High diversity of tropical peatland ecosystem types in the Pastaza-Marañón basin, Peruvian Amazonia

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[1] Very little information exists on Amazonian peatlands with most studies on tropical peatlands concentrating on Southeast Asia. Here we describe diversity of Amazonian peatland ecosystems and consider its implications for the global diversity of tropical peatland ecosystems. Nine study sites were selected from within the most extensive wetland area of Peruvian Amazonia: the 120,000 km² Pastaza-Marañón basin. Peat thickness was determined every 500 m from the edge toward the center of each site, and peat samples were collected from two cores per site. Samples from the entire central core and surface samples from the other core were analyzed for nutrient content. Topography of four peat deposits was measured. In order to study differences in vegetation, pixel values were extracted from a satellite image. The surface peat nutrient content of the peatlands varied from very nutrient-rich to nutrient-poor. Two of the peatlands measured for their topography were domed (5.4 and 5.8 m above the stream), one was gently sloping (1.4 m above the stream), and one was flat and occurred behind a 7 m high levee. Five different peatland vegetation types were detected on the basis of pixel values derived from the satellite image. The peat cores had considerable variation in nutrient content and showed different developmental pathways. In summary, the Pastaza-Marañón basin harbors a considerable diversity of previously undescribed peatland ecosystems, representing a gradient from atmosphere-influenced, nutrient-poor ombrotrophic bogs through to river-influenced, nutrient-rich swamps. Their existence affects the habitat diversity, carbon dynamics, and hydrology of the Amazonian lowlands, and they also provide an undisturbed analog for the heavily disturbed peatlands of Southeast Asia. Considering the factors threatening the Amazonian lowlands, there is an urgent need to investigate and conserve these peatland ecosystems, which may in the near future be among the very few undisturbed tropical ombrotrophic bogs remaining in the world.

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1. Introduction

[2] Peatlands are characterized by the accumulation of partially decomposed organic matter under anaerobic conditions created by water-logging. They perform a number of valuable ecosystem services, including carbon storage [e.g., Gorham, 1991], control of water quality and quantity [e.g., McNamara *et al.*, 1992], and biodiversity support [Bridgman and Richardson, 1993; Laine and Vasander, 1996; Page *et al.*, 1997; Wheeler and Proctor, 2000]. They also contain a valuable archive of biogeochemical and palaeoecological information [e.g., Ledru, 2001; Weiss *et al.*, 2002].

[3] Tropical peatlands have their greatest extent in Southeast Asia [Anderson, 1983; Page *et al.*, 1999, 2011; Rieley and Page, 2005], where almost all the studies on tropical

peatlands have been conducted. Nevertheless, a few recent studies have shown that up to 6 m thick tropical peat deposits also exist in Peruvian Amazonia [Lähteenoja *et al.*, 2009a, 2009b]. This suggests that the total area and C stock of Amazonian peatlands might be much more important than indicated by earlier vegetation studies and resource reviews that referred to Amazonian peat deposits as sporadic litter accumulations in *Mauritia flexuosa* palm swamps [e.g., Suszczyński, 1984; Duivenvoorden and Lips, 1991; Dubroeuq and Volkoff, 1998; Schulman *et al.*, 1999; Ruokolainen *et al.*, 2001; Guzmán Castillo, 2007]. Nevertheless, very little is currently known about Amazonian peatlands.

[4] Previous studies of Amazonian peatlands have indicated that they are mostly seasonally flooded, 0.1–5 m thick minerotrophic backswamps located in the river floodplains [Lähteenoja *et al.*, 2009a, 2009b]. These peatlands are influenced by large annual variations in the water level of the Amazon River and its tributaries (up to 12 m for the Amazon River in Iquitos, Peru; unpublished data obtained from SENAMHI, 2008 and Dirección Agraria Regional de

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Loreto 2008) and can also receive nutrients from the flow of surface waters (other than river floods) and capillary rise of elements in peat pores [Hill and Siegel, 1991; Romanov, 1968; McCabe, 1991]. Some of the thickest and oldest of these peatlands have evolved through minerotrophic conditions to form domed, up to 6 m thick nutrient-poor ombrotrophic bogs, and their surface peat layers (e.g., 0–175 cm, including the critical rooting zone for vegetation) currently depend entirely on atmospheric inputs of water and nutrients, despite their location in the floodplain of the Amazon River [Lähteenoja et al., 2009a, 2009b]. Reflecting their rain-fed water supply, the peat of these ombrotrophic bogs tends to have a lower nutrient content and a higher organic material and C content compared to minerotrophic peatlands. These differences create totally different growing conditions for the peatland plants, thus contributing to peatland habitat diversity.

[5] The peatlands of Southeast Asia are mostly domed, nutrient-poor ombrotrophic bogs that receive nutrients only from precipitation because of their raised shape, with relatively narrow flooded minerotrophic margins close to rivers [Page et al., 1999]. Variation in peat thickness, hydrology and nutrient supply gives rise to several different peat swamp forest types, which provide a variety of habitats for rain forest species [Page et al., 1999] including species of conservation concern [Page et al., 1997; Morrogh-Bernard et al., 2003; Sodhi et al., 2004]. Southeast Asian peatlands are currently adversely affected by habitat loss and fragmentation brought about by illegal logging, deforestation, drainage, fire, agriculture and plantations [Siebert et al., 2001; Sodhi et al., 2004; Rieley and Page, 2005; Bradshaw et al., 2009] and, as a consequence, considerable amounts of carbon have been liberated to the atmosphere [Page et al., 2002; Hooijer et al., 2010]. Tropical lowland peatlands are less well known from other continents, including Central and South America and lowland Africa [Bord na Mona, 1984; Page et al., 2011]. In Central and South America, they are known to exist in the Orinoco delta in Venezuela [Warne et al., 2002; Aslan et al., 2003; Vegas-Vilarrubia et al., 2010] and along the Caribbean coast [Cohen et al., 1989; Cameron and Palmer, 1995], although to a smaller extent than in Amazonia [cf. Schulman et al., 1999].

[6] The occurrence of different types of peatlands within the Amazon basin could make an important contribution to the maintenance of regional ecosystem and habitat diversity [Lähteenoja et al., 2009a], as well as extending the current knowledge on the distribution of tropical peatlands and their role in the global carbon cycle [Lähteenoja et al., 2009b]. Improved knowledge of these peatlands will provide a stronger basis for assessing their environmental value at both regional and global scales. The few previous studies on Amazonian peatlands [Lähteenoja et al., 2009a, 2009b] covered a geographically restricted area in Peruvian Amazonia relatively close to the city of Iquitos. In this paper, we study spatial distribution of nutrients in peat cores and ecosystem diversity of tropical peatlands in the most extensive continuous wetland area of Peruvian Amazonia: the 120 000 km² Pastaza-Marañón foreland basin [Räsänen et al., 1990, 1992, Figure 1]. The aim of the paper is to answer the following questions: (1) Do the wetlands of the Pastaza-Marañón foreland basin harbor peat deposits?

(2) How diverse are the peatland ecosystems in this area on the basis of the nutrient contents of the surface peats? (3) Can the diversity of peatland ecosystem types be detected on a Landsat TM satellite image? (4) What types of developmental histories do these peatlands represent? (5) What are the implications of these results for the ecosystem diversity of the region?

