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PEATLANDS

Peat Properties, Dominant Vegetation Type and Microbial Community Structure in a Tropical Peatland

N. T. Girkin[1,2] · R. A. Lopes dos Santos[3] · C. H. Vane[3] · N. Ostle[4] · B. L. Turner[5] · S. Sjögersten[2]

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Abstract

Tropical peatlands are an important carbon store and source of greenhouse gases, but the microbial component, particularly community structure, remains poorly understood. While microbial communities vary between tropical peatland land uses, and with biogeochemical gradients, it is unclear if their structure varies at smaller spatial scales as has been established for a variety of peat properties. We assessed the abundances of PLFAs and GDGTs, two membrane spanning lipid biomarkers in bacteria and fungi, and bacteria and archaea, respectively, to characterise peat microbial communities under two dominant and contrasting plant species, *Campnosperma panamensis* (a broadleaved evergreen tree), and *Raphia taedigera* (a canopy palm), in a Panamanian tropical peatland. The plant communities supported similar microbial communities dominated by Gram negative bacteria (38.9–39.8%), with smaller but significant fungal and archaeal communities. The abundance of specific microbial groups, as well as the ratio of caldarchaeol:crenarchaeol, isoGDGT: brGDGTs and fungi:bacteria were linearly related to gravimetric moisture content, redox potential, pH and organic matter content indicating their role in regulating microbial community structure. These results suggest that tropical peatlands can exhibit significant variability in microbial community abundance even at small spatial scales, driven by both peat botanical origin and localised differences in specific peat properties.

Keywords PLFA · GDGT · Tropical peat · Microbial community structure · Wetland

Introduction

Tropical peatlands are a critical part of the global carbon cycle representing a significant sink carbon containing 15–19% of the global peat carbon stock (Dargie et al. 2017; Page et al. 2011). Tropical wetlands in general are large sources of greenhouse gas emissions (GHGs), with annual emissions of up to 4540 Tg carbon dioxide (CO_2) and 90 Tg methane (CH_4) (Sjögersten et al. 2014). Plants are key in regulating GHG emissions, as species specific litter inputs define initial peat properties (Cooper et al. 2019; Upton et al. 2018) and rates of decomposition (Hoyos-Santillan et al. 2016b; Hoyos-Santillan et al. 2015). Plant inputs of oxygen and carbon, in the form of root exudates, have also been identified as critical regulators (Girkin et al. 2018c; Hoyos-Santillan et al. 2016a). Water table height and peat temperature are key environmental regulators, with the former determining whether anaerobic or aerobic decomposition pathways dominate, affecting the balance of CO_2 versus CH_4 production, and the latter determining the rate of biological processes (Girkin et al. 2020; Hooijer et al. 2012; Hooijer et al. 2010; Jauhiainen et al. 2005).

While peat organic matter properties have previously been found to vary substantially between dominant vegetation types (Sjögersten et al. 2011; Upton et al. 2018), peat properties can also vary on much smaller scales, between both plant species and with distance from plant stems (Girkin et al. 2019). Overall spatial variability of inputs and properties is therefore very high, with a microtopography that is also frequently visually highly heterogeneous, featuring a series of hummocks and hollows, the former of which are formed

✉ N. T. Girkin
nicholas.girkin@gmail.com

1 Environment and Agrifood, Cranfield University, Cranfield MK43 0AL, UK

2 School of Biosciences, University of Nottingham, Nottingham NG7 2RD, UK

3 Centre for Environmental Geochemistry, British Geological Survey, Keyworth NG12 5GG, UK

4 Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

5 Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Republic of Panama

predominantly by plant roots and rise above the surface of the water table, the latter of which are frequently permanently inundated. Similarly, microbial community structure has previously been found to vary between dominant vegetation types, driven predominantly by biogeochemical gradients (Troxler et al. 2012). However, smaller-scale variability in microbial community structure driven by individual plants has never been assessed in tropical peatlands.

To date, studies assessing microbial communities in tropical forests have indicated substantial differences in microbial community structure and activity on the conversion of primary or secondary swamp forest to plantation agriculture (Krashevska et al. 2015; Nurulita et al. 2016). Analysis of the 16S rRNA sequence of peats have indicated that primary tropical swamp forest features a diverse community including obligate anaerobes such as methanogenic archaea (Kanokratana et al. 2011), with bacterial community composition closely related to the availability of limiting nutrients such as phosphorus (Troxler et al. 2012). In general, most studies have identified high abundances of Gram negative bacteria, particularly Acidobacteria, and relatively low fungal abundance (Chambers et al. 2016; Jackson et al. 2009; Troxler et al. 2012). Changes in microbial community structure with depth in tropical peatlands have also been observed, with archaeal abundance more limited at increased depth (Jackson et al. 2009). Differences in microbial community structure between seasons and primary and secondary swamp forest in Malaysia, assessed through changes in specific phospholipid fatty acid (PLFA) biomarkers, have also been reported. Components of the microbial community, Gram positive and Gram negative bacteria, have in turn been positively correlated with CO_2 and CH_4 emissions respectively (Dhandapani et al. 2019). Assessing microbial community composition is therefore important in interpreting greenhouse gas dynamics within peatlands.

