Biogeosciences Discuss., 10, 14009–14042, 2013
www.biogeosciences-discuss.net/10/14009/2013/
doi:10.5194/bgd-10-14009-2013

Biogeosciences Discussions
Open Access

Microbial and metabolic profiling reveal strong influence of water table and land-use patterns on classification of degraded tropical peatlands

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Received: 21 July 2013 – Accepted: 8 August 2013 – Published: 26 August 2013

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Tropical peatlands from Southeast Asia are undergoing extensive drainage, deforestation and degradation for agriculture and human settlement purposes. This is resulting in biomass loss and subsidence of peat from its oxidation. Molecular profiling approaches were used to understand the relative influences of different land-use patterns, hydrological and physiochemical parameters on the state of degraded tropical peatlands. As microbial communities play a critical role in biogeochemical cascades in the functioning of peatlands, we used microbial and metabolic profiles as surrogates of community structure and functions, respectively. Profiles were generated from 230 bacterial 16S rDNA fragments and 145 metabolic markers of 46 samples from ten sites, including those from above and below water table in a contiguous area of 48 km^2 covering five land-use types. These were degraded forest, degraded land, oil palm plantation, mixed crop plantation and settlements. Bacterial profiles were most influenced by variations in water table and land-use patterns, followed by age of drainage and peat thickness in that order. Bacterial profiling revealed differences in sites, based on the duration and frequency of water table fluctuations and on oxygen availability. Bacterial and metabolic profiles of degraded forest and mixed crop plantations were most diverse compared to other land-use types. Metabolic profiling, being closely associated with biogeochemical functions could distinguish communities not only based on land-use types but also their geographic locations, thus providing a finer resolution than bacterial profiles. Agricultural inputs, such as nitrates were highly associated with bacterial community structure of oil palm plantations, whereas phosphates and dissolved organic carbon influenced those from mixed crop plantations and settlements. Our results provide a basis for adopting molecular marker-based approaches to classify peatlands and determine relative importance of factors that influence peat functioning. Our findings will be useful in peatland management by providing a basis to focus early efforts on hydrological interventions and improving sustainability of oil palm plantations by adopting mixed cropping practices to increase microbial diversity in the long term.

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1 Introduction

Peatlands are formed by the accumulation of partially decayed vegetation matter over thousands of years in low-lying areas that are frequently waterlogged and periodically inundated (Anderson, 1964). Peatlands are a highly vulnerable natural resource that cover 50–70 % of global wetlands (Finlayson et al., 1999) and sequester one-third of world's soil carbon (Freeman et al., 2012). In Southeast Asia, peatlands cover an area of nearly 25 million ha and store approximately 69 Gt of carbon, which is 77 % of all tropical peatland carbon pool (88.6 Gt), of which 65 % (57.4 Gt of carbon) is in Indonesia itself, distributed within 23.4 million ha of peatland (Page et al., 2011). This carbon density is relatively high in the tropics compared to temperate or boreal peatlands, which is largely because of deeper peat layer with the peat thickness up to 20 m in the tropical region (Page et al., 2002).

Southeast Asian peatlands are under threat from anthropogenic activities, predominantly drainage and deforestation for agriculture and human settlement purposes. Forest fires and biomass burning linked to land-use change exacerbate these threats, which crossed all past records in 2013 (Schmaltz, 2013). Such land-use changes and hydrological interventions have resulted in drastic decrease in water table, in many cases exposing biomass sequestered in peat to the air. Of the total area of peatlands in Indonesia, at least 2.2 million hectares has been converted to industrial oil palm plantations, which is expected to increase to 6.2 million ha by 2020 (Miettinen et al., 2012a). Interspersed within the plantations are small areas of temporary human settlements. In peninsular Malaysia and the islands of Sumatra and Borneo, some 60 % of peat swamps had been partly or completely deforested by 2007, usually accompanied by some form of drainage, and only 10 % remained in pristine condition (Miettinen and Liew, 2010). In recent years, rapidly increasing peat carbon losses from drained peatlands in Southeast Asia have been found to contribute significantly to global greenhouse gas emissions (Melling et al., 2005; Furukawa et al., 2005; Couwenberg et al., 2010). Estimates of net carbon losses and resultant CO_2 emissions from

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peatland drained for agriculture range from 30–40 $tCO_2\,ha^{-1}\,yr^{-1}$ (Murdiyarso et al., 2010; Herchoualch and Verchot, 2011) to as high as 70 $t\,CO_2\,ha^{-1}\,yr^{-1}$ (Couwenberg et al., 2010; Jauhiainen et al., 2012), excluding forest biomass losses, fire losses and biomass losses in the initial years after drainage. Carbon losses from such emissions and through fluvial processes have led to tropical peatlands being transformed from carbon sinks to carbon sources (Moore et al., 2013). The oxidation of drained peat is causing rapid subsidence by disappearance of the surface layers in the peat (Kool et al., 2006; Couwenberg and Hooijer, 2013). In a recent study from the same region of Sumatra, peat was reported to subside at a rate of $5\,cm\,yr^{-1}$, of which 92 % loss is due to oxidation and not compaction or plant respiration (Hooijer et al., 2012). Oxidation of organic matter has been shown using mesocosms of boreal peat to be due stimulation of microbial growth, thereby causing the breakdown of organic matter and release of carbon dioxide in a biogeochemical cascade (Fenner and Freeman, 2011).