2. Materials and Methods

2.1. Site Description

[7] Fieldwork was carried out in July–November 2008 in the Pastaza-Marañón foreland basin which consists of two separate areas: the southern Pastaza-Marañón basin (to the south of the Marañón River) and the Pastaza volcanogenic fan (to the north of the Marañón River) [Räsänen et al., 1990, 1992, Figure 1]. The climate of the study area is hot and humid with little seasonal variation (average yearly temperature 26°C, annual precipitation c. 3,100 mm [Marengo, 1998]). Owing to its location in a subsiding foreland basin, the Pastaza-Marañón basin is covered by extensive floodplains of the dense river and stream network of the Ucayali and Marañón rivers [Räsänen et al., 1990, 1992].

[8] Wetland distribution maps were not available for the area (except the satellite image mosaic of *Instituto de Investigaciones de la Amazonía Peruana* [2004]), but spectral reflectance recorded by high resolution (30 m) histogram equalized Landsat TM satellite images (in the near-infrared wavelength, bands 4, 5 and 7) could be visually observed as different tones of blue, orange, red, violet, and turquoise (Figures 1 and 2). Nine different study sites were selected for the field survey from different parts of the study area in order to cover as large a geographical area, as many colors of the satellite image and hence as much diversity of potential peatland ecosystem types as possible (Figure 1). Some interesting formations were observed on the satellite images: three different zones represented by different colors of the satellite image were observed at the Roca Fuerte site (Figure 2a) and alternating stripes of dark and light blue at the Nueva Alianza site (Figure 2b; alternating lines of *M. flexuosa* palms and graminaceous vegetation in open pools).

2.2. Field Methods

[9] Sites were located in the field using a handheld GPS receiver (Garmin eTrex) and rectified Landsat TM satellite images (Figure 1). If a chosen site had a clearly defined center, a transect was established from the edge of the site to its center (Nueva York, Miraflores, Roca Fuerte (Figure 2a), and Maquia; Figure 1). Some transects were established on extensive sites with an irregular shape (Aucayacu, Nueva Alianza (Figure 2b), Tacshacochoa, San Roque, and Buena Vista del Maquia; Figure 1), and, consequently, it was not possible to reach the center of these sites. Lengths of transects varied from 2 to 4 km (see Tables 3–10).

[10] At each site, peat thickness was determined with a Russian peat sampler (50 cm × 4 cm × 2 cm [Jowsey, 1965]) at study points located at every 500 m along the transect. At each study point, coring was continued from the surface to the depth where an impenetrable minerogenic deposit was encountered. The results for the central core of each

Figure 1. Location of the nine study sites (NP, nutrient-poor; NR, nutrient-rich) in Peruvian Amazonia to the southwest of the city of Iquitos ($03^{\circ}44'5''\text{S}$, $073^{\circ}14'3''\text{W}$) shown on a mosaic of 12 histogram equalized Landsat TM satellite images (WRS-2, Paths 006–008, Rows 062–065, downloaded from <http://glcfapp.glcf.umd.edu:8080/esdi/index.jsp>). Band 4 was assigned to red, band 5 was assigned to green and band 7 was assigned to blue. 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 [Räsänen *et al.*, 1990, 1992].

peatland (last core of each transect) are shown here. pH of surface peat waters and peat water table (WT) were measured (with a field meter for pH) in small holes made in the peat surface ($n = 6$: from three holes close to each of the two different cores).

[11] The topography of four peatlands was assessed (Aucayacu, Maquia (partly), Nueva Alianza (partly) and Roca Fuerte). At these sites, the elevation of the peat surface was measured in order to establish whether these deposits had a raised (characteristic of ombrotrophic sites) or a flat (characteristic of minerotrophic sites) shape. At the Nueva Alianza site, the topography transect was perpendicular to the sampling transect (owing to logistical reasons). A free boarding method was used whereby two wooden stakes were placed firmly in the soil and each end of a 35 m long hose filled with water was bound to one of the stakes. The difference between the river water level and the water level

at stake one was measured, and this water level was marked on stake two. Then the starting end of the hose was moved to a third stake, taking care that no air bubbles had formed in the hose, and the new water level was marked on stakes two and three. The difference between the two marks on stake two was measured. At each stake, the distance from the reference altitude to the peat surface was measured. Consequently, it was possible to establish a reference altitude for the peat surface that was always at known altitude above the river water. At each measurement point, there is some error involved, but these errors are not likely to be systematically biased up or downward [Lähteenoja *et al.*, 2009a].

2.3. Peat Sampling and Laboratory Methods

[12] We based our ecosystem classification on peat properties. Peat samples were collected from two cores per transect. At the Roca Fuerte site, four cores were sampled

Figure 2. Two scenes of a histogram equalized Landsat TM satellite image (WRS-2, Path 007, Row 063, downloaded from <http://glcfapp.glcf.umd.edu:8080/esdi/index.jsp>) showing (a) the Roca Fuerte transect, which goes through three different vegetation zones, and (b) the Nueva Alianza transect, which lies perpendicular to dark and light blue lines. Band 4 was assigned to red, band 5 was assigned to green and band 7 was assigned to blue.

since three vegetation zones were identified on the satellite image (two cores were collected from the central zone and one from each of the outer zones). One sample of a precise volume of 62.8 cm^3 was collected from every 50 cm section of each core from the surface to the base (see Tables 3–10). The samples were transported to Iquitos in plastic bags, dried in the laboratory (24 h at 105°C), and exported to Helsinki, Finland. In order to study the peat properties, surface samples (one from 30 to 40 cm and one from 80 to 90 cm) from two cores were analyzed for total organic content by loss-on-ignition (LOI, combustion for 2 h at 550°C), dry bulk density (g cm^{-3}), nutrient content (Ca, Mg, Mn, Fe, K, P, Zn, Cu, S) by inductively coupled plasma optical emission spectrometry (ICP-OES, Thermo Jarrel Ash IRIS Advantage with CID detector), using the $\text{HNO}_3\text{-HClO}_4\text{-HF}$ method, and total C and N content (%) using a varioMax CN Analyzer (Elementar Analysensysteme GmbH). In order to study the developmental history of each ecosystem, all the samples from each central core were also analyzed for these parameters. Even if the peat volume was precisely measured during sampling, there may have been some loss of peat on moving a sample from the sampler to a plastic bag, from the bag to the drying container, and from the drying container to another plastic bag for weighing. In addition, some volatile C may have been lost during drying at 105°C .

[13] The concentrations of chemical elements in the peat samples were analyzed in order to provide information on ecosystem trophic conditions, which, in turn provides information on the diversity of peatland types within the study area. Peat Ca content is the best indicator of ombrotrophic conditions because of its limited concentration in both rainwater and the atmosphere [Verhoeven, 1986; Muller *et al.*, 2006]. The peat Ca/Mg mass ratio was calculated and compared to that of Amazonian rainwater (1–3.5 [Furch and Junk, 1997]) and the global average for continental rainwater (0.4–6 [Berner and Berner, 1996]). The Ca/Mg ratio of ombrotrophic peat is comparable to or lower than that of rainwater; higher ratio values indicate a minerotrophic source of Ca [Weiss *et al.*, 2002; Muller *et al.*, 2006].

