The effect of drainage on organic matter accumulation and plant communities of high-altitude peatlands in the Colombian tropical Andes

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SUMMARY

The tropical Andes store and regulate water outflow that serves nearly 60 million people. Most of the water is for un-managed agricultural irrigation. In this work I report how the drainage of peatlands has adversely affected the development of plant communities and recent carbon accumulation in a páramo massif at 2500 to 3800 m altitude in the northern Andes. I surveyed vegetation and water chemistry in 26 peatlands with differing intensities of drainage. Peat cores to 50 cm from two sites with contrasting drainage histories were dated using ^{210}Pb, and used to compare historical vegetation changes and carbon accumulation rates.

(A) Species composition was much affected by drainage, which resulted in a reduction in cover of *Sphagnum* and other peat-forming species, and the encroachment of sedges and *Juncus effusus*. The ability of peat to store water and carbon was also reduced in drained peatlands. Vegetation records show a shift towards sedge-*Juncus* communities around 50 years ago when agricultural use of water increased.

(B) Peat and carbon accumulation rates were lower in drained sites, indicating either greater decomposition rates of the upper peat column or lower production by the changed plant communities. The ecological services offered by peatlands to agrarian communities downstream are important. Measures to prevent peatland destruction are needed urgently.

KEY WORDS: agriculture, diversity, carbon accumulation, peat drainage, peatland management

INTRODUCTION

The tropical Andes are home to nearly 60 million people who need and use multiple ecosystem services offered by the natural landscapes of the Andes (Bradley *et al.* 2006, Armenteras *et al.* 2011, Buytaert *et al.* 2011). The combined effects of increased human pressure and climate change are a serious threat to the persistence of natural systems, particularly at very high altitudes (Bradley *et al.* 2006, Buytaert *et al.* 2006, World Bank 2011). The tropical alpine areas of the northern Andes, also known as páramos, are important water sources for the communities and ecosystems downstream (Buytaert *et al.* 2006). Within the páramos, peatlands are small but frequent and regulate water accumulation and water outflow in most of the páramo catchments (Viviroli *et al.* 2003, Farley *et al.* 2004, Holden 2005, Chimner & Karberg 2008).

Pressures to achieve greater agricultural yields have increased during the last 25 years, particularly in developing countries, creating challenges to the conservation of natural resources (Armenteras *et al.* 2011, World Bank 2011). Of particular importance is the type of land ownership: owners of small parcels of land are more likely to tap directly into the surrounding natural resources without clear management strategies and with long-term impacts on the ecosystems (Armenteras *et al.* 2011, Sánchez-Cuervo *et al.* 2012). New crop varieties and warmer climates favour uphill migration of crops, affecting areas that were hitherto uncultivated because they have a more extreme climate (Ainsworth *et al.* 2008, Young 2009).

The main ecological effect of peatlands is to accumulate organic matter by controlling the decomposition processes in the soil (Turetsky 2004). The porous peat can accumulate to depths of as much as 5 m and store large amounts of organic carbon (Kuhry 1988)—typically 250 kg m^{-2} for every 1 m depth. In the northern Andes the high porosity and water retention in peatlands underscores their importance in the local hydrological cycles (Bosman *et al.* 1994, Holden 2005, Buytaert *et al.* 2006). Andean peatlands are in topographical depressions that are on the water outflow routes from catchments and receive inputs from both runoff and below-ground water reservoirs (Hillman 1992, Glaser *et al.* 1997). Despite their relatively small sizes, peatlands in the Andes have a disproportionate effect on water regulation because the saturated soils store and release water that is later used in human activities (Holden 2005, Jauhiainen *et al.* 2008).

There are several peatland types in the tropical Andes, a differentiation forced by hydrology and water chemistry (Chee & Vitt 1989, Halsey *et al.* 1997). Three main types of Andean peatlands are: (1) poor fens dominated by *Sphagnum* mosses; (2) rich fens dominated by minerotrophic *Sphagnum* mosses or by sedges and other vascular plants; and (3) high-altitude cushion bogs dominated by vascular plants (Cleef 1981, Bosman *et al.* 1993). Nutrient supply marks the separation between rich and poor fens (Vitt 1994). Rich fens are commonly dominated by sedges, which are more competitive and can use resources faster than *Sphagnum* mosses and at the same time accelerate below-ground processes through the oxygen brought by roots and the mechanical disturbance created by root growth (Thormann & Bayley 1997, Limpens *et al.* 2004).

The rapid degradation of peatlands in the Andes makes it urgent that we understand how different types of human activities affect their ecosystem services. In the study reported here, I investigated how a complex of high-altitude peatlands in the northern Andes is affected by drainage. This study centred on the specific questions:

(A) Are the peat-forming species and peatland plant communities affected by drawdown of the water table?
(B) How are the physical and chemical characteristics of the peat and peat water affected by drainage?
(C) How fast do the plant communities respond to disturbance by draining, and how is this reflected in the macrofossil distribution?
(D) How are the recent peat and organic matter accumulation rates affected by drainage?