In several ecosystems, changes in land-use patterns impact both microbial diversity and their activity (Wardle et al., 1998; Ollivier et al., 2011; Putten, 2012). Water table depth, which directly affects the oxygen levels in the peat layer (Lahde, 1969), is an important factor in shaping bacterial community structure. Water table depth also affects water stress, which has been shown to have direct and indirect influences on soil bacterial community composition (Fierer et al., 2003). It is, therefore, important to understand the effects of changes in water table and land-use patterns on microbial diversity in peatlands. While microbial communities influence their environment, they, in turn are influenced by the geochemical conditions in the habitat. Hence, molecular profiling approaches have been widely used to describe microbial diversity in soil (Zhou et al., 2002; Zhang and Xu, 2008; He et al., 2012), extreme environments (Bahl et al., 2011; Chan et al., 2013), rhizosphere (Drigo et al., 2007; Xiong et al., 2010), freshwater (Nold et al., 2000) and mangrove (Bai et al., 2012) ecosystems. Microbial profiling approaches that are now widely used mainly rely on DNA fingerprinting (Zhou, 2003; Nocker et al., 2007; Nazaries et al., 2013) or on pyro-sequencing of ribosomal DNA region (Chistoserdova, 2010; He et al., 2010). More recently, metabolic profiling

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has also emerged as a useful approach to report status of microbial functions in soil (Bundy et al., 2009) and rhizosphere (Lee et al., 2013). In two recent studies of pristine peatlands from Thailand (Kanokratana et al., 2011) and Malaysia (Jackson et al., 2009) used pyro-sequencing and fingerprinting approaches to describe their microbial diversity and functional properties, respectively. They demonstrated the capability of such techniques to show broad phylogenetic diversity and genetic potential to degrade biomass, respectively.

In degraded temperate peatlands, much is known about the relationship of microbial diversity to peatland functioning and greenhouse gas emissions (Opelt et al., 2007; Ausec et al., 2009; Kim et al., 2012; Tveit et al., 2013). In contrast, for degraded tropical peatlands, we have a relatively poor understanding of the relationship of microbial diversity and factors influencing community structure. Given both the ecological and economic importance of these peatlands, it will be useful to understand the differences among various land-use patterns in degraded tropical peatland. Towards this direction, it is critical to develop scientific methods to classify peat in order to conserve remaining pristine peatlands, manage the rapid change in land-use and monitor the progress of their restoration process. Our approach is based on the ability of microbial profiling to capture shifts in community structure and metabolic profiling to reflect the functional outcome of metabolic activities of microbes, plant roots and their exudates, respectively. Using these two molecular profiling approaches, we report the effects of water table and oxygen availability, land-use patterns, age of drainage and peat thickness on bacterial diversity in degraded peatlands of Indonesia. We focus on five land-use patterns from a contiguous study site: (a) degraded forest, (b) degraded land, (c) oil palm plantation, (d) settlements and (e) mixed crop plantation. In order to determine importance of various management practices of these peatlands on the structure and functioning of the bacterial communities, we studied influences eleven physiochemical parameters. Based on our findings reported here, we make recommendations that will help in classification, improved management and sustainability of the tropical peatlands.

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2 Materials and methods

2.1 Site description and sampling

The study area is located in peatlands of the eastern part of Jambi province, Sumatra, Indonesia (Fig. 1). Forested tropical peatlands are extensive in this area and a variety of land-use patterns are present due to land intensification activities. Land cover classification was performed using visual image interpretation and manual on-screen delineation of land-cover polygons. The classification scheme was mainly based on variation in physical vegetation characteristics (e.g., height, sparseness etc.) and included the main phases of the tropical peatland conversion and degradation processes (Miettinen et al., 2012b). The Landsat image and base maps of field sites were obtained from University of Jambi, Jambi, Indonesia. The coordinates of monitoring sites were recorded using handheld Global Positioning System (GPS) devices. The coordinates of these sites were inserted onto the base maps using ArcView and ArcMap programs (ArcGIS-Esri, CA, USA).

The overall mapped area in the eastern part of Jambi comprised a total of 3390 km^2 (Fig. 1), out of which water/seasonal water comprised of 11 km^2 or 0.3 % of total mapped area. For this study, the classes used in Miettinen et al. (2012b) were regrouped and the land-cover distribution was classified as (1) pristine peat swamp forest (1656 km^2 or 49 % of total mapped area), which comprises of nearly pristine and moderately degraded pristine peat swamp forest, (2) degraded forest (543 km^2 or 16 %) including heavily degraded pristine peat swamp forest and secondary forest, (3) degraded land (712 km^2 or 21 %) comprising of shrubs, fern/grass and clearance, (4) industrial plantation (279 km^2 or 8 %) including palm oil and mixed crop plantation and (5) settlement (188 km^2 or 6 %) comprising small holder mosaic and built-up areas.

The coordinates of sampling locations distributed across two broad areas, referred to as Site A and Site B, respectively, were: 103°53′52.58″ E, 1°43′12.47″ S and 103°49′32.23″ E, 1°40′58.24″ S (Fig. 1). The total areas covered by the sites were 42 and 6 km^2, respectively. Out of five land-use patterns, degraded land with similar

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peat physico-, geological and hydrological conditions was present in both Site A and Site B (Fig. 1). As part of routine management practices, fertilizers are applied to the sites that fall within oil palm and mixed crop plantations. The main categories of fertilizer are nitrogen-phosphorus-potassium (NPK 16:16:16) and urea, which are applied three times a year, and potassium chloride (KCl) and muriate of potash (MOP) that are applied once a year.

At each sampling location, a 1 m^3 pit was dug. Three subsamples were collected from 10 cm depth within each side of the wall and pooled together to make one composite sample. Replicated samples were collected by digging equidistant pits along transect, whose length ranged between 120 m to 550 m at different sampling location. Peat water samples for metabolic profiling were collected from dipwells adjacent to each pit. Peat was collected from 20–30 cm above water table (AWT) and from 20–30 cm below water table (BWT) in sterile 50 mL tubes. In order to analyze the oxygen availability at these two sampling positions (AWT and BWT), OX-N Clark-type oxygen sensor (Unisense, Aarhus, Denmark) was used and data was recorded manually. At three oil palm plantation locations, the water table was extremely low (80 cm below surface level), hence samples were collected from two positions AWT, namely 20–30 cm and 50 cm, respectively. One location within a mixed crop plantation was flooded; hence, only one sample was collected BWT and none from AWT. Samples were shipped on ice to the laboratory.

