

Dissertationes Forestales 237

Tropical peat decomposability expressed through
physical, chemical and biological properties
under varying land management intensities

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ACADEMIC DISSERTATION

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The peatlands in Southeast Asia have been impacted and turned to vast carbon dioxide sources (CO₂) by land management often involving drainage and deforestation. The amount of released CO₂ in decomposition is related to management intensity likely resulting from altered conditions for decomposition. However, the link between decomposition processes and land-use change are poorly understood.

To provide insight to the effects of land-use change intensities to decomposition processes in Central Kalimantan, Indonesia, we examined physical (dry bulk density, total pore space, particle size) and chemical properties (pH, loss-on-ignition; total concentrations of N, P, K, C, Ca, Mg, Mn, Zn, Al, Fe, S, Si, DOC and DON; organic matter quality characterized by infrared spectroscopy and on compound level), which together were used to determine the decomposition stage and decomposability (i.e., substrate quality) of peat. The peat biological properties (microbial biomass and enzyme activity) were used to provide insight to the decomposition activity at various land-use types and as a response to known peat properties. The study sites were: near-pristine swamp (i) and drained (ii) forest, deforested and drained degraded (iii), agricultural (iv) and reforested (v) sites.

At the most intensively altered deforested sites the peat was denser, finer and enriched with recalcitrant compounds. The highest enzyme activity and microbial biomass were in the surface peat of swamp forest, where the amount of labile carbohydrates was highest. The six years ago reforested site did not yet show signs of recovery in peat properties, which was likely due the limited litter production capacity of the young plantation and microbial activity limited by chemical weeding. The main conclusion is that the litter input, or rather the lack of it after land-use change, and intensive management practices forms the main factors affecting to decomposition processes and leading to poorer substrate quality and reduced biological activity.

Keywords: carbon compound composition, decomposability, decomposition stage, enzyme activity, physical and chemical properties, tropical peat

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Raija Laiho and Petra Straková, thank you both for introducing me to the fascinating worlds of multivariate analyses, soil decomposition, and fine-tuning of scientific text. Peter Spetz and Jussi Heinonsalo, thank you for bravely opening the doors of your laboratories for a person who had barely held a pipet, and later for your guidance and co-authorship.

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Thank you! I will never do this again, I promise. Unless someone offers funding.

Mari Könönen, April 11th 2017, Thorne Bay, Alaska

LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles which are referred to in the text by Roman numerals. The articles are reproduced with the kind permission from the publishers: published jointly by the International Peatland Society and the International Mire Conservation Group (I) and Springer Nature (II). The article III is an author's versions of the submitted manuscripts.

I Könönen M., Jauhiainen J., Laiho R., Kusin K., Vasander H. (2015.) Physical and chemical properties of tropical peat under stabilised land uses. *Mires and Peat* 16(8): 1–13. <http://mires-and-peat.net/pages/volumes/map16/map1608.php>

II Könönen M., Jauhiainen J., Laiho R., Spetz P., Kusin K., Limin S., Vasander H. (2016.) Land use increases the recalcitrance of tropical peat. *Wetlands Ecology and Management* 24(6): 717–731. <http://dx.doi.org/10.1007/s11273-016-9498-7>

III Könönen M., Jauhiainen J., Heinonsalo J., Strakova P., Laiho R., Limin S., Kusin K., Vasander H. (2017.) Deforestation and drainage decrease peat substrate quality and suppress microbial biomass and decomposition activity in tropical peatlands. Manuscript.

M. Könönen is responsible for the summary of the thesis. In papers **I**, **II** and **III** M. Könönen was the main person responsible for planning the study, conducting the field and laboratory work and was mainly responsible for the data analysis. She served as the main author and reviser of the published papers.

TABLE OF CONTENTS

ABSTRACT	3
ACKNOWLEDGEMENTS.....	4
LIST OF ORIGINAL ARTICLES.....	5
TERMS.....	7
1 INTRODUCTION	9
1.1 Tropical peatlands and their importance in the global C cycle.....	9
1.2 Peat formation and decomposition and the effects of land-use change.....	10
1.3 Objectives and aims.....	12
2 MATERIALS AND METHODS	12
2.1 Study area and sites.....	12
2.2 Study design and sampling.....	15
<i>2.2.1 Study design and sample analyses of peat physical and chemical properties (I, II)</i>	<i>16</i>
<i>2.2.2 Study design for peat chemical properties and samples for analyses of extracellular enzyme activity, microbial biomass, and further peat chemical properties(III).....</i>	<i>16</i>
2.3 Laboratory analyses.....	17
<i>2.3.1 Physical properties.....</i>	<i>17</i>
<i>2.3.2 Chemical properties.....</i>	<i>17</i>
<i>2.3.3 Peat biological properties.....</i>	<i>18</i>
2.4 Data analyses.....	18
3 RESULTS	19
3.1 Peat physical structure.....	19
3.2 Peat chemical properties.....	20
3.3 Chemical compound composition.....	22
3.4 Microbial biomass and extracellular enzyme activity.....	23
4 DISCUSSION	23
4.1 Peat becomes denser and finer following drainage.....	23
4.2 Decomposability of peat decreases by intensive land management.....	24
4.3 Implications of findings to peatland functions.....	26
4.4 Reliability and generalization of the results.....	28
5 PROSPECTS FOR FUTURE RESEARCH.....	29
6 REFERENCES	29

ARTICLE I (separate attachment)

ARTICLE II (separate attachment)

ARTICLE III (separate attachment)

TERMS

Al, aluminium

AIL, acid-insoluble lignin

AO, agricultural land

ASL, acid-soluble lignin

BD, dry bulk density of soil (g cm^{-3})

C, carbon

Ca, calcium

CCC, carbon compound composition CO_2 , carbon dioxide

Decomposers, in this study microbes, i.e. bacteria and fungi

DF, drained forest

DO, degraded site

DOC, dissolved organic carbon

DON, dissolved organic nitrogen

Drainage as used in this study indicates only artificial water table level drawdown

Enzyme activity as used in this study indicates extracellular enzyme activity

Fe, iron

GHG, greenhouse gas

K, potassium

LOI, loss-on-ignition

Mg, magnesium

Mn, manganese

N, nitrogen

Na, sodium

P, phosphorus

PCA, principle compound analysis

PSF, peat swamp forest

RDA, redundancy analysis

RF, reforested site

S, sulphur

SF, swamp forest

Si, silicone

TPS, total pore space % of the volume

WTL, water table level

Zn, zinc

1 INTRODUCTION

1.1 Tropical peatlands and their importance in the global C cycle

The majority (56%) of tropical peatlands are located in Southeast Asia, where the oldest still existing lowland peatlands began developing from coastal mangrove forests during the Late Pleistocene (30 000–22 000 ^{14}C yr BP) (Anshari et al. 2001; Page et al. 2004, 2011; Wüst et al. 2008;). The peat accumulation rate has varied from 0.15 mm yr^{-1} to over 2 mm yr^{-1} (7.4 and $>90 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively), being lowest during dry periods and highest during wet periods, thus indicating the dependence of peat accumulation on climatic conditions (Page et al. 2004). The long-term carbon (C) accumulation rate has been $56 \text{ g C m}^{-2} \text{ yr}^{-1}$, which is more than twice as high as reported for boreal peatlands (Turunen et al. 2002; Page et al. 2004; Loisel & Garneau 2010). Tropical peatlands are considered to actively accumulate peat or be in a steady state under the current climate without anthropologically derived disturbances (Page et al. 1999). Peat deposits up to 20 metres deep have accumulated with time, while 5.5–7 metres is an average depth and 50% of dry mass is an average carbon concentration of peat in Southeast Asia (Page et al. 2011). Due to the considerable thickness of the peatlands of Southeast Asia, covering only 6–8% ($247\,778 \text{ km}^2$) of the global peat area, they contain 11–14% (68.5 Gt) of the C stored in peat globally (Page et al. 2011). This makes peatlands of Southeast Asia globally significant C stores.

During the past decades land-use change has drastically altered peatlands in Southeast Asia, where tree-covered peat swamp forests (PSF), once a dominant peatland type, are drastically modified by land-use change (Miettinen et al. 2010). PSFs are comprised of several vegetation subtypes, which transition based on their location on the dome-shaped peatland. Low riverine forests transition into mixed swamp forest and grass or tall swamp forest towards the highest point of the dome (Page et al. 1999; Sjögersten et al. 2011). Peat swamp forest coverage in Peninsular Malaysia, Sumatra and Borneo was 4.6 Mha in 2015. This is only 29% of the PSF coverage in 1990, only 6% of which was not impacted by humans (Miettinen et al. 2016). The major drivers for land-use change are smallholder farming and, increasingly, industrial plantations especially for oil palm and acacia, which together affect 50% (15.7 Mha) of the peatlands. The largest remaining PSFs are in Central Kalimantan (40% of all PSFs in 2015), where recent changes between land-use classes have primarily occurred from degraded or secondary forest to active management (Miettinen et al. 2016). The vast degraded peat areas in Central Kalimantan are primarily a result of the Mega Rice Project implemented in the 1990s. This project aimed to drain and deforest a 1-million hectare area for rice production, but resulted in forming of vast degraded peat areas mainly because the soil properties were found unsuitable for the intended cultivation (Page & Rieley 2005). More recently, the increasing desire of land area, especially for oil palm cultivation, is likely leading to increased utilization of the formed degraded areas and the remaining swamp forests in Central Kalimantan (Miettinen et al. 2016).