METHODS

Study site

The study area is in the northern part of the Andes, in the Colombian "Cordillera Oriental" within the boundaries of the Iguaque National Park at co-ordinates 5° 41′ N, 73° 25' W (Figure 1). The Iguaque Park runs along a mountainous massif approximately 8 km long that starts at 2500 m altitude and continues up to 3800 m. The massif has numerous lateral valleys with a north-south

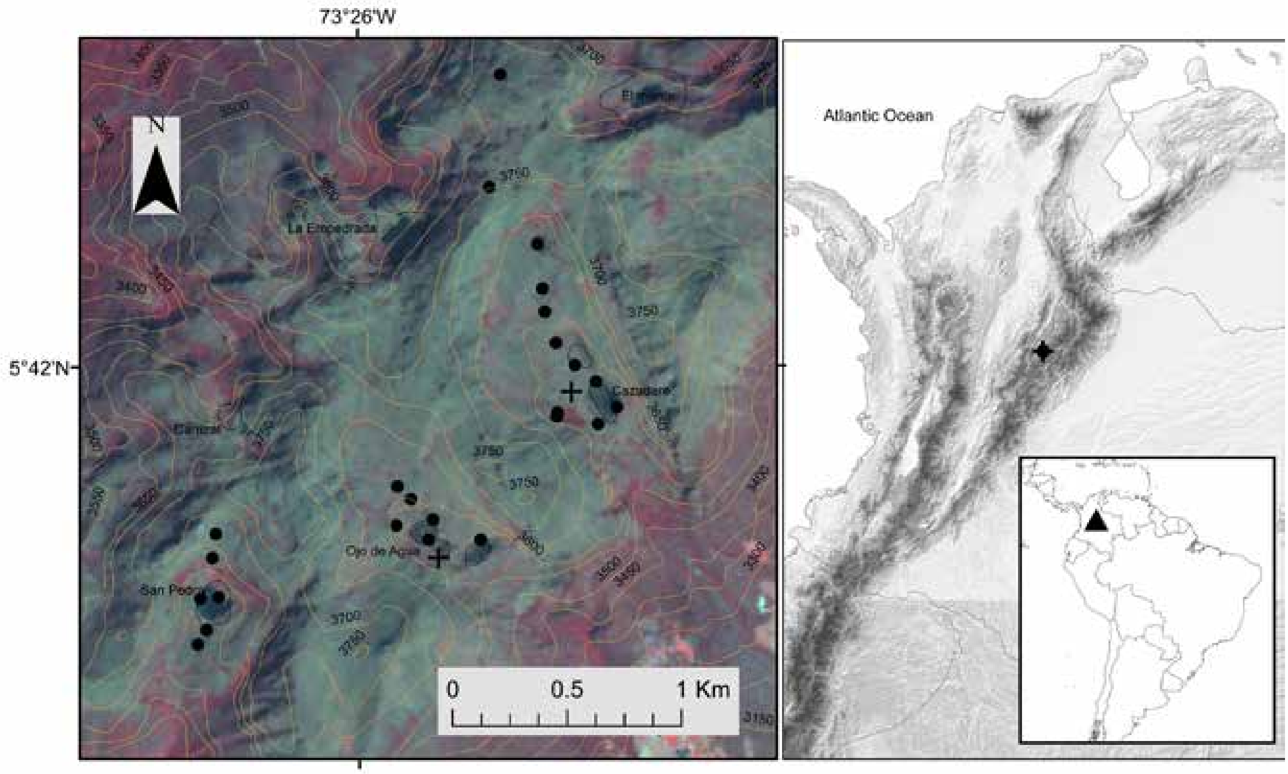

Figure 1. Left: Location of the study sites on the Iguaque páramo. The Figure is a false colour Ikonos satellite image (2001) overlaid with contours at 50 m intervals. Green (lighter) areas are open alpine vegetation and red (darker) areas are Andean montane forests. Sampling locations are marked with filled circles and sites that were cored for ^{210}Pb chronologies with crosses. Right: general location of the study sites in the northern Andes.

orientation. The valleys were created by glacier erosion, and have steep vertical sides and flat bottoms where peatlands develop. The páramo vegetation starts above the treeline at 3300 m and is fairly homogeneous up to the highest point of the Iguaque massif at 3750 m. The larger peatlands in valley bottoms have large hummocks and expanded hollows. Small peatlands, of less than 0.3 ha, are found on the flat parts of the ridges at higher altitudes. The weather of the region is highly seasonal with long periods of drought and a considerable water deficit from December to March (Figure 2) (Adler *et al.* 2003).

The valleys of the Iguaque complex face an area of highly developed potato cropping and cattle grazing. The farmers have traditionally used some of the lakes and peatlands in the valleys facing their crops as the water source for irrigation and human consumption. The cultivated area increased by more than 40 % between 1985 and 2005 (DANE 2005). The drainage of peatlands started in the 1950s, when a significant expansion of the population and the introduction of high density potato crops increased the demand for irrigation water (Morales *et al.* 2007). Crops are irrigated mostly from shallow artificial ponds dug near the cultivated area. During drought periods the water stored in the ponds is not recharged from below-ground waters and farmers directly tap water from the lakes and peatlands in the Iguaque massif (Eraso 2007).

For this work I recognised three types of peatland, namely: (i) undisturbed (undrained) valley peatlands with clear *Sphagnum* dominance, which are becoming decreasingly common; (ii) the many disturbed (drained) valley peatlands with open soil and large muddy hollows; and (iii) high-altitude (upland) peatlands with sedge-dominated vegetation and deeper water table (Figure 3). I visited a total of 26 drained, undrained and upland peatlands located along the Iguaque massif (Table 1).

Vegetation sampling

Vegetation was sampled within a central 10 × 10 m plot on each peatland. The peatlands were usually less than 0.5 ha in area, and the vegetation was fairly homogeneous. Three growth-form groups were recorded separately. (1) Ground vegetation (bryophytes and vascular plants with cushion-like growth forms) was recorded in four 1 × 1 m sub-plots at the corners of the 10 × 10 m plot. (2) Herbaceous vegetation was sampled in a 2 × 2 m sub-plot in the centre of the 10 × 10 m plot. (3) Trees and shrubs (woody vegetation with diameter at the base ≥ 2 cm) were recorded in the whole 10 × 10 m plot. Shrubs were mainly individuals of *Espeletia grandiflora* Bonpl. with a few large páramo bamboos (high *Swallenochloa tessellata* (Munro) McClure) up to 2.5 m tall.

