeler and Proctor, 2000). Both environmental conditions and spatial isolation can cause phylogenetic clustering in bacterial communities (Horner-Devine and Bohannan, 2006; Bryant *et al*., 2008; Stegen *et al*., 2013), and suggest that habitat heterogeneity can contribute to observable biogeographic patterns in microbial communities at limited (within-peatland) spatial scales. It is important to note, however, that habitat filtering (abiotic factors and biotic interactions), together with differential dispersal (connectivity among communities as a result of water run out and physical barriers) and ecological drift (stochastic changes in the relative abundance of taxa), likely act in concert (Vellend, 2010; Stegen *et al*., 2013) to produce the bacterial communities studied here.

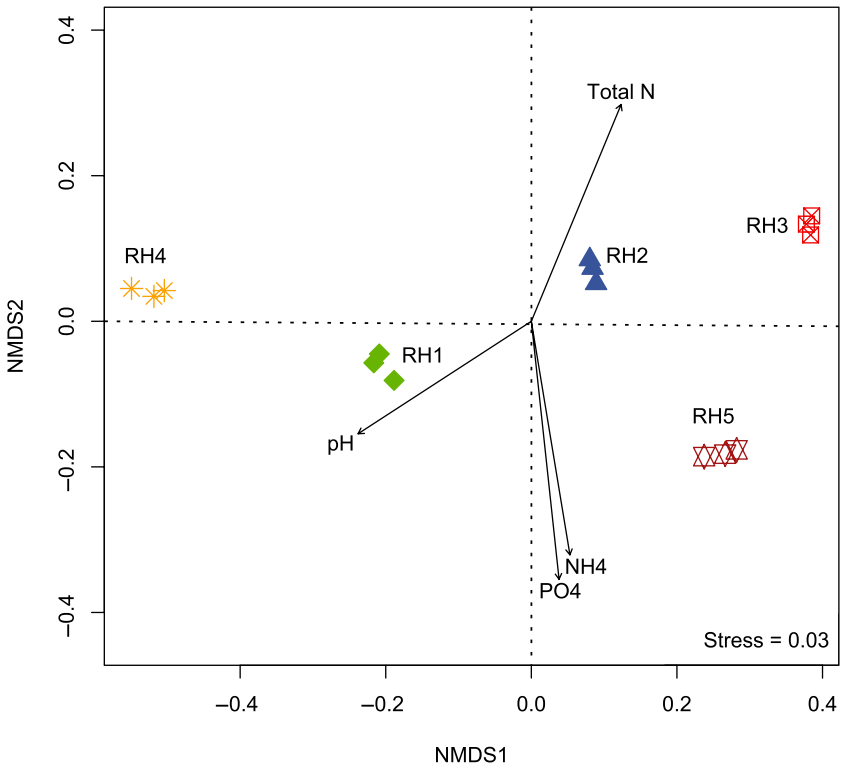

Fig. 3. nMDS ordination plot (Hellinger-transformed Bray–Curtis dissimilarity matrix). Each point represents the bacterial community of an individual sample and shapes denote different pools ($n = 5$). Environmental vectors were fit to the centroids of each pool.

Acknowledgements

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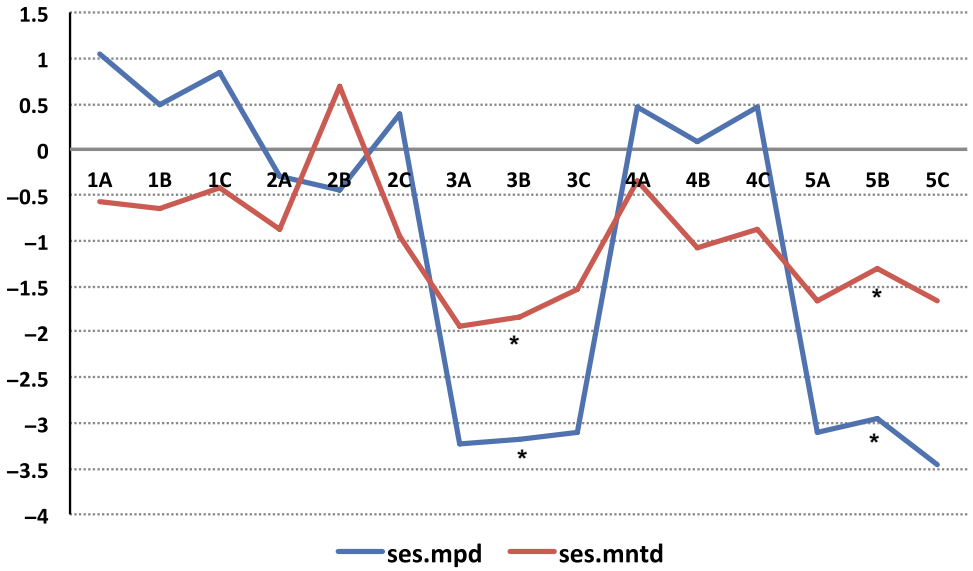

Fig. 4. Standardized effect sizes of MPD (SES.MPD) and MNTD (SES.MNTD) for bacterioplankton communities. Asterisks indicate significant results ($P < 0.05$).

Conflict of interest

The authors declare no conflict of interest.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Fig. S1. Distribution and diversity of bacterial OTUs (97% cut-off) after rarefying the data set to 2015 sequences per sample. Error bars depict standard errors. PD, phylogenetic diversity.

Fig. S2. Collector's curve (mean ± 95% confidence interval) of bacterial OTU (97% cut-off) richness versus number of samples.

Fig. S3. Taxonomic distribution of bacterial OTUs (97% cut-off). Affiliation was performed using the Ribosomal Database Project Classifier with a confidence threshold of 80%. The sequence data generated in this study were deposited in the NCBI Sequence Read Archive and are available under the project number SRP050278. A supplementary table containing sample metadata conforming to MIMARKS standards is also provided (Table S1).

Fig. S4. Frequency histogram: number of bacterial OTU (97% cut-off) that occurred in each sample (of 15 possible).

Table S1. Metadata, including the chemistry of the samples, conforming to MIMARKS standards.

Appendix S1. Materials and methods.