Land-use change led to increasing amounts of C being released to the atmosphere, especially as carbon dioxide (CO_2) (IPCC 2014). Land alteration, including drainage, coupled with increasingly strong and frequent El Niño events delaying the onset of the wet season, has led to prolonged droughts resulting in fires recurrently. Therefore, the fires are a major contributor to the amount of CO_2 released from peatlands in Southeast Asia (Page & Hooijer 2016). The combined impacts of fires and land-use change have led to the release of up to 0.25 Gt of C annually from peatlands in Southeast Asia, which is equivalent to approximately 2% of the global emissions from fossil fuel burning (Hooijer et al. 2010; Page & Hooijer

2016; Miettinen et al. 2017). In 2015, 54% (146 Mt C yr⁻¹) of the total amount of CO₂ emissions was released in decomposition processes, and the majority (113 Mt C yr⁻¹) of the CO₂ released in decomposition originated from smallholder farms and industrial plantations (Miettinen et al. 2017). Land-use change is therefore turning tropical peatlands from globally significant C sinks and stores to major C sources.

1.2 Peat formation and decomposition and the effects of land-use change

Peat may form when the litter input rate exceeds the decomposition rate (Clymo 1984). At PSFs, dead tree roots, stems and branches are major contributors to peat formation (Andriess 1988; Wüst et al. 2008; Hoyos-Santillan et al. 2015), while the most important factor regulating peat decomposition is a high water table level (WTL) that limits oxygen availability for aerobic decomposers (Clymo 1984; Laiho 2006; Jauhiainen et al. 2016a). Decomposition is most efficient in the surface peat above the WTL, where recent litter deposits and sufficient oxygen availability support aerobic decomposition (Clymo 1984; Yule & Gomez 2009; Sundari et al. 2012; Hirano et al. 2014; Hoyos-Santillan et al. 2016). Litter modified progressively by decomposition processes close to the surface will eventually be topped by more recent litter, and subsequently become buried deeper in the peat profile. The partly decomposed organic matter deeper in peat profile will decompose more slowly due to the dominance of anaerobic decomposition in more frequently waterlogged substrate closer to the water table (Clymo 1984; Page et al. 1999; Rydin & Jeglum 2013). Nowadays land-use change, which usually includes drainage and deforestation, is the largest driver of peat decomposition and formation dynamics.

Drainage is a requirement for the successful growth of most cultivated plants, because a lower WTL improves aeration in the rooting zone, while also potentiating aerobic decomposition deeper in the peat profile (Sundari et al. 2012; Hirano et al. 2014; Jauhiainen et al. 2016a). Decomposition process releases nutrients for use of vegetation and soil biota, but enhanced nutrient release in aerobic conditions also increase CO₂ emission. Enhanced aerobic decomposition leads to increased CO₂ amounts released from peat. However, the amount of released CO₂ appears to depend greatly on the time passed from the initial land-use change along with land management intensity, i.e. the effectivity of drainage and the quality of maintained vegetation (Hooijer et al. 2012; IPCC 2014). The changes in released CO₂ amount may be due to changes in substrate quality, as discussed in more detail in the next paragraph. Drainage also leads to changes in peat physical properties, as the lowering of WTL causes peat subsidence. Subsidence is a result of a combination of shrinking, compaction and consolidation of peat, which are caused by removal of support by groundwater for the peat layer above the WTL, and biological decomposition (Hooijer et al. 2012; Laiho & Pearson 2016). With time, peat subsidence is known to increase the dry bulk density of soil (BD, g cm⁻³) and decrease the total pore space (TPS, %) (Minkkinen & Laine 1998; Hooijer et al. 2012). Additionally, as a consequence of drainage and strong El Niño years leading to prolonged droughts, wild fires have become one of the greatest modifiers of peat in large areas of Southeast Asia during the past decades (Konecny et al. 2016; Page et al. 2016). The recurrent fire events surfaces progressively older peat from the deeper depths in the peat profile, as the topmost peat is impacted and consumed in the burning processes (Hoscilo et al. 2011; Hirano et al. 2014). However, peat physical properties have not been systematically compared for several differing land management types.

Land-use change typically also includes the removal of original PSF vegetation. In clear cutting, the relatively high-biomass PSF vegetation is replaced with regularly harvested plantations (i.e. acacia, oil palm) and cultivated plants with low biomass (e.g. maize, cassava). Alternatively, large clear cut and drained land areas have been abandoned, and such areas have developed into drained, but unmanaged shrub lands (Miettinen et al. 2016), where vegetation is typically formed of ferns and scattered trees. Mature oil palm and acacia plantations may reach high biomass, but the intensive management practices (i.e. weeding, and harvesting) lead to lowered litter deposition, and therefore these plantations do not support peat accumulation (Smith et al. 2012). As the litter input rate depends on vegetation type, it is unlikely that the current vegetation types on managed lands have sufficient volume and litter production capacity to maintain peat production (Hertel et al. 2009; Smith et al. 2012). Progressing decomposition will therefore take place after deforestation in existing peat depositions, and will alter the properties of the peat formed prior to land-use change. This can be expected to affect peat decomposability (i.e., quality of energy for decomposers), which is largely determined by substrate quality and determines the availability of the energy source for decomposers (Berg 2000; Straková et al. 2011; Hoyos-Santillan et al. 2016). Substrate properties generally depend on their source and decomposition stage. In PSFs, woody litter forms lignin-rich peat with up to 3.5 times higher lignin concentrations than found in typically moss- and sedge dominated boreal peatlands (Andriessse, 1988). Yet, no information exists concerning the effects of land-use change, either on peat carbon chemistry or the enzyme activity in tropical peatlands.

Nutrient availability may also regulate decomposition processes, and nitrogen (N) and phosphorus (P) in particular are thought to be the limiting nutrients for decomposition and growth in tropical organic soils (Rejmankova 2001; Sjögersten et al. 2011; Jauhiainen et al. 2016b). Therefore, productive cultivation of cropping plants on these naturally poor soils requires fertilization (Andriessse 1988). Peat nutrient concentrations in the dome-shaped PSFs are highest near rivers, as a result of nutrient input from occasional flooding and relative closeness of mineral soil due to shallow peat deposits (Page et al. 1999; Sjögersten et al. 2011). PSFs are acidic, ombrotrophic (i.e. precipitation-fed) ecosystems, where nutrients are tightly bound to the biological cycle between plants and decomposers, keeping peat itself relatively nutrient-poor (Page et al. 1999; Yule et al. 2009; Lampela et al. 2014). Deforestation and drainage breaks this biological cycle and likely cause nutrient leaching out from the system. For example, the levels of dissolved organic carbon (DOC) from older peat, deeper in the peat profile, have increased after drainage and deforestation (Moore et al. 2011). However, changes in nutrient concentrations caused by various land management have not been studied in tropical peatlands.

In the future, the utilization of degraded lands for cultivation and plantation along with reforestation acts will likely increase, due to increasing land price and awareness of the global and local consequences of unsustainable land use of tropical peatlands. Productive cultivation at degraded soils requires fertilization and reforestation increases litter input. Both added fertilizers or new litter with higher concentrations of labile carbohydrates to degraded peat soil, may trigger decomposition processes, as suggested by Comeau et al. (2016) and Jauhiainen et al. (2016b), yet the effects of reforestation to decomposition processes has not been studied. Understanding the current properties and decomposability of peat is crucial for predicting the effects of future management on C stored in peat in Southeast Asia and for planning C neutral management in Asia.

1.3 Objectives and aims

The lack of understanding concerning the tropical peat properties and decomposability may exacerbate unsustainable management practices and sustain fast peat loss especially at altered, stabilized land-use types. This study aims to identify the decomposition stage and decomposability of peat expressed through physical (dry bulk density, total pore space, particle size) and chemical properties (pH; loss-on-ignition; and total concentrations of total concentrations of N, P, potassium (K), C, calcium (Ca), magnesium (Mg), manganese (Mn), zinc (Zn), sodium (Na), aluminium (Al), iron (Fe), sulphur (S), and silicone (Si); DOC & DON; and organic matter quality characterized by infrared spectroscopy and on compound level) under common land management intensities in Central Kalimantan, Indonesia. The peat biological properties, i.e., microbial biomass and enzyme activity, were examined in response to the known peat properties to provide insight to the decomposition processes at various land-use types. We collected samples from five sites: (i) the near-pristine swamp forest, and the four other sites in order of increasing management intensity were (ii) drained forest, and deforested and drained (iii) reforested; (iv) degraded; and (v) agricultural sites.

