DEFORESTED AND DRAINED TROPICAL PEATLAND SITES SHOW POORER PEAT SUBSTRATE QUALITY AND LOWER MICROBIAL BIOMASS AND ACTIVITY THAN UNMANAGED SWAMP FOREST

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ABSTRACT

Swamp forests on deep tropical peatlands have undergone extensive deforestation and draining for agriculture and plantations, consequently becoming globally significant carbon (C) sources.

To study the effects of land-use change on peat as a biological environment, which directly affects decomposition dynamics and greenhouse gas emissions, we sampled peat from four common land-use types representing different management intensities in Central Kalimantan, Indonesia. The near-pristine *swamp forest* was used to describe unmanaged conditions, and the three other sites in order of increasing management intensity were *reforested*; *degraded*; and *agricultural*. We examined peat substrate quality (total C & nitrogen (N), dissolved organic C (DOC) and N (DON), and organic matter quality characterized by infrared spectroscopy) and microbial biomass and extracellular enzyme activity to describe both biotic and abiotic conditions in peat.

We found that the peat at altered sites was poorer in quality, i.e. decomposability, as demonstrated by the higher intensity of aromatic and aliphatic compounds, and lower intensity of polysaccharides, and concentration of DOC, total N and DON compared to the peat in the swamp forest. The observed differences in peat properties can be linked to changes in litter input and decomposition conditions altered after deforestation and draining, as well as increased leaching and fires. The quality of the peat substrate was directly related to its biotic properties, with altered sites generally having lower microbial biomass and enzyme activity. However, irrespective of management intensity or substrate quality, enzyme activity was limited primarily to the first 0–3 cm of the peat profile. Some differences between wet and dry seasons were observed in enzyme activity especially in swamp forest, where the most measured enzyme activities were higher in dry season.

Reforestation 6 years before our measurements had not yet restored enzyme activity in the peat to the level of the swamp forest, although the topmost peat characteristics in the reforested site already resembled those in the swamp forest. This is likely contributed to by the chemical weed control performed at the site, and the limited capacity of the young plantation to produce litter to support peat formation and restore the quality and structure of the peat. Therefore, we conclude that intensive land management, including deforestation and draining, leads to the surface peat becoming poorer biological environment, and it may take long time to restore the peat properties.

Keywords: decomposability; land-use; microbial biomass; enzyme activity; peat properties; tropical peat

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1 INTRODUCTION

Peatlands in Southeast Asia form globally significant carbon (C) pools comprising 11–14% of C stored in peat (Page et al. 2011). However, since 1990s land-use change, typically deforestation and draining to convert land for agriculture and industry, has occurred extensively. In Peninsular Malaysia, Borneo and Sumatra, only 29% of the original peat swamp forest area still remained forested in 2015, while only 6% of the forests lacked clear signs of human impact (Miettinen et al. 2016). The largest remaining swamp forests in Southeast Asia (40% of the land area) are located in Central Kalimantan, but the increasing demand for land, especially for cultivation, poses a major threat to their existence (Miettinen et al. 2016). Due to land-use change towards drier and more sparsely vegetated systems, altered tropical peatlands are globally significant C sources (IPCC, 2014). In 2015 in Peninsular Malaysia, Borneo and Sumatra, approximately 78% of the total amount of C (146 Mt C yr^{-1}) released in decomposition of peat was from small holder-farming and industrial plantations on peat soils (Miettinen et al.

2017). Altogether, drained tropical peatlands release approximately 200 Mt of C to the atmosphere per year (Biancalani et al. 2014; Page & Hooijer 2016).

Carbon accumulation in soil takes place when the rate of litter deposition exceeds that of decomposition; if this ratio reverses, C is released. Microbial decomposition of organic matter is mediated by extracellular enzymes, each specified to degrade certain compounds. The primary abiotic factor affecting the decomposition rate in peatlands is generally considered to be oxygen availability, which is limited by high water-table level (WT), but also substrate quality, pH, nutrient availability, and especially in boreal latitudes also temperature may further constrain decomposition (Clymo 1984; Laiho 2006). Additionally, microbial population and its composition, as a biotic factor determines the potential decomposition activity and is usually limited by the one or more of the abiotic factors. Microbial decomposition can accelerate due to WT drawdown improving oxygen availability (e.g., Freeman et al. 2001; Fenner & Freeman 2011; Ishikura et al. 2017), but it may also be suppressed by drought stress (Kwon et al. 2013; Ishikura et al. 2017). The substrate quality can also be the primary factor limiting decomposition, especially when the substrate is rich in polyphenols and other recalcitrant compounds (Berg 2000; Strakova et al. 2011; Hoyos-Santillan et al. 2016). Therefore, land-use change that alters both vegetation and draining, and thus influences both the substrate quality and WT, is likely to result in greatly modified environment for decomposers. To promote more sustainable and C-neutral management of tropical peatlands, it is crucial to increase our understanding of how peat decomposability and microbial decomposition activity (i.e. enzyme activity) in peat varies between land management types.

Mature swamp forest with closed canopy, high biomass (Sulistiyanto 2004), relatively cool and unvarying temperatures on the ground (Brady 1997; Jaya 2007) and usually moist peat up to the surface encloses abundant organic substrate resources and good environment for decomposition. In the unmanaged swamp forests, high amount of leaf litter is deposited and also mainly decomposed on the peat surface (Sulistiyanto 2004; Yule et al. 2009; Hoyos-Santillan et al. 2015). Woody litters; roots, trunks and branches, are more resistant to decomposition and partly deposited below the WT, and therefore have a higher importance in peat formation in swamp forests (Wüst et al. 2008; Hoyos-Santillan et al. 2015). The woody peat formed in swamp forests has a lignin concentration of up to 72% of dry mass (Andriesse 1988; Könönen et al. 2015). Swamp forests are ombrotrophic ecosystems (i.e., rain fed), and cycling of the limited nutrient pools within the system is tight. The majority of the nutrients are released from litter during decomposition at or close to the peat surface, and rapidly bound again to microbial and plant biomass (Page et al. 1999). Therefore, nutrients are most concentrated in the surface peat (Page et al. 1999; Andriesse 1988; Lampela et al. 2014). The slow water runoff in comparison to the amount of water received in precipitation maintains a WT close to the peat surface. The forest floor is partly waterlogged in wet seasons (Lampela et al. 2014). In dry seasons, aerobic decomposition processes are possible in the surface peat above the WT, yet, the shading of the tree canopy reduces ground temperature and loss off moisture from peat. The high WT, highest litter inputs at the peat surface especially of the easily decomposed leaf litter, and the highest availability of nutrients in the surface peat all mean that the highest microbial biomass and activity is likely restricted to the very surface layers in the unmanaged swamp forests. Yet, the fluctuation of WT between the wet and dry seasons can be high, and the impacts of this fluctuation on the biomass and activity of the microbial community has not yet been quantified for swamp forests.

Cultivation on peatlands requires removal of the original vegetation, i.e. deforestation, and draining, which ensures sufficient aeration of the rooting zone necessary for the growth of most crop plants. Permanent draining also leads to consolidation of the peat, improving its bearing capacity and thus enabling the use of cultivation machinery. Deforestation reduces the litter deposition rate, as the volume of vegetation in all subsequent land use types (small-holder farms, plantations, and abandoned areas that often develop to fern-covered shrub lands) is typically much smaller than in swamp forest (Sulistiyanto 2004; Hoscilo et al. 2011; Blackham et al. 2014; Yule et al. 2016). Although the stand biomass in mature oil palm and acacia plantations may be relatively high, harvesting and intensive management practices (slash-and-burn, weeding, tilling) reduce litter deposition (Hertel et al. 2009; Smith et al. 2012). The vastly reduced litter deposition may be one of the most important parameters influencing peat C-dynamics as it reduces the potential for C-accumulation, irrespective of potential changes in decomposition rates. It may also cause the intuitively paradoxal soil respiration patterns observed in some comparative studies, with the highest respiration coming from the large mass of litter decomposing in unmanaged swamp forests, and clearly lower rates observed for sites under intensive land use (Hirano et al. 2009; Jauhiainen et al. 2016b).

Draining enables aerobic decomposition deeper in the peat profile, consequently leading to C loss from a thicker peat layer (Hirano et al. 2009; Jauhiainen et al. 2016a). Together the enhanced draining and replacing of the swamp forest vegetation with no or patchy vegetation cover further lead to high peat surface temperatures due to the direct solar radiation reaching to and being absorbed by the dark, bare soil surface (Jauhiainen et al. 2014). High surface peat temperatures may cause drought stress thereby suppressing microbial decomposition activity (Kwon et al. 2013). Removal of the original vegetation cover and draining also upsets the tight nutrient cycle between litter and live vegetation and may exacerbate the loss of nutrients, as it is known to increase the export of dissolved organic carbon (DOC) (Page et al., 1999; Anshari et al. 2010; Moore et al. 2013; Evans et al. 2014). DOC and nutrient leaching often take place in tandem (Nieminen et al. 2015). The impoverishment of already nutrient-poor peat increases the need for fertilization for productive cultivation (Andriesse 1988). Poor soil quality for cultivation may also lead to the abandonment of the deforested and drained degraded areas, where recurrent wildfires enhance the impoverishment of peat by preventing regrowth of vegetation (Page & Hooijer 2016).

Altered WT and litter deposition rates, progressing peat decomposition, and fire occurrence all modify peat properties in complex manners, and determine the quality of the peat as a biological environment for decomposers. However, relatively little is still known about peat as a biological environment in the Tropics. Differences in substrate quality, temperature climate and WT regime may lead to different patterns from the northern peatlands, where the peat is primarily formed by *Sphagnum* mosses and *Carex* sedges. This study aims to provide insight into the factors regulating decomposition in swamp forests subject to differing land management intensities. To do so, we studied peat substrate quality (total C & nitrogen (N), DOC & DON, and organic matter quality characterized by infrared spectroscopy) as well as microbial biomass and extracellular enzyme activity under the varying environmental conditions of different land-use types in Central Kalimantan, Indonesia.