PLFA biomarker analysis is a widely used technique for determining soil microbial community structure, specifically the relative abundances of fungi, and Gram positive and Gram negative bacteria (Frostegard et al. 2011), with results broadly comparable to those derived from 16S rRNA gene metabarcoding for discerning microbial community structure (Orwin et al. 2018). Similarly, glycerol dialkyl glycerol tetraether (GDGT) can be used to characterise archaea as well as specific bacterial communities (Schouten et al. 2007), with biomarkers identified in peats (Schouten et al. 2000; Weijers et al. 2006; Zheng et al. 2015), sediments (Pancost and Damste 2003) and soils (Dirghangi et al. 2013). Both PLFAs and GDGTs are membrane spanning lipids which differ broadly in structure and size between microbial groups, thus allowing specific biomarkers to be attributed to individual communities, although this has not always been consistently applied (De Deyn et al. 2011; Nottingham et al. 2009; Tavi et al. 2013; Yao et al. 2015). Lipid biomarker analysis has several advantages over other methods of characterising soil microbial communities, including both DNA and RNA extractions. First, DNA can persist long after cell death whereas phospholipids are rapidly degraded, which means that DNA based methods of assessing total biomass therefore include a certain fraction of microbial necromass (White et al. 2009). Moreover, cell membrane lipid biomarker abundances respond to both internal and external environmental changes, meaning that PLFA and GDGT analyses provide information on both the phenotype and activity of microbial communities (Frostegard et al. 2011; Ramsey et al. 2006; Willers et al. 2015).

Recent microbial community studies in peatlands using GDGT analysis have predominantly focussed on its use as a biomarker in paleoclimate studies (Zheng et al. 2015), but distributions of branched GDGTs (brGDGTs) have also been applied as a peat-specific temperature and pH proxies (Naafs et al. 2017). brGDGTs are also thought to be produced by heterotrophic bacteria dwelling in anoxic soils, with Acidobacteria a key taxa (Damste et al. 2011; dos Santos and Vane 2016). Similarly, isoprenoid GDGTs (isoGDGTs) are broad indicators of archaeal abundance, with caldarchaeol (GDGT-0) abundance suggested as a biomarker for methanogenic archaea (Zheng et al. 2015).

In this study, we applied PLFA and GDGT biomarker analyses to assess microbial community structure in surface peats associated with two plant species, *Campnosperma panamensis*, a broadleaved evergreen tree, and *Raphia taedigera*, a canopy palm. These two species represent two dominant components of plant community structure for the Changuinola peat deposit, Panama. Peat derived from their inputs has previously been reported to vary significantly in terms of organic matter properties on both large (km) and small scales (m) across the peatland dome (Girkin et al. 2019; Upton et al. 2018), feature varying litter decomposition rates (Hoyos-Santillan et al. 2015), and autotrophic and heterotrophic respiration components (Girkin et al. 2018a). We subsequently compared microbial community structure and abundance to key environmental variables to relationships between dominant vegetation type, bulk peat properties and microbial communities. We hypothesised that: i) peats derived from contrasting botanical origins would feature distinct microbial community structure; ii) biomarker abundance would be determined by key peat biogeochemical properties including pH, redox potential, substrate availability (C:N and organic matter content) and gravimetric moisture content.

Materials and Methods

Study Sites

This study was conducted using peat samples collected in May 2016 in the 80 km^2 ombrotrophic Changuinola

peatland in Bocas del Toro province, Panama. Peat formation began 4000–5000 years ago and has resulted in a central peat dome up to 8 m deep (Phillips et al. 1997). The site is dominated by seven successive plant phasic communities beginning with a coastal belt of *Rhizophora mangle* (Linnaeus) mangrove, succeeded by *Raphia taedigera* (Mart.) dominated palm swamp, a mixed species forest swamp comprising *R. taedigera* and *Campnosperma panamensis* (Standl.), a *C. panamensis* dominated forest, a stunted *C. panamensis* forest, and a *Myrica-Cyrilla* bog-plain (Phillips et al. 1997).

The Changuinola peat deposit has previously been extensively characterised in terms of species diversity and abundances (Sjögersten et al. 2011), nutrient availability (Sjögersten et al. 2011; Troxler et al. 2012), and peat organic chemistry (Upton et al. 2018). Species composition and abundances have been reported to change over relatively short distances matching gradients in nutrient status towards the centre of the dome. Briefly, *R. taedigera* monodominant stand has a low Shannon diversity index (1.13) and low stem abundance (106 stems per hectare). The site has total phosphorus of 0.957 mg P g^{-1} higher than other stands at the site (Sjögersten et al. 2011). In contrast, *C. panamensis* monodominant stand has a higher mean stem density of 212 stems per hectare and a higher diversity of 1.53. Phosphorus concentrations are lower compared to *R. taedigera* (0.668 mg P g^{-1}), matching a gradual decline in nutrient concentrations towards the central peat dome. Details of other nutrient and vegetation trends across the entire dome are reported in Phillips et al. 1997, Sjögersten et al. 2011 and Troxler et al. 2012.

Mean annual temperature was 26 °C in the 13 years prior to sampling, with mean annual rainfall of 3207 mm. During the sampling period mean air temperature was 25 °C and rainfall was 280 mm. Soil temperature was 25 °C. There is no limited seasonality in the region, with the water table remaining close to the surface throughout the year. There are, however two periods of lower rainfall between February and April, and September and October (Wright et al. 2011). During sampling, the water table height was consistent, fluctuating ±5 cm. Central areas of the dome are consistently flooded throughout the year.