2.4. Remote Sensing Methods

[14] The dominant vegetation cover is an important indicator of ecosystem diversity. Owing to the remoteness of and difficult access to the study sites, we were not able to study the vegetation in detail during the field campaign. Remote sensing was employed, therefore, to obtain information on the vegetation of the sites studied in the field. Optical properties of the land surface detected by Landsat TM satellite images can give insights into vegetation structure, greenness (a proxy for GPP), canopy openness, canopy architecture, presence of surface water etc. [Lillesand and

Table 1. Surface Peat LOI, Dry Bulk Density, Nutrient Content (in the Order of Increasing Ca Content), pH, and WT With Standard Deviations^a

Study Site	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N	pH	WT (cm)
Miraflores (forested) ^b	98 ± 1	0.050 ± 0.024	65 ± 6	48 ± 22	1.6 ± 0.7	7.0 ± 4.8	600 ± 82	100 ± 38	118 ± 46	2.8 ± 0.5	3.6 ± 2.3	1133 ± 100	55.5 ± 1.32	1.98 ± 0.18	3.8 ± 0.1	10 ± 5 (n = 6)
Nueva York (forested)	97 ± 1	0.044 ± 0.010	75 ± 26	73 ± 19	1.1 ± 0.6	5.1 ± 2.9	725 ± 236	160 ± 52	173 ± 34	2.3 ± 0.6	6.1 ± 2.8	1180 ± 62	53.7 ± 0.70	2.43 ± 0.51	3.9 ± 0.0	3 ± 6 (n = 7)
Aucayacu (forested)	97 ± 2	0.073 ± 0.031	90 ± 42	48 ± 36	2.0 ± 1	3.0 ± 2	575 ± 171	85 ± 58	73 ± 35	3.0 ± 2	9.0 ± 12	1268 ± 648	56.5 ± 2.16	1.76 ± 0.36	3.8 ± 0.2	9 ± 3 (n = 8)
Roca Fuerte (center) ^b	97 ± 2	0.042 ± 0.012	158 ± 116	133 ± 22	1.2 ± 0.8	6.5 ± 1.0	800 ± 82	215 ± 166	200 ± 84	2.8 ± 2.0	7.0 ± 5.6	1225 ± 159	53.0 ± 0.39	1.92 ± 0.37	3.8 ± 0.1	11 ± 1 (n = 2)
(forested, high canopy)																
<i>Boundary Between Nutrient-Poor and Nutrient-Rich Conditions</i>																
Roca Fuerte (edge) ^b	82 ± 4	0.084 ± 0.015	1715 ± 1039	685 ± 163	2.4 ± 0.9	47.6 ± 23.9	4700 ± 141	970 ± 382	870 ± 325	18.9 ± 0.8	82.6 ± 2.0	1895 ± 219	45.1 ± 2.95	1.79 ± 0.17	4.5 ± 0.1	10 ± 9 (n = 2)
(floodplain forest)																
Roca Fuerte (midtransect) ^b	87 ± 4	0.055 ± 0.025	2230 ± 750	395 ± 49	5.8 ± 2.6	52.7 ± 10.0	2500 ± 424	1140 ± 424	680 ± 57	11.8 ± 1.4	52.8 ± 3.4	1535 ± 148	48.2 ± 1.98	1.90 ± 0.26	4.4 ± 0.0	8 ± 1 (n = 3)
(forested, low canopy)																
Nueva Alianza (open, scattered)	94 ± 4	0.022 ± 0.008	2818 ± 848	645 ± 138	4.3 ± 0.5	248.1 ± 61.6	3750 ± 2408	305 ± 131	338 ± 222	9.4 ± 3.1	2.6 ± 1.1	1408 ± 82	50.6 ± 2.77	2.42 ± 0.12	5.7 ± 0.2	0 ± 0 (n = 5)
<i>M. flexuosa</i>																
Tachacochoa ^c	63 ± 27	0.069 ± 0.013	4650 ± 2701	1245 ± 658	5.0 ± 4.8	44.0 ± 18.1	3850 ± 1202	4335 ± 4589	670 ± 14	20.9 ± 1.1	13.6 ± 8.9	2675 ± 2086	33.2 ± 14.7	1.85 ± 0.69	5.1 ± 0.2	0 ± 0 (n = 6)
(<i>M. flexuosa</i> palm swamp)																
Maquia (open, scattered)	96 ± 1	0.019 ± 0.007	5905 ± 849	388 ± 137	16.2 ± 3.8	105.2 ± 39.2	2425 ± 1124	565 ± 835	175 ± 124	11.0 ± 8.3	3.4 ± 5.5	2245 ± 595	51.3 ± 0.93	2.53 ± 0.40	6.1 ± 0.3	0 ± 0 (n = 8)
<i>M. flexuosa</i>																
San Roque	69 ± 14	0.087 ± 0.027	9898 ± 1158	2770 ± 1805	5.4 ± 4.2	243.8 ± 60.2	11525 ± 3090	5530 ± 3946	605 ± 76	37.7 ± 18.8	23.4 ± 12.0	3650 ± 175	36.9 ± 7.97	2.04 ± 0.51	5.8 ± 0.2	14 ± 6 (n = 5)
(<i>M. flexuosa</i> palm swamp)																
Buena Vista del Maquia	74 ± 23	0.075 ± 0.047	10250 ± 2328	2410 ± 2082	8.8 ± 7.6	70.1 ± 23.4	6150 ± 4835	5100 ± 6321	433 ± 126	39.1 ± 35.2	36.1 ± 37.3	5510 ± 2579	40.1 ± 12.5	2.18 ± 0.77	6.0 ± 0.2	7 ± 6 (n = 7)
(<i>M. flexuosa</i> palm swamp)																

^aThe values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.^bFor the edge and middle parts of the Roca Fuerte site (NR), n = 2 for the nutrient content, because only one core was collected from these zones. For the center (NP), n = 4.^cFor the Tachacochoa site (NR), n = 2 for the nutrient content measurements because of the shallow peat.

Figure 3. Topography of four peat deposits. The black deposits include peat intersected by minerogenic intrusions (see Tables 5–8). The locations of the entire cores analyzed for nutrient content are indicated with arrows. (a) Aucayacu (NP) (peat thickness below WT was extrapolated), (b) Roca Fuerte (NP + NR), (c) Nueva Alianza (NR) (peat thickness was measured in the center (1 km) and the rest was extrapolated), and (d) Maquía (NR). (The topography was measured from 0 km to 5 km, and the rest was extrapolated.) Note different scales on the x axis.

Keifer, 2000]. Also, pixel values of satellite images have been shown to be efficient in predicting landscape-scale floristic and edaphic patterns in other western Amazonian forest types [Tuomisto *et al.*, 2003]. We applied a posterior remote sensing analysis on the sites studied in the field in order to assess indirectly their vegetation properties. A Principal Components Analysis (PCA) of a Landsat TM satellite image (WRS-2, Path 007, Row 063, downloaded from <http://glcfapp.glcf.umd.edu:8080/esdi/index.jsp>) was performed using the program Erdas Imagine 9.1. PCA was chosen 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). The PC1 values were extracted from the image for further analyses in the area of each field site by using areas of interest (AOI).