We hypothesized that: (i) deforested and drained sites have lower surface peat substrate quality, and thus lower microbial biomass and enzyme activity, than unmanaged swamp forest. However, due to improved oxygen conditions via WT drawdown, we also assumed that (ii) enzyme activity continues deeper in the peat profile at the drained sites than in the swamp forest. Since decomposition in peatlands is also in great extent controlled by WT, we assumed that (iii) the high WT during the wet season will suppress enzyme activity in the undrained swamp forest, whereas the drought during the dry season will suppress enzyme activity at the drained sites. We expected (iv) the reforestation of degraded peatland with a relatively high WT to restore peat quality and thus improve conditions for decomposers, reflected as higher microbial biomass and enzyme activity.

2 MATERIALS AND METHODS

2.1 Study area and sites

Our study area was located on the upper parts of the Sabangau River catchment in Central Kalimantan, Indonesia. (Fig. 1). During the period 2002–2010, the mean annual temperature in the area was 26.2 ± 0.3 ºC and mean rainfall 2540 ± 596 mm yr^{-1} (Sundari et al. 2012). The high precipitation received in the region is normally interrupted by a dry season occurring from June to September. However, in recent decades, strong El Niño events have prolonged the dry seasons and caused extreme droughts, which have led to the spread of wildfires. Our four study sites were within c. 20 km distance in same catchment area on two ombrotrophic peat domes located on opposite sides with similar distances from Sabangau River with peat depth exceeding 3 m at the sites.

At three of the sites, the vegetation and hydrology had been altered for at least 6 years and up to three decades prior to the sampling. It was assumed that the conditions at these transformed sites had stabilized after land-use change; as it has been considered to take five years before the peat physical properties and greenhouse gas dynamics stabilize after deforestation and draining (Hooijer et al. 2012; IPCC 2014). The sites in order of increasing management intensity were: near-pristine swamp forest (SF; 2º19’16.96” S, 113º 53’43.29” E), reforested site (RF, 2º18’54.94“S, 114º 03’31.76”E), degraded site (DO 2º19’25.11”S, 114º1’5.15” E), and agricultural site (AO; 02° 17′ 25.21″, E114° 0′ 41.20″) (Fig. 2). Degraded and agricultural site together are referred to as *open sites.*

Figure 1. A satellite photo of the study area with study sites indicated. The location of the study area in Southeast Asia is shown on the inserted map. The dark green areas are swamp forests and lighter green areas deforested areas with some ground vegetation. Copyrights of the photo: ©2016 Google.

Figure 2. Description of study sites with management intensity increasing from left to right.

In the swamp forest, the hydrology and original swamp forest vegetation were almost pristine. However, due to selective logging prior to 1997 and remnants of small ditches, it cannot be considered fully intact. The topmost layer of the tree canopy reached 35 m height, and ground vegetation consisted of a few, scattered *Pandanus spp*. palm thickets (Page et al. 1999). The soil microtopography was characterized by open, low peat surfaces, which formed pools during high WT, and higher hummock-like surfaces mainly around tree bases (Lampela et al. 2014). Two of the altered sites, reforested and degraded, were clear-felled and drained in 1997 during the so-called Mega Rice Project, a failed project attempting to convert 1 million hectares of peatlands into arable land (Page & Rieley 2005). The degraded site was abandoned following draining without further land use, while the other site was reforested in 2008. The hydrology at both of these altered sites was affected by the same approximately 10-meter-wide and 3–4-meter-deep canal dug in 1997. However, draining at the reforested site has been less efficient due to its lower elevation, consequently leading to higher annual WT and frequent flooding events. Both of these sites had burned after land-use change, but the reforested site not since 1998. The degraded site had burned recurrently with the most intense fires occurring in 1997, 1999, 2002, 2006 and 2009. At the degraded site, at least 0.5 m of the topmost peat had been lost due to fire (Hoscilo et al. 2011). At the time of sampling in the reforested site, 10-meter-tall *Shorea balangeran* trees grew in rows at 3*3-meter intervals at a density of c. 500 trees ha^{-1}. Herbaceous understorey vegetation was kept low by cutting and occasional application of herbicides containing mainly glyphosate. The dominant vegetation at the degraded site was composed of ferns and scattered small trees with crowns extending approximately 3 meters above the land surface. The most intensively managed site with the longest history of management in this study was the agricultural site (AO), which was deforested and drained for smallholder cultivation in the beginning of the 1980s. The main cultivated species were corn, tomatoes and cassava. Controlled draining at the site maintained the WT below but rather close to the soil surface (Hirano et al. 2009). The agricultural site has been repeatedly fertilized mainly with urea and by burning the surface peat and previous crop residues. At all three altered sites, the microtopography was flat. Further information on peat properties at the sites is presented in Table 1 and information on WT depth in Figure 3.

We chose managed sites that would be as comparable as possible in conditions where detailed soil and vegetation analyses prior to land-use change were not available. Our view of the comparability was based on the distance to the river, since the vegetation is known to gradually change with distance from the river due to the changes in hydrology and nutrient conditions (Page et al. 1999: Sjögersten et al. 2011), and peat properties that were rather uniform in the deepest layers studied at the sites, which best reflect the pre-draining properties as land-use impacts are usually most evident in the surface layers (Könönen et al. 2015, 2016). All sites have been previously forested judged by the high amount of wood and organic substrates characteristic to woody peat (e.g. Könönen et al. 2016). However, since the site status before land-use change has not been recorded, we cannot rule out site-specific variation in the properties studied here. This is a basic problem in nearly all space-for-time substitution studies on land-use impacts (Oksanen 2001). This problem is even more emphasized in our study due to the limited number of sites. However, since research in this region is logistically challenging we consider that our data are yet among the best currently available for this area, and provide valuable information on peat as a biological environment in managed former swamp forests. Recurrent burning of some sites may also be seen as a confounding factor in our comparisons; however, since wild fires in this region are common and are known to target especially the degraded drained sites, we consider that they should be accepted as a typical part of the land-use change impact in these sites.

Figure 3. Average monthly water-table level during the sampling year (2014) at the sites based on 1–2 monthly monitoring events.

Table 1. Selected soil properties at the study sites corresponding to the sampling depths in this study. Data from this and other studies (source mentioned under the table).

2.2 Sampling

We established five permanent square-shaped 1m^2 sampling plots at the swamp forest, degraded and reforested sites. The permanent plots were located at approximately ten-meter intervals. In the swamp forest and degraded site, four of the permanent plots were situated at the corners and one in the middle of a square-shaped sampling area covering approximately 400 m^2. At the reforested site, the plots were arranged in a row along the midsection of the reforested area covering approximately 300 m^2. At the agricultural site, permanent sample plots could not be established because they would have disturbed farming, and samples were thus taken from three randomly chosen spots.

Soil samples for determining enzyme activity were taken at the middle of the wet and at the end of the dry season, mid-March and mid-September in 2014, respectively, except for the agricultural site where samples were only taken at the end of the dry season. Sampling for total N and C, infrared spectroscopy, microbial biomass C and N, and dissolved organic N and C (DON and DOC, respectively) analyses was carried out at the end of the dry season. In the swamp forest and reforested site, samples were extracted from low, vegetation-free surfaces between the trees, as they covered the majority of the land area. At the open sites (agricultural and degraded), both vegetated and unvegetated surfaces were sampled (ferns at degraded site and maize at agricultural site).

The samples included the first 30 cm of the peat from the surface divided into four sections (0-3 cm, 3-10 cm, 10-20 and 20-30 cm). The rationale for this was that we expected to see different patterns right at the surface than in the deeper layers, since for instance the temperature variations are the most extreme in the topmost layer in the managed sites. Non-volumetric samples from the topmost peat (0–3 cm) were collected by hand. Volumetric samples (68.7 cm^3 from 3–10 cm depth and 98.2 cm^3 from 10–20 and 20–30 cm depth) were extracted from deeper depths using a Russian peat auger 5 cm in diameter. The total number of undivided samples (n) per season was 5 at the swamp forest, degraded and reforested sites, whereas at the agricultural site the total number of undivided samples was 3.

Samples were sealed in plastic bags immediately after extraction. Since the time needed to transport samples from the field to the laboratory located at the University of Helsinki, Finland was long, samples were stored in coolers or in a refrigerator at 4 ºC temperature for a maximum period of two weeks prior to analyses, if not mentioned otherwise. Prior to analyses, the living roots were removed.

2.3 Laboratory analyses

2.3.1 Infrared spectroscopy

Subsamples were air-dried before milling to fine powder. Infrared spectra were obtained with a Bruker VERTEX 70 series FTIR (Fourier Transform InfraRed) spectrometer (Bruker Optics, Germany) equipped with a horizontal attenuated total reflectance (ATR) sampling accessory. Dried and powdered samples were inserted directly on the ATR crystal and a MIRacle high-pressure digital clamp was used to achieve even distribution and contact of the sample and crystal. Each spectrum consisted of 65 averaged absorbance measurements between 4000 and 650 cm^{-1}, with a 4 cm^{-1} resolution. Summed absorbance values of the following bands were used as representative of the different organic compounds in the ordination diagram of Figure 7: 2920 and 2850 cm^{-1} (wax, lipids); 1612, 1513, 1450 and 1265 cm^{-1} (lignin and other phenolics); 3340, 1150 and 1034 cm^{-1} (polysaccharides. Offsets in baseline and slope between the different runs (samples) were removed by standard normal variate transformation and the second derivative using the Unscrambler software (CAMO, Norway). The individual bands were assigned according to Artz et al. (2008).

2.3.2 Total C and N and C/N-ratio

Total C and N concentrations (mg g^{-1} of dry mass) and, consequently, the C/N-ratio were determined from approximately 0.3 g of homogenized, air-dried sample with LECO CHN-1000. The peat C and N pools for each sampled layer were calculated by multiplying the C and N concentrations with the thickness and bulk density of the layer, and transforming the values per m^2. The peat bulk density used in these calculations is from Table 1.