Peat Sampling and Characterization

The microtopography under both *C. panamensis* and *R. taedigera* plants featured a mix of shallow water pools (hollows) and raised areas (hummocks), the formation of which is primarily driven by the presence pneumatophores and roots. Ten peat samples were collected from peat under both *C. panamensis* trees and *R. taedigera* palms using a hand trowel to excavate the acrotelm (approximately 0–10 cm). Samples were collected from slight depressions between roots which at the time of sampling were water-saturated but not flooded. Samples were stored in zip-lock bags and transported to the University of Nottingham where they were stored at 4 °C prior to analysis.

Sub-samples from each site were used to characterise physiochemical properties in the laboratory. Peat moisture content was determined through gravimetric analysis of the mass of water lost from 10 g wet weight peat oven dried at 105 °C for 24 h. Organic matter content was determined as the mass lost after ignition for 7 h at 550 °C. Total peat carbon (C) and total nitrogen (N) were determined from 0.2 g of dry, homogenised peat combusted using a total element analyser (Flash EA 1112, CE Instruments, Wigan, UK). Peat pH and redox potential were measured using a Hanna 209 pH meter coupled with separate pH and redox probes. Electrical conductivity was measured simultaneously using a conductivity meter.

PLFA Analysis

PLFAs were extracted from 20 peat samples following the Bligh and Dyer (1959). Total lipids were extracted from 500 mg of freeze-dried soils using citrate buffer (0.15 M, pH 4), 1.9 ml chloroform ($CHCl_3$), 3.8 ml methanol (MeOH) and 2 ml Bligh and Dyer reagent ($CHCl_3$: MeOH: citrate buffer; 1: 2: 0.8 volume ratio). Extracts were vortexed for one minute and left at room temperature to separate for two hours. Subsequently, extracts were centrifuged for 10 min at a relative centrifugal force of 650 before the supernatant was transferred to a $CHCl_3$ rinsed glass tube. This step was repeated twice to ensure complete extraction of lipids from the soil pellet. Citrate buffer and chloroform (1:1 volume ratio) were added and left overnight to allow separation of aqueous and organic phases. The chloroform layer was transferred to a clean glass tube and blown dry under a stream of N_2 at room temperature (Bligh and Dyer 1959).

Lipids were separated using a silica solid phase extraction cartridge. The cartridge column was rinsed first with 15 ml methanol followed by 2.5 ml chloroform. The dry lipid extract was re-suspended in 0.5 ml chloroform and added to the column. Lipids were separated into neutral lipids, glycolipids and phospholipid fractions using chloroform, acetone and methanol solutions respectively. The PLFA fraction was collected and evaporated under a stream of N_2 at 36 °C.

Phospholipid samples were re-suspended in 1 ml MeOH: toluene (1:1 volume ratio) and trans-esterified to fatty acid methy esthers (FAMEs) using 1 ml 0.2 M KOH dissolved in methanol. For liquid extraction, 2 ml of hexane:chloroform (4:1 volume ratio), 0.3 ml acetic acid (1.0 M), and 2 ml ultrapure water were added. C13 and C19 internal standards were

added to the samples before evaporating FAMEs under a stream of compressed N_2 and re-suspension in hexane prior to GC analysis. PLFAs were identified and quantified using gas-chromatography.

Standard PLFA nomenclature is applied (A:BωC) where A is total number of carbon atoms, B is the number of double bonds, and C is the position of double bond from the methyl end of the molecule. 'C' and 'T' indicate cis and trans isomers, and 'A', 'I' indicates iso- and anteiso-, and 'Me' and 'Cy' indicate methyl groups and cyclopropyl rings respectively (Kong et al. 2011). C15:0i, C15:0a, C16:0i, C17:0i and C17:0a PLFA biomarkers were assigned to Gram positive bacteria. C16:1ω7, C17:0, C18:1ω7, and 7,8Cy-C19:0 were assigned to Gram negative bacteria. Fungal PLFA biomarkers were C18:2ω6c, C18:1ω9c. C14:0, C15:0, C16:1ω6, C16:0, C17:1ω8, 10Me-C16:0, C17:1, 10Me-C17:0, and C18:0, biomarkers were unclassified due to a lack of specificity to any microbial group.

GDGT Analysis

GDGTs were extracted from 20 freeze-dried peat samples (500 mg) using an Accelerated Solvent Extractor (ASE) 200, Dionex, operated at 100 °C and 7.6×10^6 Pa with a mixture of dichloromethane (DCM): methanol (MeOH) (9:1, v:v) to obtain a total lipid extract (TLE). Internal standards squalane and C_{46} GDGTs were added to the TLE, which was subsequently separated into an apolar and polar fraction in an alumina oxide column (Al_2O_3), using *n*-hexane/DCM 9:1, and methanol/DCM 1:1 as eluents. The polar fractions were filtered through a polytetrafluoroethylene filter (PTFE - 0.45 μm) and analysed using a Thermo TSQ Quantiva coupled to an Ultimate 3000 series U-HPLC following a slightly modified method of Schouten et al. (2007) described in Lopes dos Santos and Vane (2016). Shortly, separation was achieved on a Prevail Cyano column (2.1 × 150 mm, 3 Am; Alltech, Deerfield, IL, USA), maintained at 30 °C. Tetraethers were eluted isocratically with 99% A and 1% B for 5 min, followed by a linear gradient to 1.8% B in 45 min, where A is hexane and B is isopropanol. Flow rate was 0.2 ml min^{-1}. Detection was achieved using atmospheric pressure positive ion chemical ionization mass spectrometry (APCI-MS) of the eluent. Conditions for APCI-MS were as follows: sheath gas 20, auxiliary gas 2, ion transfer tube temperature 325 °C, vaporiser temperature 400 °C, pos. Ion discharge 2. Relative GDGT distributions were determined by integrating the summed peak areas in the respective $[M + H]^+$. IsoGDGTs (GDGT-0, GDGT-1, GDGT-2, GDGT-3, crenarchaeol and isocrenarchaeol) were assigned to archaea, and brGDGTs (brGDGT-IIIa, brGDGT-IIa, brGDGT-IIb, brGDGT-IIc, brGDGT-Ia, brGDGT-Ib and brGDGT-Ic) were assigned to bacteria (Fig. 1).