The hypotheses were:

- 1) As a result of land-use change, peat physical structure changes
- 2) Deforestation and drainage leads to enrichment of recalcitrant compounds in peat.
- 3) Enzymatic activity and microbial biomass are lower at intensively altered sites compared to swamp forest covered sites with high WTL due to poorer peat quality.
- 4) Reforestation modifies peat chemical properties and biological activity towards those in unaltered swamp forests.

2. MATERIALS AND METHODS

The methods applied here are described in detail in **I–III**.

2.1 Study area and sites

The study area was located on lowland peatland within the same watershed divided by Sebangau River in the province of Central Kalimantan, Borneo Island, Indonesia (Fig. 1). During the period of 2002–2010, annual rainfall in the area was 2540 ± 596 mm yr⁻¹ and annual temperature was 26.2 ± 0.3 °C (Sundari et al. 2012). Annual precipitation is usually divided into two seasons, with a drier season normally occurring from June to October.

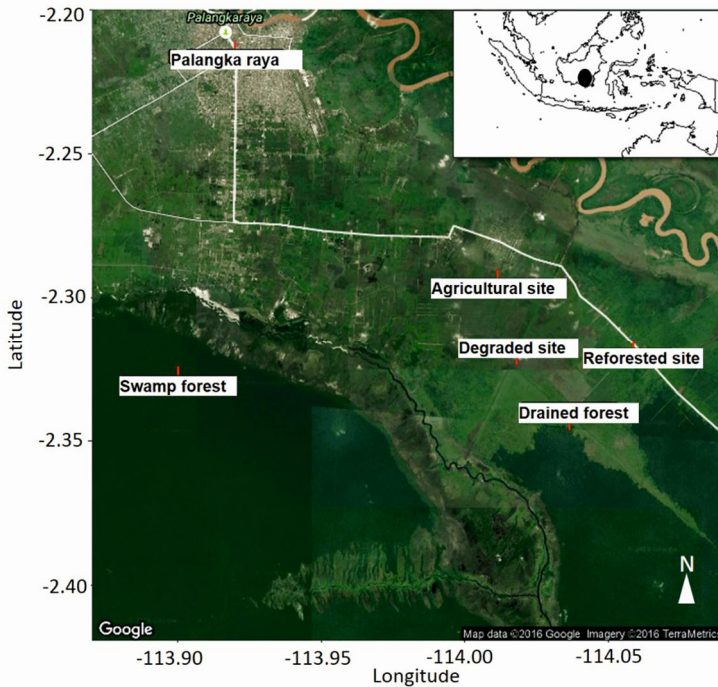


Figure 1. A satellite photo of the study area with study sites indicated. The dark areas are swamp forests and lighter areas deforested areas with ground vegetation. Copyrights of the photo: ©2016 Google.

A total of five study sites were located within a 10-km radius forming a continuum of common land-use types with varying management intensities (Fig 1; Table 1). The hydrological conditions, vegetation and peat chemistry graduates from the nutrient-rich parts near the river towards the nutrient-poor central areas of the peat dome. The study sites on the two peat domes located on opposite sides with a similar distances, from the Sebangau River, and the peat depth exceeding 3 m at all sites, and the sites can therefore be assumed to originate from comparable ombrotrophic mixed PSFs. The sites in order of increasing land management intensity were: near-pristine swamp forest (SF; referred to as undrained forest in **I** & **II**, and as swamp forest in **III**), drained forest (DF; **I**, **II**), reforested site (RF; **III**), degraded site (DO; **I**, **II**, **III**) and agricultural site (AO; **I**, **II**, **III**).

The vegetation of the swamp forest and drained forest sites comprised of steady-state forest cover with the topmost canopy layer reaching a height of 35 m and some scattered *Pandanus* spp. palm thickets as ground vegetation (Page et al. 1999). Neither of the forests was fully pristine, due to selective logging that occurred in the 1990s. The soil surface microtopography in the swamp forest was formed of a mosaic of open, low peat surfaces (i.e. base level), and hummock-like formations, which were mainly around tree bases (Lampela et al. 2014). Microtopography was less notable in the drained forest due to drainage. At the reforested site, a canopy height of approximately 10 metres was formed by *Shorea*

balangeran-trees planted in lines at three-metre intervals six years prior to the study. The understorey vegetation was suppressed by cutting and occasionally by utilizing herbicides containing glyphosate and parquat. At the degraded site the vegetation was formed of ferns and scattered trees reaching approximately a height of three metres.

The drained forest and degraded site were drained by the same 3–4-metre deep and approximately 15 m wide canal, while the reforested site was drained by other parts of the same canal system. The canal system was established in 1997, during the Mega Rice Project (Page & Rieley 2005). In comparison to the drained forest and degraded site, with very deep WTLs during dry season, the reforested site was only moderately affected by draining due to its location at a lower elevation on the peat dome, and thus resulting in higher average WTL and a higher flooding frequency. Both the reforested and degraded sites had burned after deforestation, but fires on the reforested site had occurred only before 1998, prior to reforestation. The degraded site had burned recurrently (most intensively in 1997, 1999, 2002 and 2006) prior to sampling, and the fire events had oxidized several decimetres of the topmost peat and resurfaced older peat (Hoscilo et al. 2011).

The most intensively and longest managed site was the agricultural site, which had been deforested and drained for smallholder cultivation (i.e. cassava, maize) in the early 1980s. Drainage at the agricultural site was controlled and rather shallow (Table 1). The agricultural site had been fertilized mainly with urea and by burning a mixture of surface peat and crop-plant residues.

Table 1. Study sites referenced in articles including site location, vegetation type and management history.

Site	Co-ordinates	Management history	Vegetation	WTL ⁽¹⁾	Articles
Swamp forest	2°19'16.96"S 113°53'54.29"E	Selective & illegal logging (1990–2000), small ditches	Swamp forest	-10 / -4	I, II, III
Drained forest	2°20'45.89"S 114°2'11.12"E	Drained (1996à), selective logging (1996–1998)	Swamp forest	-39 / –	I, II
Reforested site	2°18'54.94"S 114°3'31.76"E	Clear-cut & drained (1996à), reforested 2008	<i>Shorea balangeran</i> plantation	– / -30	III
Degraded site	2°19'25.11"S 114°03'31.76"E	Clear-cut & drained (1996à), burned several times	Ferns, shrubs	-17 / -58	I, II, III
Agricultural site	2°17'25.21"S 114°1'5.15"E	Clear-cut & drained (1987à), since cultivation	Crops, ever under	i.e. -22 / -41	I, II, III

⁽¹⁾WTL data on the right is long-term data used in papers **I, II** (original data from Dr. Hidenori Takahashi and Dr. Takashi Inoue) and on the left data from year 2014 used in paper **III** (unpublished data from Dr. Jyrki Jauhiainen).

2.2 Study design and sampling

Two study designs were utilized, one in articles I and II (Fig. 2), and the other in article III (Fig. 3). Both set-ups covered conditions from mostly aerobic conditions closer to the peat surface to mostly anaerobic, waterlogged conditions deeper in the peat profile.

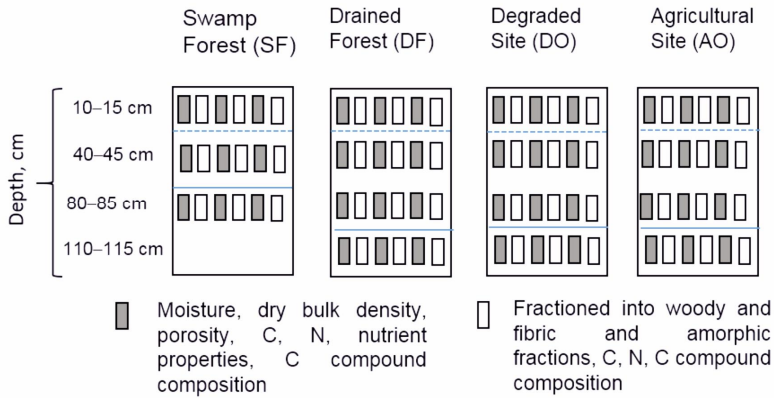


Figure 2. The figure presents the study design for articles I and II. Sampling depths for each site are presented as a cross-section in peat profile. Predominantly aerobic conditions are pictured above the dotted blue line in the sampling profile, the permanently anaerobic conditions beneath the solid blue line, and frequently aerobic conditions in-between. The grey and white boxes present the parallel subsamples collected from each depth. The conditions analysed from each subset are explained beneath the figure.