2.2 Bacterial community structure (Terminal Restriction Fragment Length Polymorphism (T-RFLP) analysis)

Bulk peat gDNA was extracted using ZR Soil Microbe DNA MidiPrep™ extraction kit (Zymo Research Corporation, Irvine, USA) based on the manufacturer's protocol, with minor modifications. The extracts were quantified spectrophotometrically (Nanodrop ND-1000, Nanodrop Technologies, Wilmington, DE, USA). Bacterial 16S rRNA genes were amplified using universal primer, BSF517-GCCAGCAGCCGCGGTAA and BSR1541/20-AAGGAGGTGATCCAGCCGCA (Wilmotte et al., 1993). For T-RFLP anal-

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ysis, forward primer was labeled with 6-carboxyfluorescein (FAM) at the 5'-end and reverse primer was labeled with photoinduced electron transfer (PET) at 3'-end. PCR was performed in triplicate (50 µL reaction) using 50 ng of template DNA and following parameters: initial denaturation at 95 °C for 10 min, followed by denaturation 95 °C for 1 min, annealing at 58 °C for 30 s, extension at 72 °C for 1 min and final extension of 72 °C at 7 min. Agarose gel electrophoresis, followed by staining of products with SYBR Green (Invitrogen, USA) was performed to check amplified product size and concentration. Amplicons from three replicates of PCR were pooled and cleaned up using NucleoSpin® Extract II according to manufacturer's instructins. 500 ng of each amplicon was digested with restriction enzymes *Alu I* and *Bsu RI* (Fermantas) at 37 °C for 16 h. Digests were then purified using NucleoSpin® Extract II kit and an aliquot of 1 µL was mixed with 8.5 µL HiDi formamide (Applied Biosystems, Foster City, CA, USA) and 0.5 µL of internal size standard (Applied Biosystems) for T-RFLP reactions. The labeled terminal-restriction fragments (TRFs) were detected on an ABI 3730XL automatic DNA sequencing machine (Applied Biosystems) in the GeneScan mode. For data collection from the DNA sequencing machine, Genemapper software (Applied Biosystems) was used to compare relative lengths of TRFs with the internal size standard. For profile comparison, minimal and maximal cut-offs of 50 bp and 600 bp, respectively, were set and fragments with peak height below 75 were removed as filter noise.

2.3 Chemical analysis

Five gram of peat was mixed with 40 mL of analytical grade water. The mixture was shaken at 200 rpm overnight to obtain a bioavailable extract for microorganisms from peat (Reynolds and Clarke, 2008). These extracts were used for analysis of total dissolved organic carbon (DOC) and inorganic carbon using a total organic carbon analyzer (TOC-V CPH E200V 220V, Shimadzu). Aliquots from the same remaining extracts were also analyzed for anions such as fluoride, chloride, nitrite, nitrate, phosphate, sul-

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fate and cations such as sodium, ammonium, potassium, magnesium, calcium using ion chromatography analyzer (ICS-5000, Dionex).

Peat water samples were run through a Solid Phase Extraction cartridge using an Oasis® HLB cartridge (1 cc/30 mg; 30 µm, Waters, USA) in order to extract, concentrate and clean-up the metabolites (Parab et al., 2009). The samples were analyzed using Ultra Performance Liquid Chromatography (UPLC) in a Waters ACQUITY UPLC™ system (Waters Corp., MA, USA), equipped with a binary solvent delivery system and an autosampler. The chromatography was performed on a Waters ACQUITY C_{18} 1.7 µm column (100 × 2.1 mm). Mass spectrometry was performed based on MS conditions using a mass spectrometer equipped with electrospray ionization source (UPLC-TOF-Bruker Daltonics). Data was extracted using Bruker Daltonics-Profile Analysis software.

2.4 Data analysis

To analyze the variation in bacterial community structure as well as difference in metabolic functions, due to influence from analyzed parameters (namely, water table, land-use patterns, age of drainage and peat thickness), multivariate statistical techniques (PRIMER 6, PRIMER-E, Ltd., Plymouth, UK) were used to calculate distance matrices using Bray–Curtis similarity indices and one-way ANOSIM (Analysis of Similarity) coefficients (Legendre and Legendre, 1998). Unconstrained ordination plots with 100 iterations using nonmetric multidimensional scaling (nMDS) based on Bray–Curtis similarity were used to represent the outcome (Kruskal, 1964; Shepard, 1962). To analyze the relative influence of different parameters over bacterial communities, two-way ANOSIM (Clarke, 1993) was used. The global R statistic value (generated using one-way or two-way ANOSIM) indicates the degree of separation between the two communities, with values close to unity indicating more separation and a zero value indicating no difference between the groups.

To analyze influences of geochemical traits over the bacterial community structure, CCA (Canonical Correspondence Analyses) was performed using Canoco (version 4.5

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for Windows, PRI Wageningen, the Netherlands) (Lepš and Šmilauer, 2003). Presence/absence of TRFs was used as "species" data. Geochemical data (anions, cations, DOC and inorganic carbon) were included in the analysis as "environmental" variables. Ordination biplots approximating the weighted differences between the individual communities (T-RFLP patterns) with respect to each of the geochemical factors (represented as arrows) were drawn. The relative importance of geochemical factors in explaining variation in the bacterial T-RFLP profiles was explained by the length of the corresponding arrows and the angle between arrows indicated the degree to which they were correlated. The impact of geochemical variables over bacterial community structure was calculated using Monte Carlo permutation test based on 1000 random permutations (Rasche et al., 2011).

To predict the phylogeny of the bacterial species at the taxa level from the TRFs of 16S rDNA, Fragment Sorter Suite (FRAGSORT) (ver. 5.0; Agricultural Research and Development Center, Ohio State University) and Phylogenetic Assignment Tool (PAT) (Kent et al., 2003) was used, adopting the methodology described in Lefebvre et al. (2010). Microbial Community Analysis (MiCA) – a virtual digest program (Shyu et al., 2007) was used to construct a reference database for each set of primers.