Statistical Analysis

A one-way ANOVA was used to assess differences properties and biomarker abundances between peat types. Principal component analyses (PCAs), based on correlation matrices, were used to visualise microbial community profiles for both peat types and were applied separately for individual PLFA and GDGT biomarkers. Backwards stepwise regression was used to identify which biogeochemical variables best described PLFA and GDGT biomarker abundance for specific groups of microorganisms. The groups used were total, Gram positive and Gram negative bacteria, and fungi calculated from PLFA biomarker abundance and PC-1 and PC-2 from the PLFA PCA, archaea (total IsoGDGTs) and bacteria (total brGDGTs) from GDGT biomarker abundance, and PC-1 and PC-2 from the GDGT PCA. For each regression, the maximal model comprised all measured biogeochemical properties included pH, redox potential, electrical conductivity, total carbon and nitrogen, moisture content and organic matter content. Non-significant variables were eliminated individually using backwards elimination regression using $p > 0.05$ as a cut-off. Non-linear models were also tested using the same data. R^2 values reported in text are adjusted R^2 derived from multiple regression models. All statistical analyses were conducted in GenStat v17.1, and figures produced in GraphPad Prism v7.04.

Results

Peat Properties

Peats from under both species were acidic, with pH significantly lower under *C. panamensis* (4.2) compared to *R. taedigera* (4.7) ($p < 0.005$, Table 1). Electrical conductivity was low, and both peat types were weakly reducing (< 300 mV) with neither property differing significantly between species. Moisture content and organic matter content were high for both peats (> 80%), with organic matter content significantly greater in *C. panamensis* peats (92.7%) compared to *R. taedigera* (87.7%) ($p < 0.05$). Total carbon ($p < 0.001$) and total nitrogen ($p < 0.05$) were both greater in *C. panamensis* peats (40.8% and 2.4%) compared to *R. taedigera* (35.3% and 2.1%). C:N ratios were similar between peat types (17.2–17.3).

Microbial Community Composition

Microbial communities from under both plant species had broadly profiles (Fig. 2a). Total PLFA biomarker abundance was somewhat higher in *C. panamensis* peats (74.7 ± 7.0 μg g^{-1}) compared to *R. taedigera* peats (62.3 ± 4.9 μg g^{-1}) but there were no significant differences between