One AOI was drawn on the image in the central part of each field site. Three AOIs were drawn on the Roca Fuerte site: one on each of the three different vegetation zones represented by different colors on the satellite image (Figure 2a). The Maquía and Buena Vista del Maquía sites were excluded from the analysis, because they were located on a different satellite image. Thus, the total number of AOIs was nine. Subsequently, the PCA image was subset with each AOI. Pixel values from ten random pixels of each subset AOI area were extracted for further analyses. In order to study whether the nine AOIs were different as regards their pixel values (representing potential differences in vegetation), the variance of the pixel values between and within the peatlands was analyzed with one-way analysis of variance (ANOVA) using SPSS 16.0. Tukey pairwise comparisons

Table 2a. Results of the Principal Components Loadings (Eigenmatrix)

	PC1	PC2	PC3	PC4	PC5	PC6	Total
Band 1	0.45	0.47	0.075	0.69	−0.11	−0.29	
Band 2	0.32	0.4	0.01	−0.12	0.1	0.84	
Band 3	0.24	0.52	−0.09	−0.67	0.14	−0.45	
Band 4	0.69	−0.5	0.47	−0.19	−0.1	−0.04	
Band 5	0.37	−0.31	−0.71	0.11	0.5	−0.03	
Band 7	0.16	−0.05	−0.5	−0.12	−0.84	0.05	
Eigenvalue	5474.17	108.34	28.46	4.32	1.56	0.97	5617.82
Percent of the variance	97.44	1.93	0.51	0.08	0.03	0.02	100.00
Cumulative percent of the variance	97.44	99.37	99.88	99.95	99.98	100.00	

Table 2b. Results of the ANOVA of the Pixel Values Extracted From the PCA Image

	Sum of Squares	df	Mean Square	F	Significance
Between peatlands	6857.222	8	857.153	134.293	0.000
Within peatlands	517.000	81	6.383		
Total	7374.222	89			

were used to assess which AOIs were different from each other.

3. Results

3.1. Nutrient Content in the Surface Peat and Topography of the Peat Deposits

[15] The LOI values of the surface peat samples were high (mostly 82–98%), confirming that the sites were peatlands according to the definition of the Geological Survey of Finland (min. 30 cm peat with more than 75% pure organic material). Only at the Tacshacocha, San Roque and Buena Vista del Maquia sites was the LOI of the surface samples lower than this (63%, 69%, and 74%, respectively), suggesting that these sites were wetlands with clayey peat. On the basis of the Ca, Mg, Mn and Fe contents of the surface peats (<90 cm), the study sites could be divided into either a nutrient-poor (NP, four sites) or a nutrient-rich (NR, six sites) group (Table 1). At the Roca Fuerte site, the two outer vegetation zones were part of the nutrient-rich group and the center was nutrient-poor.

[16] The boundary between the two groups was most strikingly shown by a tenfold increase in the surface peat Ca content: from 65–158 mg kg⁻¹ (NP) to 1715–10250 mg kg⁻¹ (NR). No overlap in the ranges of the groups was observed either in the contents of Mg (NP: 48–133 mg kg⁻¹; NR: 388–2770 mg kg⁻¹), Mn (NP: 3–7 mg kg⁻¹; NR: 44–248 mg kg⁻¹) and Fe (NP: 575–800 mg kg⁻¹; NR: 2425–11525 mg kg⁻¹). The boundary was also observable (although with some overlap in the ranges shown by standard deviations) in the surface peat LOI values (NP: 97–98%; NR: 63–96%), in the contents of K (NP: 85–215 mg kg⁻¹; NR: 305–5530 mg kg⁻¹), P (NP: 73–200 mg kg⁻¹; NR: 175–870 mg kg⁻¹), Zn (NP: 2.3–3 mg kg⁻¹; NR: 9.4–39.1 mg kg⁻¹), and C (NP: 53–57%; NR: 33–51%), and in the Ca/Mg ratio (NP: 1.1–2; NR: 2.4–16.2) (Table 1). The boundary was only weakly observable in the surface peat dry bulk density (NP: 0.042–0.073 g cm⁻³; NR: 0.019–0.087 g cm⁻³) and in the contents of Cu (NP: 3.6–9 mg kg⁻¹; NR: 2.6–82.6 mg kg⁻¹), S (NP: 1133–1268 mg kg⁻¹; NR: 1408–5510 mg kg⁻¹) and N (NP: 1.76–2.43%; NR: 1.79–2.53%).

[17] The surface peat Ca/Mg ratio of the nutrient-poor group was comparable to that of Amazonian rainwater (1–3.5 [Furch and Junk, 1997]) and the global average for continental rainwater (0.4–6 [Berner and Berner, 1996]). The surface peat Ca/Mg ratio of the nutrient-rich group was higher than or comparable to rainwater (Table 1).

[18] Within the nutrient-rich group, a clear gradient of increasing surface peat Ca content with a sixfold difference between the extremes of the group was detected (Table 1). A gradient of increasing surface peat Mg, Fe and Mn contents

was also observed within this group, but the ordering of the sites based on gradients for these elements was different compared to that for Ca.

[19] Surface peat water pH was lower at the nutrient-poor sites (3.8–3.9) than at the nutrient-rich sites (4.4–6.1), a reflection of the greater exchangeable alkalinity and the smaller amount of organic acids present in the minerotrophic peat [Siegel and Glaser, 1987, Table 1]. Water table of the nutrient-poor sites (3–11 cm) was below the soil surface. Water table of the nutrient-rich sites (0–14 cm) was sometimes above or on the soil surface, forming large pools (Table 1).

[20] At the Aucayacu (NP) (Figure 3a), Roca Fuerte (NP + NR) (Figure 3b), and Nueva Alianza (NR) (Figure 3c) sites, the peat surface at the center was located 576 cm, 536 cm, and 136 cm, respectively, above the water level of the closest stream. Consequently, these sites had a domed shape typical of ombrotrophic bogs. By contrast, the Maquia peatland (NR) was located in a depression behind a 7 m high levee and had a relatively flat peat surface (Figure 3d).

3.2. Remote Sensing Results

[21] According to the Eigenmatrix (Table 2a), the PC1 values were much more important in explaining the variability of the data than the other principal components: 97% of the variance could be explained by the PC1 values. Band 4 had the strongest correlation with PC1 (0.69), while the other bands had weaker correlations (band 1: 0.45; band 5: 0.37; band 2: 0.32; band 3: 0.24; band 7: 0.16). The PC1 values derived from the satellite image were statistically different between the different AOIs ($p < 0.0001$, Table 2b). The AOIs could be divided into five different groups (Tukey pairwise comparisons; Table 2c), of which, nutrient-rich sites were found in four and nutrient-poor sites in three groups. Thus, the grouping of the sites made on the basis of the pixel PC1 values was different compared to the one made on the basis of surface peat nutrient content. No consistent trend or correlation between these two was observed.