2.5 Clone library sequencing of 16S rDNA gene

In order to validate the presence of predicted species evaluated from FRAGSORT analysis, a clone library using 16S rDNA from two randomly chosen sites that differed in water table, land-use pattern and oxic conditions was prepared. The sites chosen belong to settlement with high water table and oil palm plantations with low water table. The samples were taken from both oxic and anoxic zones.

The cleaned PCR product (using same non-labeled primer sequences as described earlier) of 16S rDNA from settlements and oil palm plantation sites was cloned into 3956bp pCR® 4-TOPO® vector using TOPO TA Cloning kit for sequencing (Invitrogen, USA) according to the manufacturer's protocol. One Shot® TOP 10 Competent

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Cells (Invitrogen, USA) was used in order to transform the recombinant plasmid. DNA Sequencing was performed on a DNA sequencer (ABI 3130x/Genetic Analyzer) using forward or reverse M13 primers, on plasmid DNA extracted using Wizard® Plus SV MiniPrep DNA Purification System (Promega, USA) from individual clones. DNA sequence data was analyzed as described previously (Reuben et al., 2012). Briefly, sequences were trimmed and edited using MEGA 5 (Tamura et al., 2011). MAFTT (Katoh et al., 2009) was used for aligning the sequences and identifying reverse orientation. Sequences were then reverse-complemented using MEGA5. Vector contamination was checked using Vector screening tool in Sequin (http://www.ncbi.nlm.nih.gov/Sequin/sequin.hlp.html) and chimera check was performed using Bellerophon (Katoh et al., 2009) followed by Mallard 1.2. (Ashelford et al., 2006). Sequences of 301 clones were submitted to Genbank and the nucleotide sequence data reported in this paper is published in the GenBank nucleotide database under accession numbers JF739556-JF739857.

3 Results

3.1 Influences of peat characteristics on bacterial community structure

3.1.1 Oxygen availability and water table

Oxygen availability was lower in the below water table (BWT) samples compared to above water table (AWT) samples by a factor of three or more (Fig. 2a). The BWT oxygen levels were similar across all land-use types. Based on these, henceforth, we use the terms “oxic” and “anoxic” conditions to refer to oxygen availability in AWT and BWT zones, respectively. Effects of oxygen levels on bacterial DNA profiles were analyzed (Fig. 2b). In the ordination plot, samples from the low water table sites (across all oil palm plantations) tended to cluster together, regardless of oxic and anoxic zones. The remaining samples clustered roughly into oxic and anoxic zones, although samples

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from degraded land were mixed within oxic and anoxic zones. However, only one site of anoxic zone from mixed crop plantation (indicated by dashed arrow) did not fall into the anoxic zone group, as this site was flooded at the time of sampling. Anoxic zones supported more complex bacterial communities than oxic zones, although this was not the case for samples from degraded land (Table 1).

Continuous monitoring of the water table and rainfall revealed that variation in water table over a one-year period (August 2009–August 2010) was influenced by rainfall in that period, with maximal rainfall in February 2010 of 370 ± 25 mm, averaged over all sites (Fig. 3a). Sampling of bacterial communities was performed when the water table was high. Variation in the water table pattern was similar for all sites except for five oil palm plantation sites that had low water table (> 50 cm). Water table varied more in the low water table sites than in high water table sites, thereby, exposing the low water table sites to different durations of oxic and anoxic regimes compared to high water table sites. Between-site comparisons of bacterial community composition showed statistically significant clustering based on water table level in oxic zones (Fig. 3b; Table 2 – one-way ANOSIM values).

Water table depth greatly influenced bacterial diversity in both oxic and anoxic zones, with the influence being greater in the oxic zone. In order to determine the relative influences of different peat characteristics, we analyzed pair-wise combinations of peat characteristics using two-way ANOSIM analysis. It revealed major influence of water table and land-use pattern over other characteristics, namely, age of drainage and peat thickness (Table 2: two-way ANOSIM values). The variations in bacterial communities due to water table differences for both oxic and anoxic zones were significant across land-use, peat thickness and age of drainage (Table 2: two-way ANOSIM values).

3.1.2 Land-use pattern, age of drainage and peat thickness

Unlike the oxic zone, where water table was the predominant factor influencing bacterial community structure, in the anoxic zone, land-use pattern had an equally strong influence as water table on bacterial community structure (Table 2). In such anoxic

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zones, the bacterial diversity decreased in different land-use types in the following order: mixed crop plantations > degraded forest > settlements > degraded land > oil palm plantations (Table 1). In both oxic and anoxic zones, highest diversity of bacterial communities was found in mixed crop plantations, whereas, least diversity was present in oil palm plantations.

Age of drainage and peat thickness had a weaker yet statistically significant affect as compared to water table and land-use patterns in shaping the bacterial community profiles in both oxic and anoxic zones (Table 2: one-way ANOSIM values). In the ordination plot of the bacterial communities based on age of drainage, two sub-groups dominated by low water table sites and mixed crop plantations, respectively, revealed that these two parameters had additional influences (Supplement Fig. S1). As in the case of age of drainage, in the ordination plot based on peat thickness, there was a sub-group of low water table sites in oxic zones (Fig. 3b).

3.2 Distribution of bacterial taxa

In order to identify the dominant members of the bacterial communities, we predicted the taxa using the TRFs. To validate the taxa group identified, a clone library was created that revealed differences in abundance of taxa based on water table, land-use pattern and oxygen availability (Table 3), which was consistent with our previous findings (Figs. 2 and 3b). *Acidobacteria* had 100 % similarity with the predicted taxa as mentioned above for all the sites sampled for clone library. The coverage between the predicted taxa and clones identified for Gammaproteobacteria ranged from 56.7 % to 89.3 % between the sites sampled. The highest coverage between the predicted taxa and clones identified was found in the site with settlements in oxic zones. Based on sequence database searches with the clone sequences, two species were identified based on identities to known entries. *Brevundimonas* sp., reported initially from saline soils (Wang et al., 2012) was found abundant in settlements. Interestingly, a beneficial plant growth promoting species, *Stenotrophomonas* sp. was found abundant in the clones identified from all three types of samples where cloning was performed.