2.3.3 Soil DOC and DON and microbial C and N

Two comparable samples, approximately 3 g of homogenized fresh peat, were prepared. One sample set was used to measure the total DOC and DON concentrations of soil, and the other to measure soil microbial C and N after chloroform ($CHCl_3$) fumigation (Vance et al. 1987). DOC and DON concentrations were measured from non-fumigated samples after extraction with K_2SO_4 at the start of the fumigation process of the other sample set. Fumigated samples were incubated at 25 ºC for 24 hours with $CHCl_3$ prior to extracting with 0.05 M K_2SO_4. A TOC-analyser was used to analyse the C and N concentrations of the filtered (Whatman No. 42-filters) non-fumigated and fumigated samples. To calculate the microbial C and N, the C and N concentrations of non-fumigated samples were subtracted from the fumigated samples. To estimate the microbial biomass, a correction factor of 2.64 was used for unrecovered microbial C (Vance et al. 1987) and a correction factor of 1.86 for microbial N (Brookes et al. 1985).

2.3.4 Extracellular enzyme activity

Extracellular activity of five enzymes was determined from peat with a fluorescence method modified from Pritsch et al. (2011). The measured enzymes, their abbreviations and substrates used in analysis (in parentheses) were:

(i) b-Xylanase (Xyl, 4-methylumbelliferyl-β -D-xylopyranoside, 3.2.1.37),

(ii) b-Glucosidase (Gls, 4-Methylumbelliferyl-β-D-glucuronide, 3.2.1.21),

(iii) N-acetyl-b-glucosaminidase (Nag, 4-Methylumbelliferyl N-acetyl-β-D-glucosaminide, 3.2.1.14),

(iv) Phosphomonoesterase (Pho, 4-Methylumbelliferyl phosphate, 3.1.3.2),

(v) Arylsulfatase (Sulf, 4-Methylumbelliferyl sulfate potassium salt, 3.1.6.1)

The activity of these enzymes is used to describe the enzymatic decomposition activity related to degradation of C (b-xylanase and b-glucosidase), N (N-acetyl-b-glucosaminidase), P (phosphomonoesterase) and S (arylsulfatase) compounds.

One day (24 h) prior to the analyses, approximately 2 g of peat of each sample stored in a refrigerator was weighed in small plastic bags (10×10 cm^2) and incubated in the sealed bags at room temperature (22^oC) in darkness. On the day of analyses, 7 mL of deionized water was added to the bags, mixed throughout for three minutes, and filtered through a cellulose acetate filter (Whatman, 0.45 µm). Then 50 µL of universal buffer prepared as in Pritsch et al. (2011) (pH 4.5 for all substrates), 50 µL of filtered sample aliquot and 50 µL of enzyme substrate were added to a microplate (Optiplate 96F HB, Perkin-Elmer) having separate microplates for each substrate. Plates were incubated on a microplate shaker for 15 min (b-Glucosidase and N-acetyl-b-glucosaminidase) or 30 min (b-Xylanase, Phosphomonoesterase and Arylsufatase). After incubation, 100 µL of incubated aliquot was added on a microplate on top of 100 µL TRIS-buffer (1M; pH 10-11) to stop the fluorescence assay. All used buffers were prepared as in Pritsch et al. (2011). Fluorescence values were measured with a Wallac 1420 Victor2 (PerkinElmer, Inc., USA) multilabel plate reader. The aliquot of substrate in deionized water was used as the background value in calculations.

2.4 Data analyses

To test the first and second hypothesis, the differences in measured variables between sites at each sampling depth were tested with one-way analysis of variance (ANOVA). When the effect of site was significant, ANOVA was followed by Games-Howell post hoc test, which is suitable for testing differences between groups having unequal sample sizes and heterogeneous variances, and when normality cannot be assumed. Due to values below detection limits, enzymatic data had zero-values and were thus transformed as log(x+1) to improve the strength of statistical tests. Differences were statistically significant if the p-value was less than 0.05.

Multidimensional ordination methods were applied to further analyze the data, where several variables were presumably intercorrelated. Before analysis, the data were centered and standardized to make the different scales commensurable. To test the first, second and fourth hypothesis, redundancy analysis (RDA) was used to test the effect of land management type on substrate quality (the infrared spectroscopy-derived peat quality). In this RDA, the interaction of site and depth was used as explanatory variable. The summed absorbance values of some main compound groups, e.g. polysaccharides; waxes and lipids; lignin and other phenolics, were used as supplementary variables to better visualize the correlation of substrate quality with the site and depth. This means that they were not affecting the analysis as such, but their correlations with the ordination axes were projected in the graphs. To test further the first, second, and third hypothesis, constrained redundancy analysis (RDA) with variation partitioning was conducted to analyze how much of the total variation in enzyme activity was explained first by site and depth, and then by the substrate quality (pH, and total C and N, DOC and DON, microbial C and N concentration) and to analyze how much of the total variation (inertia) was explained by each environmental variable. Last, we tested the effect of spectroscopy data-derived peat quality on enzyme activity from the dry season (for which data from all sites were available) with RDA. In all analyses, a Monte Carlo permutation test with 999 permutations was applied to evaluate the significance of the canonical axes; permutations were constrained by the covariates. All ordination analyses were made using Canoco 5 for Windows.

3 RESULTS

3.1 Peat as an environment

3.1.1 Carbon and nitrogen

The total C concentration of peat varied in the range 48.7–61.1 mg g^{-1} (of dry peat) and the total N concentration in the range 0.81–1.61 mg g^{-1}, depending on sampling depth and site (Fig. 4). The total C concentration was lowest in the topmost peat (0–3 cm) and increased with depth at all sites (Fig. 4). In the degraded and reforested sites, the C concentration was generally higher than at other sites throughout the sampling profile (Fig. 4). The N concentration of swamp forest peat was higher and also rather constant at all sampled depths as compared to the altered sites, where the N concentration showed a clear maximum in the topmost peat (Fig. 4). The C/N-ratio varied in the range 32–76, being at its highest deeper in the peat profile at all sites (Fig. 4). Generally, the ratio was lowest in the swamp forest and highest in the agricultural site. The total C and N pools for the 30 cm peat layer sampled varied between the sites from 16.8 to 22.8 kg C m^{-2} and 0.30 to 0.51 kg N m^{-2} (Fig. 4). The C pool was typically smaller and the N pool was greatest in the swamp forest than at the other sites. The highest C pool was in agricultural site and the lowest N pool was at reforested site.

The concentrations of DOC and DON extracted from the peat varied in the range 0.52–1.80 mg g^{-1} and 0.15–0.50 mg g^{-1} of peat dry mass, respectively (Fig. 4f & g). In the topmost peat layer (0–3 cm), the DOC concentration in the swamp forest and reforested site was up to three times higher than at the open sites (Fig. 4f). The swamp forest, however, showed the highest DOC concentration in the deepest layer studied (20–30 cm), while the reforested site had its maximum in the topmost layer. The degraded site had the highest peat DOC concentration in the deepest layer. The agricultural site showed a clear maximum in the 3-10 cm layer. The DON concentration was highest in the topmost peat layer (0–3 cm) at all sites and decreased towards the deeper layers. DON concentration was overall highest in the swamp forest (Fig. 4g). The DOC/DON –ratio was lowest in swamp forest throughout the peat profile (Fig. 4h). The total N and DON concentration correlated positively (R=0.90, p=).

Figure 4. From top to bottom, peat total pool carbon and nitrogen pool; and total, dissolved and microbial concentrations of carbon and nitrogen at various depths in peat during the dry season at sites. Bars indicate the mean ± SE. Different letters next to bars indicate significant ($p < 0.05$) difference between sites at the same depth. The number of samples for each depth was five (n=5) at swamp forest, reforested and degraded sites and three (n=3) at agricultural sites.

3.1.2 Peat characterization with infrared spectroscopy

The strongest gradient in RDA, axis–1, explained 51.1% of the total variation in infrared spectroscopy data and separated most of the layers at altered sites from the swamp forest (Fig 5). This indicates that generally, the peat in all managed sites differed from the unmanaged swamp forest peat. The second strongest gradient, axis–2, explained 24.4% of the variation and separated the swamp forest and reforested site from the open sites. This indicates that the peat of the reforested site was closer in some respects with the swamp forest peat than the peat of the open sites. The topmost peat layer (0–3 cm) showed higher intensities of polysaccharide absorption bands at the swamp forest and reforested site and higher intensities of absorption bands assigned to lignin and other phenolic compounds at the open sites (Fig 6). Differences between forest-covered and open sites were most apparent in the surface peat (0–10 cm), while deeper layers revealed less contrast. RDA also indicated that generally, the topmost peat layers differed from deeper layers of the same site. The exception was the agricultural site, where peat chemical composition varied little between the sampled depths.

Figure 5. Redundancy analysis summarizing the variation in peat quality characterized by infrared spectroscopy as explained by site and depth (used as interaction factor). Axis 1 explained 51.1% and Axis-2 24.4% of the total variation in peat quality characterized by infrared spectroscopy. Carbon compound groups were used as supplementary variables, i.e., their correlation with the axes is shown but they did not affect the analysis. SF= swamp forest, RF=reforested site, DO=degraded site, AO=agricultural site.

Figure 6. Peat carbon characteristics described by infrared spectra for each depth and site. Each carbon compound group associated with a specific wavelength is indicated on the top of the respective peak (i.e., polysaccharides at the wavenumber 3340).

3.3 Microbial N and C

At all sites, the microbial C and N concentrations were highest in the topmost peat (0–3 cm) and decreased with depth (Fig. 4). Generally, the concentrations were highest in the swamp forest and decreased following the intensity of land management, thus being lowest at the agricultural site. In the surface peat of the swamp forest, concentrations of microbial C were 0.5–2.7 times higher and microbial N 0.82–2.46 times higher than at other sites at the respective depths (Fig. 4).