[22] The three different concentric vegetation zones of the Roca Fuerte site (NP + NR) (see Figure 2a) were significantly different from each other (Table 2c). Our visual field observations support the finding that the vegetation of the

Table 2c. Results of the Tukey Pairwise Comparisons of Means by Groups

	N	Subset for Alpha = 0.05				
		1	2	3	4	5
Nueva Alianza (NR)	10	142.90				
Nueva York (NP)	10		153.40			
Miraflores (NP)	10		154.10			
Tacshacocha (NR)	10		155.80			
Aucayacu (NP)	10			160.80		
San Roque (NR)	10			162.10		
Roca Fuerte (NR)	10			163.50		
(midtransect)						
Roca Fuerte (NP)	10				169.70	
(center)						
Roca Fuerte (NR)	10					173.70
(edge)						
Significance		1.000	0.465	0.304	1.000	1.000

Table 3. LOI, Dry Bulk Density, and Nutrient Content of the Miraflores Core^a

Depth (cm)	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N
30–40	97	0.059	60	80	0.8	10.6	500	150	140	3.0	2.3	1000	53.6	2.12
80–90	97	0.015	70	40	1.8	11.6	600	70	50	3.0	1.4	1200	55.8	1.80
130–140	98	0.072	90	50	1.8	2.7	900	100	70	4.5	13.7	1150	55.5	1.48
180–190	95	0.075	30	140	0.2	3.2	700	280	100	1.6	14	800	53.0	0.90
<i>Mineral Sediment Intrusion (No Samples)</i>														
280–290	74	0.143	150	1110	0.1	15.9	6300	2410	400	34.2	42.6	2180	41.5	1.12

^aNP, 360 cm thick, located in the center of the site at the end of a transect of 2.5 km. The values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.

sites was very variable: the nutrient-poor sites were forested peatlands, and the nutrient-rich sites were *M. flexuosa* palm swamps, open peatlands with scattered *M. flexuosa* palms or forested peatlands (see the first column in Table 1).

3.3. Nutrient Content in the Peat Cores

[23] The thickness of the studied cores collected from central positions in the peatlands varied from 60 cm to 745 cm, including pure peat, clayey peat and mud layers. Of the four peatlands classified as nutrient-poor on the basis of the surface peat nutrient content, the Miraflores core (NP, 360 cm thick, Table 3) had a high LOI (95–98%), a high C content (53–56%), low Ca, Mg, Mn, Fe, K, P, Zn, Cu and S contents and a low Ca/Mg ratio (all comparable to those of the nutrient-poor group) from the peat surface to a depth of 180–190 cm. Below an intrusion of minerogenic sediments (between 180 and 280 cm), a buried peat deposit was observed, with Mg, Fe, K, P, Zn, Cu and S contents, LOI (74%) and C content (42%) comparable to the nutrient-rich group (but Ca and Mn contents and a Ca/Mg ratio comparable to the nutrient-poor group). By contrast, the N content of the core decreased toward the base.

[24] The Nueva York core (NP, 310 cm thick, Table 4) had a high LOI (96–99%), a high C content (54–55%), low Ca, Mg, Mn, Fe, K, P, Zn, Cu and S contents and a low Ca/Mg ratio (all comparable to the nutrient-poor group) from the surface to a depth of about 230 cm (180 cm for Cu), exhibiting an increasing trend toward the base. At the base of the core, the LOI (89%), C (49%), Mg, Mn, Fe, K, P, Zn and S contents and the Ca/Mg ratio were at the level of the nutrient-rich group. The Ca content also increased toward the base of the core but did not reach the level of the nutrient-rich group, while the N content decreased.

[25] The central core of the highest raised bog, Aucayacu (NP, 745 cm thick, Table 5), had a high LOI (97–99%), a high C content (54–58%) and low Ca, Mg, Mn, Fe, K, P,

Zn, Cu and S contents (all comparable to the nutrient-poor group) from the surface to a depth of about 340–380 cm. Nevertheless, at 230–240 cm, we observed a peak in Ca, Mg, Mn, Fe, K, P, Cu and S contents (corresponding to a lower LOI and C content). At about 380–440 cm, the Ca, Mg, Mn, Fe, K, P, Zn, Cu and S contents gradually increased (and LOI and C content decreased) to the level of the nutrient-rich group and remained high (low) until the base of the core. The intrusion of minerogenic sediments (mixed with peat) at 490–540 cm was characterized by very high Fe, K, Zn, Cu and S contents, relatively high Ca, Mg, and Mn contents, a high dry bulk density (0.232–0.239 g cm⁻³), a low LOI (45–47%) and a low C content (25–42%). For both Ca/Mg ratio and N content there was no discernable trend.

[26] The Roca Fuerte core (NP, 535 cm thick, Table 6) had a high LOI (97–99%), a high C content (53–55%), low Ca, Mg, Mn, Fe, K, P, Zn and Cu contents and a low Ca/Mg ratio (all comparable to the nutrient-poor group) from the surface to a depth of 170–180 cm. At 230–240 cm, the Ca, Mg, Mn and Fe contents and the Ca/Mg ratio started to increase and reached soon the level of the nutrient-rich group. Despite this, the LOI (90–98%) and C content (50–58%) stayed at the level of the nutrient-poor group throughout the core. For K, P, Zn, Cu, S and N contents, we could not observe any discernable trend (except a peak for P at 230–240 cm, for Zn at 230–270 cm and for Cu and S at 230–240 cm and at the base).

[27] Of the five peatlands classified as nutrient-rich, the Nueva Alianza core (NR, 200 cm thick, Table 7) had high Ca, Mg, Mn, Fe, K, Zn and S contents and a high Ca/Mg ratio throughout the core (all comparable to the nutrient-rich group). A low peak of Fe, K, P, Zn and Cu contents was observed at 80–90 cm. The Mg, Fe, Zn and Cu contents were very high at the base of the core, while LOI (64–96%) and C content (34–53%) were comparable to the nutrient-

Table 4. LOI, Dry Bulk Density, and Nutrient Content of the Nueva York Core^a

Depth (cm)	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N
30–40	99	0.054	60	60	1.0	9.3	700	180	140	1.5	3.8	1150	54.1	2.63
80–90	97	0.035	110	60	1.8	4.6	400	100	160	2.4	7.3	1110	54.1	2.25
130–140	97	0.073	70	60	1.2	5.4	800	120	120	2.5	7.8	900	55.1	1.78
180–190	96	0.043	120	140	0.9	8.7	1000	250	120	1.9	13.3	1170	53.5	1.83
230–240	96	0.042	340	180	1.9	17.6	1500	170	120	1.3	16.2	1330	53.8	1.48
280–290	89	0.065	810	360	2.3	38.8	3500	350	470	8.8	53.2	1610	48.7	1.51

^aNP, 310 cm thick, located in the center of the site at the end of a transect of 3 km. The values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.

