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Carbon Dynamics and Ecosystem Diversity of Amazonian Peatlands

by

Outi Lähteenoja

TURUN YLIOPISTO
UNIVERSITY OF TURKU
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From

Section of Biodiversity and Environmental Science
Department of Biology
University of Turku
FI-20014 Turku, Finland

Supervised by

Dr Kalle Ruokolainen
Department of Biology
University of Turku, Finland

Dr Leif Schulman
Finnish Museum of Natural History
University of Helsinki, Finland

Reviewed by

Dr Viviana Horna
Ecological Botanical Gardens
University of Bayreuth, Germany

Dr Jyrki Jauhiainen
Department of Forest Sciences
University of Helsinki, Finland

Dissertation opponent

Professor Dan Charman
College of Life and Environmental Sciences
University of Exeter, UK

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- II Lähteenoja O, Ruokolainen K, Schulman L, Alvarez J (2009) Amazonian floodplains harbour minerotrophic and ombrotrophic peatlands. *Catena*, 79, 140–145.
- III Lähteenoja O, Page SE (2011) High diversity of tropical peatland ecosystem types in the Pastaza-Marañón basin, Peruvian Amazonia. *Journal of Geophysical Research, Biogeosciences*, 116, G02025.
- IV Lähteenoja O, Reategui YR, Räsänen M, del Castillo Torres D, Oinonen M, Page SE (2011, published on-line) The large Amazonian peatland carbon sink in the subsiding Pastaza-Marañón foreland basin, Peru. *Global Change Biology*.

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Introduction

Atmospheric carbon has accumulated in the earth's ecosystems, oceans and rocks over hundreds of millions of years, and these function as carbon stores in the global carbon cycle. Until the industrial revolution, the global carbon cycle was largely influenced by biological, physical, chemical, and geological factors, which caused significant but slow changes in the concentration of atmospheric carbon during the earth's history. During the last decades, however, excessive burning of fossil fuels, deforestation, and intensified agriculture have led to the liberation of considerable amounts of carbon into the atmosphere at previously unequalled rates and, thus, to the intensification of global warming. The global carbon cycle has attained increasing attention as a consequence.

Terrestrial ecosystems play a crucial role in the global carbon cycle as carbon stores, sinks, and sources (Schimel 1995). When an ecosystem accumulates carbon, it acts as a net carbon sink from the atmosphere and has a cooling effect on the global climate. When an ecosystem releases carbon, it acts as a net carbon source to the atmosphere and has a warming effect on the global climate.

Significant carbon stocks are stored, for example, in forests, especially in boreal and tropical regions (Phillips et al. 1998, Malhi and Grace 2000, Clark 2002, Malhi et al. 2008). However, the most important "carbon hotspot" ecosystems on a per area basis are probably peatlands (Yu et al. 2011), which form when water-logging produces anoxic soil conditions and the accumulation of organic deposits of partially decomposed litter, i.e. peat. Global peatlands contain approximately 650 Gt of carbon (Yu et al. 2010 for northern peatlands, Page et al. 2011 for tropical ones), which is about 80 times more than the global annual carbon emissions from the burning of fossil fuels (8 Gt of carbon per year, IEA 2010).

Peatlands should be of major concern to policymakers and global change scientists, because their significant carbon stores may be converted into strong carbon sources under climate change induced drought and fires (Page et al. 2002). However, different types of feedbacks may be expected in the world's peatlands in the future, because increased temperatures (with sufficient air humidity) increase both plant growth and decomposition rates (Hirano et al. 2008). Some peatlands may be converted into even more efficient carbon sinks than they are at present, owing to increased plant growth in a warmer climate, especially if water-logged, anoxic conditions are maintained (Yu et al. 2010, 2011).

To estimate the role of peatlands in the global carbon cycle, a global picture of the extent, thickness, ecosystem characteristics, carbon stores, and

carbon accumulation rates of the earth's peatlands is necessary. The world's largest peatland areas are located in boreal and subarctic regions, especially in western Siberia, central Canada, northwestern Europe, and Alaska (Gorham 1991, Yu et al. 2010, 2011). The development of these northern peatlands began 16,500 years ago and they expanded during the Holocene (the past 12,000 years after the last ice age) on land exposed by the melting of continental ice sheets (MacDonald et al. 2006). By contrast, a 26,000–27,000 year old, 9.8 m thick peat core from a massive peat deposit in the Sebangau River catchment on the island of Borneo proves that tropical peatlands were involved in the global carbon cycle prior to the last glacial maximum (LGM, between 26,500 and 19,000 years ago) (Page et al. 2004).

Currently, Southeast Asian tropical peatlands form a globally important carbon store of approximately 70 Gt (Page et al. 2011). These ecosystems can accumulate carbon at very high rates and thus act as strong carbon sinks (Maltby and Immirzi 1993, Sorensen 1993, Neuzil 1997, Page et al. 2004, Rieley and Page 2005). Nevertheless, Southeast Asian peatlands are being very negatively affected by drought, fire, logging, deforestation, drainage, agriculture, and plantations, which have converted them from long-term carbon sinks and stores into strong short-term carbon sources (Siegert et al. 2001, Page et al. 2002, Sodhi et al. 2004, Bradshaw et al. 2009, Hooijer et al. 2010). For example, due to extensive fires during El Niño-related drought in 1997, Indonesian tropical peatlands released 0.81–2.57 Gt of carbon into the atmosphere, which represented 13–40% of global anthropogenic carbon emissions at the time (Page et al. 2002). This contributed considerably to the largest annual increase in atmospheric CO₂ since the beginning of the records and, consequently, the carbon dynamics of Southeast Asian peatlands became an issue of global importance.

In contrast, the world's most extensive continuous area of humid tropical rainforest, Amazonia, has hardly been considered in discussions on the role of tropical peatlands in the global carbon cycle (Schulman et al. 1999, Ruokolainen et al. 2001). At the outset of the current study, knowledge on Amazonian peatlands was limited to a few sporadic observations of peat in ecological studies focusing on other aspects of the rainforest ecosystem (Junk 1983, Suszczynski 1984, Shier 1985, Andriessse 1988, Kahn and Mejía 1990, Duivenvoorden and Lips 1991, Kahn and Granville 1992, Dubroeuq and Volkoff 1998, Batjes and Dijkshoorn 1999, Schulman et al. 1999, Ledru 2001, Ruokolainen et al. 2001, Del Castillo et al. 2006; but see Guzmán 2007, Lähteenoja 2007). On the basis of such sporadic observations, satellite images, and land cover maps, Schulman et al. (1999) and Ruokolainen et al. (2001) suggested that 150,000 km² of practically unknown peatlands may exist in Amazonia. This is about 60 % of the current best estimate of the

Southeast Asian tropical peatland area (247,778 km²; Page et al. 2011), suggesting that the carbon dynamics of Amazonian peatlands may also be significant in a global context. However, as the authors pointed out, this estimate of Amazonian peatland area was highly uncertain, as it was not based on systematically collected field data (Schulman et al. 1999, Ruokolainen et al. 2001).

In addition to their carbon storage function, peatlands increase regional and global biodiversity by providing a diversity of ecosystem types that are different from those on minerogenic soils (Bridgham and Richardson 1993, Laine and Vasander 1996, Page et al. 1997, 1999, Wheeler and Proctor 2000). In Southeast Asia, variation in peat thickness, hydrology, and nutrient supply gives rise to several different peat swamp forest types, which provide a variety of habitats for rainforest species, including species of conservation concern (Morley 1981, Anderson 1983, Page et al. 1997, 1999, Morrogh-Bernard et al. 2003, Sodhi et al. 2004). Although a high diversity of rainforest and wetland ecosystem types has been described from Amazonia (Junk 1983, Kahn and Mejia 1990, Kalliola et al. 1991, Ruokolainen and Tuomisto 1993, Mäki and Kalliola 1998, Tuomisto 1998), the existence of diverse peatland ecosystems has not really been considered.