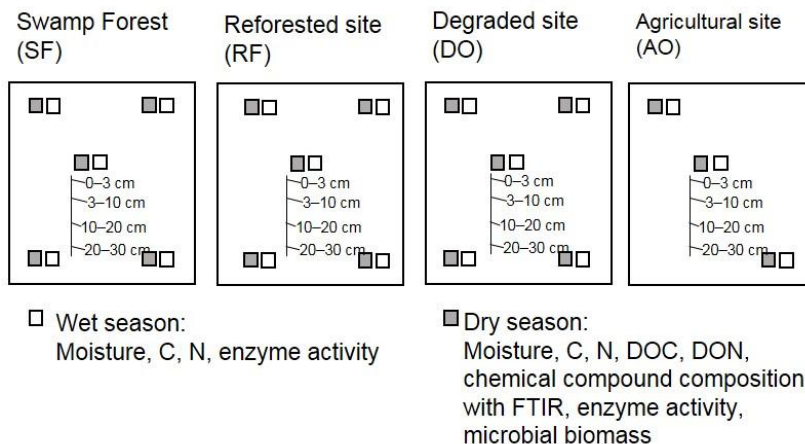


Figure 3. The study design for article III. The study plots are pictured from above. Each site had five permanent plots – except for the agricultural site, where only three plots were established. Samples were taken from four depths (0-3, 3-10, 10-20 and 20-30 cm) at each plot.

2.2.1 Study design and sample analyses of peat physical and chemical properties (I, II)

Samples to study peat physical (**I**) and chemical properties (nutrient properties in **I**, carbon compound composition in **II**) were collected from the swamp and drained forests, and degraded and agricultural sites. Sampling took place in September 2009 at the end of the dry season when annual WTL was at its lowest. Samples in the swamp and drained forest sites were taken from the low peat surface between trees, and from the flat vegetation-free surfaces at the open sites. Samples were taken at pre-set depths (10–15, 40–45, 80–85, and 110–115 cm below the soil surface) from one pit hole from each site immediately after reaching each sampling depth. The topmost depth (10–15 cm) was mostly above the WTL, and was thus mainly aerobic at all sites, while deeper peat (40–45 cm) was mostly waterlogged and thus anaerobic at all sites. In the swamp forest, the 80–85 cm depth was under permanent anoxia due to relatively high WTL, and it provided the deepest sampling depth at the site. At the other sites, where the WTL was lowered due to enhanced drainage, the 80–85 cm depth provided a sampling depth with mostly waterlogged conditions and 110–115 cm with permanently waterlogged conditions. From each depth six volume-exact (10 x 10 wide and 5 cm high) samples ($n = 24$ per site, except for swamp forest $n = 18$; total $n = 90$) were collected.

After removing living roots, samples from each site and depth were divided into two subsets (total $n = 45$ per subset, $n = 3$ for a subset from each depth for each site). Subset 1 was used to determine the BD and TPS; nutrient properties approached through pH, loss-on-ignition (LOI) and total concentrations of N, P, K, C, Ca, Mg, Mn, Zn, Na, Al, Fe, S, and Si; and carbon compound composition. Subset 2 was fractionated to determine the peat physical decomposition stage.

2.2.2 Study design for peat chemical properties and samples for analyses of extracellular enzyme activity, microbial biomass, and further peat chemical properties (III)

Samples to study peat chemical (DOC, DON, C, N, chemical composition with infrared spectroscopy) and biological properties (enzyme activity, microbial biomass) were collected in two sampling events in 2014 (**III**). The first sampling event occurred close to the end of the wet season in mid-March and the second at the end of the dry season in mid-September. Extracellular enzyme activity was measured from samples of both sampling events. Samples collected at the end of the dry season were also used to analyse peat chemical properties and microbial biomass. Five representative sample plots were established in the swamp forest, and at reforested, degraded, and agricultural sites. The permanent plots were located at approximately ten-metre intervals, forming a ca. 400-m² square in the swamp forest and the degraded site, and a 300-m² rectangle forming a cross-section of the reforested site. Samples were collected only once from three randomly chosen spots at the agricultural site. Samples at the forest and reforested site were taken from low, vegetation-free surfaces between the trees covering the majority of the land area. Both vegetation-free surfaces and surfaces covered by vegetation (ferns at the degraded site and maize at the agricultural site) covered large proportion of the land area at the open sites (agricultural and degraded), and samples were therefore collected from both surface types.

We studied peat chemical and biological properties only on the surface peat (topmost 30 cm), because decomposition-related functions are generally most active in the surface soils. Sampling covered the first 30 cm of the peat profile, where peat was divided into four sections: 0–3 , 3–10 , 10–20 and 20–30 cm. Non-volumetric samples from the topmost peat

(0–3 cm) were collected with glove-covered hands, while the volumetric samples (68.7 cm^{-3} from the 3–10 cm depth and 98.2 cm^{-3} from 10–20 cm and 20–30 cm depths) from deeper depths were extracted using a Russian auger with a diameter of 5 cm ($n = 20$ per site except for the agricultural site $n = 12$). Samples were sealed in plastic bags and stored at 4°C for a maximum of two weeks prior to analyses. Previous studies have not found that storing samples in a cool environment for comparable time periods would affect the microbiological sample quality of tropical soils (Turner & Romero 2010; Sjögersten et al. 2011). Living roots were removed from the collected samples prior to any further analyses.

2.3 Laboratory analyses

2.3.1 Physical properties

Peatlands are important flood regulators due to the hydraulic conductivity of peat (Rieley & Page 2005), and this peat function is largely dependent on peat physical properties (Päivänen 1973). Drainage affects the peat physical properties due to shrinkage, compaction, consolidation, and enhanced decomposition (Minkinen & Laine 1998; Laiho et al. 1999; Kurnain et al. 2001; Hooijer et al. 2012; Laiho & Pearson 2016).

To study peat physical properties (**I**), we measured the peat dry bulk density (g cm^{-3} , BD) and the decomposition stage, i.e. particle size distribution. First, the samples from each site and depth were divided into two subsets ($n = 45$ per subset). Subset 1 was used to determine the BD and to derive the total pore space (TPS, %). Subset 2 was used to describe the physical decomposition stage of peat by fractioning the samples gently with running water and two sieves (mesh \varnothing 1.5 mm and 0.15 mm). The larger mesh diameter captured the physically least decomposed matter, called the ‘woody’ sample, while the smaller mesh captured the more decomposed matter, called the ‘fibric’ sample. The finest matter, called ‘amorphic’, was washed through the smaller mesh, but its share of the non-fractioned sample was calculated by subtracting the masses of the woody and fibric fractions from the average total mass of the non-fractioned samples taken from the same site and sampling depth. Thus, the woody, fibric and amorphic fractions together accounted for 100% of the mass of the non-fractioned sample. The mass of each fraction per sample volume (i.e., density of fraction, g cm^{-3}) was calculated. Each sample type is discussed in article **I**, but only non-fractioned, woody, and fibric samples are utilized in article **II**.

2.3.2 Chemical properties

Peat properties generally largely depend on the properties of the organic matter forming peat, and are altered with progressing decomposition (Berg 2000; Rydin & Jeglum 2013). In addition, substrate quality and nutrient availability regulate the decomposition of peat (Laiho 2006; Sjögersten et al. 2011; Straková et al. 2011; Hoyos-Santillan 2016). Peat chemical properties can therefore predict the decomposability, i.e. quality of energy for decomposers. To reach an understanding of chemical peat properties, we analysed peat nutrient properties and compound composition, with a primary focus on C compounds.

Peat nutrient properties were approached through pH (**I**, **III**), LOI (**I**) and total concentrations of N, P, K, Ca, Mg, Mn, Zn, Na, Al, Fe, S and Si (**I**). We analysed peat total C concentrations and determined the C/N-ratio (**I**, **II**, **III**). Peat total concentrations (g g^{-1}) of DOC and dissolved organic nitrogen (DON) were estimated (**III**). Analyses conducted for papers **I** and **II** were performed on three laboratory replicates of combined samples per site

and depth, and analyses performed for paper **III** were made from five field replicates at swamp forest, reforested and degraded sites and from three samples at agricultural sites.