Table 5. LOI, Dry Bulk Density, and Nutrient Content of the Aucayacu Core^a

Depth (cm)	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N
30–40	98	0.036	60	30	2.0	2.4	400	70	110	2.6	1.2	1070	54.0	2.25
80–90	98	0.062	60	20	3.0	1.7	500	60	60	2.1	3.0	1060	55.9	1.83
130–140	99	0.088	120	30	4.0	2.8	600	80	60	2.5	2.3	1140	56.0	1.64
180–190	98	0.091	50	20	2.5	1.1	700	20	40	0.6	7.6	1250	57.1	1.69
230–240	89	0.096	160	340	0.5	5.8	1500	920	170	4.0	37.1	2970	50.4	1.45
280–290	99	0.073	40	30	1.3	1.3	700	40	40	0.9	4.8	1400	57.9	1.52
330–340	97	0.091	70	50	1.4	2.5	1100	70	60	0.5	9.2	1290	58.1	1.63
380–390	92	0.064	100	200	0.5	5.2	1800	460	150	5.8	18.9	1480	54.1	1.59
430–440	80	0.109	260	690	0.4	12.3	3800	1420	410	22.1	59.6	1890	45.9	1.14
490–500	45	0.239	910	1880	0.5	37	13000	5290	380	72.6	110	1810	24.8	0.91
530–540	47	0.232	2160	2580	0.8	66.3	17800	6440	300	118.9	130	3150	41.9	1.32
580–590	75	0.129	930	1000	0.9	34.8	9800	1950	200	78.4	103.9	6230	25.5	0.91
630–640	77	0.137	2430	1220	2.0	60.9	13400	1560	430	66	197.4	8550	42.4	1.24
680–690	91	0.080	2360	620	3.8	51.2	13200	700	120	32.5	37.2	11940	51.5	1.61
720–730	67	0.122	1320	1910	0.7	48.6	11400	3530	180	31.4	73	4040	37.2	1.20

^aNP, 745 cm thick, located at the end of a transect of 3.5 km. The values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.

rich group throughout the core. The N content was about the same as in the nutrient-poor sites and no consistent trend was observed.

[28] The Tacshacocha core (NR) was very shallow (60 cm thick), and thus only surface peat samples (shown in Table 1) were collected (at two study points along a transect of 2.5 km).

[29] The Maquía core (NR, 430 cm thick, Table 8) had high Ca, Mg, Mn, Fe, Zn and S contents and a high Ca/Mg ratio throughout the core. An increasing trend toward the base of the core was observed, especially for Ca and S. The LOI and C content were high at the surface (94–97% and 50–52%, respectively) and decreased toward the base of the core (80–93% and 43–51%, respectively). Low peaks of Mn, K, P and Cu were observed at 80–150 cm. The P content was relatively low throughout the core. One intrusion of minerogenic sediments was encountered between 340 and 380 cm, and the peat deposit under the intrusion had notably high Ca, Mg, Fe, K and S contents and a low LOI (51%) and C content (28%). The N content was about the same as in the nutrient-poor sites and no consistent trend was observed.

[30] The San Roque core (NR, 635 cm thick, Table 9) had a complex stratigraphy of peat and minerogenic intrusions. Ca, Mg, Mn, Fe and S contents and Ca/Mg ratio were very high throughout the core. The K, P, Zn and Cu contents were relatively high, but the P content decreased surprisingly to the level of the nutrient-poor group at the base of

the core (430–540 cm). The LOI (62–91%) and C content (30–53%) were quite low throughout, while the N content was lower than in the other cores.

[31] The Buena Vista del Maquía core (NR, 170 cm thick, Table 10) was intersected by one minerogenic intrusion. The core had very high Ca, Mg, K and S contents, relatively high Mn, Fe, P, Zn, Cu contents, a Ca/Mg ratio comparable to the nutrient-rich group, a relatively low LOI (61–93%) and a low C content (32–50%). The N content was about the same as in the other sites and no consistent trend was observed.

4. Discussion

4.1. Current Diversity of Peatland Ecosystems

[32] Our results show that the Pastaza-Marañón basin harbors (1) several previously unstudied peat deposits (up to 7.5 m thick) and (2) a considerable diversity of peatland ecosystems, indicated by differences in surface peat nutrient content, topography and vegetation. The study sites can be placed on a gradient of surface peat nutrient content ranging from very nutrient-poor to nutrient-rich. A sharp change in the surface peat nutrient content on this gradient indicates the boundary between a nutrient-rich and a nutrient-poor group. In this Amazonian environment, the most likely explanation for the marked change in surface peat nutrient content between the two groups is the change from river- to atmosphere-influenced conditions [cf. Page *et al.*, 1999; Weiss *et al.*, 2002; Muller *et al.*, 2006; Lähteenoja *et al.*,

Table 6. LOI, Dry Bulk Density, and Nutrient Content of the Roca Fuerte Core^a

Depth (cm)	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N
30–40	98	0.048	90	110	0.8	6.2	800	100	150	1.2	2.7	1100	53.0	1.77
80–90	99	0.024	330	140	2.4	5.8	700	170	110	5.4	4.8	1290	53.3	1.48
120–130	97	0.077	50	60	0.8	2.3	600	90	310	1.2	9.4	1450	54.0	2.05
170–180	97	0.040	90	90	1.0	3.9	800	140	130	1.8	9.5	1220	55.1	1.67
230–240	90	0.103	290	190	1.5	10.9	2900	180	460	6.4	48.6	2380	49.8	1.66
260–270	97	0.065	480	140	3.4	13.4	1500	140	210	9.6	8.4	1810	57.0	2.27
310–320	97	0.076	1560	430	3.6	41.3	2900	190	50	2.1	5.6	600	58.0	1.46
360–370	98	0.048	670	250	2.7	29.1	1800	320	60	3.0	6.9	910	56.1	0.88
410–420	98	0.034	760	240	3.2	22.5	1500	100	40	1.1	7.4	850	56.3	0.88
470–480	96	0.065	2630	880	3.0	101	7000	130	130	5.3	27.7	1830	55.9	1.55
510–520	93	0.094	3200	1070	3.0	126.7	9300	180	130	9.1	138.1	2000	50.9	1.44

^aNP, 535 cm thick, located in the center of the site at the end of a transect of 4 km. The values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.

Table 7. LOI, Dry Bulk Density, and Nutrient Content of the Nueva Alianza Core^a

Depth (cm)	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N
30–40	96	0.024	3180	670	4.7	306.3	3700	240	440	11.6	2.7	1510	51.8	2.36
80–90	96	0.018	3830	830	4.6	295.7	1500	220	120	5.0	1.1	1410	52.5	2.29
130–140	90	0.053	3220	650	5.0	216	2500	710	470	17.3	10.2	1470	48.4	2.33
180–190	64	0.103	3380	1190	2.8	150.4	10100	1970	660	35.6	93	1480	33.7	1.63

^aNR, 200 cm thick, located at the end of a transect of 2 km. The values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.

2009a]. The nutrient-poor peatlands are rain-fed ombrotrophic bogs (with a domed topography), which have a peat nutrient content similar to bogs of other tropical regions [Page *et al.*, 1999; Weiss *et al.*, 2002]. In contrast, the nutrient-rich sites are minerotrophic ecosystems fed by river, surface or groundwater. Accordingly, we interpret that at the Roca Fuerte site, the two outer vegetation zones (NR) are covered by the floods of the nearby San Luis stream, while the central zone (NP) is dependent on atmospheric water and nutrient inputs only.

[33] The extractable Ca, Mg and K contents of the fluvial sediments of the rivers Tigre (Ca: 1000 mg kg⁻¹, Mg: 270 mg kg⁻¹, K: 740 mg kg⁻¹) and Ucayali (Ca: 4000 mg kg⁻¹, Mg: 180 mg kg⁻¹, K: 1370 mg kg⁻¹) [Kalliola *et al.*, 1993] were higher than those of the ombrotrophic bogs, and lower than or comparable to those of the nutrient-rich peatlands. This supports our interpretation of the boundary between river- and atmosphere-influenced conditions.