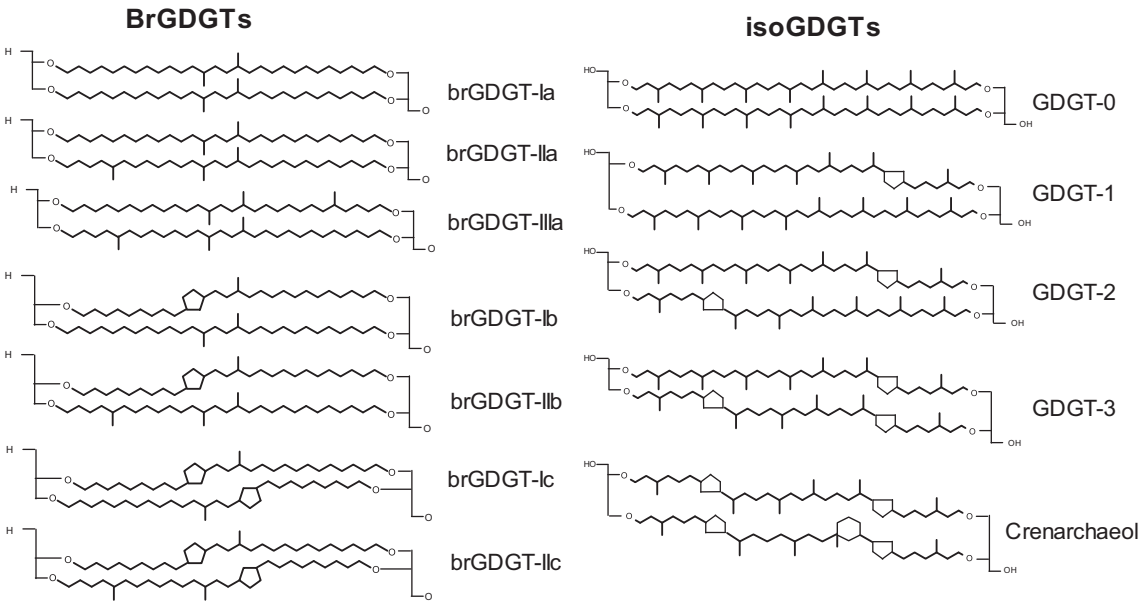

Fig. 1 Molecular structure of identified br- and isoGDGTs

peat types for any specific PLFA biomarker groupings (Fig. 2b). The ratios of fungi:bacteria (0.12–0.13) and Gram positive:Gram negative bacteria (0.65–0.68) were consistent between peat types. Fungal biomarkers were the smallest group relative to total biomarker abundance (Fig. 2c). Gram negative biomarkers were most abundant, accounting for 38.9–39.8% of total biomarkers. PCA broadly separated both peat types, with separation along the first principal component (PC-1) separated by C15:0i, as well as several non-specific biomarkers. PC-2 separated loadings by C16:1ω7, C16:0, 10Me-C17:0, amongst others. Collectively PC-1 and PC-2 accounted for 77% of variance (Fig. 2d-e).

GDGT biomarker profiles indicated only limited differences in archaea (isoGDGTs) and bacteria (brGDGTs) abundance between peats (Fig. 3a) with no significant differences ($p > 0.05$). GDGT-0 was the most abundant isoGDGT for both peat types, and brGDGT-Ia was the most abundant brGDGT. Overall brGDGT abundance was greater than isoGDGT abundance (Fig. 3b). There were no significant differences in total abundances of isoGDGTs, or brGDGTs between peat types ($p > 0.05$). The ratio of caldarchaeol:crenarchaeaol was greater under *C. panamensis* (13.0) than for *R. taedigera* (6.0) but was not significantly different ($p > 0.05$). PCA conducted using GDGT biomarkers again indicated limited broad scale differences in microbial community structure between peat types. With the exception of crenarchaea, the second principle component predominantly separated isoGDGTs from brGDGTs. Collectively PC-1 and PC-2 accounted for 72% of variance (Fig. 3c-d).

Table 1 Biogeochemical properties from *C. panamensis* and *R. taedigera* derived peats. Means ± one SE ($n = 10$). * = $p < 0.05$, ** = $p < 0.005$, *** $p < 0.001$

Peat botanical origin	*C. panamensis*	*R. taedigera*
pH	4.2 ± 0.07	4.7 ± 0.1 **
Conductivity (μS cm^{-1})	63.3 ± 20.8	85.9 ± 10.3
Redox potential (mV)	226.4 ± 9.0	239.9 ± 2.2
Moisture content (%)	86.0 ± 1.2	84.8 ± 0.9
Organic matter (%)	92.7 ± 1.6	87.7 ± 1.3 *
Total carbon (%)	40.8 ± 1.1	35.3 ± 1.6 ***
Total nitrogen (%)	2.4 ± 0.1	2.1 ± 0.1 *
C:N	17.3 ± 0.8	17.2 ± 0.3

Environmental Regulation of Microbial Communities

The results of multiple linear regression indicated several significant relationships between key environmental variables and biomarker abundance (Table 2). A significant positive linear relationship was identified between fungi:bacteria and redox potential ($p < 0.05$). In addition, a significant positive linear relationship was identified between total carbon and PLFA PC-2 ($p < 0.001$). Significant relationships were also identified between GDGT-0 abundance and pH ($p < 0.05$), and moisture content ($p < 0.01$), with decreasing pH but increasing moisture content associated with greater abundance. Similar relationships were identified for GDGT PC-2 ($p < 0.05$). Crenarchaeol abundance decreased significantly with increasing organic matter content ($p < 0.01$). Caldarchaeol:crenarchaeaol ($p < 0.05$) and isoGDGT abundance ($p < 0.05$) both increased significantly with moisture content. The ratio of iso:brGDGTs, however, was significantly related to pH ($p < 0.05$), the ratio decreasing at higher, less acidic, pH.