On the basis of their nutrient status, peatlands can be placed on a gradient from nutrient-rich (eutrophic) to nutrient-poor (oligotrophic) ecosystems, and on the basis of the origin of their nutrient inputs, peatlands can be divided into minerotrophic swamps and ombrotrophic bogs (Heinselman 1970, Verhoeven 1986, Bridgham and Richardson 1993, Wheeler and Proctor 2000, Clarkson et al. 2004, Bragazza et al. 2003, 2005). Minerotrophic swamps form in depressions and floodplains (or when lakes become overgrown), and these ecosystems receive mineral nutrients with inflowing surface water or from the capillary rise of the groundwater in peat pores (Hill and Siegel 1991; Romanov 1968 in McCabe 1991). Minerotrophic swamps range from eutrophic to oligotrophic, reflecting the nutrient level of their water sources. In contrast, the only nutrient and water inputs of ombrotrophic bogs are from wet and dry atmospheric deposition and, consequently, these ecosystems tend to be very nutrient-poor (except when affected by volcanic ash, Yeloff et al. 2007). No surface or groundwater can enter ombrotrophic bogs because the convex form of the peat dome forces water to run off the bog and because the peat layer is too thick and porous for capillary rise of ground water to near the surface. These two peatland types typically have distinct species compositions, and their coexistence contributes to the regional diversity of ecosystems and habitats (Wheeler and Proctor 2000, Bragazza et al. 2005, Hájek et al. 2006).

Peatlands are also good palaeoecological archives of information for detecting past changes in climate, atmospheric deposition, hydrology, and vegetation, especially if the peat deposit has accumulated during several centuries or millennia (Tolonen and Turunen 1996, Weiss et al. 2002, Page et al. 2004). Peatlands also influence the hydrological dynamics and water quality of surrounding drainage systems by storing considerable amounts of water within the peat itself and by affecting the direction of surface water flow (McNamara et al. 1992). Finally, peatlands have many direct economical uses, such as agriculture and forestry on peat soils, as well as peat mining for energy production and for horticultural and industrial use. During the last decades, these uses of peatlands have had a negative impact on their carbon storage and habitat diversity, increasing carbon emissions and enhancing global warming (Page et al. 2002, Rieley and Page 2005, Holmgren et al. 2008, Minkkinen et al. 2008).

The aim of this study

My overall aim was to initiate peatland research in Amazonia, which has been referred to as “one of the large white spots on the global peatland map” (Couwenberg and Joosten 2001). Specifically, I aimed to clarify how common peat accumulation is on Amazonian floodplains, and how extensive and thick peat deposits can be encountered. Secondly, I aimed to study how rapidly Amazonian peatlands sequester carbon, and how much carbon they store. Thirdly, I aimed to gain some understanding of the diversity of peatland ecosystem types and of the processes forming these ecosystems. I discuss these aspects of Amazonian peatlands in the four papers included in this thesis, to which I hereafter refer with Roman numerals in superscript:

- I** In the first paper, I address the question of the thickness of Amazonian peatlands on the basis of fieldwork carried out in Peru. I also present some data on how rapidly these Peruvian peatlands accumulate carbon.
- II** In the second paper, I show that the peatlands of the first paper can be divided into two different ecosystem types: nutrient-rich minerotrophic swamps and nutrient-poor ombrotrophic bogs. These are new ecosystem types for the Amazonian lowlands and increase regional ecosystem and habitat diversity.

- III** In the third paper, I deepen our knowledge of Amazonian peatland ecosystem diversity by describing a series of peatland ecosystem types ranging from very nutrient-poor ombrotrophic bogs through several stages of increasing nutrient-content to very nutrient-rich floodwater-influenced minerotrophic swamps in the 120,000 km² Pastaza-Marañón foreland basin (Peru). I also study the developmental histories of the peatlands and show that this diversity of peatland ecosystem types not only exists in geographical space but can be detected within some peat cores in time.
- IV** In the fourth paper, I readdress the question of the thickness of Amazonian peatlands and how rapidly they accumulate carbon. I present an estimate of the total peatland area and total peat carbon store that can be currently encountered in the Pastaza-Marañón basin. I conclude that the basin functions as a long-term biogeological peatland carbon sink.

Materials and methods

Study area and selection of field sites

I carried out the field work in two phases (July–September 2006 and July–November 2008) in the hot, humid, and nearly aseasonal northern part of Peruvian lowland Amazonia (Fig. 1). The elevation of the area is between c. 90 m and 130 m above sea level, the yearly mean temperature is 26 °C, and annual precipitation is c. 3,100 mm (Marengo 1998). With the help of colleagues who had visited the area previously, I identified as potential peat accumulation areas the floodplains of the Amazon River and its tributaries influenced by large annual variations in the river water level (up to 12 m for the Amazon River in Iquitos, Peru; unpublished data obtained from SENAMHI, 2008 and Dirección Agraria Regional de Loreto 2008) as well as small depressions in the middle of the non-flooded rainforest (*terra firme*). During both fieldwork phases, my base was the town of Iquitos (Loreto). From there I made several field trips to the wetland areas of Peruvian Amazonia.

The focus of the first phase^{I,II} was the river floodplains relatively close to the city of Iquitos (within about 5–200 km from the town). The focus of the second phase^{III,IV} was the 120,000 km² Holocene sedimentation area of the subsiding Pastaza-Marañón foreland basin (Fig. 1), which is the