Peat chemical composition was analysed with two different methods from two sample sets collected at different times (**II**, **III**). Infrared spectra were obtained to reach the entire spectrum and variation in peat chemical composition, including waxes and lipids, carboxylic acids and aromatic esters, polysaccharides, lignin and phenolics (**III**) (Artz et al. 2008). To study peat C chemistry on the compound level, we analysed peat carbon compound composition (CCC, mg g⁻¹) with gravimetric and gas chromatographic methods (**II**). The same methods were used to explore CCC variation at physically different decomposition stages of peat (non-fractionated peat and woody and fibric fractions) fractionated in paper **I**. The analysed compounds, in order of decreasing decomposability, were: hemicelluloses and uronic acids (including pectin), cellulose, extractives (hydrophilic and hydrophobic soluble compounds, i.e. soluble carbohydrates, waxes and lipids), acid-soluble lignin (ASL) and acid-insoluble lignin (AIL), which is often referred to as Klason's lignin. The analysed hemicelluloses were arabinose, rhamnose, xylose, mannose, galactose, and glucose, while analysed uronic acids were glucuronic, galacturonic, and 4-O-Me-glucuronic acid. The methods are described in Sundberg et al. (1996, 2003) and Brunow et al. (1999).

2.3.3 Peat biological properties

Microbial C and N (i.e. C and N bound to the cell walls of microbes) can be derived to estimate microbial biomass (Vance et al. 1987). Extracellular enzymes catalyze microbial decomposition processes of organic matter and each enzyme degrades specific compounds (Bruns 2013). Microbial biomass and enzyme activity are therefore used to describe the quality of peat as a biological environment reflecting substrate quality for microbes.

Microbial C and N concentrations were determined with a chloroform fumigation-extraction method modified from Vance et al. (1987) (**III**). Correction factors of 2.64 and 1.86 were used for unrecovered microbial C (Vance et al. 1987) and microbial biomass N, respectively, when estimating the microbial biomass (Brookes et al. 1985).

Extracellular enzyme activity related to C, N, P and S decomposition in peat were measured with a fluorescence method modified from Pritch et al. (2011) (**III**). The method provides information concerning potential activity in optimal conditions, and pH is therefore regulated with a buffer for each enzyme. The enzymes related to C degradation were b-Xylanase (4-methylumbelliferyl- β -D-xylopyranoside) and b-Glucosidase (4-Methylumbelliferyl- β -D-glucuronide); enzymes related to N cycle N-acetyl-b-glucosaminidase (4-Methylumbelliferyl N-acetyl- β -D-glucosaminide), P degradation Phosphomonoesterase (4-Methylumbelliferyl phosphate) and S degradation Arylsulfatase (4-Methylumbelliferyl sulfate potassium salt).

2.4 Data analyses

It is acknowledged that the demanding sampling conditions at field and laborious analyses forced us to limit sampling design from the optimal, and thus some of the applied analyses are not optimal for the collected data. However this is much of the condition in large number of ecological studies, and when the predicted response is strong enough the replication can be kept relatively small (Oksanen 2001).

We analysed several intercorrelated peat properties and therefore most statistical analyses performed in this study are multivariate analyses (**I**, **II**, **III**), performed using Canoco for

Windows version 5.0 (ter Braak and Smilauer, 2012). Unconstrained principal component analyses (PCA) were used to examine the variation in peat properties and their relationship to sample and sampling depth that were applied as passive explanatory variables. Constrained redundancy analyses (RDA) were used to test how much of the variation in peat properties was explained by explanatory variables. RDA with variation partitioning was used to test the unique effect of each explanatory variable. Variation partitioning partitions the variation attributable to a given explanatory variable along with the shared variation, thus pointing the amount of variation explained each by explanatory variable independently by also taking into account the shared amount of variation explained by two or more variables.

In paper **I**, we applied a two-way analysis of variance (ANOVA) followed by Tukey's post hoc test to test the effect of site and depth and their interaction to peat properties. Three field replicates from each depth were used as measurement variable and site and depth as nominal variables. In paper **II**, the effect of sample type to peat carbon compound composition was tested with a t-test. The test was conducted between all samples of the same type was separately for each measured variable.

In paper **III**, the differences in peat chemical or biological properties between sites at each 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. Games-Howell post hoc test 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, which were transformed as $\log(x+1)$. The analysis were performed with RStudio version 0.98.1102. Differences were statistically significant if the p-value was less than 0.05. Data analyses are described in more detail in the papers (**I**, **II**, and **III**).

3 RESULTS

3.1 Peat physical structure

The differences in peat physical properties between the sites were greatest near the peat surface (10–15 cm) and differences generally decreased with depth (Fig. 4; **I** Table 2). Peat BD correlated negatively with the concentration of the woody and fibric fractions (**I** Fig. 3). The surface peat of the swamp forest and drained forest were more similar compared to peat at the open sites. The lowest BD in the surface peat was observed in the swamp forest, as the BD was 54% higher at the degraded site, 38% higher at the agricultural site, and 31% higher in the drained forest at the respective depth. The swamp forest had the coarsest structure in surface peat, which contained twice as much wood as peat from the drained forest and up to six times more wood than peat from the degraded or agricultural sites from the respective depth. This also contributed to the highest peat porosity values detected at the swamp forest. Fibric material content was highest in the two topmost sampling depths (10–15 and 40–45 cm) in the drained forest at all the sites and depths. Peat BD in the drained forest at a depth of 40–45 cm was 29–88% higher than at the other sites at the respective depth, while porosity was lowest and the concentration of fibric particles was highest compared to peat at the other sites at the respective depth. The amorphous fraction concentration of the surface peat (10–15 cm) was up to three times higher at the degraded and agricultural sites than at the swamp and drained forest.

3.2 Peat chemical properties

RDA with variation partitioning showed that site, depth and physical structure (concentrations of wood, fibre and amorphous fraction) accounted for 28.7% ($F=10.7$, $p=0.002$), 20.8% ($F=8.0$, $p=0.002$) and 13.8% ($F=5.7$, $p=0.002$) of the variation in peat nutrient properties, respectively (Fig. 5). The strongest gradient in the data (x axis) showing the joint effect of site, depth and physical structure separated the topmost peat layer (10–15 cm) from the deeper layers, and the swamp forest and agricultural site from the drained forest. The second strongest gradient (Y-axis) separated, and the forest-covered (swamp and drained) and the topmost peat layer from open sites (degraded and agricultural) and deeper layers. Two clear trends were observed in the measured elements: concentrations of C, ash and cations (Mg, Ca, Zn, Mn) were highest at the agricultural site, and N and P concentrations were highest at the forested sites, especially the undrained swamp forest (Fig 5; **I** Fig. 3, and Appendix 1A and 1B).

One sample set was used to measure C and N concentrations and C/N-ratio within peat depths from 0 cm to 30 cm (**III**), the other from depths of 10–15, 40–45, 80–85 and 110–115 cm (**I**, **II**), resulting in relatively similar values for comparable sections of the peat profile. C concentration was 49–61%, and it increased with depth at forest-covered sites and was more stable throughout the sampling profile at open sites (**I**, Appendix A1; **III** Fig. 4g). N concentration was 0.68–1.67% being lower at deeper depths (**I**, Appendix A1; **III** Fig. 4h). The C/N-ratio varied from 29 to 89 in both data sets, and was lowest at the swamp forest site for all sampling depths (**I**, Appendix A1; **III** Fig. 4g). Generally, peat C/N-ratio increased with advanced decomposition stages of peat, and this could be seen as higher C/N-ratios in deeper peat with higher BD and smaller particle size, and as a similarity of the non-fractionated peat and the fibric fraction samples (**II**, Fig. 4). Interestingly, the C/N-ratio of the woody fraction increased notably with depth, and was between 111 and 167 in the deeper layers, but remained less than 100 in the other sample types deeper in the peat (**II**, Fig. 4).

DOC and DON concentrations were measured only from a depth of 0–30 cm in the peat profile and during the dry season (**III**, Fig. 4d, 4e & 4f). DOC concentration varied between 0.52 and 1.80 mg g⁻¹, and DON concentration varied between 0.15 and 0.50 mg g⁻¹ of dry peat (**III**, Fig. 4d & e). DOC concentrations were up to three times higher in the topmost peat at the swamp forest and reforested site than at open sites at respective depth. Only within the swamp forest did the DOC concentration increase with depth. The DON concentration in peat decreased with depth at all sites, and was highest at the swamp forest at all sample depths.