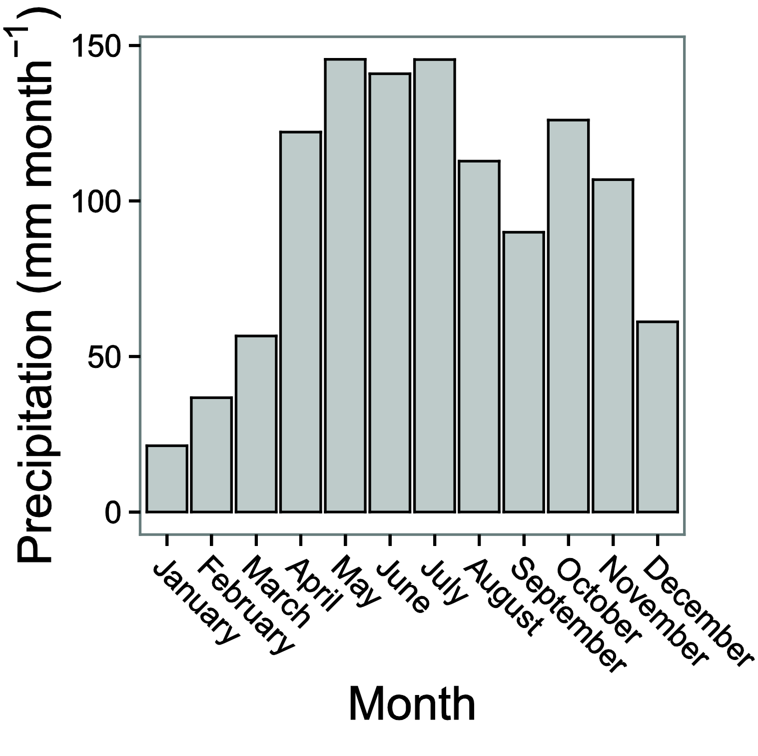

Figure 2. Monthly precipitation (1950–2005 averages) from the Global Precipitation Climatology Centre (GPCC) dataset (Adler *et al.* 2003).

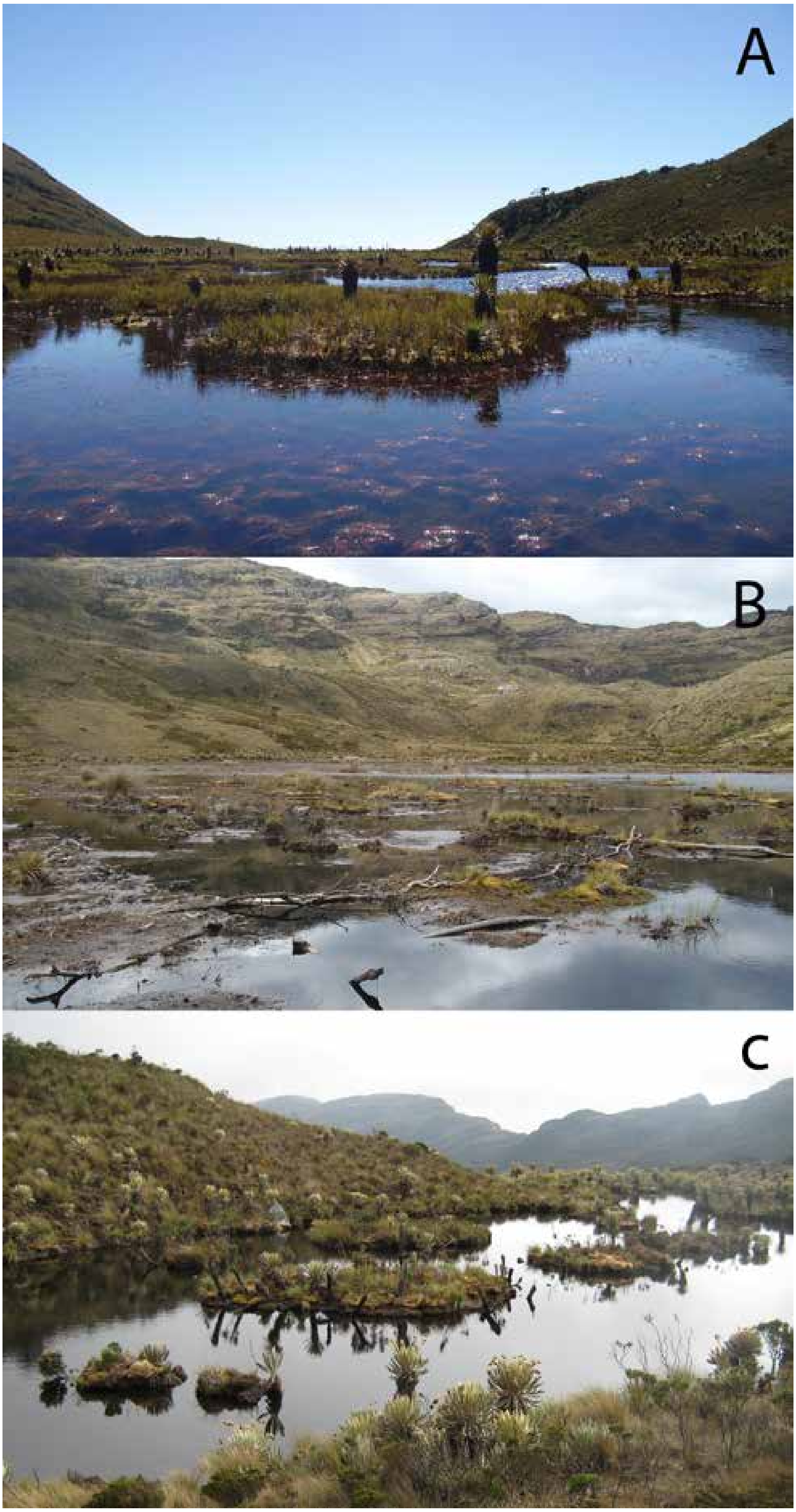

Figure 3. Photographs of peatland types visited during the present study. A: undisturbed (undrained) valley peatland; B: drained peatland at valley bottom; and C: ridge-upland peatland.