3.4 Enzyme activity

Enzyme activity greatly depended on the site, sampling depth and substrate quality. The variation partitioning, showed that of the total variation in enzymatic activity 23.4% was explained by the sampling depth and the interaction of site and season together, and 19.0 % was explained by soil properties (pH, and total C and N, DOC and DON, and microbial C and N). The enzyme activities positively correlated with the absorption intensities of the bands assigned to polysaccharides, and the variation in spectroscopy data explained 22.2% of variation in enzyme activities (data not shown).

If detected, extracellular enzyme activity was highest in the topmost peat (0–3 cm) and there was hardly any activity at deeper depths. In the wet season, the measured extracellular enzyme activities in peat were significantly higher in the swamp forest than at the degraded and reforested sites (Fig. 7, Supplementary table. 2). In the dry season, the reforested site showed the lowest overall activity. Interestingly, in the dry season, the degraded and agricultural sites had similar or higher C-related enzyme activity, slightly lower N- and much lower P related activity than in the swamp forest.

In the swamp forest, where activities were detected in both seasons, some differences between the seasons occurred. In the topmost peat, the enzyme activity related to N degradation (N-acetyl-b-glucosaminidase) was two times higher during the wet season than the dry season. The activities of enzymes related to P (acid phosphatase) and C (ß-glucosidase) release, in turn, were 2.5 and 2 times lower, respectively, during the wet season than dry season (Supplementary table 2).

The enzyme allocation clearly differed between land management types (Figure 8). In the swamp fores,t allocation to P acquisition was highest in both seasons, despite the contrasting differences in the activities of the enzymes between seasons described above. In the degraded and reforested sites, the allocation patterns differed between seasons, with higher allocation to C acquisition in the wet season and P acquisition in the dry season.

Figure 7. The extracellular enzyme activity in peat samples according to season (wet or dry). On the x-axis, activity is expressed as µmol min-1 g-1 (dry mass) and sampling depth (cm) is indicated on the y-axis. Enzyme activity at the agricultural site was only measured during the dry season. SF= swamp forest, RF= reforested site, DO= degraded site, AO= agricultural site. (mean ± SE).

Figure 8. Enzyme allocation on the topmost (0-3 cm) peat during the wet and dry season at the sites.

Supplementary table 2. The mean extracellular enzymatic activity in peat samples according to season. (mean ± standard error). Different letters indicate significant ($p < 0.05$) difference.

4 DISCUSSION

In order to improve the sustainability of tropical peatland management, decomposition dynamics and environmental conditions resulting in C loss need to be understood. Therefore, we studied peat as a biological environment under common land management types by focusing on both the major abiotic (substrate composition and moisture conditions) and biotic (microbial biomass and enzyme activity) factors that influence organic matter decomposition (Clymo 1984; Berg 2000; Laiho 2006; Hoyos-Santillan et al. 2016). The results of this study, which cover four land management types but only few sampling events, reflect the current biotic and abiotic peat conditions modified up to several decades by the present land management type. Therefore, the results cannot be used to estimate the effects of land use change as a dynamic process, but instead they can be used to describe the differences between land management types and to discuss of the potential effects of the changes in land management practices.

4.1 Deforestation and draining lead to peat becoming poor biological environment

As hypothesized, intensive land management including deforestation and draining have led to an overall lower microbial biomass and enzyme activity. This was likely due to the peat quality showing advanced peat decomposition degree at the altered sites, i.e., increased recalcitrance, being richer in aromatic and aliphatic compounds and poorer in of polysaccharides, DOC and nutrients (total N, NO_{3-}, NH_{4+}, DON) compared to the peat in the undrained swamp forest. The observed changes in peat properties can be linked to changes in litter input, conditions influencing decomposition in soil, and loss of the original surface peat in recurrent fires. In the swamp forests, net formation of peat is supported by a high and continuous litter deposition rate into environment where aerobic decomposition is seasonally reduced by high WT (Page et al. 1999; Wüst et al. 2008; Hoyos-Santillan et al. 2015), which was reflected in the high concentration of labile C compounds throughout the sampled peat profile in the swamp forest. At open sites, decomposition progresses primarily in older peat substrates as the litter input rates are low, hence the topmost peat is enriched with recalcitrant compounds as the labile compounds have already been consumed during earlier period after the land-use change. Similar effects of land-use change on the carbon compound characteristics of tropical peat have also been reported earlier (Könönen et al. 2016). The N and DON concentrations were higher in the swamp forest than at the altered sites, which likely implies biomass removals, fires and leaching leading to the losses of N from peat at altered sites.

In tropical peatlands, the availability of labile carbohydrates (Hoyos-Santillan et al. 2016; Jauhiainen et al. 2016b; Sangok et al. 2017), along with N and P (Rejmánková 2001; Sjögersten et al. 2011) has been emphasized in the regulation of organic matter decomposition, which is in line with our findings of generally lower enzyme activity in the impoverished peat at the altered sites. The enzyme allocation patterns can be used to estimate the substrate demand of microbes as well as availability of the nutrients (Sinsabaugh et al. 1994). Interesting differences were observed between the sites in this respect. The high allocation to P-acquisition in the swamp forest indicates that P is likely the limiting factor for microbial activity, despite this site having the highest peat P concentration (Könönen et al. 2015). At the open sites, the acquisition of C was highest in the wet season and P in the dry season. This may imply different limiting factors between the seasons, possibly caused by varying qualities or quantities of litter input or released root exudates.

Draining of the swamp forest, where the peat contains a high concentration of labile carbohydrates (this study; Könönen et al 2016; Sangok et al. 2017) and has relatively high pore space (Page et al. 1999; Lampela et al. 2014; Könönen et al. 2015), has led to high C-loss especially during the first years after draining and deforestation, and to subsequent decrease in the level of C-loss rate with time (Hooijer et al. 2012). Therefore, it appears that the WT is the most important parameter limiting the decomposition processes when the labile carbohydrates are available, and later especially in deforested areas with reduced input of new litter, with proceeding decomposition, the substrate quality becomes more important parameter regulating decomposition of peat. The sites studied here appear to have reached the latter stage. However, increased availability of labile substrates or decomposition-limiting nutrients, for example through reforestation or fertilization, may again boost microbial decomposition and lead to increased decomposition of the recalcitrant compounds through priming (Kuzyakov 2010; Dungait et al. 2012). The peat at the agricultural site has been fertilized with urea and residues of plants burned as part of land management. This may have boosted decomposition, consequently resulting in higher enzyme activity than at the other altered sites. Both ex situ and in situ studies have demonstrated that the addition of N alone or together with a labile C source (glutamate and glucose) to peat from intensively managed land-use types enhances decomposition rates in peat (Jauhiainen et al. 2014, 2016b; Comeau et al. 2016). Additionally, in drainage-affected plantations with high-biomass production, e.g. acacia and oil palm plantations, the fresh root litter input and N-binding ability of Acacia-family may boost the decomposition processes deeper in peat; however, such information is still lacking.

The enzyme activity was limited primarily to the topmost 0–3 cm of the peat profile at all sites. In line with this result, decrease in microbial enzyme activity and microbial population richness with increasing depth from the peat surface has been reported previously from tropical peatlands (Jackson et al. 2009; Hoyos-Santillan et al. 2015). This phenomenon has been linked to the lack of oxygen and reduction in substrate quality in deeper peat layers (Hoyos-Santiallan 2016; Jauhiainen et al. 2016b). Therefore, we had expected to find higher enzyme activity in deeper soil layers at the altered sites due to the assumedly improved conditions for decomposition via increased soil aeration following draining. The diffusion of oxygen to deeper layers may, however, be slow at the open drained sites, where the surface peat has typically shown to have higher bulk density, higher proportion of small particles and lower porosity than at swamp forest, and thus smaller proportional airspace in peat (Iiyama et al. 2010; Hooijer et al. 2012; Könönen et al. 2015). Overall, it seems that draining and deforestation have made the surface peat a poor biological environment, that does not inherently support high rates of peat decomposition in the studied sites. This may appear beneficial from the point of view of conserving the peat C stores. However, when substantial inputs of litter are lacking, even lower rates of decomposition will lead to loss in peat stores (Hooijer et al. 2010; Wijadasa et al. 2017).

4.2 Reforestation had not yet restored microbial activity

In opposition to our hypothesis, reforestation had yet to restore microbial enzyme activity in peat, despite the fact that the topmost peat characteristics were already rather similar in the swamp forest and the reforested site. Potentially, glyphosate applied regularly to remove understorey vegetation has leached into the surface peat and suppressed the activity of the microbial community (Zaller et al. 2014; Druille et al. 2016). Additionally, the trees planted six years prior still likely require more time to significantly increase their biomass and produce coarse, slowly decomposing root litter, which is the largest contributor to peat formation in swamp forest (Niiyama et al. 2010). Over time, if the vegetation cover will grow and increasingly promote the input of both above- and belowground litters and associated labile carbohydrates, the accumulation of new surface peat with lower BD may commence. This may eventually restore the quality and structure of the surface peat, yet, long-term monitoring will be needed to evaluate the potential of reforestation to restore the C-sink function in degraded areas.