[34] The gradient of increasing nutrient content within the nutrient-rich group of peatlands indicates that these sites are influenced by waters of different nutrient status and/or over different durations. Consequently, considerable diversity of peatland ecosystems also exists within the nutrient-rich group. Some variation in nutrient content was also observed within the nutrient-poor group, which may be due, e.g., to a different extent of bioaccumulation in the surface peat layer [Page *et al.*, 1999; Weiss *et al.*, 2002; Muller *et al.*, 2006] due to differences in the age, duration of the ombrotrophic phase and vegetation of the sites.

[35] We interpret the significant variation in pixel values as being indicative of differences in peatland vegetation types [cf. Tuomisto *et al.*, 2003]. When taken together with the considerable variation in peat biogeochemistry, this offers strong evidence that the diversity of peatland ecosystems in the study area is very high. The grouping of sites on the basis of surface peat nutrient contents was different compared to that obtained from the analysis of pixel values.

Thus the various qualities of the vegetation cover obtained using a remote sensing approach were not directly reflected by the nutrient contents of the peat substrates. The vegetation diversity of these sites clearly requires more detailed investigation. Nevertheless, we can confidently conclude that the Pastaza-Marañón basin currently harbors not only a large variation in peat chemical and physical characteristics but in peatland ecosystem types.

4.2. Developmental Histories

[36] Surface peat nutrient content provides information on the current properties of the ecosystem and the growing conditions for the vegetation. The changes in nutrient content in peat profiles provide information on ecosystem history and developmental phases. This basic information on peatland ecosystem characteristics can be applied in subsequent palynological, geological and carbon-cycling studies.

[37] The four peatlands classified as ombrotrophic had variable developmental histories based on the variation of the concentrations of chemical elements. The Miraflores site (NP) was originally a minerotrophic peatland, which was subsequently buried under minerogenic river sediments. However, the Ca and Mn contents and Ca/Mg ratio comparable to the nutrient-poor group suggests that initial peatland may also have been ombrotrophic. After the burial event, peat accumulation started again and the ecosystem developed (with no further interruptions) into a very nutrient-poor ombrotrophic bog.

[38] By contrast, the Nueva York peatland (NP) developed gradually and without interruption to a nutrient-poor ombrotrophic bog. The relatively high nutrient content close to the base of the Nueva York core probably represents an initial minerotrophic phase in peatland development and/or capillary rise (max. 30–40 cm) of groundwater in the peat pores [Hill and Siegel, 1991; Romanov, 1968; McCabe, 1991].

[39] The raised Aucayacu bog (NP) was initially a very nutrient-rich minerotrophic peatland, which was subse-

Table 8. LOI, Dry Bulk Density, and Nutrient Content of the Maquía Core^a

Depth (cm)	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N
30–40	94	0.015	6140	570	10.8	160.4	3900	1810	360	23.5	11.7	2810	50.2	2.71
80–90	97	0.013	6260	350	17.9	68	1600	110	130	7.3	1.3	2680	52.4	2.94
140–150	96	0.026	8030	410	19.6	55.2	2200	100	260	7.1	4.1	3680	51.7	2.62
180–190	88	0.055	9680	1030	9.4	45.4	4300	1790	300	8.9	19.6	6910	48.1	2.60
230–240	93	0.043	12090	630	19.2	77.3	4800	460	220	5.3	5.1	9060	51.1	2.29
280–290	93	0.030	14210	680	20.9	133.5	4500	250	200	7.8	3.9	8150	50.8	2.47
330–340	80	0.063	14810	2280	6.5	168.7	7500	4680	280	71.3	22.9	9710	43.4	2.03
<i>Mineral Sediment Intrusion</i>														
380–390	51	0.175	14760	4680	3.2	237.4	32300	10640	450	94.4	63.5	39300	27.7	1.62

^aNR, 430 cm thick, located in the center of the site at the end of a transect of 4 km. The values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.

Table 9. LOI, Dry Bulk Density, and Nutrient Content of the San Roque Core^a

Depth (cm)	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N
30–40	84	0.064	10610	970	10.9	229.2	8000	1400	530	18.9	10.9	3740	44.8	2.57
80–90	62	0.069	9200	3310	2.8	176.4	11700	7490	580	35.9	29	3480	32.3	1.74
120–130	72	0.097	11130	2430	4.6	197.2	11700	4690	480	28.4	27.4	4510	37.7	1.83
<i>Mineral Sediment Intrusion</i>														
170–180	56	0.078	9590	4040	2.4	178.3	13900	7880	470	94.1	45.9	5370	29.8	1.39
<i>Mineral Sediment Intrusion (No Samples)</i>														
330–340	88	0.140	11100	570	19.5	164.2	13500	670	330	11.7	41.7	8020	51.0	1.53
380–390	84	0.078	10580	1260	8.4	169.1	10600	1880	190	20.3	33.4	5710	48.5	1.23
430–440	91	0.121	14930	880	17.0	299.6	8300	320	70	6.9	29.8	3910	53.1	1.33
480–490	86	0.161	14640	1610	9.1	315.3	7300	1720	60	14.2	33.1	2680	50.0	1.17
530–540	91	0.153	15920	1280	12.4	323.5	5300	350	50	8.5	39.4	4060	52.9	1.40

^aNR, 635 cm thick, located at the end of a transect of 2 km. The values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.

quently buried under (and mixed with) minerogenic sediments (at 490–540 cm). After the burial event, peat accumulation started again and the ecosystem gradually turned to a nutrient-poor ombrotrophic bog. Ombrotrophic peat accumulation was interrupted by a minor minerotrophic phase at 230–240 cm (shown by the peak in Ca, Mg, Mn, Fe, K, P, Cu and S contents), probably induced by an especially massive flood or a change in the position of the nearby river channel, resulting in surface water influence. The Aucayacu peatland subsequently reverted to an ombrotrophic system, its current state.

[40] The Roca Fuerte bog (NP + NR) was a minerotrophic, river-influenced peatland for more than half of its developmental history, shown by the high Ca, Mg, Mn and Fe contents and the high Ca/Mg ratio of the lower part of the core. During the last phase of peat accumulation (0–180 cm), the center of the peatland attained ombrotrophic status, shown by the low nutrient contents. Interestingly, all four nutrient-poor bogs developed on nutrient-rich volcanic soil composed of pyroclastic debris from the Pastaza fan, originating from the Ecuadorean volcanoes [Räsänen *et al.*, 1990, 1992; Neller *et al.*, 1992, and references therein].

[41] The five peatlands classified as nutrient-rich also had variable developmental histories. The high nutrient content of the Nueva Alianza site (NR) (especially the considerably higher Ca content compared to the nutrient-poor sites) indicates that this peatland has been minerotrophic throughout its developmental history and subject to likely frequent inundation by the floodwaters of the nearby Sábalo stream despite having a raised peat surface (136 cm above the stream water level). Consequently, the Nueva Alianza site (NR) could provisionally be defined as a transitional “minerotrophic raised bog.”

[42] The Tacshacocha site (NR) may represent an early developmental phase of an ombrotrophic bog because of its relatively low Ca content and low Ca/Mg ratio and, consequently, may develop into an ombrotrophic bog over time as more peat accumulates.

[43] The high nutrient content of the Maquía core (NR) indicates that this peatland has been minerotrophic throughout its developmental history. Owing to its location in a depression and the flat peat surface, the annual floods of the nearby Maquía river probably flow onto this peatland on a regular basis. The very high Ca, Mg, Fe, K and S contents in the buried peat deposit probably indicate past sedimentation from the nearby sediment-rich Ucayali river.