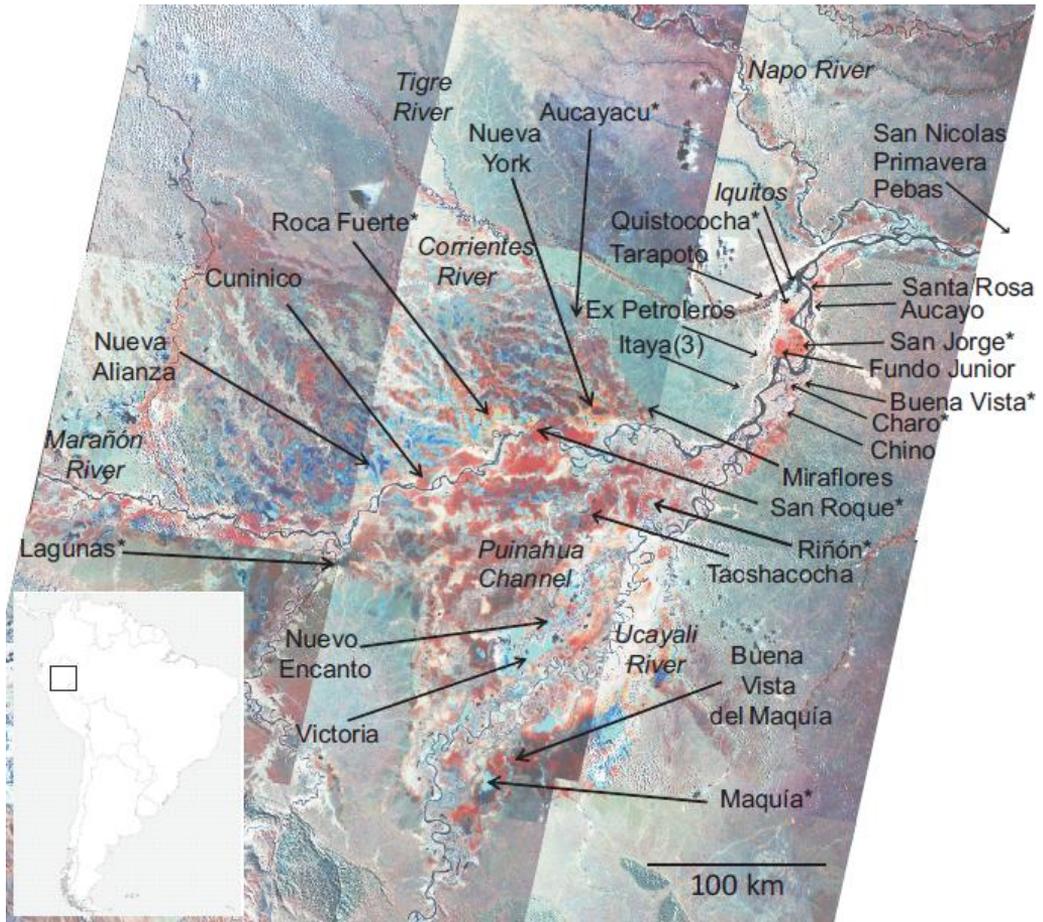


Figure 1. A satellite image mosaic of all the study sites of the first and second fieldwork phases located in Peruvian Amazonia (a modified version from Lähteenoja and Page 2011^{III}). The figure is composed of 12 histogram-equalized Landsat TM satellite images (NASA Landsat Program, GeoCover, Orthorectified, WRS-2, Paths 006-008, Rows 062-065, <http://glcfapp.glc.f.umd.edu:8080/esdi/index.jsp>, band 4: red, band 5: green, band 7: blue). The Holocene sedimentation area of the Pastaza-Marañón basin is the colourful leaf-shaped area in the middle. The southern Pastaza-Marañón basin is located to the south of the Marañón River and the Pastaza volcanogenic fan is located to the north of the Marañón River. *) The sites where radiocarbon age was measured.

most extensive Amazonian wetland area and also forms the largest modern tropical system of fluvial aggradation (Räsänen et al. 1990, 1992). The basin belongs to a belt of subsiding Andean foreland basins formed during the uplift of the Andes (Räsänen et al. 1987, 1990, 1991, 1992, Dumont and García 1991, Dumont 1996, Roddaz et al. 2005). Since the Cretaceous

period, rivers originating from the Andes have accumulated several kilometer thick minerogenic sediment deposits in these basins (Räsänen et al. 1987, 1990, 1992). The Holocene sedimentation area consists of two main areas: 1) the fluvial distal part of the Pastaza alluvial fan, composed of black volcanoclastic debris originating from Ecuadorean volcanoes (to the north of Marañón River, Fig. 1), and 2) the southern Pastaza-Marañón flood basin, dominated by meandering and laterally migrating suspension-rich rivers originating from the Andes (to the south of the Marañón River, Fig. 1, Villarejo 1979, Räsänen et al. 1990, 1992, Kalliola et al. 1992). The subsiding geological system has been active for most of the Quaternary period (the past 2.6 Ma, Dumont and García 1991, Räsänen et al. 1992, Dumont 1996).

Wetland distribution maps were not available for Peruvian Amazonia (except for the satellite image mosaic of IIAP 2004), but it has been observed that different wetlands in the study area have different spectral values in Landsat TM satellite images (Mäki and Kalliola 1998, IIAP 2004). I selected 17 study sites in the first phase^{I,II} and 13 in the second one^{III,IV}, using geo-referenced high resolution (30 m) histogram-equalized Landsat TM satellite images (Fig. 1). I based the selection on four criteria: 1) Ability to define the site as a wetland (and, thus, a potential peatland) on the basis of its distinctive reflectance compared to the non-flooded rainforest, 2) Accessibility of the site with a reasonable amount of time and effort, 3) Representation among the sites of as wide a range of spectral signatures as possible (and hence as much diversity of potential peatland ecosystem types as possible), visually observed as different tones of red, violet, blue, orange, and turquoise in the near-infrared wavelength (bands 4, 5 and 7), and 4) Representation of as large a geographical area as possible, considering the time and resources available.

Peat sampling in the field

I delimited each site in a Landsat TM satellite image, where most sites could be distinguished as patches differing in colour from the non-flooded rainforest. Subsequently, I established a 0.2–4.2 km long transect from the edge of each site towards its centre. I did not always reach the centre because some sites were very extensive or were continuous floodplain wetland areas without a clearly defined centre. At those sites, I studied an accessible part.

On each transect, I established study points at every 100–500 m. At these points I determined the thickness of the organic soil layer with a Russian peat sampler (Jowsey 1965). I classified the deposits into three

categories by visual examination: peat (organic matter consisting mostly of partially decomposed vegetation), clayey peat (peat mixed with minerogenic sediments), and mud (deposit dominated by minerogenic sediments). I continued coring from the surface until I encountered an impenetrable deposit. I measured pH and the conductivity of surface peat waters with a field meter, and the peat water table in small holes made in the peat.

I collected peat samples from a total of 15 peatland sites (five sites in the first phase^{I,II} and ten sites in the second phase^{III,IV}) from 2–4 cores per site. I collected one or two samples of a precise volume (10 cm bar from the Russian peat sampler: 62.8^{III,IV} or 98.2^{I,II} cm³) per each meter of peat from the surface to the base of the core. After having collected samples from 1–4 peatlands, I returned to Iquitos and transported the fresh peat samples in closed plastic bags to a laboratory of the local university (Universidad Nacional de la Amazonía Peruana, UNAP). If I had to conserve wet peat samples for more than a week in hot and moist field conditions, I froze the samples and conserved them in a portable cooler during the rest of the field trip. I dried the samples in the laboratory (24 h at 105 °C), and conserved them in closed plastic bags in a dry and cool place in Iquitos. After this, I returned to a different field site to collect more samples. Within a few months of the end of each of the two fieldwork phases, I transported all the samples by air to Finland for further analyses.

Topographic measurements

I measured the topography of five peat deposits with a method called free boarding or levelling, to establish whether they had a raised shape (characteristic of ombrotrophic sites) or a flat one (characteristic of minerotrophic sites). I performed levelling on a transect running from the shore of an adjacent river towards the centre of each peatland. I first placed one wooden stake in the soil at the water's edge and a second one about 30 m along the transect. I subsequently bound each end of a 35-m-long clear plastic hose filled with water vertically along each stake. I measured the difference between the river water level and the water level inside the hose at stake one, and I marked this water level on stake two. I then moved the end of the hose from stake one to a third stake located another 30 m further along the transect, and I marked the new water level inside the hose on stakes two and three. I measured the difference between the two marks on stake two and the distance from the water level in the hose to the peat surface. Consequently, I was able to establish a reference level for the peat surface that was always at a known height above the river water. I repeated these

steps until I arrived at or near the centre of the peatland. At each measurement point, there is some error involved, but these errors are not likely to be systematically biased up- or downwards.

Loss-on-ignition (LOI), dry bulk density, and carbon content

I analysed the peat-core samples for total organic content by loss-on-ignition (LOI, combustion for 2 h at 550 °C, Andrejko et al. 1983) to check whether the collected material was actually peat or not. In this study, I used the same threshold to define peat as that used by the Geological Survey of Finland: 75–100 % organic content indicated peat, whilst a soil with lower organic content was classified as clayey peat or mud. I analyzed peat carbon and nitrogen contents using a LECO Carbon Analyzer ®^{I,II} or a varioMax CN Analyzer^{III,IV} (Elementar Analysensysteme GmbH).

Finally, I measured the dry bulk density of the peat samples by dividing the dry weight of each peat sample by its field volume (the volume before drying). Although I precisely measured the peat volume during sampling, some peat was lost on moving the sample from the Russian peat sampler to a plastic bag, from the plastic bag to the drying container, and from the drying container to another plastic bag for weighing. In addition, some volatile carbon may have been lost during drying at 105 °C. Consequently, the weights used in calculating the dry bulk densities are lower than the true weights of the sampled volume, and the dry bulk density values are thus somewhat lower than the real ones.