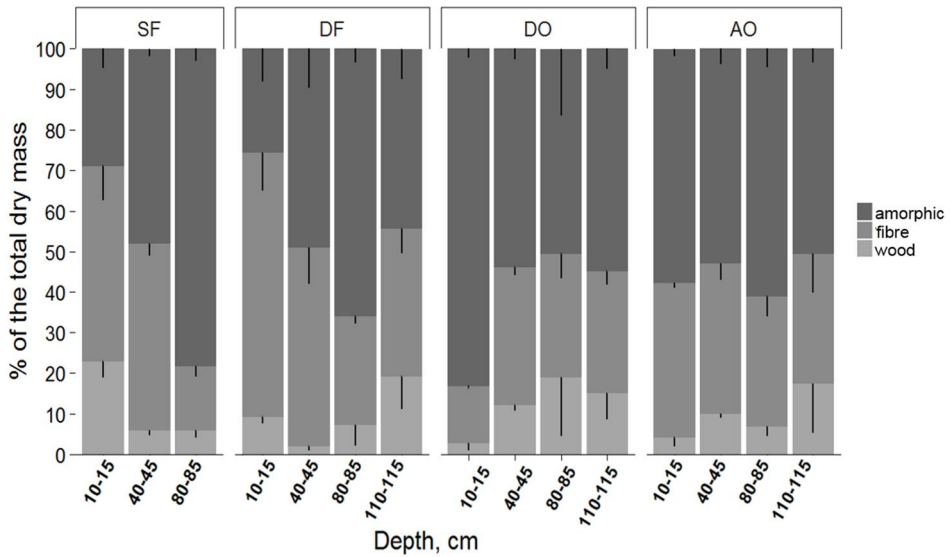


Figure 4. The cumulative proportions of woody, fibric and amorphous fractions from the mass (g/g) of the bulk sample from each site and depth (mean \pm SE). SF= swamp forest, DF=degraded site, DO=degraded site, AO=agricultural site.

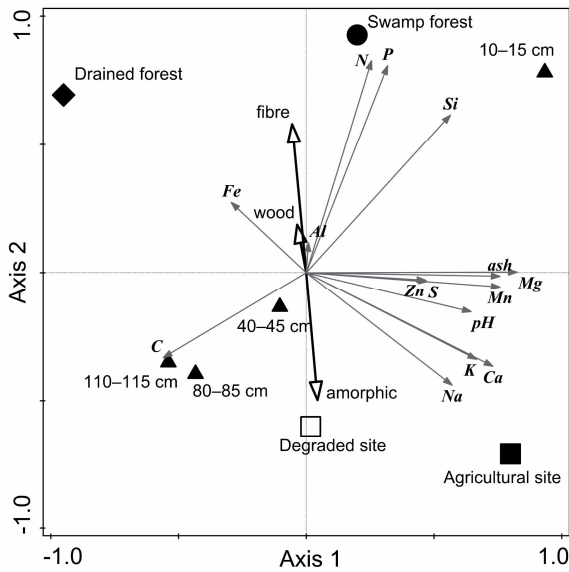


Figure 5. The joint effect of the site, depth and physical structure (proportion of wood, fibre and amorphous matter) used in RDA with variation partitioning together with the residual variation explained 63.4% of the variation in peat nutrient properties.

3.3 Chemical compound composition

Both methods used to analyse peat chemical composition indicated that the differences between sites were most prominent in the surface (10–15 cm in **II**, 0–3 cm in **III**) peat, and the surface peat properties at each site differed from those of the deeper layers of the same site (Fig. 6; **III**, Fig. 6 & 7).

Infrared spectroscopy showed that the topmost peat (0–3 cm) at the swamp forest and reforested site was rich in polysaccharides in comparison to peat at the open sites, which were enriched with lignin and other phenolic compounds (**III**, Fig. 6 & 7). At a depth of 3–10 cm the compound composition at the reforested site differed from both swamp forest and open sites, yet, it resembled more the open sites as it was richer in lignin and poorer in polysaccharides (**III**, Fig. 6 & 7). The differences between the swamp forest and other sites were less notable below the 10 cm depth in peat.

The effects of environmental variables on peat CCC were analysed using RDA with variation partitioning, which showed that site explained 27.3% ($p=0.056$), physical structure 23.6% ($p=0.066$) and depth 9.7% ($p=0.124$) of the total variation (**II**). On average, the concentrations of extractives, total hemicelluloses and ASL in peat were higher in the swamp forest and drained forest sites (38%, 647% and 38% higher, respectively), and the concentrations of cellulose, and ASL were lower (4% and 11% lower, respectively) than at the degraded and agricultural sites (Fig. 7; **II** Fig. 5, Supplementary Table 3). The total hemicelluloses were divided into sugars and uronic acids, while peat contained compounds in the following order: glucose > xylene > mannose > galactan > galacturonic acid > arabinose > rhamnose > glucuronic acid > 4-O-Me-glucuronic acid (**II** Fig. 3, Table 4).

Of the fractions indicating physical decomposition stage, the woody sample differed significantly ($p<0.05$) from the non-fractionated bulk soil and the fibric fraction (**II** Fig. 3 & 6, Table 5). On average, non-fractionated samples and fibric fractions had higher concentrations of extractives, AIL and ASL (33.8%, 12.7% and 68.4%, respectively) than the woody samples. Cellulose concentration was 4.5 times higher and total hemicellulose concentration was nearly three times higher in the woody samples than in the other samples.

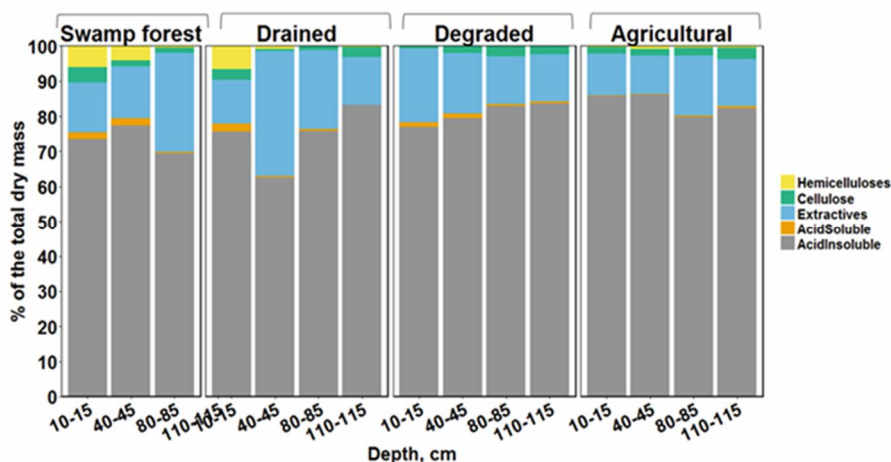


Figure 7. Cumulative proportions (y-axis) of hemicelluloses, celluloses, extractives, acid-soluble lignin and acid-insoluble lignin at each site and depth (x-axis) from swamp forest, drained forest, degraded site and agricultural site, respectively..

3.4 Microbial biomass and extracellular enzyme activity

At all sites the microbial biomass C and N concentrations were highest in the surface peat (0–3 cm) and decreased with depth (**III**, Fig. 4a & b). The concentrations varied between 0.03 and 8.5 mg g⁻¹ of soil (d.w.) for microbial C and between 0.00 and 0.55 g g⁻¹ of soil (d.w.) for microbial N, both being highest in the swamp forest (**III**, Fig 4a & b).

Extracellular enzyme activity correlated positively with microbial biomass, pH and N and DON concentrations (**III**, Fig. 9b). The measured enzyme activities were detected mainly in the topmost peat (0–3 cm) and they were generally higher in the swamp forest than at altered sites (**III**, Figs. 8 & 9b). Differences in enzyme activity between the wet and dry season varied between sites (**III**, Figs. 8 & 9a). Seasonality was most evident in the swamp forest. Enzyme activity in the open sites was mainly detected during the dry season, while activities remained relatively low throughout both seasons at the reforested sites.

4 DISCUSSION

4.1 Peat becomes denser and finer following drainage

Physical processes, i.e. modification and relocation of materials, and improved conditions for biological decomposition, i.e. chemical breakdown of peat leading to gaseous and waterborne C losses, following drainage greatly modify peat physical properties over time. This could be seen especially at the most intensively altered deforested and drained sites (**I**) as increased BD, and decreased porosity and particle size composition in peat. Similar changes in peat physical properties following drainage have been reported in earlier studies both from tropical and boreal regions (e.g. Minkinen & Laine; 1998; Hooijer et al. 2012). According to Hooijer et al. (2012), the physical effects of drainage leading to changes in peat physical properties, can be divided into two phases: (1) immediately following drainage, the subsidence is rapid due to physical re-arrangement of particles and the released CO₂ emissions are relatively large especially from the decomposition of labile carbohydrates. This is followed by the second phase (2), where peat becomes denser and finer mainly due to progressing biological decomposition. Additionally, at the agricultural site, land management practices, including shallow tilling, that mixes and aerates the surface peat, had also modified the peat properties. In a longer time span, most of the subsidence (up to 92%) is concluded to result from decomposition and the amount of released CO₂ per time unit decreases (Hooijer et al. 2012). This observed decrease in carbon loss rate is likely due to the increase of peat recalcitrance (**II**, **III**), which will be discussed in more detail in the next chapter.