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Oxygen availability had a strong influence on the abundance of bacterial taxa in high and low water table depths (Supplement Fig. S2). In the oxic zones, the water table did not affect taxa abundance, whereas, in the anoxic zones, all major taxa were more abundant in the low water table sites. Among the five most abundant taxa (*α*-, *β*- and *γ*-*proteobacteria*, *Actinobacteria* and *Firmicutes Bacillales*), *Actinobacteria*, had the largest difference in abundance between different water table depths in both oxic and anoxic zones.

3.3 Relationship of environmental and geochemical parameters with bacterial community structure

Canonical correspondence analysis was used to identify the association of environmental and geochemical traits with bacterial communities from different land-use patterns (Fig. 4a, b and Supplement Table S1). Bacterial communities from the oil palm plantations were associated with nitrate levels in both oxic (Fig. 4a) and anoxic (Fig. 4b) zones. Bacterial communities in the mixed crop plantations, on the other hand, were mainly associated with DOC, ammonium and phosphates. Salinity had a major influence on bacterial communities from mixed crop and settlement sites; latter corroborated the identified salinity associated species from settlements.

Metabolic profiling of peat water and bacterial profiling of TRFs from peat based on land-use patterns were performed to directly compare the effects of bioavailable organics that influence the bacterial communities (Fig. 5). Bacterial communities were separated based on habitat, as revealed by separation of the flooded site (indicated by arrow) from the non-flooded sites (Fig. 5a). However, when comparing the functional data from metabolic profiling (Fig. 5b), distinct clusters of different land-use types were formed. Metabolic profiling not only differentiates the land-use patterns but also clearly distinguishes samples based on geographical sampling position. For example, two sites from degraded land in Site B formed a distinct cluster from the other two sites from degraded land in Site A (DHAN in Fig. 1). Similarly, two oil palm plantation sam-

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ples (extreme left of Fig. 5b) though belonging to different peat thickness (MHPN and DHPN in Fig. 1) were clustered very close as they were from the same transect.

4 Discussion

Microbial and metabolic markers that represent the complex nature of bacterial communities and their metabolic processes, respectively, provided the resolving power to distinguish different habitats. This resolution ranged from centimeter scale in depth measurements to kilometer scale, where sites were distributed within the 48 km^2 of the study area. Thus, the same set of molecular markers provided a dynamic range of resolution at four orders of magnitude. Microbial markers have been extensively used to study alteration in community structures due to changes in land-use patterns at large scales of spatial distribution, such as, in Pacific Northwest marine sediment communities (Braker et al., 2000), in high levels of nuclear waste-contaminated vadose sediments at the Hanford Site in the US (Fredrickson et al., 2004), in Western Amazon soils (Jesus et al., 2009) and in Antarctic dry valley (Chan et al., 2013), among other biogeographic locations. In comparison, there are relatively few studies that have used metabolites as function-based markers for understanding variation at large scale of spatial distribution. Both sets of molecular markers distinguished different land-use types, but with different levels of resolution. Compared with microbial profiles, those of metabolites were additionally able to separate land-use types from locations that are separated by nearly 8 km distance. Our findings about bacterial profiling have led us to identify geochemical factors that influence the state of degraded peatlands. In addition, metabolic profiling, which relies on markers derived from bacterial functions provide a finer classification of peatland sites. Metabolic profiling can, therefore, be used in developing better practices for mapping peatlands, which can be a tool for both management and policy development.

While there have been reports of effects of land-use change on emissions (Jauhiainen et al., 2012) and hydrology on subsidence (Hooijer et. al., 2010, 2012), our

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approach allows multiple parameters to be evaluated simultaneously using a single molecular profiling approach. Our findings show that microbial profiles from peatland sites are most influenced by variations in water table and land-use patterns. These two are followed by age of drainage and peat thickness in influencing the bacterial community structure. Along peat dome, water table fluctuates due to drainage, rainfall and other physical parameters (Jauhiainen et al., 2008; Hooijer et al., 2010). The ability of microbial markers to distinguish the low and high water table sites shows their robustness despite the fluctuations in water level at these sites. Incidentally, sampling was done when the water table was at its highest levels and prior month received the highest rainfall. Such changes in microbial community structure along a hydrological gradient have been reported in other natural ecosystems, such as in wetlands (Yu and Ehrenfeld, 2010). However, rapid fluctuations in water table, as seen here, were not present in the wetland study. Hence microbial profiling presents a good approach to monitor peat responses to both rapid short-term and long-term hydrological changes. Land-use changes are discussed later.

Oxygen availability for microbial communities vary with both depth and seasonal fluctuations of water table. Low water table sites undergo more pronounced cycles of drying and wetting compared to high water table sites, which mostly have low oxygen availability. The oxic zones from these sites will, therefore, have less pronounced differences in oxygen availability. Variations in oxygen availability can explain the differences in the bacterial community structure from anoxic zones of the high and low water table sites. Both diversity index and abundance of taxa in oxic and anoxic zones of these sites corroborate this trend. Among the five most abundant taxa, *Actinobacteria* had the largest variation between different water table depth in both oxic and anoxic zones. Hence, it seems to be the most sensitive taxa group in the peat habitats to oxygen availability, which is consistent with the finding in freshwater ecosystems (Garcia et al., 2013). Members of this taxa group have been shown to actively reduce N_2O to N_2 and thus sequester nitrogen not only in the anoxic zone of palsa peat (Palmer and Horn, 2012), but also in other habitats, such as, agricultural soils (Philippot et al., 2002) and