Total peatland area and current peatland carbon stock within the Pastaza-Marañón basin

I classified the two Landsat TM satellite images on which the study sites of the second field work phase were located into different peatland types using the supervised classification method in Erdas Imagine 9.1^{IV}. I used the peatland sites studied in the field as training areas. I also attributed training areas to *terra firme* forests, flooded forests on minerogenic soils, water bodies, beaches, river shores, and villages.

To establish the total peatland area on each image, I extracted the number of 28.5 m x 28.5 m -sized pixels belonging to each peatland class. With this information, I calculated the total area of each class. Using the total area, and the median, minimum and maximum peat thickness, carbon content and dry bulk density of each field site, I calculated a best estimate,

minimum, and maximum carbon stock for each peatland class, respectively (as in Page et al. 2011)^{IV}. In this kind of extrapolation, the peat thickness estimates must be used with caution. In field sites where the centre of the peatland was reached, median peat thickness is likely to have been over-estimated, because peripheral areas with shallow peat, which are spatially most extensive, will be underrepresented in the samples, compared to central areas with deep peat^I. In the extensive and continuous floodplain peatlands where the centre was not reached, in contrast, median peat thickness is likely to have been under-estimated^{I,IV}.

In addition, the occurrence of minerogenic intrusions inside the peat deposits complicates total carbon stock calculations owing to the lower carbon content and higher bulk density of minerogenic deposits compared to peat^{I,IV}. With regular sampling depths (sampling every 50 cm within cores), I managed to capture minerogenic deposits too, and their carbon content and dry bulk density values are represented in the calculations of total carbon stocks. However, for one site of the second fieldwork phase (San Roque^{IV}), I did not sample one meter of the central core (at 200–300 cm), because those depths were entirely dominated by minerogenic sediments. This may bias the calculation of the carbon stock of the peatland in question, because I used the total core depth in calculations, but the carbon content and dry bulk density values of the peat parts only. Afterwards, I realized that a regular sampling depth should be maintained when minerogenic intrusions are encountered. However, the total carbon stock estimates of the Pastaza-Marañón basin are not likely to be significantly affected by this inconsistency.

Radiocarbon dating

A total of 42 samples were dated from the central cores of ten sites using the AMS radiocarbon dating method in the Dating Laboratory of the Finnish Museum of Natural History, University of Helsinki^{I,IV}. At the sites of the second phase of field sampling^{IV}, two basal samples for each core were dated to gain additional confidence in the results. AMS ¹⁴C ages of the various organic fractions can be significantly different in tropical peatlands with deep root penetration, which transports young carbon into older peat layers (Wüst et al. 2008). Visible root remains were removed from the samples in order to reduce this effect.

The samples were treated with the acid-alkali-acid-method (Olsson 1980), dried, ground, and combusted with CuO at 520 °C for 10 h. The resulting CO₂ was trapped with liquid nitrogen and purified prior to measuring the ¹³C/¹²C ratio ($\delta^{13}\text{C}$). The CO₂ was converted into CO in the

presence of zinc, and subsequently into graphite in an iron-catalyzed reduction process. The radiocarbon content of the graphite samples was measured with the AMS technique (Tuniz et al. 1998). The radiocarbon ages, corrected for isotopic fractionation, were calibrated into calendar ages (cal yr BP, before present = 1950) with the program Oxcal 3.10 based on the IntCal04 calibration data set (Reimer et al. 2004). The measured double basal ages were combined with Oxcal 3.10 to obtain averaged basal calendar ages. The median values of the calibrated ages of the 1σ range were used for calculating peat and carbon accumulation rates.

Accumulation rates

Peat accumulation rate was calculated for peat layers between the dated depths of the profiles, and the carbon accumulation rate was obtained from the following equation (Tolonen and Turunen 1996, Page et al. 2004):

$$CA = r/1000 \times \tilde{n} \times c$$

where CA = carbon accumulation rate ($\text{g m}^{-2} \text{yr}^{-1}$); r = peat accumulation rate (mm yr^{-1}); \tilde{n} = dry bulk density (g m^{-3}); c = carbon content (g C g^{-1} dry weight).

The long-term apparent carbon accumulation rate (LORCA, Tolonen and Turunen 1996) and long-term peat accumulation rate were calculated by dividing the total amount of accumulated carbon and peat by the basal age using the median carbon content and dry bulk density of each core:

$$\text{LORCA} = (h/1000 \times \tilde{n} \times c) / \text{ba}$$

where h = peat depth (mm); \tilde{n} = dry bulk density (g m^{-3}); c = carbon content (g C g^{-1} dry weight); ba = basal age (cal yr BP).

Median absolute deviations were used to describe variation in median carbon content and median dry bulk density, which were used to calculate the carbon accumulation rates and LORCA. The uncertainties of the accumulation rates were estimated using the law of error propagation (Taylor 1997). The largest error contribution to individual accumulation rates arose from the radiocarbon calibration procedure^{IV}. There were other less important uncertainties due to peat depth measurements (± 5 cm), weighing of samples (± 0.2 mg), volume of samples (± 10 %), and carbon content (± 5 %).

Peat accumulation rates calculated with this method give rough estimates of past peat accumulation rates, but they do not tell us the true current or past accumulation rates. Peat is formed in a continuous process, where fresh falling litter is gradually transformed into homogeneous organic

matter of varying degrees of decomposition. A peat deposit is roughly divided into two sections: the active aerobic surface peat layer called the acrotelm and the lower anoxic peat layer called the catotelm. Above these two peat layers, there is a layer composed of recently fallen litter. The degree of water-logging may vary in the acrotelm, whilst the catotelm is permanently water-saturated. According to the definition of Clymo (1965), the true peat accumulation rate would be the annual insertion of organic matter from the acrotelm to the catotelm. Owing to the aerobic conditions and constant inputs of fresh litter, the decomposition process in the acrotelm is relatively fast. Consequently, peat accumulation rates calculated for the acrotelm are higher than the true peat accumulation rates from the acrotelm to the catotelm. Only a minor fraction of this material will become part of the permanent peat deposit. By contrast, owing to the prevailing anoxic conditions and to the poor quality of the partly decomposed organic matter entering, the decomposition process in the catotelm is very slow or inexistent. However, during several centuries or millennia, some decomposition usually does occur within the catotelm, and, consequently, the accumulation rates recorded for the catotelm are lower than the true accumulation rates at the time organic matter enters the catotelm.

The autocompaction of peat (Aaby and Tauber 1974) and seasonal fluctuations in hydrology (Pakarinen 1975) also influence bulk density and, thus, peat (but not carbon) accumulation rates. Leaching of carbon in run-off water (Baum et al. 2007, Moore et al. 2010) affects both peat and carbon accumulation rates. These possible error sources are unavoidable consequences of the chosen method, and direct comparisons should be made only to values obtained in a similar manner. Despite these error sources, I chose this method because I considered it more important to obtain rough data on numerous Amazonian peatlands fairly rapidly, rather than exact and detailed data on just one or two sites.

Nutrient content

To obtain information on trophic conditions and on the diversity of peatland ecosystem types, I sent numerous samples (from both the peat surface and entire cores) to be analysed for their nutrient contents (Ca, Mg, Mn, Fe, K, P, Zn, Cu, S) with an inductively coupled plasma optical emission spectrometer (ICP-OES, Thermo Jarrel Ash IRIS Advantage with CID detector, HNO₃-HClO₄-HF method) in the laboratory of MTT Agrifood Research Finland, in Jokioinen^{II,III}. The nutrient content of surface peat samples provides information on the current trophic conditions of a peatland, whilst the

nutrient content of the core samples provides information on the developmental history of a peatland ecosystem^{ii,iii}.