4.3 Seasonality in microbial enzyme activity

The samples to study the seasonal variation in microbial enzyme activity were collected in the end of the rainy and dry seasons. Therefore, we assume that the measured enzyme activity reflect the acclimation of microbial decomposition on longer lasting seasonal WT conditions. However, we acknowledge that the measurements reflect a snapshot in both space and time, and may be affected by both spatial and temporal variation caused by other factors as well. In any case, some seasonal differences were observed in the enzymatic decomposition activity. In the swamp forest, enzyme activity was primarily lower during the wet season than the dry season. This observation is in line with decreased CO_2 emissions released through decomposition when the WT lies close to the soil surface (Fig. 2 in Jauhiainen et al. 2016 and references therein), and may in principle be caused by either low oxygen or substrate availability. Interestingly, in the swamp forest the activity of N-acetyl-β-glucosaminidase, which is involved in microbial breakdown of N-rich chitin, was higher during the wet season when peat was water saturated. The N released in chitin breakdown, may partly contribute to the efficient denitrification and CH_4 consumption noticed under the anaerobic conditions (Adji et al. 2014; Jauhiainen et al. 2016b), and thus the differences in enzyme activities may also indicate that different parts of the microbial community with differing enzyme activity profiles are active during the wet and dry seasons. Overall, however, the microbial communities and their activities in tropical peatlands still warrants further and more thorough study.

Although we expected drought stress to suppress enzymatic activity at the degraded site, there the highest activity actually occurred during the dry season. In the agricultural site, where only dry-season samples were taken, the enzymatic activity was comparable to the degraded site. The absence of shading combined with the solar radiation-absorbing capacity of dark soil at these sites elevates soil temperatures (Jauhiainen et al. 2014), which probably influenced positively in activity in the recalcitrant, fire-affected peat. Notably, the surface peat properties at these sites actually resembled those of biochar (Könönen et al. 2015, 2016), and accelerated decomposition of biochar has been observed in temperatures over 40°C in substrate in aerobic conditions (Nguyen et al. 2010; Fang et al. 2015). Although the long-term average soil temperature during the dry season did not exceed 28°C in the degraded site in this study (Table 1), it is very likely that the topmost peat temperatures can rise above 40°C momentarily during the hottest hours of the day.

4.5 Implications for C balance of tropical peatlands

We conclude that the land management greatly modifies the biotic and abiotic conditions for decomposition in peat as a result of altered litter input and WT level. Enzymatic activity is especially related to substrate quality (compound composition and nutrient availability) and WT. The observed positive relation between microbial decomposition activity and substrate quality may partly explain the relatively low CO_2 emissions from peat reported for land uses characterized by low vegetation cover and extensive time since deforestation (Hirano et al. 2009; IPCC 2014). Yet, we suggest that deforestation and draining weaken both the *biotic and abiotic* conditions supporting peat C stores, because new peat formation is negligible due to reduced litter input rates at deforested sites, fire events (either controlled or uncontrolled) promote peat oxidation, and fertilizer applications on cultivated lands may enhance decomposition of recalcitrant compounds.

Even though the relatively young reforested site still clearly differed from the swamp forest both functionally and in regard to peat properties, over time and under seasonally high WT, the growth of forest vegetation may be expected to increase litter input to peat, and eventually this ecosystem may become functionally capable of suppressing the loss of C and increasingly supporting the formation of peat, however the time span for this to happen remains to be evaluated.

The results of this study concern the biotic and abiotic conditions on the time of sampling at the annual WT extreme on four sites each representing different land use types. To fully understand the annual dynamic in the decomposition processes long-term monitoring is still needed.

ACKNOWLEDGMENTS

We acknowledge the Centre for International Cooperation in Sustainable Management of Tropical Peatland (CIMTROP) for providing facilities and assistance during field sampling. We thank Marjut Wallner from the University of Helsinki for her patience and expertise in the laboratory analyses. We acknowledge Meeri Pearson for polishing the language of this paper.

FUNDING

This research was supported by the Academy of Finland –funded 'Restoration Impact on Tropical Peat Carbon and Nitrogen Dynamics' -project (RETROPEAT; Decision number 253933), Jenny and Antti Wihuri Foundation, Finnish Cultural Foundation, and University of Helsinki prize money for Peatlanders.

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Table1

Table 1. Selected soil properties at the study sites corresponding to the sampling depths in this study. Data from this and other studies (source mentioned under the table).

	Season	Swamp forest				Reforested site				Degraded site				Agricultural site			
Sampling depth, cm		0 –5	5 –15	15 –25	25 –30	0 –5	5 –15	15 –25	25 –30	0 –5	5 –15	15 –25	25 –30	0 –5	5 –15	15 –25	25 –30
BD, g cm^{-3} (1		0.11	0.10	0.11	0.11	0.13	0.11	0.10	0.09	0.17	0.12	0.13	0.12	0.13	0.12	0.10	0.9
pH (2		3.5	3.49	3.49	3.46	3.4	3.41	3.43	3.43	3.55	3.47	3.52	3.48	3.43	3.44	3.46	3.44
Moisture %	*wet (3*	76.6	86.2	87.3	87.3	70.7	74.6	80.8	82.4	42.7	64.1	75.4	80.7	-	-	-	-
Moisture %	*dry (3*	81.4	82.7	85.6	88.6	63.3	77.0	79.8	83.1	19.3	66.5	65.2	79.3	34.1	78.9	81.9	83.8
Moisture, %	*long term (1*	88.3	88.2	87.4	87.0	76.8	81.7	83.6	84.3	76.4	81.9	84.4	84.9	83.7	85.0	86.9	88.1
Soil temp, °C	*wet (1*	25.4	25.6	25.4	25.6	27.5	27.5	27.3	27.1	27.9	27.4	27.2	27.3	-	-	-	-
	dry (1	24.4	24.6	24.7	24.5	26.3	26.6	26.6	26.5	27.2	26.9	27.2	27.2	-	-	-	-
NO_{-3}-N, mg g^{-1}	*wet (5*	0.016	-	0.013	-	0.007	-	0.008	-	0.008	-	0.007	-	-	-	-	-
	dry (5	0.050	-	0.047	0.056	0.007	-	0.016	0.010	0.008	-	0.008	0.008	-	-	-	-
NH_{+4}-N, mg g^{-1}	*wet (5*	0.092	-	0.068	-	0.041	-	0.033	-	0.020	-	0.024	-	-	-	-	-
	dry (5	0.154	-	0.160	0.122	0.038	-	0.037	0.028	0.019	-	0.029	0.030	-	-	-	-

1) Peat dry bulk density, soil temperature and moisture are from data collected monthly for 1+ year (Jyrki Jauhiainen, unpublished). Soil temperature for wet season was measured in March and dry season in August by loggers set to 1-hour recording intervals. The soil temperatures at the agricultural and degraded sites can be assumed to be similar due to their close location and similar shading effect.

2) pH was determined from peat: deionized water solution (1:2) in field conditions. Measured from the samples collected for this study.

3) Moisture concentration was determined by drying samples at 105 ºC for 24 h. Wet and dry season moisture was measured from the samples collected for this study

4) Total NO3-N and NH4-N were extracted from approximately 2 g of fresh peat (dry mass concentration approximately 24 ± 14 %) with 2M KCl and analysed with Lachat Instrument (Method 12-107-06-2-A for NH4 and 12-107-04-1-E for NO3). Wet season samples were collected in March and dry season samples in September in 2014.

Supplementary Table 1. The mean extracellular enzymatic activity in peat samples according to season. (mean ± standard error). Different letters indicate significant ($p < 0.05$) difference between sites at the respective depths.