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in Uranium contaminated sediments (Akob et al., 2008). Independent of the role of *Actinobacteria*, our findings show large influence of nitrates and phosphates on overall bacterial diversity in oil palm plantations. Both nitrates and phosphates are likely to originate from mineral fertilizers used in these peatland sites under agriculture. Such fertilizers and organic manure affect the soil microbial biomass, their activity and diversity (Zhong et al., 2010). Since nitrogenous fertilizers are heavily used in the management of plantations on tropical peatlands, N_2O is likely to be released, as demonstrated from other agricultural lands, such as, from Australia (Dalal et al., 2003), India (Aggarwal P.K., 2008) and Africa (Hickman et al., 2011) agricultural soil, among many others. Hence, it will be important to estimate N_2O emissions from tropical peat plantations that use mineral fertilizers and also the utility of N_2O reducing bacteria in such plantations. In contrast to plantations, salinity is a major influencing factor in settlements, possibly due to anthropogenic activities. This land-use type covers nearly 6 % of the total mapped area in this study (3390 km^2), thus representing a significant influence on the microbial communities in this region. Hence, microbial profiling can help reveal influences of both management and anthropogenic activities on peat.

In the anoxic zones of peat layer, the differences among the bacterial communities are more influenced by land-use patterns than by water table. It is likely that these differences in land-use pattern are linked to their plant communities and the nature of dissolved organic carbon (Bardgett et al., 2005). Dissolved organic carbon has recently been shown to be a major source of carbon loss via fluvial processes (Moore et al., 2013). Based on levels of dissolved organic carbon and metabolic profiles from different land-use types, we propose that the plant communities associated with each habitat contribute significantly diverse metabolites in the form of exudates and biomass degradation products, as reported from many plant systems (Weston and Mathesius, 2013). These organic resources then contribute to the bioavailable nutrient pool for the microbial communities. Nutrients from the root exudates such as carbohydrates, organic acids, amino acids and secondary metabolites from lignin and flavonoid classes are required for the growth of soil microbes (Narasimhan et al., 2003; Dennis et al.,

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2010). This relationship between plant and microbial communities is corroborated by the trend in bacterial diversity in our study, which was the highest in mixed crop plantations and degraded forest followed by settlements, degraded land and oil palm plantations in that order. The degraded forest has undergone partial deforestation, drainage and burnt since 2003. Mixed crop plantations have been shown to increase the soil microbial biomass in the rhizosphere resulting in enhanced plant yield in mineral soil (Zarea et al., 2009). Low bacterial diversity in oil palm plantations can, therefore, lead to reduction in their productive period. Rhizosphere microbial community consists of plant growth promoting organisms among others, which can contribute significantly to sustainable growth of plant community. In oil palm plantations and settlement sites in our study, a plant growth promoting microorganism, *Stenotrophomonas* sp. was one of the most abundant species found. These findings provide a good basis to adopt microbial ecology principles to encourage mixed crop planting in the existing plantations, in order to increase their microbial diversity, especially of beneficial microbes, which can lead to sustainable use of these plantations.

Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/10/14009/2013/bgd-10-14009-2013-supplement.pdf.

Acknowledgements. We thank NUS Environmental Research Institute (NERI), Department of Biological Sciences, NUS and Singapore-Delft Water Alliance (SDWA) for their funding and infrastructure support. We thank Choon Nam Ong for his insightful comments and kind support throughout the program. We also thank Ryan Chisholm for his suggestions during critical reading of the manuscript. Thanks also to Lee Li Kheng and Kalyan Mynampati for their support on GIS and metabolic profiling software, respectively. Lastly, we thank Sugino, research staff from University of Jambi, for his assistance during the field work. The research presented in this work was supported by funding from National Research Foundation and the Economic Development Board (SPORE, COY-15-EWI-RCFSA/N197-1), NERI (WBS: R-706-000-008-646) and SDWA (R264-001-011-490).

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Table 1. Shannon diversity indices for different land use patterns based on 16S rDNA.

Land use patterns	Above water table (Oxic zones)	Below water table (Anoxic zones)
Degraded forest	3.14	3.53
Degraded land	3.44	3.27
Settlements	3.19	3.38
Oil palm plantations	2.62	2.68
Mixed crop plantations	3.48	3.62

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Table 2. One-way (bold cells) and two-way (roman cells) ANOSIM showing variation in bacterial community structure due to individual parameter across other parameter tested in oxic and anoxic zones. The top value in each roman cell refers to influence by the individual parameter across others (left to right), whereas bottom value in the same roman cell shows vice versa (right to left). Values in roman cells can be directly compared within same roman cells or between roman cells of oxic and anoxic zones. As an example of within-roman cell comparison: in oxic zones, the influence of water table was much higher across different land-use patterns (Global R: 0.702), peat depth (0.946) and age of drainage (0.609) than vice versa (0.189, 0.344, NS: −0.009), respectively. However, in anoxic zones, land-use pattern had high influence across water table (0.468), peat depth (0.636) and age of drainage (0.532), respectively.

Global R statistics									
	Above water table (oxic) zones					Below water table (anoxic) zones			
	Water table	Land use	Peat depth	Age of drainage		Water table	Land use	Peat depth	Age of drainage
Water table	**0.527**^{c}	0.702^{b} 0.189^{a}	0.946^{b} 0.344^{a}	0.609^{c} −0.009	Water table	**0.359**^{b}	0.541^{a} 0.468^{b}	0.878^{a} 0.266^{a}	0.66^{b} 0.247^{a}
Land use		**0.267**^{a}	0.485^{b} 0.358	0.361^{b} 0.76^{b}	Land use		**0.413**^{b}	0.636^{c} 0.268	0.532^{c} 0.101
Peat depth			**0.214**^{b}	0.433^{c} 0.574^{b}	Peat depth			**0.165**^{a}	0.563^{b} 0.643^{b}
Age of drainage				**0.389**^{c}	Age of drainage				**0.192**^{a}

Level of significance is: ^{a} $p < 0.05$, ^{b} $p < 0.01$, ^{c} $p \leq 0.001$.

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Table 3. Correspondence of clone data in comparison to predicted species. "AWT": above water table samples and "BWT": below water table samples.