Table 1. Geographical locations, altitudes and types of the 26 sampled peatlands in the Iguaque massif.

Plot code	Altitude / m	Type	Latitude	Longitude	Cored
IGU1	3589	Drained	5.69092	-73.439	
IGU2	3589	Drained	5.69087	-73.44	
IGU3	3660	Drained	5.69342	-73.439	
IGU4	3563	Undrained	5.69898	-73.425	yes
IGU5	3576	Undrained	5.69817	-73.426	
IGU6	3576	Undrained	5.69801	-73.426	
IGU7	3626	Undrained	5.70481	-73.426	
IGU8	3831	Upland ridge	5.71151	-73.428	
IGU9	3755	Upland ridge	5.70706	-73.428	
IGU10	3574	Drained	5.69245	-73.43	
IGU11	3596	Undrained	5.69318	-73.431	yes
IGU12	3595	Undrained	5.69373	-73.432	
IGU13	3594	Drained	5.69396	-73.431	
IGU14	3594	Drained	5.69317	-73.429	
IGU15	3665	Drained	5.69476	-73.431	
IGU16	3568	Undrained	5.69528	-73.432	
IGU17	3581	Undrained	5.69772	-73.424	
IGU18	3581	Undrained	5.69838	-73.423	
IGU19	3631	Upland ridge	5.69939	-73.424	
IGU20	3836	Upland ridge	5.70004	-73.425	
IGU21	3760	Upland ridge	5.70092	-73.426	
IGU22	3579	Upland ridge	5.70215	-73.426	
IGU23	3601	Undrained	5.70307	-73.426	
IGU24	3600	Undrained	5.68963	-73.439	
IGU25	3560	Undrained	5.68906	-73.44	
IGU26	3565	Undrained	5.69247	-73.439	

Percentage cover of the different species was estimated ‘by eye’ for ground vegetation and herbs. Height and diameter at breast height (DBH) of individuals was recorded for shrubs.

^{210}Pb chronologies

Two peatlands with contrasting disturbance characteristics (one drained, the other undrained) but similar climate and geology were selected for coring. Cores were taken with a PVC pipe, 50 cm long and 10 cm in diameter, with one sharpened end. The cores were taken from the centres of the two peatlands. Cores were frozen within 48 hours of collection and cut into 2.5 cm thick slices using a bench saw. Half of the core was used for ^{210}Pb analysis and the other half was kept for macrofossil and peat chemistry analyses.

^{210}Pb inventories were made for each peat slice and used to make an age-depth profile of each core. ^{210}Pb dating uses the activity of ^{210}Pb across the peat profile *versus* the unsupported ^{210}Pb activity to estimate the time at which the peat section was at the surface. ^{210}Pb is part of the ^{235}U disintegration process, and is mainly of atmospheric origin. ^{210}Pb isotopes have a half-life of 22.2 years, and after 200–250 years (10 half-lives) all but 0.01 % of the ^{210}Pb of atmospheric origin has decayed, and ^{210}Pb is below the detection limit. The ^{210}Pb that can be detected after that is from background sources and part of the disintegration of uranium in the soil matrix or bedrock. This background activity is termed the supported ^{210}Pb. The proportion of unsupported ^{210}Pb activity with depth allows the calculation of the age-depth profiles assuming a constant rate of supply (CRS) of atmospheric ^{210}Pb (Appleby *et al.* 1997, Turetsky 2004). A competing model describing the changes in ^{210}Pb with depth assumes a constant rate of production-accumulation; but due to changes in primary production, and compression and the mass loss from decomposition of deeper peat layers, a constant rate of supply model (CRS) is usually preferred (Appleby *et al.* 1997).

^{209}Po was added to the peat sample as a yield tracer at the beginning of the process. ^{210}Pb inventories were measured after digesting approximately 3 g of peat with concentrated acids and H_2O_2. Samples were first digested with a mix of HCl, HNO_3 and H_2O_2 kept overnight on a hotplate at approximately 35 °C. A 1.5 cm square of copper was put into the digest for 12 hours, during which ^{209}Po and ^{210}Pb isotopes plated themselves on the copper. Activity of the ^{209}Po and ^{210}Pb was then measured on the copper squares using an ORTEC 576A alpha spectrometer. ^{210}Pb chronologies in peatlands have successfully been estimated from bogs and have shown no secondary mobilisation in *Sphagnum* peat soils (Vile *et al.* 1999, Turetsky 2004). One of the most important assumptions of the ^{210}Pb dating technique is that lead particles are non-mobile and once they have fallen they remain attached to the peat without secondary mobilisation. Compared to other metals Pb is particularly stable in the peat column (Novak *et al.* 2011). The roots of vascular plants can, in theory, act as conduits that mobilise particles including lead from the surface to deeper layers rendering the ^{210}Pb chronologies useless. However, studies from peatlands dominated by sedges and other vascular plants have shown that, despite the greater proportion of roots, the chronologies are still useful and ^{210}Pb secondary mobilisation is absent, at least in the timespan covered by the experiments (Vile *et al.* 1999, Vitt *et al.* 2009).