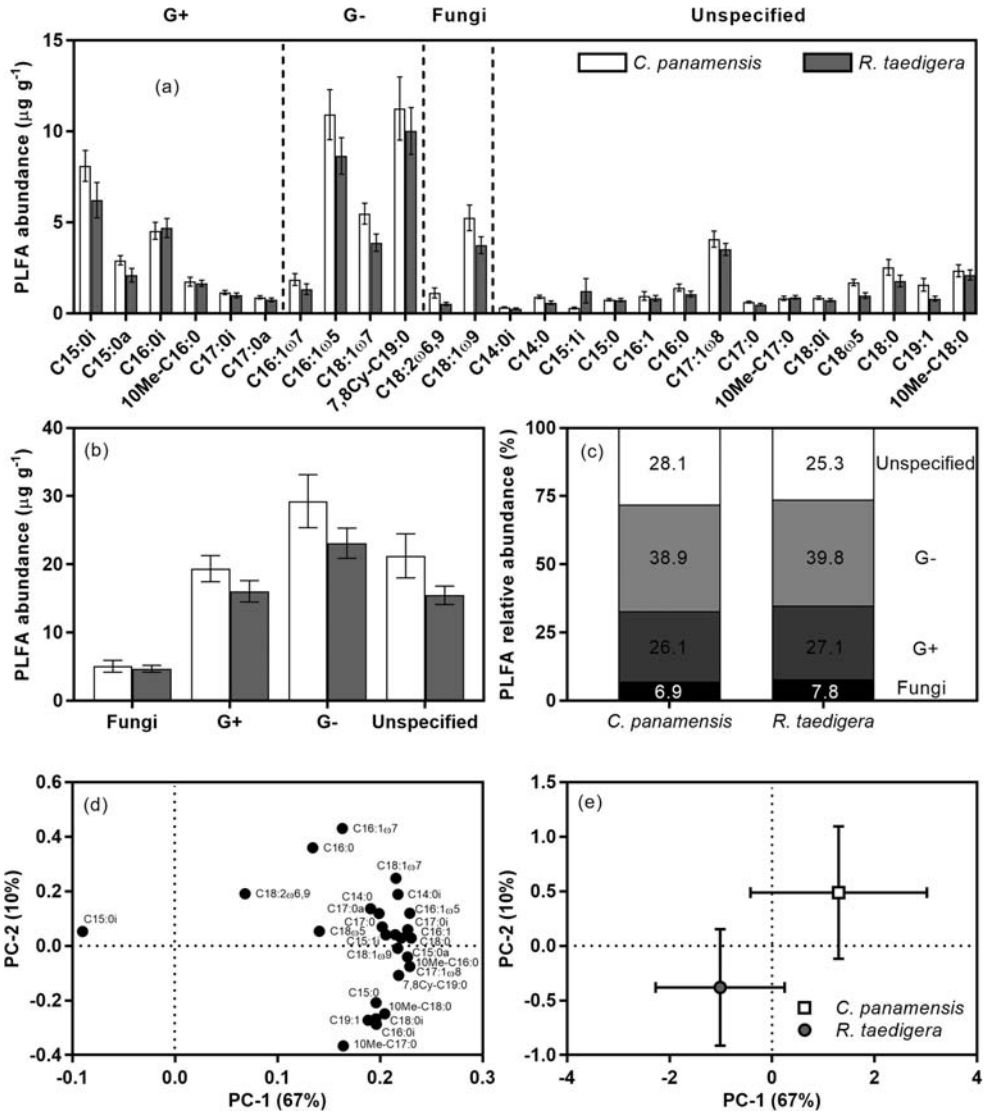

Fig. 2 (a) PLFA biomarker abundance for *C. panamensis* and *R. taedigera*. (b) Net abundance of fungal, Gram positive (G+), Gram negative (G-) and unspecified PLFA biomarkers. (c) Relative abundance of fungal, Gram positive, Gram negative and unspecified PLFA biomarkers. (d) PCA loadings for PLFA biomarkers. (e) PCA scores for PLFA biomarkers. Means ± one SE ($n = 5$)

Discussion

Peat Botanical Origin and Microbial Community Structure

The PLFA and GDGT biomarker profiles of peats collected under *C. panamensis* and *R. taedigera* were broadly similar, with both microbial communities featuring a dominance of Gram negative bacteria, and lower abundances of fungi and archaea. Previous studies have identified stronger differences in microbial community structure between peats derived from contrasting botanical origins (Borga et al. 1994; Troxler et al. 2012), or have alternatively identified differences in microbial activity (Sjögersten et al. 2011). These processes are generally driven by strong gradients in peat properties (for example, pH and phosphorus). Substantial small-scale variation in peat properties (including pH and organic matter properties) has also previously been reported, with some differences between peats predominantly derived from different plant species (Girkin et al. 2019). However, it is now clear that these differences in peat properties between dissimilar plant species do not necessarily result in contrasting microbial community profiles.

The consistently high abundance of Gram negative bacteria may be driven by the dominance Acidobacteria, which are critical components of the microbial community of both tropical (Jackson et al. 2009; Troxler et al. 2012) and temperate peats (Dedysh et al. 2006), with their ubiquity reflecting their oligotrophy (Fierer et al. 2007). High abundances of brGDGTs were also found, which have previously been reported as indicative of Acidobacteria in peats and soils (Damste et al. 2011).

Methanotrophs are a key microbial group in peatlands (Hanson and Hanson 1996), with specific PLFA biomarkers previously proposed in the literature, including C16:1ω5, C16:1ω7, C16:1ω8c and C16:1ω11c for type I