Species distribution (Taxa level)	MLPO-AWT (from oxic zones) (Medium peat–Low water table–Oil palm plantations–Old age of drainage)			DHTO-AWT (from oxic zones) (Deep peat–High water table–Settlements–Old age of drainage)			DHTO-BWT (from anoxic zones) (Deep peat–High water table–Settlements–Old age of drainage)		
	No. of Clones (102)	No. of predicted taxa by FRAGSORT	% Coverage	No. of Clones (104)	No. of predicted taxa by FRAGSORT	% Coverage	No. of Clones (96)	No. of predicted taxa by FRAGSORT	% Coverage
Environmental (Unclassified)	71	313	22.7	60	278	21.6	74	281	26.3
Gammaproteobacteria	19	34	56.7	25	28	89.3	15	23	65.2
Alphaproteobacteria	5	45	11.2	10	41	24.4	3	41	7.3
Acidobacteria	5	5	100.0	3	3	100.0	2	2	100.0
Actinobacteria	0	53	0.0	1	49	2.0	0	22	0.0
Betaproteobacteria	2	44	4.5	2	37	5.4	2	41	4.9
Planctomycetes	0	12	0.0	1	9	11.1	0	14	0.0
Proteobacteria	0	4	0.0	2	3	66.7	0	1	0.0

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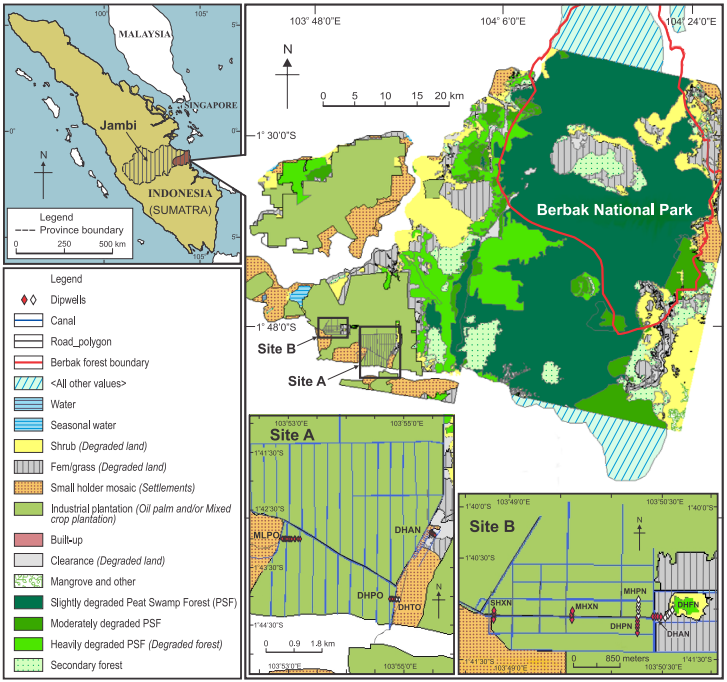

Fig. 1. Map showing the Sumatra Island in Indonesia (top left) and land cover present in eastern part of Jambi province (right). Study sites in this region of Jambi, Site A and Site B are located at geographical locations: 103°53′52.58″ E, 1°43′12.47″ S and 103°49′32.23″ E, 1°40′58.24″ S, respectively. Abbreviations are: D, deep peat thickness (> 7 m); M, medium peat thickness (3–7 m); S, shallow peat thickness (< 3 m); H, high water table(between 0–45 cm); L, low water table (> 45 cm); F, degraded forest; A, degraded land; P, oil palm plantations; T, settlements; X, mixed crop plantations; N, new age of drainage (drained < 10 yr); O, old age of drainage (drained > 10 yr ago). Land-use patterns described in this study are italicized in the legends of land cover.

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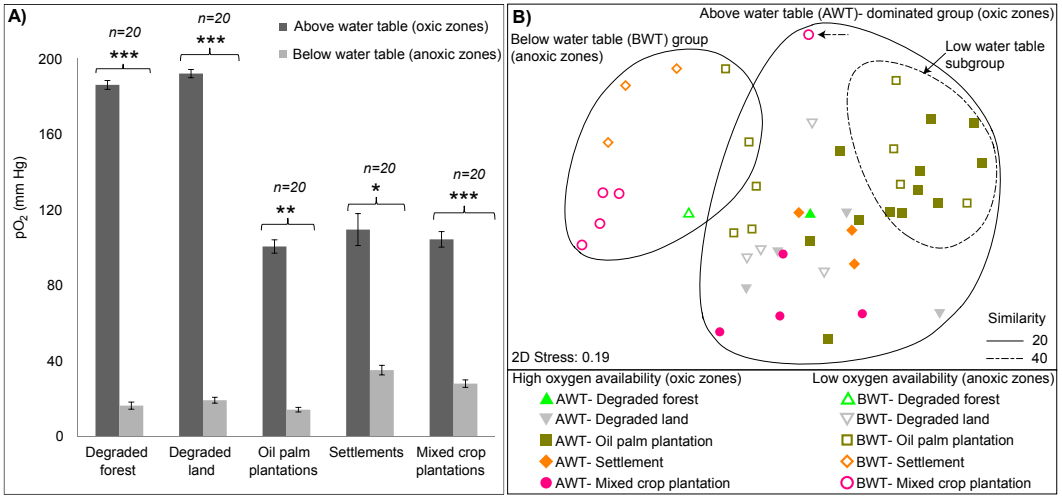

Fig. 2. Oxygen levels (pO_2), mm Hg **(A)** and nonmetric multidimensional scaling (nMDS) ordination plot based on Bray–Curtis similarities calculated from presence/absence data of 16S rDNA TRFs abundances **(B)** at above (oxic zones) and below (anoxic zones) water table positions in different land-use types. Level of significance in **(A)** is: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