I compared the peat Ca/Mg mass ratio to that of Amazonian rainwater (1–3.5; Furch and Junk 1997) and the global average of continental rainwater (0.4–6; Berner and Berner 1996)^{ii,iii} because peat Ca content is the best indicator of ombrotrophy, owing to its limited concentration in rainwater and in the atmosphere (Verhoeven 1986, Muller et al. 2006). The Ca/Mg ratio of ombrotrophic peat is comparable to or lower than that of rainwater, whilst higher ratios indicate a minerotrophic Ca source (Weiss et al. 2002).

Remote sensing of peatland vegetation

Owing to the remoteness of and difficult access to the study sites as well as limited resources, I was not able to study any characteristics of the peatland vegetation in the field (except by taking photographs and descriptive notes). I employed, therefore, a simple posterior remote-sensing analysis to obtain information on the vegetation of the studied peatlands located in the northern part of the Pastaza-Marañón foreland basinⁱⁱⁱ. Optical properties of the land surface detected by Landsat TM satellite images can provide insights into vegetation structure, greenness (a proxy for GPP), canopy openness, canopy architecture, presence of surface water, etc. (Lillesand and Keifer 2000). First, I performed with Erdas Imagine 9.1 a Principal Components Analysis (PCA) of a Landsat TM satellite image (WRS-2, Path 007, Row 063, downloaded from <http://glcfapp.glc.f.umd.edu:8080/esdi/index.jsp>), where most study sites of the second fieldwork phase were locatedⁱⁱⁱ. I used PCA in order to compress the six-band (1–5, 7) Landsat TM image into more effective dimensions that define the greatest variability in the data (PC1 component). Subsequently, I extracted the PC1 values in the area of each field site by drawing an area of interest (AOI) on the image in the central part of each field site. Subsequently, I subset the PCA image with each AOI, and extracted the pixel values from ten random pixels of each AOI. In order to study whether the AOIs were significantly different as regards their mean pixel values (representing potential differences in vegetation), I analysed the variance of the pixel values between and within the peatlands with one-way analysis of variance (ANOVA). I used Tukey pairwise comparisons to assess which AOIs were different from each otherⁱⁱⁱ.

Results and discussion

Peat thickness

The results of both fieldwork phases show that peatlands are common in the floodplains of Peruvian Amazonia. Sample core thickness in the studied sites varied from 0 to 7.5 m, including peat, clayey peat, and minerogenic intrusions^{I,IV}. Only one of the 30 studied sites did not have any kind of organic deposit^I. The majority of the peat deposits were notably thicker than any peat deposit previously reported from anywhere in Amazonia (Junk 1983, Suszczyński 1984, Shier 1985, Andriessse 1988, Dubroeuq and Volkoff 1998, Schulman et al. 1999, Ledru 2001, Ruokolainen et al. 2001). It is interesting that this kind of basic ecosystem characteristic has been practically ignored in Amazonia. Some satellite image-derived maps already existed for parts of the Peruvian Amazon prior to this study, in which peat areas appear as something completely different from the non-flooded rainforest (Mäki and Kalliola 1998, IIAP 2004). However, since these areas were not visited for field verification, they were not identified as peatlands.

Even though measured maximum peat thicknesses were high, they were not as high as those measured in Southeast Asian tropical peatlands (up to more than 10 m, see Maltby and Immirzi 1993, Sorensen 1993, Page et al. 1999, 2004, Rieley and Page 2005). There are at least two possible explanations for this: 1) There are peat deposits in Amazonia as thick as those in Southeast Asia, but I did not happen to visit them, or, alternatively, I could not reach them owing to difficult access to the peatland centres, where the thickest peats are probably located^I. For example, a 9.6 m thick Indonesian peat deposit in the catchment of the river Sungai Sebangau was not reached on foot but using the railway of a logging concession (Page et al. 1999). If I were to run one of my 4–5 km long transects beginning at the margin of that particular Indonesian peat deposit, measured peat thickness along the transect would vary from 1 to 4 m (data from Page et al. 1999). This is in line with the peat thicknesses measured in my Amazonian transects. Consequently, the extensive Amazonian peatland areas where I did not reach the centre (especially in the Pastaza-Marañón basin), as well as other unstudied Amazonian peatlands, may potentially harbor peat deposits as thick as those found in Southeast Asia. 2) Amazonian peat deposits do not reach the thicknesses found in Southeast Asia owing to unstable conditions created by the active lateral migration of rivers. The undisturbed conditions necessary for peat accumulation may have not prevailed long enough in the area to allow very thick peat deposits to form (see below)^I.

The role of Amazonian peatlands as a carbon store

The existence of thick peat deposits with a high carbon content^{I,III,IV} indicates that their role as a carbon store can be significant. Giving an estimate of the total carbon stored in Amazonian peatlands is a long-term project, which I have begun by providing a rough estimate of the total carbon stored in the peat deposits of the 120,000 km² Holocene sedimentation area of the Pastaza-Marañón basin^{IV}.

The total peatland area and the total peat carbon stock in the area covered by the two satellite images on which my Pastaza-Marañón basin study sites were located were 21,929 km² and 3.116 Gt (with a range of 0.837–9.461 Gt), respectively^{IV}. These two satellite images cover about half of the Holocene sedimentation area of the Pastaza-Marañón foreland basin (see Fig. 1), so assuming a similar distribution of peatlands in the rest of the area, the total peat carbon stock would be closer to double these values: 43,858 km² of peatlands and 6.2 Gt of carbon (Table 1)^{IV}.

Table 1. Comparison of the peat carbon stock of this study to that of other peatland areas (a modified version^{IV}).

	Carbon stock (Gt)		
	Minimum	Best estimate	Maximum
Northern peatlands*	473	547	621
Southern peatlands in Patagonia*	13	15	18
<u>Total of the northern and southern peatlands*</u>	486	562	639
African tropical peatlands**	3.536	6.934	8.131
Southeast Asian tropical peatlands**	66.341	68.516	69.853
Asian other tropical peatlands**	0.303	0.427	0.497
Central American & Caribbean peatlands**	2.888	3.048	3.167
Pacific tropical peatlands**	0.007	0.007	0.007
South American tropical peatlands**	8.604	9.667	10.219
<u>Total of the tropical peatlands**</u>	<u>81.679</u>	<u>88.599</u>	<u>91.874</u>
<u>Total of the global peatlands***</u>	<u>568</u>	<u>651</u>	<u>731</u>
<u>Pastaza-Marañón basin (extrapolated)^{IV}</u>	<u>1.674</u>	<u>6.232</u>	<u>18.922</u>
- % of the South American best estimate	17.3 %	64.5 %	195.7 %
- % of the tropical best estimate	1.9 %	7.0 %	21.4 %
- % of the global best estimate	0.3 %	1.0 %	2.9 %

*) data from Yu et al. 2010

**) data from Page et al. 2011

The Pastaza-Marañón peatland carbon stock is about 65 % of the current best estimate of the South American tropical peatland carbon stock, about 7 % of the best estimate of the global tropical peatland carbon stock, and about 1 % of the global peatland carbon stock (Table 1). A new total carbon stock value for South American tropical peatlands cannot be calculated on the basis of this study because it is not clear how large a proportion of the carbon stock of the peatlands of the Pastaza-Marañón basin was included in the previous value for Peru: 4.41 Gt of carbon (Page et al. 2011 based on Ruokolainen et al. 2001 for peatland area and on I for peat thickness). An estimate of the total area of Peruvian Amazonian peatlands is thus necessary. Either way, 4.41 Gt of carbon is a clear underestimate for Peru because the estimated peatland carbon stock in the Pastaza-Marañón basin alone was larger than this.