Peat chemistry and organic matter

Peat from the plots was collected as cores: 0–10 cm and 10–20 cm. Samples of peat from these homogenised cores were analysed for several variables. (1) Organic matter proportion of dry mass by combustion in a muffle furnace for 16 hours at 350 °C. Carbon proportion of dry mass was assumed to be 48 % of the combusted organic matter (Burt 2004). (2) Dry bulk density was calculated from peat dry mass and core volume. (3) The concentrations of the most abundant cations (Ca^{++}, K^{+}, Mg^{++} and Na^{+}) in the peat were estimated in samples of measured mass (about 1 g). The samples were digested for 8–16 hours in concentrated HCl (12M) at 50 °C in a sand bath. Digested samples were diluted to 100 ml. Cation concentration was then measured by atomic absorption spectrometry (Varian SpectrAA 220FS). Reported concentration is the average of three consecutive readings with a two-second delay between readings.

Peat water table was measured on site in excavated pits, using a ruler. Peat water storage was estimated from the mass of 8 cm diameter by 10 cm deep cores, saturated with water and allowed to drain freely for about one hour (peat dry mass + water mass + corer mass). The peat dry mass and corer mass were measured separately. Water proportion is then water mass / peat dry mass.

Water chemistry

Electrical conductivity (EC) and pH were determined in the field (Orion 4-Star pH/Conductivity meter). Water samples were collected at each plot from 30 cm deep pits in 125 ml HDPE bottles. Samples were filtered through a 5 µm membrane and stored at 5 °C until analysis. Cation concentration (Ca^{++}, K^{+}, Mg^{++}, Na^{+}) was measured by atomic absorption spectrometry (Varian SpectrAA 220FS). Reported concentration is the average of three consecutive readings.

Statistical analyses

Species composition was analysed after combining the ground and herbaceous vegetation records in a single species matrix. Differences in composition were analysed using Non-Metric Multidimensional Scaling (NMDS). This is a numerical technique that best preserves the ranked dissimilarities among samples in a predetermined (small) n-dimensional space. NMDS ordination optimisation uses a monotonic regression between ranked dissimilarities and distances on the ordination until a (local) minimum is found. The residuals of the local minimum are the stress and can be used to indicate the disagreement between the ranked dissimilarities and their representation in the ordination (Faith *et al.* 1987, Minchin 1987). In this study I used the Bray & Curtis dissimilarity matrix for the ordination. The NMDS ordination was made by the metaMDS function from the vegan package in the statistical software R (Oksanen *et al.* 2012, R Development Core Team 2012). The environmental vectors fitted to the NMDS ordination represent the degree of correlation between positions of samples in the ordination spaces and variation of the environmental variables (Minchin 1987, Kantvilas & Minchin 1989). Significance of the fitted vectors was tested using a Monte-Carlo procedure with 999 pseudoreplicates (Minchin 1989).

Environmental variables were compared among the different peatland types using one way ANOVAs after checking for normality of the residuals and variance homogeneity. Variables with significant differences among the peatland types were explored using Tukey's Honest Significant Difference (HSD) *post hoc* test (Crawley 2007). Peat soil samples from 0–10 cm and 10–20 cm depths were combined and the means of the two values were used as input to the ANOVA analysis.

Peat and organic matter accumulation during the last 25, 50 and 100 years was estimated from the intersection of the year with the interpolated line connecting successive dated core sections (Vitt *et al.* 2009). Confidence intervals (95 %) were constructed from the date errors obtained in the ^{210}Pb chronologies (Wieder 2001). Differences in the peat and organic matter accumulated at the different year intervals were estimated directly from the 95 % confidence intervals. It is worth noting that there are only two cores, and this study should be regarded as a preliminary one describing emerging patterns in peat chemistry and peat accumulation rates in the tropical Andes. Vertical profiles of cations, organic matter proportion, dry bulk density and macrofossils were compared between the two cores. All the statistical and numerical analyses were done in the R statistical environment (R Development Core Team 2012).

RESULTS

Species richness and composition

The mean number of species in drained sites was larger than in undrained sites, but similar to the number of species in ridge upland peatlands (Table 2). There was a negative correlation between cover of *Sphagnum* and the number of species

Table 2. Mean percentage cover and growth form group for the ten most abundant species from 26 plots in a complex of drained, undrained and high-altitude (upland) rich fens in the northern Andes. Values are means ± standard error.

Group	Species	Disturbance		
		Drained	Undrained	Upland
Herb	*Calamagrostis effussa*	5 ± 2.2	1 ± 1.5	27 ± 11.8
Herb	*Puya santonii*	7 ± 1.4	11 ± 1	6 ± 1.7
Herb	*Valeriana plantaginaceae*	5 ± 1.9	5 ± 1.7	2 ± 1.1
Sedge	*Carex bomplandii*	12 ± 3.2	33 ± 3.2	2 ± 2.6
Sedge	*Cortaderia nitida*	3 ± 1.3	16 ± 2.8	16 ± 4.4
Shrub	*Diplostephium revolutum*		1	10 ± 0.7
Shrub	*Espeletia grandiflora*	3 ± 0.2	3 ± 0.4	12 ± 2.3
Sphagnum moss	*Sphagnum cf. falcatulum* Besch.		1	19 ± 8.1
Sphagnum moss	*Sphagnum magellanicum*	27 ± 6.2	11 ± 3.3	21 ± 6.2
Sphagnum moss	*Sphagnum oxyphyllum*		57 ± 6.8	
Sphagnum moss	*Sphagnum sancto-josephense*	1	15 ± 8.3	3 ± 1.8

(r = -0.45, p = 0.02). *Sphagnum oxyphyllum* (60 %), *Sphagnum magellanicum* (20 %) and *Sphagnum sancto-josephense* were the three species with the largest mean cover. Undrained peatlands had larger cover values for ground vegetation and *Sphagnum* than drained or ridge upland peatlands (Table 2), although the differences for ground vegetation were not significant.