Physical processes and biological decomposition simultaneously cause physical breakdown of the peat, leading to a progressively higher proportion of smaller-size particles in further decomposed peat. This could be seen in the swamp forest with increasing peat depth and the open sites already at the surface peat as a decrease in particle size composition (**I**). However, peat decomposition stage does not necessarily increase with depth in the swamp forests, as more decomposed layers in the peat profile may be interspersed with less decomposed layers, due to variation in peat formation speed related to changes in climate and vegetation over time (Page et al. 1999; Wüst & Bustin, 2004; Dommain et al. 2015). In the surface peat at the open sites, where new coarse litter deposition rates cannot notably support peat accumulation and thus decomposition takes place mainly in the “old” peat, the particle size was smaller than at the forest sites and deeper layers in the open sites. Yet,

among the fire-affected open sites, combustion certainly was the single most important factor affecting surface peat properties as the repeated fires had progressively consumed peat from the surface, and thus resurfaced “older” peat deeper from the peat profile (Hoscilo et al. 2011; Page et al. 2016). Present surface peat properties may therefore have actually been subject to primarily anaerobic, slow decomposition for centuries, if not for thousands of years prior to recent recurrent fires at the sites.

In the drained forest, where original forest vegetation was still present, the most distinct peat bulk density increase was close to the new WTL median (-40 cm from soil surface) (**I**). This is likely due to a combination of tree biomass compression and enhanced decomposition after water table drawdown, and relocation of small particles deeper in peat profile with the water movement (Lampela et al. 2014; Laiho & Pearson 2016). Tree mass sets considerable weight on porous surface peat above the typical WTL, and thus may have compressed the peat close to the WTL median after drainage, leading to increased BD. As also the concentration of woody matter decreased and the amount of fibric matter increased in the drained forest, it is more likely that with time the breakdown of peat through enhanced decomposition is the main factor leading to increased BD. Additionally, the annual high WTL fluctuation may have led to the relocation of small-sized particles from the surface close to the median WTL, as Lampela et al. (2014) suggested to happen in swamp forests.

4.2 Decomposability of peat decreases by intensive land management

Peat chemical properties correlated with its physical decomposition stage, as expected. This relation was seen as a higher amount of labile carbohydrates in the physically less decomposed woody fraction, and as an enrichment of recalcitrant compounds in the physically further decomposed fibre fraction and non-fractionated peat (**II**). Between land management types these differences could be seen as higher concentrations of labile compounds and N and P in the surface peat at sites with original forest cover, and as enrichment of recalcitrant compounds and cations along with a slightly higher concentration of C in further decomposed surface peat at deforested sites. Various compounds are decomposed at different rates due to the variation in the strength of their chemical bonds leading to enrichment of recalcitrant compounds in organic substrate (such as lignin) due to faster consumption of more labile compounds (such as hemicelluloses) during the early stages of decomposition (Berg 2000). This has led to the noted differences in compound composition at various physical decomposition stages of peat and between sites. However, cellulose is often bound to more recalcitrant compounds (i.e. lignin), and therefore some of the cellulose remains nearly intact with progressing decomposition (Berg 2000). This can explain why notable changes were not detected in cellulose concentrations in peat with increasing depth within sites or between land management types (**II**). The decrease in the concentration of labile carbohydrates and enrichment of recalcitrant compounds with progressing decomposition has been reported in earlier studies on tropical PSFs (Hoyos-Santinllan et al. 2016), but this is the first time when peat chemical properties have been studied at various land management intensities or on a compound level (CCC).

The fully developed forest vegetation provides a high and continuous input of litter rich in labile carbohydrates on the peat surface and in the upper peat profile (Sulistiyanto 2004), and was seen as high hemicellulose concentration at the surface peat (10–15 cm depth in paper **II**, 0–3 cm depth in paper **III**) at the swamp and drained forests. At the forest-covered sites, the recently deposited leaf litter is decomposed relatively quickly on the surface, as suggested by the observed highest enzyme activity and microbial biomass measured in the

swamp forest (III). Therefore leaf litter can potentially contribute to surface peat properties, yet less to peat accumulation (Chimner & Ewer 2005; Yule & Gomez 2009; Hoyos-Santillan et al. 2016). However, fine and structural tree roots provide litter input largely below the peat surface, and are known to decompose slower, thus having a major role in peat formation (Chimner & Ewer 2005; Hoyos-Santillan et al. 2016). This may explain the relatively high hemicellulose concentrations deeper in peat (40–45 cm) in the swamp forest compared to other sites. However, combined effect from the decrease in litter input by depth together with efficient decomposition in the aerobic conditions close to the peat surface likely leads to the observed decline in labile carbohydrate concentration with depth in the peat profile also in the swamp forest (II, III, Hoyos-Santillan et al. 2016). The poorer substrate quality, together with decrease in oxygen availability explains the observed decrease in activity with depth at the original forest-covered sites (III, Hoyos-Santillan et al. 2016). In the drained forest, the effects of improved conditions for decomposition following WTL drawdown were present at the 40 cm depth, where the hemicellulose concentration was significantly smaller than at a respective depth at the undrained swamp forest, where longer periods of wet anaerobic conditions are prevalent close to the peat surface (I).

At the degraded and agricultural sites, frequent fires had combusted several decimetres of the topmost peat (Hoscilo et al. 2011; Hirano et al. 2014). The current fire-affected surface peat was additionally further modified by preceding decomposition leading to enrichment of recalcitrant substrates and cations (II, III). At the open sites, the surface peat properties resembled biochar to some extent, which is produced with the combustion of organic matter at high temperatures without air (Shrestha et al. 2010; Lehmann et al. 2011). Biochar is used as a soil amendment substance due to its properties, and is considered as a way of increasing C sequestration in soil to help mitigate climate change (Lehmann et al. 2011). Yet, biochar decomposition is observed to accelerate at temperatures of 40°C or higher (Nguyen et al. 2010; Fang et al. 2015). This may partly explain the higher measured enzyme activities among open sites during the dry season, when the black soil surface absorbs solar radiation, and undoubtedly leads to momentarily higher surface temperatures. Additionally, soil management at the agricultural site, including fertilization, has likely improved conditions for enzyme decomposition at otherwise impoverished soil conditions (I, III). Therefore, despite peat recalcitrance and due to the lack of peat-forming litter input, progressing decomposition and fires inevitably lead to C losses at open peatlands. With time this imbalance will lead to loss of the existing peat deposits.

At the reforested site, despite the planted tree vegetation and a relatively high WTL, the peat compound composition (infrared spectroscopy) resembled the swamp forest only in the topmost surface peat (0–3 cm), while deeper in the profile (3–30 cm) it was more similar to the degraded and agricultural sites (III). Both swamp forest and reforested sites had higher hemicellulose, DOC and DON concentrations in the topmost surface compared to respective depths at the degraded and agricultural sites (III). The peat samples for this study were taken from trees at the reforested and swamp forest-covered sites, which likely overlooks the importance of the role of root litter in peat formation and substrate contribution. Additionally, in the reforested site, the relatively young tree vegetation unlikely produces larger, slowly decomposing woody roots, which comprise a large portion of the total root systems at mature swamp forests (Niiyama et al. 2010). This suggests that the altered ecosystems requires time to recover after reforestation to support peat production comparable to peat swamp forests.

The nutrient properties were found to differ between land management types, being particularly dependent on vegetation (I). In the swamp and drained forest, the N and P concentrations were highest in the topmost peat close to the main rhizosphere (sampling

depths 10–15 cm and 40–45 cm). This is likely due to the tight nutrient cycling between living vegetation, deposited litter and decomposers in the surface peat, which quickly drain most of the easily extractable nutrients from the peat substrate (Page et al. 1999; Lampela et al. 2014). However, in the drained forest, the total N and P concentrations were lower closer to the peat surface than at the swamp forest, which is likely a consequence of enhanced aerobic decomposition and leaching following drainage. Despite nutrient leaching not having been studied in tropical peatlands, the amount of DOC in runoff waters is notable soon after drainage, then decreasing and remaining relatively low with a longer time horizon (Moore et al. 2013; Evans et al. 2014). In this study, the DON and DOC concentrations and N/DON ratio were notably higher at the swamp forest than at open and reforested sites altered a long time ago (III), which is likely because of impoverishment following the removal of nutrients binding vegetation and drainage causing leaching. Additionally, the high K level throughout the peat profile at the agricultural site (I) is likely a result of soil tilling and leaching of added mineral fertilizers towards deeper layers. At the open sites, fire events resurfacing the nutrient-poor peat from deeper layers, together with leaching, also explains the significantly lower N and P concentration than at the sites with swamp forest cover (I).