Even if the calculation of the total area and carbon stock in the Pastaza-Marañón basin are extrapolations with several uncertainties, these estimates suggest that globally significant amounts of carbon are stored in just one Amazonian peatland area^{IV}. 6.2 Gt is still much less than the carbon stored in the Southeast Asian tropical peatlands (about 70 Gt, Page et al. 2011), but even so, it is undoubtedly worth finding out how much carbon is stored in the peatlands of the Amazon Basin.

The role of Amazonian peatlands as carbon sinks

The historic peat and carbon accumulation rates recorded for these Amazonian peatland sites (from 0.5 to 9.3 mm yr⁻¹, and from 26 to 195 g C m⁻², respectively^{I,IV}) were comparable to those of other tropical peatlands (Neuzil 1997, Page et al. 2004, Wooller et al. 2007, Chimner and Karberg 2008) and warm-temperate peatlands (Newnham et al. 1995, Goman and Wells 2000)^{I,IV}. They were usually higher than those of boreal peatlands (Tolonen and Turunen 1996, Turunen et al. 2002; Borren et al. 2004; but see Yu et al. 2003, 2009)^{I,IV}.

The high accumulation rates combined with the relatively smooth and continuous age-depth curves of the dated peat cores^{I,IV} suggest that these Amazonian peatlands have acted as steady and relatively strong carbon sinks during their developmental history^{I,IV}. With the method used it is only possible to give rough estimates of historic peat and carbon accumulation rates. It is not possible to determine whether the peatlands are currently net accumulators of carbon, have balanced carbon accumulation and loss rates, or are net carbon emitters (Pakarinen 1975, Page et al. 1999, Yu et al. 2003). However, there is evidence that the last millennium represents an especially

rainy epoch in the Holocene history of Peruvian Amazonia (Bush et al. 2007). This suggests that environmental conditions are still favourable for peat accumulation^{I,IV}. Consequently, Peruvian Amazonian peatlands probably continue to act as carbon sinks, thus having a cooling effect on the global climate. This is a previously unidentified carbon sink, which could contribute to “the missing sink” detected in the carbon fluxes among the four major global carbon pools: fossil carbon, atmosphere, oceans, and terrestrial biosphere (Schimel 1995). Nevertheless, their cooling effect may be counteracted if Amazonian peatlands emit large amounts of methane (see below).

On the basis of the high observed frequency of peat deposits buried under minerogenic sediments^{I,IV}, I suggest that another type of carbon sink function also operates in Peruvian Amazonia, especially in the Pastaza-Marañón basin: burial and subsidence of peat^{IV}. In the burial process, carbon is stored in a relatively stable reserve, where it is protected by over-lying minerogenic sediments (see e.g. the observations of Hoorn 2006). When buried peat slowly subsides in a foreland basin under an increasing amount of minerogenic sediments deposited by rivers, carbon is removed from the short-term carbon cycle between the biosphere and atmosphere^{IV}. Consequently, I suggest that the subsiding Pastaza-Marañón basin currently acts, and has acted for most of the Quaternary period at least, as a long-term bio-geological peatland carbon sink^{IV}.

The potential role of Amazonian peatlands as carbon sources

A carbon store is always a potential carbon source to the atmosphere. Although I visually observed that my Amazonian peatland sites were still in a relatively natural, undisturbed condition, climate change, deforestation, large-scale land-use projects (like damming, road construction, and oil palm plantations), and extensive gas and oil exploration threaten these ecosystems (Malhi et al. 2008)^I. Even if the peatlands are not directly affected, all of these factors could contribute to the desiccation of regional climate, thereby increasing the risk of fire (Siegert et al. 2001)^{I,IV}. This could convert them from steady long-term carbon sinks into carbon sources, and, simultaneously, change their cooling effect into a warming one (as has already happened in Indonesia, Page et al. 2002, Hirano et al. 2007)^{I,IV}. For example, if all the carbon stored in the peat deposits of the Pastaza Marañón basin (6.2 Gt) was liberated into the atmosphere, it would correspond to ca 80 % of global annual carbon emissions from the burning of fossil fuels (8 Gt of carbon per year, IEA 2010).

Nevertheless, of the whole Amazon Basin, northwestern Amazonia (where the Pastaza-Marañón basin and all the other studied peatland sites are located) is least likely to experience major droughts in the future, even under severe scenarios (Malhi et al. 2008). It is not thus probable that these Amazonian peatland sites will be suddenly converted from carbon sinks into sources. The future of Peruvian Amazonian peatlands seems thus more optimistic than that of the Indonesian ones (Li et al. 2007).

The potential risk of oxidation mainly threatens the current (unburied) peatlands^{IV}. Buried peat is less vulnerable to oxidation caused by hydrological change, drought or fire because it is protected by over-lying minerogenic deposits (Smith et al. 1989; Morozova and Smith 2003). However, it is important to note that the action of laterally migrating rivers does not always lead to the burial of peat^{IV}. Peat can also be eroded and transported by rivers, whereby it may decompose in the presence of oxygen or become redeposited on the floodplain (Dunne et al. 1998). This natural geological process can cause the liberation of stored carbon into the atmosphere and convert a peatland from a carbon sink into a sudden and strong carbon source regardless of the prevailing climatic conditions^{IV}. Nevertheless, this rarely happens simultaneously over large areas. The erosion of a single peatland would obviously not have a global effect, provided other peatlands continue to act as carbon sinks.

Even if Amazonian peatlands continue acting as carbon sinks by actively accumulating peat, they might have a warming effect on the global climate by liberating methane (CH₄). Methane is a potent greenhouse gas (with a 56-fold global warming potential compared to that of carbon dioxide over 20 years), which forms to a significant extent in the world's wetlands (especially in the northern peatlands) as a result of anaerobic decomposition in water-saturated conditions (Bubier and Moore 1994). Nothing is currently known about the role of Amazonian peatlands as methane sources. In a gas-exchange study in a tropical peatland in Central Kalimantan (Indonesia), the role of carbon dioxide for atmospheric processes was detected to be clearly more important than that of methane (Jauhiainen et al. 2005). Methane emissions were low and they were detected in water-saturated peat only. Nevertheless, these results cannot be directly extrapolated to Amazonian peatlands. Some of my peatland sites were very watery, and some are covered by river floodwaters during several months of each year. Consequently, they are potential methane sources. Another important peatland-related greenhouse gas is nitrous oxide (N₂O). However, N₂O is liberated into the atmosphere in significant quantities only in disturbed peatlands (Martikainen et al. 1993).

Basal ages, peat initiation and river dynamics in Peruvian Amazonia

The basal radiocarbon ages of my Amazonian peatland sites varied considerably, from 672 to 8870 cal yr BP^{I,IV}. The basal ages mark the initiation of a peat deposit and are generally attributed to a wetter and/or warmer climatic phase or high seasonality (Page et al. 2004, MacDonald et al. 2006, Chimner and Karberg 2008, Yu et al. 2010). In the western Amazonian lowlands, however, I suggest that the dynamic lateral migration of rivers (Kalliola et al. 1992) is an even stronger control on the timing of peat initiation^{I,IV}. Laterally moving rivers may bury or erode a peat deposit, after which peat accumulation can restart on a fresh minerogenic surface.

The oldest basal age in this study, 8870 cal yr BP in the Aucayacu site in the northeast corner of the Pastaza fan^{IV}, is comparable to the depositional ages (7658 cal yr BP and 8180 cal yr BP) of the minerogenic fan sediments along the nearby Corrientes River (Räsänen et al. 1990, 1992). These sediments were deposited when the former Pastaza River flowed eastwards through this area. Hence, the subsoil of the Aucayacu bog^{IV} probably originates from this stage of active minerogenic deposition, which preceded the relatively stable conditions enabling peat accumulation. Similarly, the basal age of each peatland in the Pastaza fan probably indicates the moment when the Pastaza River moved over the site during its east-west migration towards its current channel in the western part of the Pastaza fan (Räsänen et al. 1990, 1992)^{IV}.