Species composition differed markedly among the three peatland types (drained, undrained, ridge upland). The MDS ordination separated the three peatland types into distinct groups, with low similarity of species composition between sites with different disturbance intensities and topographical positions. Altitude, water EC, calcium (both dissolved and in peat) and organic matter proportion were the environmental variables that had significant correlation with the variation in species composition. The selected environmental variables had correlation values above 0.5 and significance below 0.05 (Figure 4).

Peat and water chemistry

Water pH was similar among undrained, drained and ridge upland peatlands, but water EC was greater at drained sites and ridge upland peatlands (Table 3). The concentrations of Ca^{++} and Mg^{++} in water were greater at drained sites (Table 3). Water EC was correlated with Mg^{++} concentration in water (r = 0.77, p < 0.001). Total charge from the cations and H^{+} activity was weakly correlated with water EC (r = 0.28, p = 0.15) mostly due to the higher EC at two sites with low cation activity and Ca^{++} concentration.

Peat density in the first 20 cm was greater in drained peatlands than in undrained and ridge upland sites (Table 3). The same pattern was observed for mass of organic matter in the first 20 cm, with greater values in drained peatlands when compared to undrained and ridge upland sites (Table 3). Water storage was greater in undrained and ridge upland peatlands, at up to 22 times the dry mass compared to 14 times the dry mass in drained

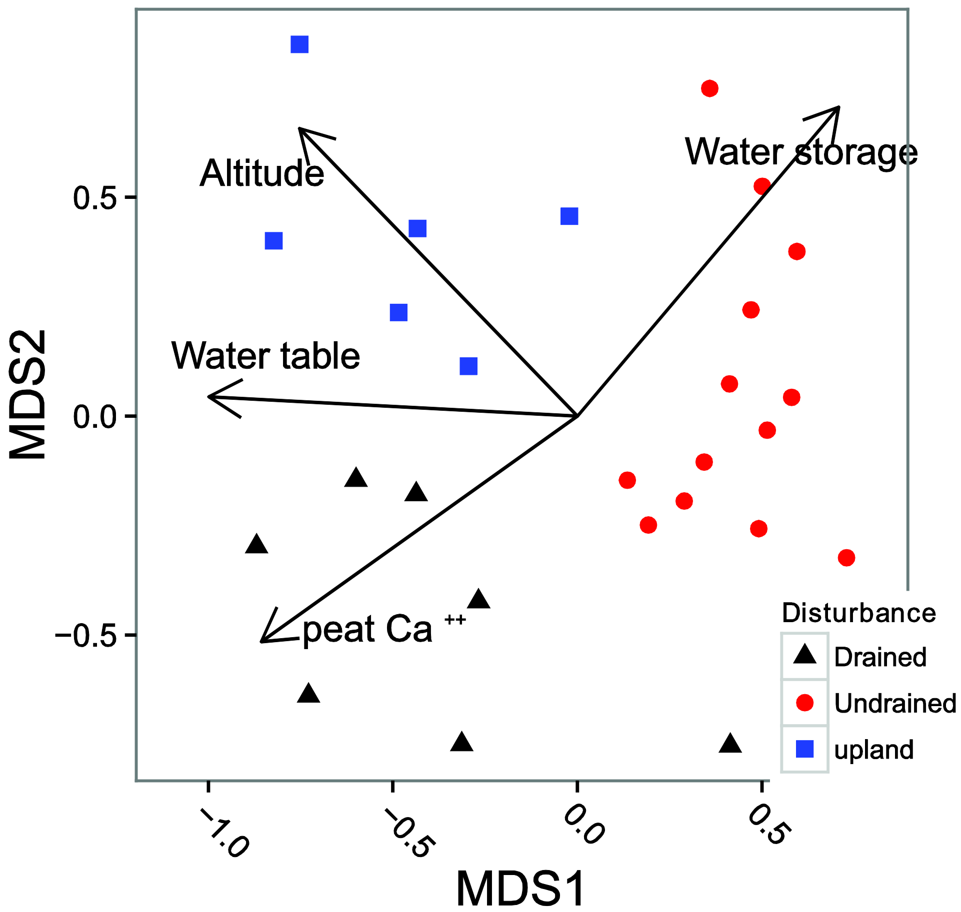

Figure 4. Non-metric multidimensional scale ordination for 26 peatlands in the northern Andes under different intensities of drainage and in contrasting topographical positions (stress = 0.12). Arrows in the ordination diagram represent environmental variables fitted to the ordination (*r* > 0.4, *P* < 0.05). Length of the arrow represents strength of the correlation.

Table 3. Physical and chemical characteristics of peat soils and peat interstitial water from 26 plots in a complex of drained, undrained and high-altitude (upland) rich fens in the northern Andes. Values are mean ± standard error and the last two columns represent $F_{2,23}$ values from Anova analyses and the respective *P* values. Superscript letters mark homogeneous groups after Tukey HSD *post hoc* test. Star (*) indicates significant difference ($P < 0.05$).