[44] In the San Roque peatland (NR), peat accumulation has always been characterized by minerotrophic conditions. Peat accumulation was interrupted by several intrusions of minerogenic sediments, which explains the large periodic inputs of Ca, Mg, Mn, Fe and S throughout the core.

[45] The Buena Vista del Maquía peatland (NR) has also been minerotrophic throughout its history, with peat accumulation interrupted by one minerogenic intrusion. These factors together explain the very high Ca, Mg, K and S contents throughout the core. While the Nueva Alianza (NR) and Maquía (NR) peatlands have clearly received water and nutrients from nutrient-rich flood waters, the San Roque (NR) and Buena Vista del Maquía (NR) peatlands have also been affected by sediment inputs from adjacent river courses.

[46] In summary, the developmental histories outlined above indicate that parts of the Pastaza-Marañón basin have been sufficiently stable to allow the development of thick ombrotrophic peat, while other parts have been so intensively affected by the flooding or sedimentation of the adjacent

Table 10. LOI, Dry Bulk Density, and Nutrient Content of the Buena Vista del Maquía Core^a

Depth (cm)	LOI (%)	BD (g cm ⁻³)	Ca	Mg	Ca/Mg	Mn	Fe	K	P	Zn	Cu	S	C	N
30–40	93	0.028	10130	750	13.5	41.9	1700	230	300	10.8	6.7	3170	50.0	2.87
80–90	67	0.101	9530	2990	3.2	61.5	8200	6550	530	84.1	85.1	9140	36.5	1.79
<i>Mineral Sediment Intrusion</i>														
130–140	61	0.139	9890	3410	2.9	90.4	38200	8330	270	56.5	56	42700	32.2	1.68

^aNR, 170 cm thick, located at the end of a transect of 3 km. The values of the chemical elements are mg kg⁻¹ dry peat (with an uncertainty of ±5%) and % for C and N. BD, bulk density.

river courses that peat accumulation has been interrupted on several occasions, creating minerogenic intrusions.

4.3. Significance of This Study for Amazonian Ecosystem Diversity and Ecology

[47] The existence of this diversity of peatland ecosystems has several consequences for the ecology of the Amazonian lowlands. The variation in peatland ecosystem types provides a diversity of habitats, which are very different from nonflooded (*terra firme*) rain forest habitats and from other wetland habitats on the floodplains. Consequently, a thorough species survey would probably reveal important information on the importance of these peatlands as wildlife habitats [cf. *Nicholson*, 1997; *Page et al.*, 1997, 1999; *Morrogh-Bernard et al.*, 2003]. For example, the ombrotrophic bogs may provide a habitat for unique species adapted for oligotrophic environments [*Lähteenoja et al.*, 2009a] that are otherwise only known from the so-called white-sand forests occurring on nonflooded, nutrient-poor quartz sands [*Anderson*, 1981].

[48] Ombrotrophic bogs in other areas of the world are known to be excellent sources of information on Holocene climate variability, atmospheric deposition, palaeohydrology and rain forest vegetation dynamics [*Weiss et al.*, 2002; *Muller et al.*, 2006]. Currently, there are no other detailed, high resolution palaeoecological records in this region, and, consequently, future palynological studies of these peatlands could reveal important long-term trends of the Amazonian rain forest biome, extending back to the time of peat initiation [cf. *Ledru*, 2001; *Hoorn*, 2006]. The extensive peatlands must also affect the hydrological dynamics of the surrounding dense network of streams and rivers (see Figure 1) by storing a considerable amount of water in the peat and by affecting the direction of the surface water flow as well as river water chemistry through release of DOC [e.g., *McNamara et al.*, 1992; *Page et al.*, 1999; *Moore et al.*, 2010].

4.4. Comparison to Tropical Peatlands of Other Geographic Regions

[49] Of our study sites, 40% were ombrotrophic and 60% minerotrophic, while the Southeast Asian tropical peatlands are currently almost exclusively ombrotrophic. Consequently, the diversity of Amazonian peatland ecosystem types may be even higher than that in Southeast Asia, where, owing to a longer period of disturbance, many of the minerotrophic, freshwater peat swamps fringing rivers and lakes have already been lost [*Wüst and Bustin*, 2004]. A higher representation of minerotrophic peatlands in Amazonia probably implies significant differences in ecosystem function compared to Southeast Asia, including e.g., C storage and trace gas exchange. Hence, the research results obtained for Southeast Asian peatlands cannot be directly applied to Amazonian peatlands.

[50] In contrast to the peat swamp forests of Southeast Asia, our Amazonian peatland sites are still relatively undisturbed ecosystems. They are located in remote areas with difficult access and are currently not notably affected by anthropogenic activities such as logging, deforestation, drainage, fire or agriculture (even though moderate hunting and collecting by the local villagers does occur especially in the *M. flexuosa* palm swamps [*Nicholson*, 1997; *Guzmán*

Castillo, 2007]). Consequently, they provide an undisturbed analog for the increasingly heavily impacted peatlands of Southeast Asia.

5. Conclusions and Implications

[51] This study demonstrates a high diversity of peatland ecosystem types (with a maximum recorded peat thickness of 7.5 m) within the Amazonian lowlands, thus emphasizing that extensive and diverse tropical peat bogs are not limited to the Southeast Asian lowlands. The most important finding of this study is that the peatlands in our study area can be placed on a gradient of surface peat nutrient content ranging from nutrient-poor to nutrient-rich. A sharp increase in the surface peat nutrient content at one point on this gradient marks the boundary between atmosphere- and river-influenced conditions. Our results greatly expand on earlier observations of these systems [*Lähteenoja et al.*, 2009a] and support the conclusion that some peatlands in the Amazonian floodplain are true tropical ombrotrophic peat bogs.

[52] These peatlands may cover an extensive area, because, in addition to our limited field observations, visual observation of the satellite image mosaic (see Figure 1) suggests that a large part of the 120 000 km² Pastaza-Marañón foreland basin [*Räsänen et al.*, 1990, 1992] is covered by similar ecosystems. Consequently, on the basis of the high C content of the peat, their total C stock may be regionally important. Future research should focus on establishing the total area of peatlands in the basin as well as the C storage and C and trace gas exchange of the different types of peatland ecosystems.

[53] Climate change, deforestation, large-scale land use projects (like damming, road construction and oil palm plantations), and especially extensive gas and oil exploration in the Pastaza fan [*Malhi et al.*, 2008] potentially threaten these newly described ecosystems. Even if the peatlands were not affected directly by anthropogenic activities, all of these factors could contribute to the desiccation of the regional climate, generating changes in the flow of rivers and an increased risk of fire [cf. *Siegert et al.*, 2001; *Page et al.*, 2002]. The experience demonstrates that these factors can be very detrimental to the existence of tropical peatlands in Indonesia, where disturbance has resulted in a loss of habitat [*Sodhi et al.*, 2004] and the release of globally significant amounts of carbon from long-term storage [*Page et al.*, 2002]. In conclusion, the results of the present study indicate an urgent need to further investigate and especially to conserve these varied and poorly known Amazonian ecosystems, which may in the near future be among the few undisturbed tropical ombrotrophic bogs remaining in the world.

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