I did not find thick and continuous peat deposits between the Puinahua Channel, the Ucayali River, and the Marañón River in the southern Pastaza-Marañón floodbasin. This is probably due to the migration of the Marañón River over this area during the last few thousands of years (Räsänen et al. 1992), interrupting the process of peat formation and causing peat burial and erosion^{IV} (see Fig. 1). In contrast, the peatlands in the southern periphery of the Pastaza-Marañón floodbasin (to the south of the Ucayali River) were relatively thick, probably because they have been less exposed to moving rivers^{IV}.

Ecosystem diversity of Amazonian peatlands

On the basis of their surface peat nutrient contents, the study sites could be placed on a gradient from nutrient-poor to nutrient-rich^{II,III}. The difference in Ca content was 270-fold between the nutrient-poor and nutrient-rich ends of the gradient: from 65 to 17 400 mg kg⁻¹ dry peat^{III} (Fig. 2). A steady increase in surface peat water pH was also observed along the gradient^{II,III}.

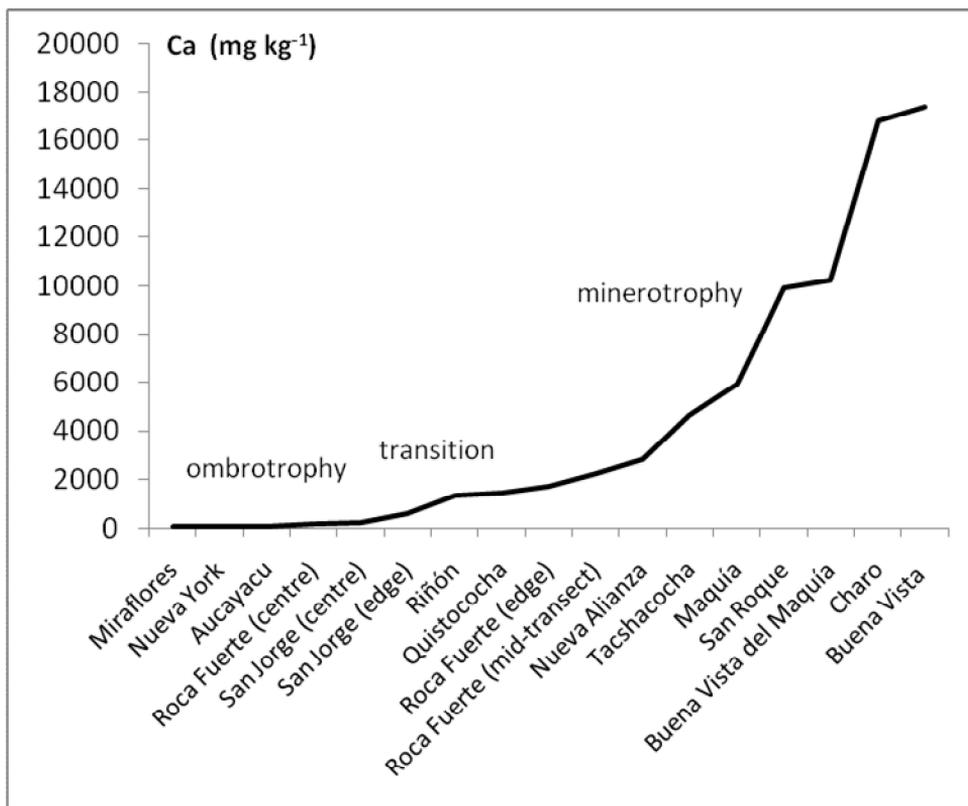


Figure 2. Peatland gradient in Peruvian Amazonia on the basis of the average surface peat (< 100 cm) Ca content. All the study sites where samples were collected are included.

In this Amazonian environment, the most likely explanation for such a nutrient-gradient is a gradual change from atmosphere- to river-influenced conditions^{III}. In other words, the five or six most nutrient-poor peatlands were rain-fed ombrotrophic bogs, whilst the other peatlands were minerotrophic swamps with an inflow of river, surface or ground water^{II,III}. This interpretation was confirmed by the domed topography of those three nutrient-poor sites for which topography was measured^{II,III}. In addition, peat nutrient content and pH values of the nutrient-poor sites were similar to those of other tropical ombrotrophic bogs (Anderson 1983, Page et al. 1999, Weiss et al. 2002, Muller et al. 2006), and their surface peat Ca/Mg ratio was comparable to that of Amazonian rainwater (1–3.5; Furch and Junk 1997)^{II,III}. In some peatland sites, the nutrient-poor and nutrient-rich types co-existed as separate zones^{II,III}. One site was a nutrient-rich peatland, despite having a slightly raised peat surface^{III}. That site is likely to be subject

to frequent inundations of a nearby stream, and could thus be defined as a “minerotrophic raised mire”.

The most likely explanation for the high variability in nutrient content within the nutrient-rich river-influenced sites is the influence of surface waters of different nutrient statuses and over different durations^{III}. By contrast, the variation in nutrient content within the surface peat of the ombrotrophic sites is probably due to a variable degree of bioaccumulation, which will arise due to differences in age, duration of the ombrotrophic phase and vegetation (Page et al. 1999, Weiss et al. 2002, Muller et al. 2006)^{II,III}.

According to the remote-sensing analysis of peatland vegetation, the study sites could be divided into five different groups, of which nutrient-rich sites were found in four groups and nutrient-poor sites in three groups^{III}. I interpret the significant variation in pixel values as being indicative of differences in peatland vegetation type^{III}. The grouping of the sites on the basis of their pixel values was not compatible with the surface peat nutrient gradient. Thus, the various qualities of the vegetation cover obtained using a remote-sensing approach were not directly reflected by peat nutrient content. The vegetation of these sites requires more investigation. However, on the basis of this simple analysis combined with the nutrient data, I suggest that the Pastaza-Marañón basin currently harbours a large variation not only in peatland soils but in peatland ecosystem types.

In summary, these results indicate that the Amazonian lowlands harbour a high diversity of previously unidentified ecosystem types^{II,III}. Their existence increases the ecosystem diversity of the Amazonian lowlands and they provide a variety of species habitats, which can be very different from *terra firme* rainforests and minerogenic wetlands^{II,III}. Interestingly, in one ombrotrophic bog a colleague observed plant and bird species typical of white-sand forests that grow in non-flooded areas on extremely nutrient-poor quartz sand soils (Anderson 1981)^{II}. I visually observed that the slender physiognomy of the trees at this and the other ombrotrophic sites was similar to that of the white-sand forests. The ecological conditions of the nutrient-poor ombrotrophic bogs may thus be somewhat analogous to those of the white-sand soils, and thereby extend the very restricted habitat range of specialized white-sand species^{II}.

The existence of a high diversity of peatland ecosystems in Amazonia has global implications: it confirms that diverse tropical peatlands are not limited to the Southeast Asian lowlands, and that true tropical ombrotrophic bogs also exist in Amazonia^{III}. Outside the Amazon Basin, other neotropical lowland peatlands are known to exist at least in the Orinoco delta in Venezuela (Warne et al. 2002, Aslan et al. 2003, Vegas-

Vilarrúbia et al. 2010) and along the Caribbean coast (Cohen et al. 1989, Cameron and Palmer 1995). Very little is known about tropical lowland peatlands in Africa (Bord na Mona 1984, Page et al. 2011).