	Drained	Undrained	Upland	*F* statistic	P	
n (number of plots)	7	13	6			
Species	44	31	38			
Species per plot	14.1 ± 0.962 [a]	10.2 ± 0.553 [b]	16.8 ± 1.249 [a]	17.3	< 0.001	*
Cover of *Sphagnum* (%)	48.4 ± 12.6 [b]	84.1 ± 6.9 [a]	45.7 ± 14.1 [b]	5.1	0.015	*
Ground vegetation cover (%)	105.8 ± 13	118.8 ± 6.8	100.6 ± 9.3	1.1	0.345	
Herbaceous vegetation cover (%)	55.9 ± 7.5	70.3 ± 3.79	86.7 ± 9.3	5.1	0.015	*
Tree/shrub basal area (cm^2)	932.6 ± 612	693.1 ± 456.9	0 ± 0	17.3	< 0.001	*
pH	4.96 ± 0.24	4.72 ± 0.055	4.74 ± 0.162	0.9	0.435	
Conductivity (μS cm^{-1})	6.6 ± 0.44 [a]	4.4 ± 0.39 [b]	6.9 ± 1.17 [a]	5.4	0.012	*
Altitude (m)	3609 ± 14 [b]	3583 ± 5.3 [b]	3732 ± 43 [a]	15.6	< 0.001	*
Ca^{++} in peat (mg/kg)	8.9 ± 0.457 [a]	5.3 ± 0.255 [b]	4.84 ± 0.775 [b]	23	< 0.001	*
Ca^{++} in water (mg/l)	8.5 ± 0.694 [b]	17.6 ± 1.714 [a]	11.7 ± 2.855 [b]	6.5	0.006	*
K^{+} in peat (mg/kg)	1.06 ± 0.374	0.48 ± 0.025	0.74 ± 0.144	2.7	0.09	
K^{+} in water (mg/l)	0.46 ± 0.111	0.33 ± 0.046	0.21 ± 0.032	2.7	0.091	
Mg^{++} in peat (mg/kg)	0.23 ± 0.017 [a]	0.17±0.013 [b]	0.17 ± 0.027 [b]	3.9	0.035	*
Mg^{++} in water (mg/l)	0.16 ± 0.016 [a]	0.18 ± 0.017 [a]	0.1 ± 0.026 [b]	3.7	0.042	*
Na^{+} in peat (mg/kg)	1.01 ± 0.052	1.12 ± 0.026	1 ± 0.062	2.6	0.1	
Na^{+} in water (mg/l)	0.59±0.036	0.59±0.023	0.51±0.021	2	0.158	
Organic matter content (%)	0.79 ± 0.015 [b]	0.84 ± 0.008 [a]	0.78 ± 0.023 [b]	7.1	0.004	*
Organic matter in first 20 cm (kg m^{-2})	7.3 ± 0.763 [a]	5.3 ± 0.357 [b]	5.2 ± 0.859 [b]	3.6	0.043	*
Dry bulk density (g cm^{-3})	0.05 ± 0.005 [a]	0.03 ± 0.002 [b]	0.03 ± 0.005 [b]	4.2	0.028	*
Water table depth (cm)	40.1 ± 2.521 [a]	19.1 ± 1.416 [b]	41.8 ± 2.626 [a]	45.5	< 0.001	*
Water temperature (°C)	9.6 ± 0.642	9.5 ± 0.218	8.9 ± 0.191	0.7	0.498	
Water mass / dry mass	14.9 ± 1.389 [a]	21.9 ± 1.014 [b]	23 ± 2.695 [b]	6.9	0.004	*

sites. Water table depth at undrained sites (20 cm) was half that in drained sites (40 cm).

Recent peat accumulation and variation in peat chemistry

Net peat accumulation rates were similar between the two cored sites, with approximately 35 cm of accumulation in the last 110 years (Figure 5). Rates of organic matter accumulation were greater for the undrained core, with stronger differences in the deeper layers (Figure 5). Overall peat accumulation was similar for undrained and drained sites during the last 100 years, but was greater for the undrained sites during the last 50 and 25 years (Figure 6). The differences indicate a greater rate of accumulation for the drained site in the interval between 100 and 50 years ago, and a greater rate for the undrained site later on. Organic matter accumulation was greater in the undrained peatland during the last 100, 50 and 25 years (Figure 6).