The current study shows that compared to the swamp forest (III), peat microbial decomposition activity and biomass is reduced at the altered sites, where peat quality and abiotic conditions had been drastically and permanently changed several years prior sampling (I, II, III). This is likely due to changes in substrate quality (i.e. enrichment of recalcitrant substrates) and less suitable moisture conditions for decomposers, which are known to limit microbial activity (Berg 2000; Rejmankova 2001; Anshari et al. 2010; Strakova et al. 2011; Sjögersten et al. 2011; Hoyos-Santillan et al. 2016). Despite higher litter input rates being re-established in the reforested site, the microbial biomass and enzyme activity still remained low, which is very likely due to management practices, including chemical weeding with glyphosate having a negative effect on the microbial population (Zaller et al. 2014; Druille et al. 2016).

4.3 Implications of findings to management of peatlands

Changes in peat properties and decomposition conditions affect the ecological, functional and economical services provided by tropical peatlands.

Land use alters processes supporting peat formation and peat preservation, and has turned peatlands of Southeast Asia from globally significant C stores to C sources (IPCC 2014). Additionally, in cultivated sites either the vegetation does not provide sufficient litter input to support peat accumulation or management practices prevent the accumulation of litter as peat (Hertel et al. 2009; Smith et al. 2012; Jauhiainen et al., 2016MP). This study observed this phenomenon indirectly as a decreased concentration of labile carbohydrates at the intensively altered sites, where litter production does not sufficiently support peat production. Therefore, after removal of the PSF vegetation, decomposition occurs primarily in the “old” peat releasing C to the atmosphere as CO₂.

It is likely that land management and recurrent fires, leading to subsidence of the surface peat, as seen to happen in this study (I), will severely affect peat hydrological properties, because peat hydraulic conductivity and water storage capacity are greatly dependent on peat physical properties (Päivänen 1973). Especially the high density and small particle size and low porosity are lead to low hydraulic conductivity and high water retention capacity (Päivänen 1973). Additionally, the water-repellency (i.e hydrophobicity) of organic soils increases due to extreme drought or burning (Doerr et al. 2000; Kettridge et al. 2014). Due

to land-use change, especially the risk of flooding is thought to increase at the lowland peatlands of Southeast Asia. For example, Sumarga et al. (2016) have estimated that long-term oil palm cultivation will make lowland peatlands in Central Kalimantan subject to regular flooding within a century of the establishment of the plantation. With time, continued subsidence and peat loss will lead to the expansion of salt sea water intrusion into the lowland areas (Sumarga et al. 2016; Wijedasa et al. 2017), which undoubtedly will lead to land area losses due to cultivation and restoration, and yet, the economic benefits of oil palm plantations are short-term and mainly profit only a small number of stakeholders (Sumarga et al. 2016).

Besides the increased vulnerability for flooding, denser hydrophobic peat may also further increase the risk of severe droughts, leading to a higher likelihood of fire risk. Fires are currently the fastest and largest contributing factor releasing tremendous amounts of CO₂ and other gaseous compounds into the atmosphere and causing health problems to people around Southeast Asia (Koplitiz et al. 2016; Konecny et al. 2016; Page et al. 2016). Future climate scenarios predict higher drought occurrence within Southeast Asia, which, coupled with less predictable and stronger El Niño events, will increase fire event occurrence on peatlands (IPCC 2014). Fire prevention is therefore extremely important in tropical peatlands in reducing potential negative effects to the climate.

Land management practices are another way of affecting the volume of CO₂ released through decomposition, as the amount of CO₂ emissions is known to depend on land management type (IPCC 2014; Miettinen et al. 2017). Interestingly, CO₂ emissions have been observed to decrease with time due to land alteration from PSF, being the lowest at stabilized, most intensively altered open sites (Hooijer et al. 2012 and references within; IPCC 2014). The decrease in CO₂ emissions is very likely related to peat decomposability, which was seen to decrease with land management intensity in this study (**I**, **II**, **III**). Therefore, the highest measured CO₂ emissions from high biomass oil palm and acacia plantations (IPCC 2014) are likely explained by the availability of labile carbohydrates and nitrogen-based fertilizers (Smith et al. 2012). Yet, intensive management practices, e.g. weeding and harvesting, reduce potential litter deposition and do not support the accumulation of new, stable C as peat (Smith et al. 2012). Despite the current low CO₂ emissions released during decomposition from intensively altered open sites, decomposition processes may be accelerated by management practices.

Productive utilization of these nutrient-poor peatlands as cropland requires fertilization (**I**; Andriesse 1988; Rieley & Page 2005). However, as a side effect, the breakdown of recalcitrant compounds may accelerate as a result of increased availability of decomposition-limiting nutrients or labile carbohydrates. This has been observed in *ex situ* studies by the addition of N together with labile glutamate and glucose (Jauhiainen et al. 2016b), and *in situ* by the addition of N-fertilizer and urine (Jauhiainen et al. 2014, Comeau et al. 2016) to peat from intensively managed land-use types. Similarly, the relatively high enzyme activities observed at the topmost peat of the agricultural site (**III**), is likely due to triggered decomposition caused by urine and burned plant residues used as fertilizers.

Land management methods supporting maintenance of peat C store should be promoted and implemented as the alternative is that decomposition in peat is the dominant process in C-cycle until the peat deposit becomes depleted. The easiest way to maintain tropical peatlands C storing capacity is to maintain the high WTL and vegetation with high biomass and litter deposition capacity. Among degraded sites, land management by vegetation that has high below-ground litter input rates and tolerates maintained high WTL are likely the best options to reduce peat C store loss and potentially enabling the re-establishment of net

peat C store accumulation. However, the recovery of peat C accumulation, even after successful reintroduction of high litter input and high WTL, will likely require several decades if not centuries (Warren et al. 2016). The restoration of peat lands has primarily been studied in boreal peatlands, where the restoration of natural functions on altered peatland has been found challenging, but possible with time (e.g. Holdens et al. 2004). In tropical areas the changes in peatland ecosystems are usually more dramatic (draining depth, annual water table level changes, fire intensity and occurrence, vegetation type change) and restoration will very likely be more challenging, yet possible with proper tree species and restoration of the WTL (Lampela et al., 2017).

4.4 Reliability and generalization of the results

Results of this study clearly show that peat physical, chemical and biological properties at intensively altered drained and deforested sites differ greatly from the properties at the swamp forest.

To gain information concerning the effects of long-term land management, the focus of this study was on stabilized conditions that form over time after the initial land management change. Originally, all of the study sites have been PSF forest-covered sites, which can be assumed to present the same mixed swamp forest type due to their similar locations on the peat domes at comparable distances from the river. Therefore, the observed differences in peat properties between the sites have resulted from the initial land alteration (drainage, deforestation, cultivation) that had taken place over a decade ago and processes following it (decomposition, fires, changes in litter input), which are found to form stable conditions about within five years after the initial land alteration (Hooijer et al. 2012; IPCC 2014). The reforested site can be assumed to be stabilized from the initial land management change, but the planted forest had not reached maturity, therefore the conditions for litter production and soil functions will develop with time with tree growth.

The data collection for papers **I** and **II** was conducted only from one pit hole at each site and the sample sets were relatively small, which may have caused under- or overestimation to some measured properties. Yet, the two different methods used to analyse peat chemical compound composition (**II**, **III**) from samples collected at various times from the same sites, and also from a wider area at each site in paper (**III**), led to similar results, indicating that this study still managed to capture the variation in the field.

The samples used for determined peat enzyme activity were analysed in a laboratory in Finland. Despite transportation of the samples in a cool box in a stabilized temperature and storing them for no longer than two weeks in a refrigerator (approximately + 4°C) prior to the analyses, the conditions for microbial activity were certainly different from field conditions. We therefore measured optimal enzyme activity using buffers (regulating the pH) and in standardized conditions (in dark and in room temperature).

To prevent further losses in peat swamp forests, the future utilization of tropical peatlands should be implemented at previously altered sites. This study provides detailed information of peat properties under stabilized conditions at several land management types. The results of this study can therefore be utilized to predict the longer term outcomes formed by land management practices on peat decomposition processes. Results can be regarded representative to most common land management types (degraded land, agricultural land and young reforested area) found today in ombrotrophic peatlands in Southeast Asia.

5 PROSPECTS FOR FUTURE RESEARCH

This study clearly shows that various land management intensities have different effects on peat chemical and physical properties determining peat decomposability, and thus the properties of peat as a biological environment for decomposers. To form tools for the sustainable management of tropical peatlands, focus to the following issues is recommended:

- 1) Studying the decomposition and decomposition activity of various land management types under various WTL levels, vegetation covers and management practices (e.g. weeding, not weeding, fertilizing, not fertilizing) to find a combination of conditions producing lowest peat C loss and forming potential to peat accumulation, yet simultaneously providing economic benefits, particularly for local communities.
- 2) To reach the first aim, above- and below-ground litter production and decomposition processes should be further studied at various land management types.
- 3) Increased focus should be given to clarify actual microbial groups in tropical peat to create deeper understanding of the effects of land management on the dynamics between microbial community and decomposition processes.

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