ENZYME	Season	Depth, cm	Swamp forest	Reforested site	Degraded site	Agricultural site
b-Xylanase	wet	**0-3**	10.3 ± 2.19 ^{a}	2.90 ± 0.50 ^{b}	0.21 ± 0.70 ^{c}	–
		3-10	2.83 ± 0.65 ^{a}	1.81 ± 0.85 ^{a}	0 ± 0 ^{b}	–
		10-20	1.71 ± 0.65 ^{a}	1.52 ± 1.22 ^{ab}	0.04 ± 0.29 ^{b}	–
		20-30	1.51 ± 0.68 ^{a}	1.52 ± 0.75 ^{ab}	1.32 ± 0.66 ^{b}	–
	dry	**0-3**	10.9 ± 2.55 ^{a}	0.86 ± 0.85 ^{b}	20.6 ± 4.30 ^{ab}	19.10 ± 5.41 ^{ab}
		3-10	3.10 ± 0.50 ^{a}	1.11 ± 0.76 ^{ab}	0.01 ± 0.21 ^{b}	1.66 ± 1.12 ^{ab}
		10-20	3.22 ± 0.54 ^{a}	0.99 ± 0.58 ^{ab}	0.02 ± 0.18 ^{b}	0.96 ± 0.80 ^{ab}
		20-30	3.68 ± 0.32 ^{a}	0.93 ± 0.49 ^{ab}	0.03 ± 0.18 ^{b}	1.96 ± 1.54
b-Glucosidase	wet	**0-3**	16.56 ± 3.97 ^{a}	2.28 ± 0.29 ^{ab}	0.01 ± 0.16 ^{b}	–
		3-10	4.50 ± 0.53 ^{a}	3.77 ± 0.69 ^{b}	0.59 ± 0.92 ^{c}	–
		10-20	4.18 ± 0.39 ^{a}	3.77 ± 0.37 ^{a}	0.75 ± 0.70 ^{b}	–
		20-30	3.59 ± 0.70 ^{a}	3.56 ± 0.69 ^{a}	0.38 ± 0.61 ^{b}	–
	dry	**0-3**	43.16 ± 7.02 ^{a}	7.76 ± 1.41 ^{b}	43.05 ± 5.90 ^{a}	39.39 ± 7.62 ^{a}
		3-10	2.33 ± 0.77 ^{a}	3.03 ± 0.51 ^{a}	0 ± 0 ^{b}	0.52 ± 0.92 ^{ab}
		10-20	1.35 ± 1.63 ^{b}	2.54 ± 0.56 ^{a}	0 ± 0 ^{c}	0.43 ± 0.57 ^{bc}
		20-30	2.95 ± 3.49 ^{ab}	3.59 ± 0.69 ^{a}	0 ± 0 ^{b}	0.09 ± 0.42 ^{bc}
N-acetyl-b-glucosaminidase	wet	**0-3**	72.92 ± 7.98 ^{a}	3.27 ± 1.09 ^{b}	0.09 ± 0.43 ^{c}	–
		3-10	3.94 ± 1.48 ^{a}	3.02 ± 1.34 ^{b}	0.48 ± 0.93 ^{c}	–
		10-20	3.73 ± 0.81 ^{a}	1.16 ± 0.86 ^{b}	0.90 ± 0.96 ^{b}	–
		20-30	1.68 ± 1.18	0.87 ± 0.70	1.94 ± 0.65	–
	dry	**0-3**	36.10 ± 2.90 ^{a}	6.87 ± 2.14 ^{b}	12.32 ± 3.42 ^{b}	22.38 ± 5.98 ^{ab}
		3-10	3.39 ± 2.42 ^{ab}	0.45 ± 1.32 ^{b}	0.23 ± 0.55 ^{b}	5.12 ± 1.06 ^{a}
		10-20	0.78 ± 1.26 ^{a}	0.01 ± 0.24 ^{a}	0.40 ± 0.79 ^{a}	4.22 ± 0.35 ^{b}
		20-30	0.49 ± 1.50	0.04 ± 0.29	0.63 ± 1.36	3.81 ± 1.84
Phospho-monoesterase	wet	**0-3**	861.4 ± 1.83 ^{a}	0 ± 0 ^{b}	0 ± 0 ^{b}	–
		3-10	68.97 ± 11.89 ^{a}	9.54 ± 6.91 ^{b}	7.31 ± 5.95 ^{b}	–
		10-20	58.66 ± 11.37 ^{a}	0 ± 0 ^{b}	0 ± 0 ^{b}	–
		20-30	4.08 ± 4.04 ^{a}	0 ± 0 ^{b}	0 ± 0 ^{b}	–
	dry	**0-3**	1696.3 ± 39.01 ^{a}	40.81 ± 4.63 ^{b}	80.24 ± 1.52 ^{b}	75.13 ± 10.72 ^{b}
		3-10	103.07 ± 4.44 ^{a}	0.23 ± 1.08 ^{b}	6.80 ± 1.08 ^{c}	2.15 ± 2.54 ^{d}
		10-20	77.10 ± 7.18 ^{a}	0.35 ± 1.32 ^{b}	9.69 ± 2.10 ^{c}	7.05 ± 2.39 ^{d}
		20-30	52.61 ± 7.91 ^{a}	0 ± 0 ^{b}	5.23 ± 3.36 ^{c}	14.33 ± 3.78 ^{c}
Arylsulfatase	wet	**0-3**	6.09 ± 2.37	1.67 ± 1.27	0.26 ± 1.01	–
		3-10	5.82 ± 0.57 ^{a}	3.05 ± 0.62 ^{b}	0.00 ± 0.09 ^{c}	–
		10-20	5.92 ± 0.55 ^{a}	3.07 ± 0.57 ^{b}	0.12 ± 0.35 ^{c}	–
		20-30	5.61 ± 0.39 ^{a}	2.53 ± 0.29 ^{b}	0.24 ± 0.48 ^{c}	–
	dry	**0-3**	4.94 ± 3.32 ^{a}	1.60 ± 0.25 ^{a}	0.82 ± 0.51 ^{b}	3.15 ± 0.01 ^{ab}
		3-10	1.67 ± 0.48 ^{a}	1.38 ± 0.49 ^{a}	0.22 ± 0.51 ^{b}	2.20 ± 0.74 ^{a}
		10-20	1.33 ± 0.62 ^{ab}	1.24 ± 0.31 ^{b}	0.14 ± 0.81 ^{c}	1.92 ± 0.40 ^{a}
		20-30	1.81 ± 0.47	1.34 ± 0.25	0.25 ± 0.39	2.18 ± 0.05

Figure1

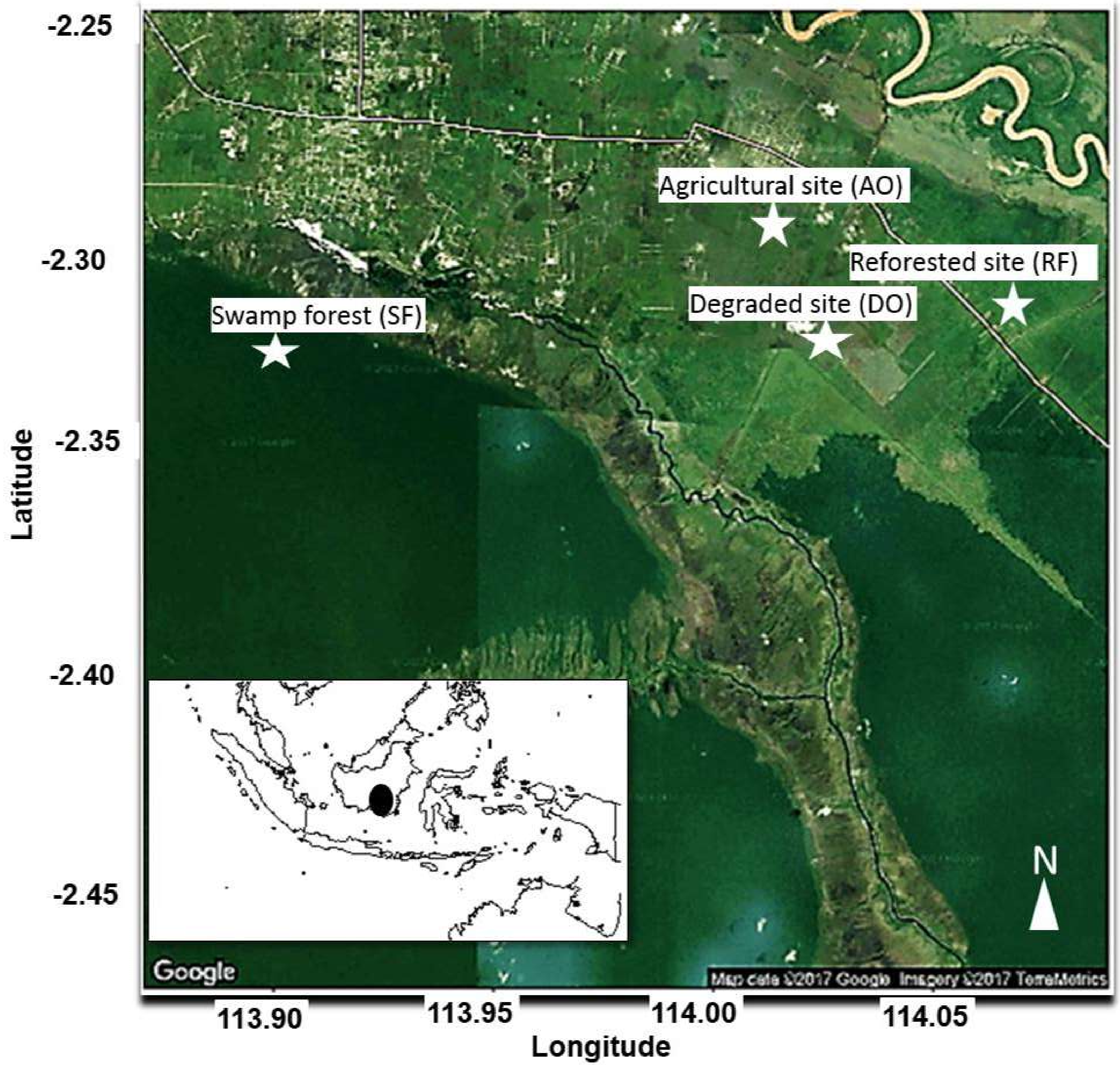
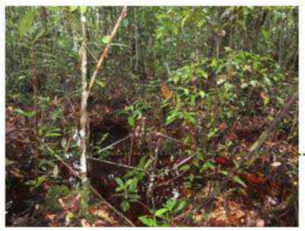
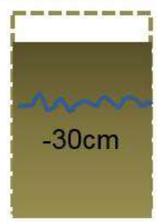

-2.25
-2.30
-2.35
-2.40
-2.45
Latitude
Agricultural site (AO)
Reforested site (RF)
Degraded site (DO)
Swamp forest (SF)
N
Google
Map data ©2017 Google Imagery ©2017 TerraMetrics
113.90
113.95
114.00
114.05
Longitude