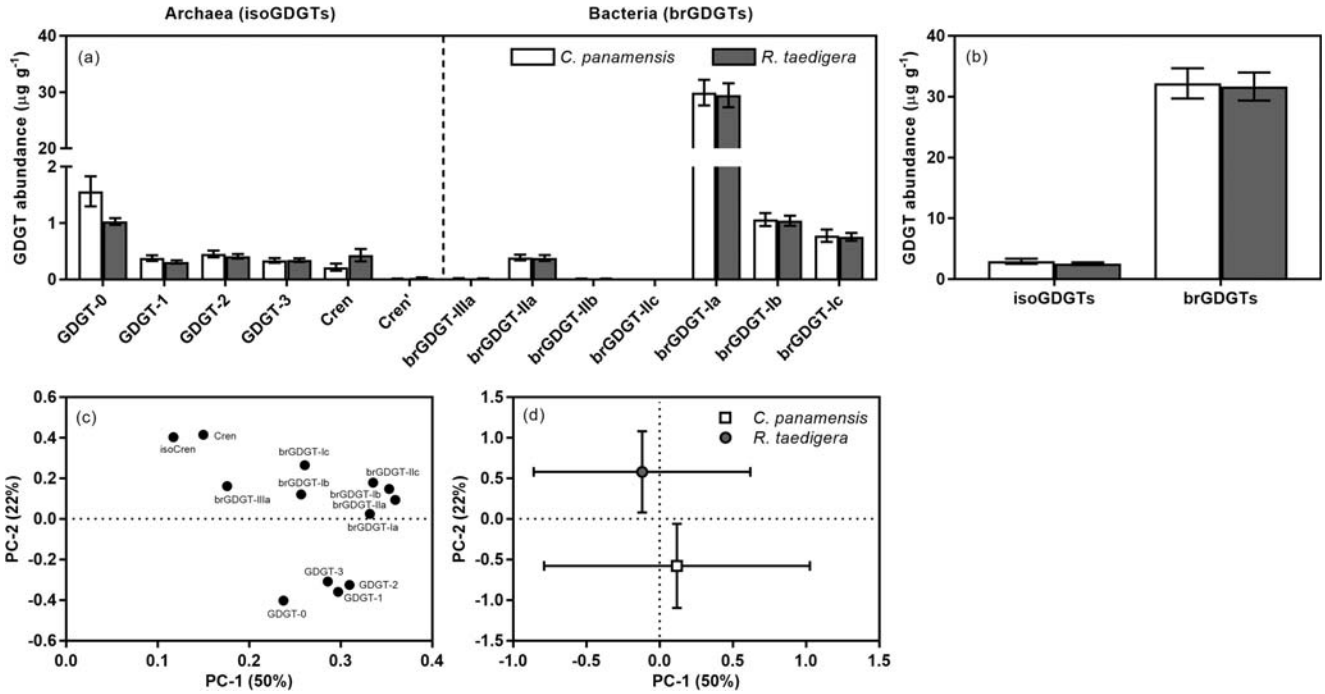

Fig. 3 (a) GDGT biomarker abundance for *C. panamensis* and *R. taedigera*. (b) Net abundance of br- and isoGDGT biomarkers. (d) PCA loadings for GDGT biomarkers. (e) PCA scores for GDGT biomarkers. Means ± one SE (n = 5)

methanotrophs, and C18:1ω7c and C18:1ω8c for type II methanotrophs (Maxfield et al. 2006; Mills et al. 2013; Roslev and Iversen 1999; Singh et al. 2007). Both C16:1ω5 and C18:1ω7c were detected in both *C. panamensis* and *R. taedigera* peats in this study and were the most abundant Gram negative biomarkers, accounting for approximately 73% (21.2 μg g^{-1}) of total Gram negative PLFA abundance (Fig. 2a). High methanotroph abundance would also imply large CH_4 production, which has previously been reported from both in situ and ex situ studies of CH_4 production/fluxes (Girkin et al. 2018b; Girkin et al., 2018; Sjögersten et al. 2011).

Fungal biomarkers were generally present at much lower abundances than other PLFA biomarkers, accounting for only 7.6–7.7% of total PLFAs, a finding possibly driven by the largely anoxic conditions. Fungi have previously been

Table 2 Backwards stepwise linear regression, reporting *p* value and B for multiple regression models. Total carbon and total nitrogen were included in the maximal model but were not significant ($p > 0.05$). + and – B indicate direction of linearity

Parameter		Fungi: bacteria	PLFA PC-2	GDGT-0 (Caldarchaeol)	Crenarchaeol	Caldarchaeol: crenarchaeol	isoGDGTs	isoGDGT: brGDGTs	GDGT PC-2
Redox potential	p value	0.042							
	B	+2.23							
Total carbon	p value		< 0.001						
	B		+5.63						
pH	p value			0.02				0.041	0.047
	B			−2.56				−2.20	−2.42
Moisture content	p value			0.006		0.039	0.031		0.027
	B			+3.15		+2.22	+2.33		+2.14
Organic matter content	p value				0.006				
	B				−3.10				
F-statistic		4.98	31.7	9.18	9.6	4.93	5.44	4.82	5.84
d.f.		1,14	1,14	2,17	1,18	1,18	1,18	1,18	2,17
p value		0.042	< 0.001	0.002	0.006	0.039	0.031	0.041	0.012
Adjusted-R^2		0.15	0.65	0.40	0.27	0.13	0.14	0.12	0.26

proposed as critical decomposers of organic matter in tropical peatlands, with groups identified which can decompose organic compounds ranging from simple polymers to complex phenolics including lignins and tannins (Thormann 2006). Woody wetland plants frequently form mutualisms with arbuscular mycorrhizal fungi (AMF), including in mangrove swamps (Wang et al. 2010) and in high altitude Andean wetlands (Vanesa et al. 2013) amongst others (Xu et al. 2016), although AMF biomarkers were not identified in this study.

Overall, archaea (isoGDGT) biomarkers were present at relatively low concentrations compared to bacteria (brGDGT) biomarkers, accounting for up to 8% of total GDGT compounds (Fig. 3b). This low abundance may, in part, be driven by regular changes in water table height at the site (−20–9 cm from February – May 2016), resulting in alternating oxic and anoxic conditions (Weijers et al. 2006). Low archaeal abundances have previously been reported in surface tropical peats, with archaea accounting for only 1.6% of the total microbial community in a peat swamp forest in Thailand, as identified by pyrosequencing (Kanokratana et al. 2011), although much higher abundances have been reported with parity with total bacteria (Espenberg et al. 2018).