Of the peatland sites for which I collected nutrient data, approximately 40 % were ombrotrophic and 60 % minerotrophic^{III}, whilst the Southeast Asian tropical peatlands are almost exclusively ombrotrophic (Page et al. 1999). Consequently, the diversity of Amazonian peatland ecosystem types may be even higher than that in Southeast Asia, where many minerotrophic peat swamps have already been lost (Wüst et al. 2004). On the other hand, considering the high degree of human influence on Southeast Asian peatlands, Amazonian ombrotrophic bogs may also soon be among the few undisturbed tropical ombrotrophic bogs remaining in the world^{III}.

Development and history of Amazonian peatlands

Whilst surface peat nutrient contents provide information on current ecosystem properties and growing conditions for vegetation, changes in nutrient content in vertical peat cores provide information on the history and developmental phases of a peatland.

All the peat cores taken from the ombrotrophic bogs revealed that their ombrotrophic conditions had arisen after a minerotrophic phase^{II,III}. For example, the highest raised bog, Aucayacu, was initially a very nutrient-rich minerotrophic peatland, which was subsequently buried under (and mixed with) minerogenic sediments^{III}. After the burial event, peat accumulation started again and the ecosystem gradually turned into a nutrient-poor ombrotrophic bog. Subsequently, the ombrotrophic phase was interrupted by a minor minerotrophic intrusion (probably induced by an especially massive flood or a change in the position of the nearby river channel, resulting in surface water influence)^{III}. Finally, the Aucayacu bog reverted into an ombrotrophic system, which is its current state. In summary, in the Aucayacu bog, peatland ecosystem types of different nutrient statuses could be detected – not in space but in time. This kind of alternation of minerotrophic and ombrotrophic phases may be typical of floodplain peatlands (e.g. Morozova and Smith 2003), but, in the absence of river influence, it is more common to encounter only one minerotrophic layer below an ombrotrophic one (see, e.g., Weiss et al. 2002, Muller et al. 2006).

All the minerotrophic peatlands had a minerotrophic history with no detectable ombrotrophic phases in the peat cores^{III}. By contrast, their peat nutrient content tended to increase towards the base. This indicates these

ecosystems may currently be approaching ombrotrophic conditions as more and more peat accumulates. In the future, their peat deposits may become so thick that they surpass the maximum floodwater level. This is the most likely mechanism of ombrotrophic bog formation in Amazonia, although this hypothesis still needs to be confirmed. Lake overgrowth has been proposed as an alternative mechanism (Lähteenoja 2007).

Conclusions, future research and conservation of Amazonian peatlands

This study includes five major new findings. First, thick and extensive but previously unstudied peatlands exist in the Amazonian lowlands^{I,IV}. Surprisingly, such a basic ecosystem characteristic as peat accumulation has remained practically unrecognized from Amazonia until today. It is understandable that the remote corners of the Pastaza-Marañón foreland basin have not been studied for peat accumulation, but it is difficult to understand why there are no previous published studies of the 5-m-thick Quistococha peat deposit located next to the public beach of the city of Iquitos.

Second, Peruvian Amazonian peatlands, especially in the Pastaza-Marañón basin, form a significant carbon store^{IV}. Similar studies carried out in other parts of the Amazon Basin and a more extensive remote-sensing analysis are necessary to be able to estimate the total carbon store of Amazonian peatlands. On the basis of my unpublished observations in the Rio Negro basin in Brazil, peat accumulation is also common in central Amazonia. Recently, thick Amazonian peatlands have also been reported from the Madre de Dios basin in southern Peru (Householder et al., in review).

Third, these peatlands act as carbon sinks and potential sources^{I,IV}. On the basis of this study, I suggest that peatland-related fluxes of greenhouse gases in the Pastaza-Marañón foreland basin are likely to be significant at both South American and global scales. Once their total area and carbon stock are better known, it would be possible to estimate the role of all Amazonian peatlands in the global carbon cycle and in the carbon balance of the Amazon Basin as a whole. Whilst the carbon dynamics of the Amazon Basin have been under active recent debate (Phillips et al. 1998, Tian et al. 1998, Cox et al. 2000, Malhi and Grace 2000, Clark 2002, Malhi et al. 2008), the existence of peatlands has not been included in these discussions (Schulman et al. 1999). Further research should especially be targeted towards clarifying how probable is the risk that Amazonian peatlands will be converted from carbon sinks into carbon sources and how

this could be prevented. With measurements of carbon dioxide exchange, it would be possible to estimate the annual carbon flux from these peatlands and seasonal variation in their carbon cycling (Jauhiainen 2005). It would also be useful to estimate methane and nitrous oxide emissions from Amazonian peatlands, since these two gases have high global warming potential.

Fourth, the extensive peatlands in the Pastaza-Marañón basin in Peruvian Amazonia not only act as a major current carbon sink, but also a long-term biogeological carbon sink^{IV}. Drilling should be undertaken in the basin to extract cores a few hundreds of metres deep in order to be able to estimate the amount of buried and subsided peat, which is likely to be significant.

Fifth, Amazonia harbours a high diversity of previously undescribed peatland ecosystem types^{II,III}. The fact that it is still possible to describe not only new species but also totally new ecosystems from the Amazonian lowlands highlights our very poor knowledge of the region. Further research should be targeted towards clarifying whether there are other peatland ecosystem types that have yet not been described, what kinds of vegetation the different peatland ecosystem types support, and what kinds of roles the different peatland ecosystem types play in carbon cycling (Page et al. 1999). It would also be interesting to find out how their existence affects the regional distribution patterns of species and whether ombrotrophic bogs really are suitable habitats for white-sand forest species^{II}. Future palynological studies of the peat deposits could reveal long-term trends in the Amazonian rainforest biome (Ledru 2001), even though they will more probably reflect changes in the floodplain environment than those in *terra firme*. On the other hand, there are currently no other high resolution palaeoecological records for this region.

On the basis of these five major points, I suggest that Amazonian peatlands need to be included in discussions on the role of the tropical peatlands in the global carbon cycle, on the carbon dynamics of the Amazon Basin, and on the diversity of ecosystems and habitats in Amazonia. Experience from Southeast Asian peatlands demonstrates that excessive human influence in combination with drought and fires can lead to the loss of the tropical peatland habitat and convert these valuable ecosystems from long-term carbon sinks and stores into strong carbon sources (Page et al. 2002, Rieley and Page 2005). This should be taken seriously and lead to the active conservation of Amazonian peatlands. The peatland sites of this study were still relatively intact, which indicates that their conservation in a natural state is possible. Probably the most extensive Amazonian peatland area, the Pastaza-Marañón foreland basin, currently belongs in part to several

different conservation areas: The Pastaza fan is included in the Ramsar Convention on Wetlands, whilst the central and southern parts of the basin are protected by the Pacaya-Samiria national park (also a Ramsar site) and the Yanayacu-Maquía Conservation Concession, respectively. Unfortunately, these conventions do not guarantee the effective conservation of these areas, especially owing to oil exploration in the Pastaza-Marañón basin. Consequently, active national conservation is needed and it will hopefully be supported by international involvement.

In conservation planning, it is necessary to recognize that peatlands are strongly connected to surrounding water systems, which, in minerotrophic peatlands, originate not only from local rainfall but from melting snow waters originating from the peaks of the Andes and from rainfall in the catchments of the rivers upstream of the peatland in question. By contrast, constancy of regional rainfall is crucial for the permanence of ombrotrophic bogs. Although rainfall scenario models predict a relatively wet future climate for western Amazonia, drought and subsequent fires may well threaten central and eastern Amazonian peatlands (Li et al. 2007, Malhi et al. 2008). Ultimately, the effective conservation of Amazonian peatlands requires wise conservation of the systemic characteristics of the Amazon Basin as a whole. Simultaneously, the existence of these peatland ecosystems in the Amazonian lowlands provides an additional strong motive to conserve the world's largest, most diverse and least known rainforest area.

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