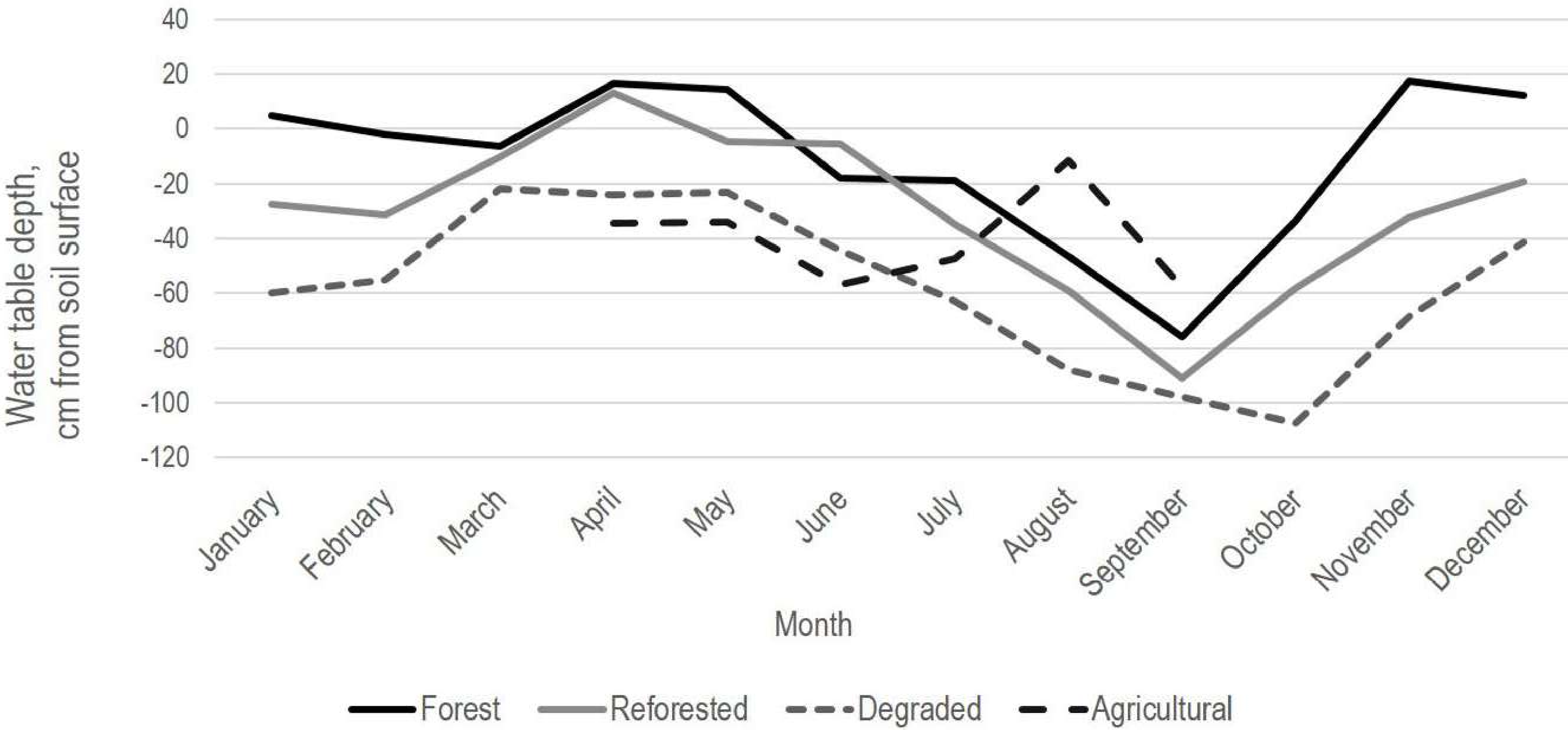
Figure2

Intensity of land management increases

Site	Swamp forest 2°19'16.96''S, 113°53'54.29''E	Reforested site 2°20'43.24''S, 114°3'31.76''E	Degraded site 2°19'25.11''S, 114°1'5.15''E	Agricultural site 2°17'25.21''S, 114°0'41.20''E
Management history	Selective logging practices prior to 1997, when small ditches were also dug	Drained and clear-felled in 1997, fires only prior to 1998, reforested in 2008, addition of herbicides	Drained and clear-felled in 1997. Burned repeatedly since then (1997, 1999, 2006, 2009)	Deforested and clear-felled and under smallholder cultivation since 1980s
Current vegetation	Near-pristine peat swamp forest	*Shorea balangeran* trees 2000 trees ha^{-1}	Ferns and scattered trees	During sampling maize, cassava, tomatoes
Photos from field				
Original peat surface indicated with dotted line and current surface with solid box. Annual median WTL represented by wavy line. [1]				
Causes of peat deposit depletion at altered sites	No depletion caused by management	Peat subsidence	Peat loss ~0.5m due to fires	Peat loss ~0.5m due to fires and tilling
Reported CO_2 emissions from related sites	Considered as C-neutral (IPCC, 2014)	Shallow drained plantation 1.5 tons CO_2 ha^{-1} yr^{-1} (IPCC, 2014)	Degraded peatlands 5.0–5.3 tons CO_2 ha^{-1} yr^{-1} (Hirano et al. 2012; IPCC, 2014)	Croplands 14 tons CO_2 ha^{-1} yr^{-1} (IPCC, 2014)

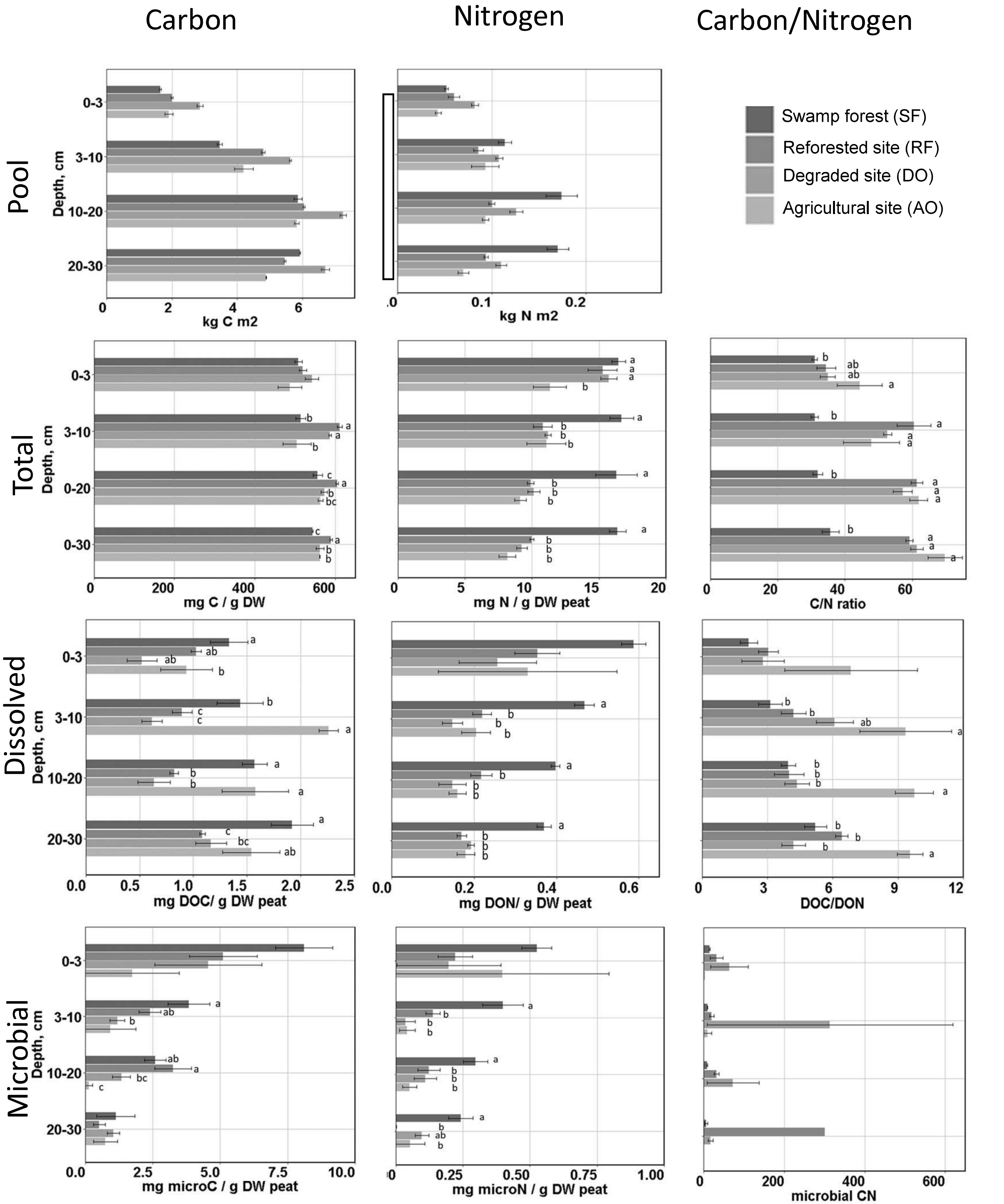
[1]WT measured twice monthly in swamp forest, reforested site and degraded site, and between March and August in agricultural site in 2014.

Figure3



Water table depth, cm from soil surface
40
20
0
-20
-40
-60
-80
-100
-120
January
February
March
April
May
June
July
August
September
October
November
December
Month
Forest
Reforested
Degraded
Agricultural

Figure 4



Carbon
Nitrogen
Carbon/Nitrogen
Pool
Total
Dissolved
Microbial
Depth, cm
Swamp forest (SF)
Reforested site (RF)
Degraded site (DO)
Agricultural site (AO)
kg C m2
kg N m2
mg C / g DW
mg N / g DW peat
C/N ratio
mg DOC/ g DW peat
mg DON/ g DW peat
DOC/DON
mg microC / g DW peat
mg microN / g DW peat
microbial CN