The ratio of caldarchaeol:crenarchaeol has previously been reported as a good indicator of whether GDGTs in soils and sediments are dominated by methanogenic or non-methanogenic Euryarchaeota, with higher ratios (> 1.4) indicating the production of caldarchaeol and thus the presence of methanogenic archaea (Zhang et al. 2016). Mean ratios were 13.0 and 6.0 under *C. panamensis* and *R. taedigera* respectively, likely explaining the high CH_4 production potential of the peat soils previously reported (Girkin et al. 2018c; Hoyos-Santillan et al. 2016b). This ratio has also been explicitly linked to the concentrations of dissolved oxygen in sediments (Zhang et al. 2016), and in this study was significantly correlated with soil moisture content (Table 2). High relative abundance of methanogenic archaea may explain high CH_4 surface fluxes previously reported from the Changuinola deposit (Wright et al. 2013a), and would likely also support the large methanotroph community identified in this study from C16:1ω5 and C18:1ω7 PLFA biomarkers. These two communities likely coexist in low oxygen and high oxygen microsites throughout the peat profile, with oxygen inputs from surface diffusion and root inputs (Girkin 2018).

Environmental Regulation of Microbial Community Structure

While microbial community structure did not differ between peat types, variation in several peat properties was key in determining the abundance of several microbial groups. Redox potential and pH were identified as significant regulators of caldarchaeol:crenarchaeol isoGDGTs:brGDGTs, fungi:bacteria, and isoGDGT abundance (Table 2). Both variables are closely linked, with redox potential, measuring the activity of electrons within the peat, and pH assessing proton activity (Reddy and DeLaune 2008). Redox potential is also closely linked to soil moisture content, as waterlogged soils are low in oxygen, except for inputs derived from root oxygen loss and atmospheric diffusion at the surface boundary (Hoyos-Santillan et al. 2016a). Plant root inputs of carbon (root exudates) are also able to directly influence peat properties, and may therefore also exert an indirect control on microbial community structure and function, but the precise effect is dependent on the composition and concentration of the input (Girkin et al. 2018b). Moreover, peat properties are also strongly linked to the properties and quantity of leaf, root and shoot inputs and the influence of their decomposition products on their immediate environment (Hoyos-Santillan et al. 2015).

The significant link between redox potential and fungi:bacteria abundance is important because under oxic conditions fungi are key decomposers (Thormann 2006). The inhibitive role of waterlogged conditions on tropical peat fungal abundance has been previously demonstrated, with significant increases in fungal gene copy numbers following a drought event (Kwon et al. 2013). Low redox potential indicates increasingly anoxic peat which may limit the presence of fungi, which are frequently obligate aerobes. Organic matter content, indicating the broad availability of substrate for microbial respiration, was also positively correlated to crenarchaeol GDGT biomarker abundance, suggesting a possible role as a limiting factor for its abundance. This may be because crenarchaeaol are limited by the availability of specific components of the available organic matter pool, which may increase in line with total organic matter availability (Girkin et al. 2019; Hodgkins et al. 2018), as it is unlikely that total organic matter content is limiting in a tropical peatland system. In addition, the significant linear regression between PLFA PC-2 and total carbon, and GDGT PC-2 and moisture content and pH broadly matches those of previous studies of tropical peatland microbial community structure, which have identified substrate availability (C, N and P), and pH as key for determining diversity (Krashevska et al. 2015; Troxler et al. 2012).

Previous studies in tropical soils and peats have noted that microbial community structure and abundance can exhibit a tendency towards seasonality (Dhandapani et al. 2019; Smith et al. 2018). Tropical peatlands are subject to distinct wet and dry seasons which can exert a strong influence on water table height in particular, altering the balance between oxic and anoxic processes (Wright et al. 2013b). Peats in this experiment were collected from hollow, which, in general, are more consistently water-saturated throughout the year compared to hummocks formed by root material (Jauhiainen et al. 2005). As a consequence, we speculate that the significant relationships between redox potential and soil moisture and a variety

of PLFA and GDGT biomarker abundances mean that seasonal changes in precipitation will influence on community structure in this ombrotrophic peatland, with potential consequences for GHG emissions. This has been previously demonstrated to be the case in temperate peatlands, with significant changes in microbial community structure with changes in water table depth (Zhong et al. 2015), and has recently been reported in two tropical peatlands in Malaysia (Dhandapani et al. 2019).

Conclusion

Our results indicate that botanical origin can result in substantial differences in peat bulk properties, specifically total carbon and nitrogen, pH, and organic matter content. However, while many of these properties significantly affected the abundance of specific components of the peat microbial community, overall community structure did not vary significantly between peat types. The PLFA and GDGT biomarker profiles for *C. panamensis* and *R. taedigera* derived peats are amongst the first for Neotropical peatlands and indicate a dominance of Gram negative bacteria (38.9–39.8%). Prevailing environmental conditions, particularly soil moisture content and small changes in pH exerted a significant control on the abundance of specific microbial groups which are known as key drivers of ecosystem GHG fluxes, including methanogens and methanotrophs. This is important in the wider context of land use change in the tropics, as these processes alter peat properties and subsequent GHG production.

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Author Contributions NTG, BT, NO and SS devised the study. NTG conducted the fieldwork. NTG, RLS and CHV analysed the samples. NTG analysed the data and wrote the first draft of the manuscript. All authors contributed to subsequent revisions.

Compliance with Ethical Standards

Conflict of Interest The authors declare no competing interests.

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