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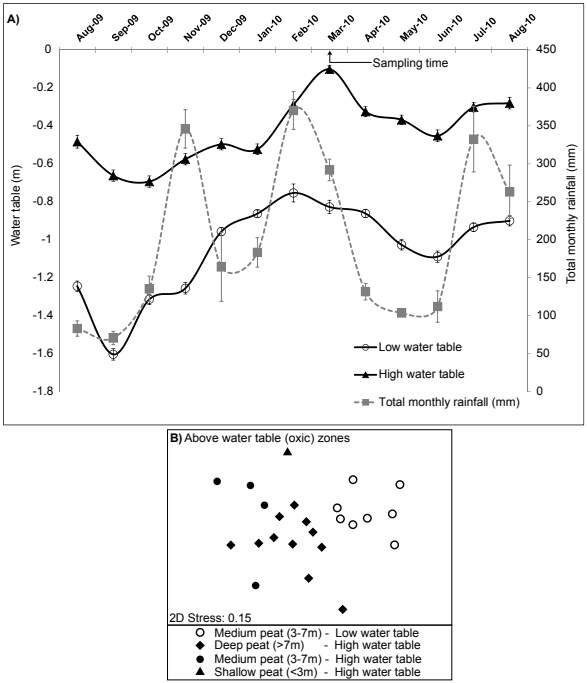

Fig. 3. (A) Rainfall and water table data from August 2009 to August 2010 at all sampling locations from Site A and Site B. The locations are shown in Fig. 1. Water table levels were averaged across locations with high water table (between 0–45 cm) and low water table (> 45 cm), respectively. The averaged values are represented as "high water table" and "low water table", respectively. **(B)** Nonmetric multidimensional scaling (nMDS) ordination plot, based on Bray–Curtis similarities calculated from presence/absence data of 16S rDNA TRFs abundances, showing variation between bacterial community across different water table depth and peat thickness, respectively, from above (oxic zones) and below (anoxic zones) water table positions. Low water table (LWT), high water table (HWT) and different peat thickness samples are represented by open symbols, closed symbols and different shapes, respectively.

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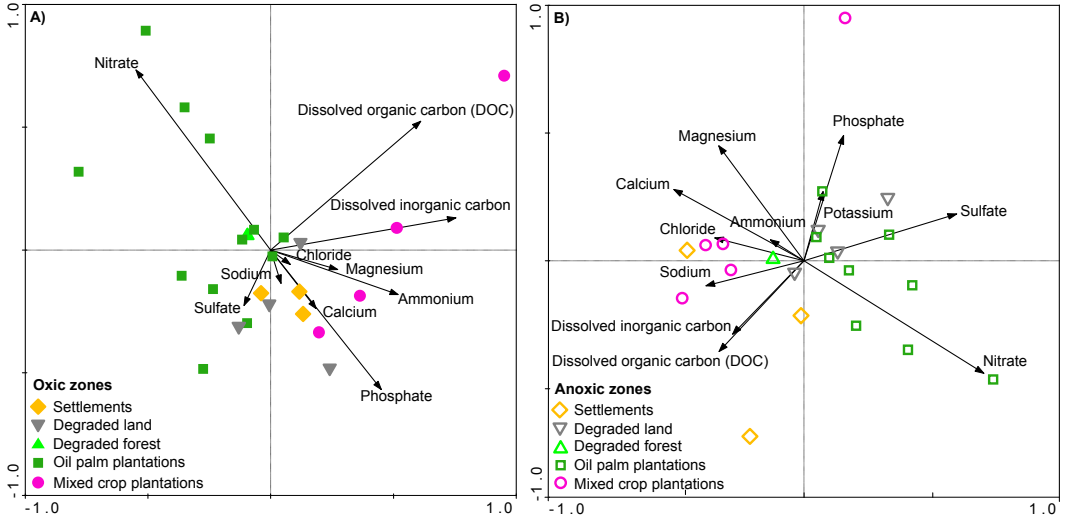

Fig. 4. Canonical correspondence analysis of 16S rDNA gene based T-RFLP datasets and environmental data in different land-use patterns from oxic **(A)** and anoxic **(B)** zones. Environmental and geochemical data, represented with arrows are: nitrates, dissolved organic carbon (DOC), dissolved inorganic carbon, chloride, magnesium, ammonium, sodium, calcium, sulfate and phosphate. Test of significance (*p* value) of all canonical axes is 0.05 and 0.009 in oxic **(A)** and anoxic **(B)** zones, respectively.

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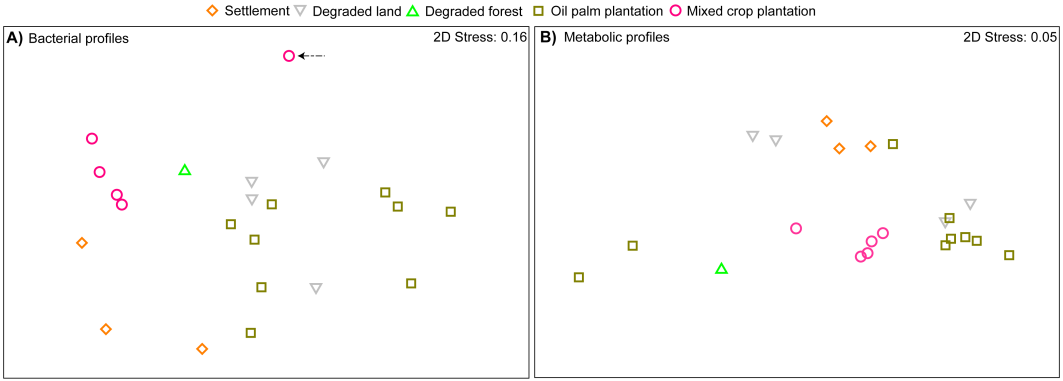

Fig. 5. Nonmetric multidimensional scaling (nMDS) ordination plot, based on Bray–Curtis similarities calculated from presence/absence data of 16S rDNA TRFs from anoxic zones **(A)** and based on Euclidean distance calculated from intensity of metabolites extracted from peat water from dipwells **(B)** in different land-use patterns.

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