Figure 5_earlier numb 6

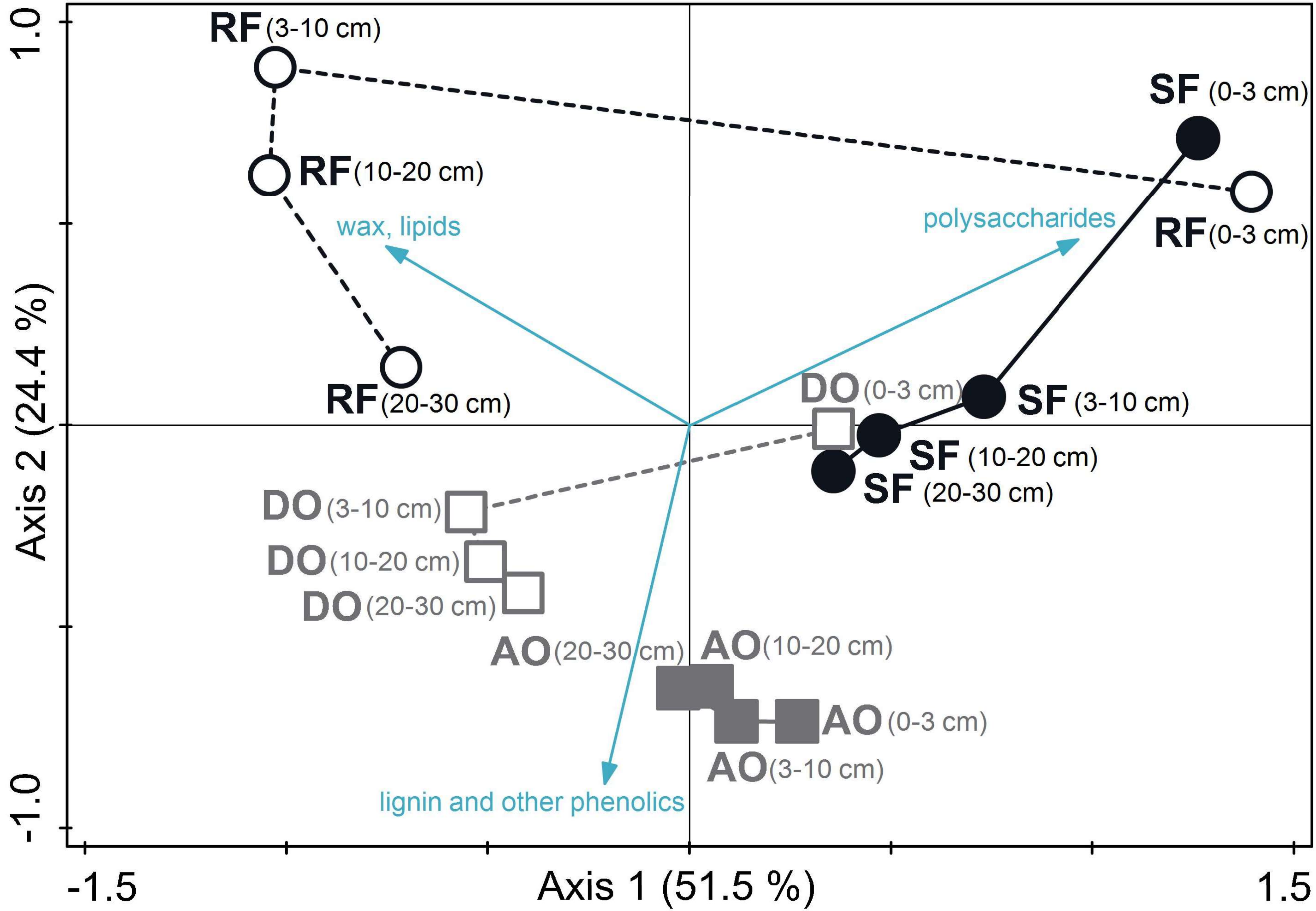


Figure 6_previous numb 7

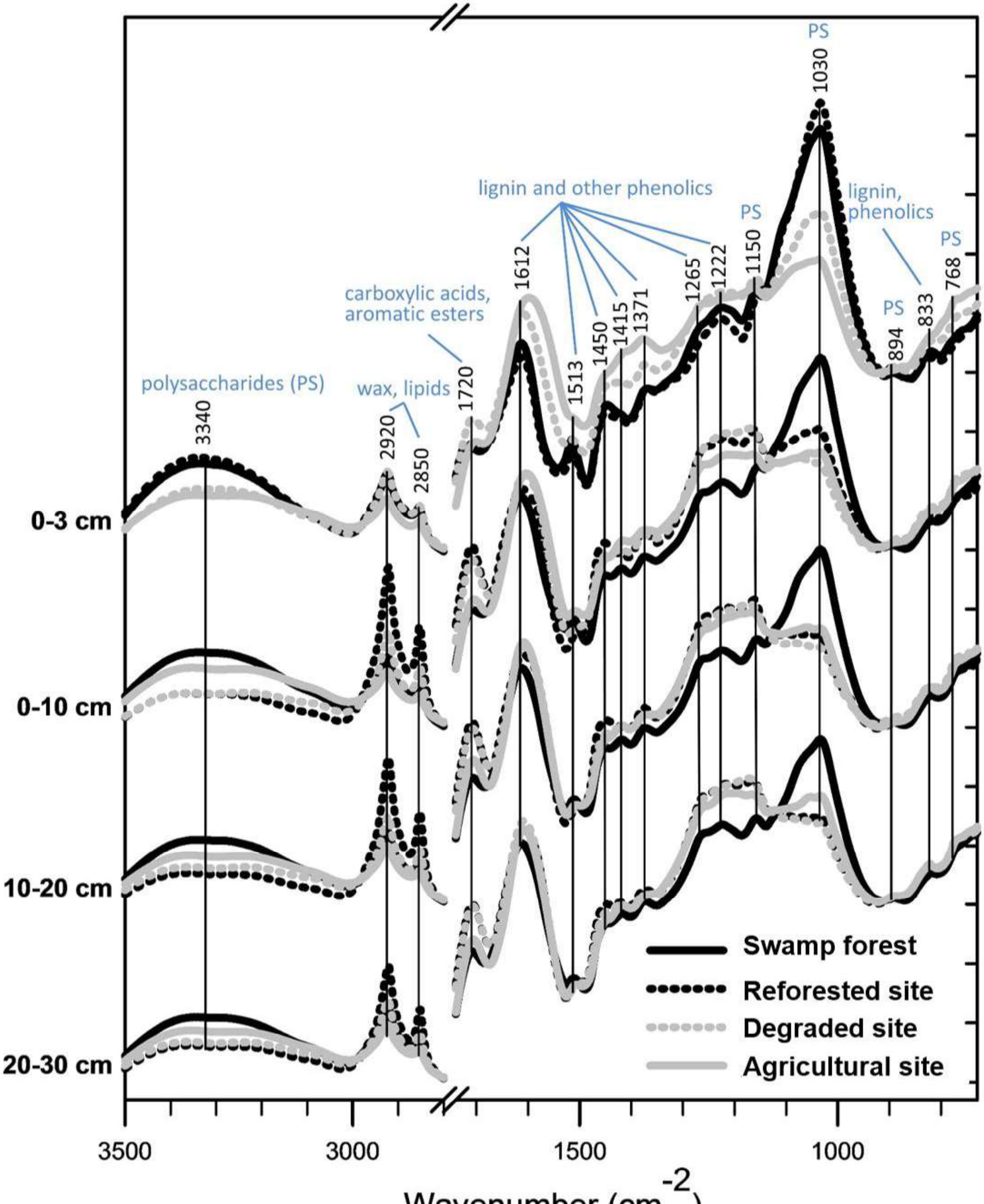


Figure 7_previous numb 8

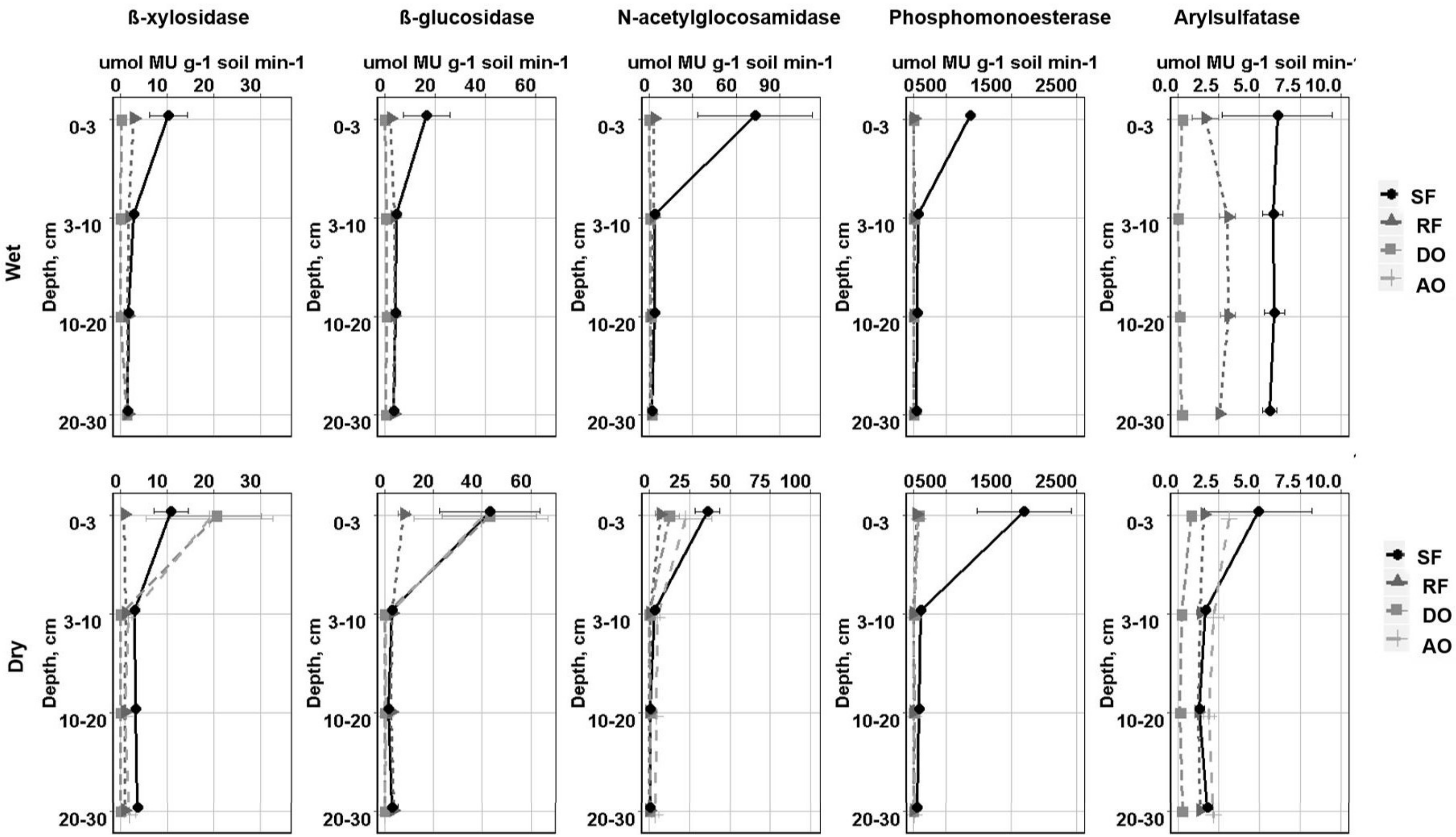


Figure 8

Figure 8