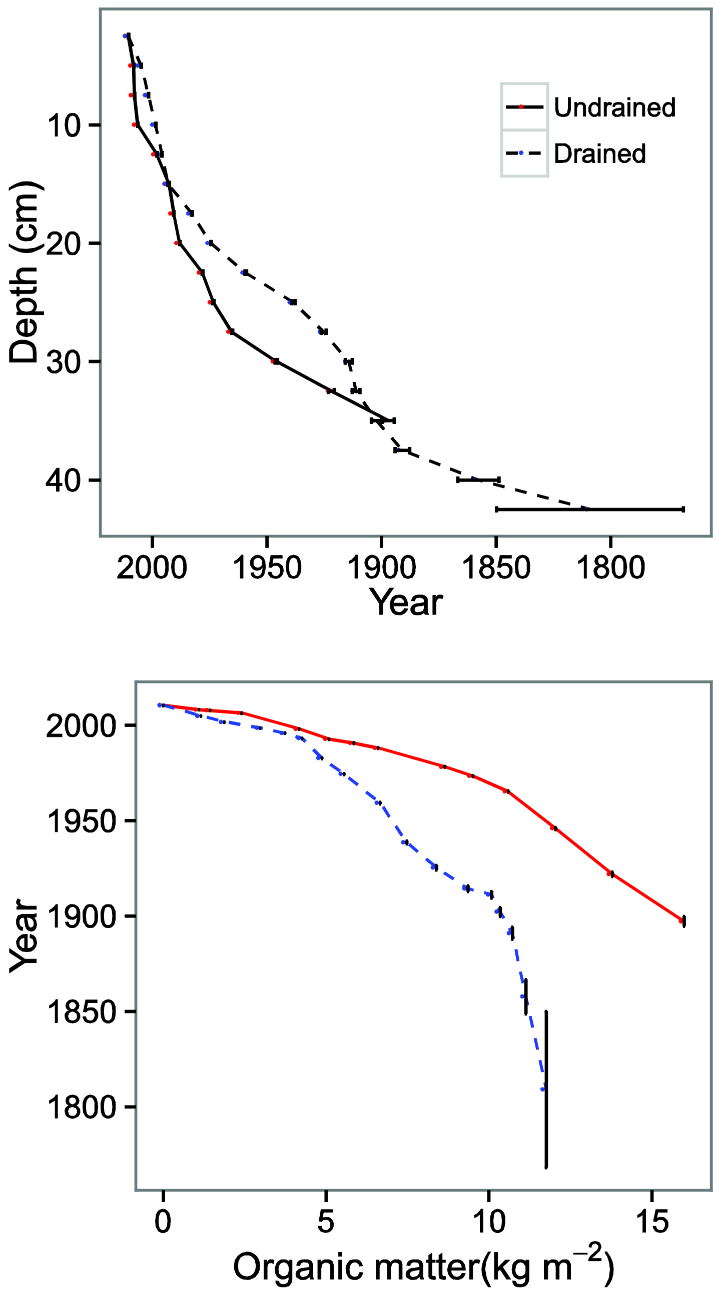

Figure 5. Peat age - depth (top) and organic matter - age (bottom) curves for the last 200 years from two peatlands with contrasting disturbance patterns: drained and undrained. Chronologies are reconstructed using ^{210}Pb dating. Error bars represent errors of the ^{210}Pb disintegration counts for age estimation.

The vertical distributions of main cation concentrations within the peat were stable with peaks at the undrained site 40 years ago. The only cation with greater concentrations at drained sites was Ca^{++}. The concentration of K^{+}, Mg^{++} and Na^{+} was greater at the undrained site with peaks at 10 cm and 30 cm depth corresponding to the years 1990 and 1960 respectively (Figure 7). Calcium in peat and water can be linked to the regional geology, which is dominated by calcareous shale and sandstones (Patarroyo-Camargo *et al*. 2009).

Dry bulk density was greater at the undrained site below 20 cm depth. Organic matter proportion was greater in the top 25 cm at the drained site (Figure 8), but the reverse was observed at greater depths. The vertical distribution of macrofossils shows a greater proportion of *Sphagnum* remains at the undrained site. The drained site has greater dominance of vascular plants and unrecognisable debris. The proportions of vascular-plant remains in the two cores are similar below 20 cm, which corresponds to the early 1980s; but differ in the upper layers, indicating greater dominance of vascular plants in the drained site.

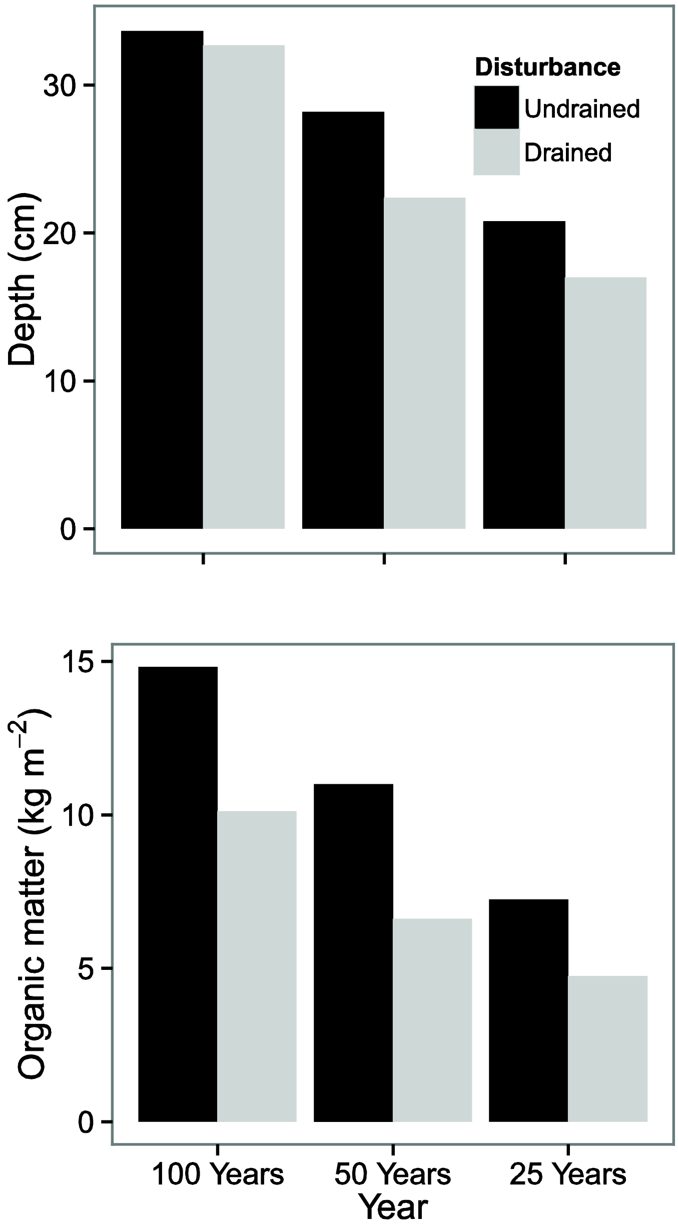

Figure 6. Rate of peat accumulation (top) and of organic matter accumulation (bottom) during the most recent 25, 50 and 100 years, for two north Andean peatlands with contrasting human disturbance patterns: drained and undrained.

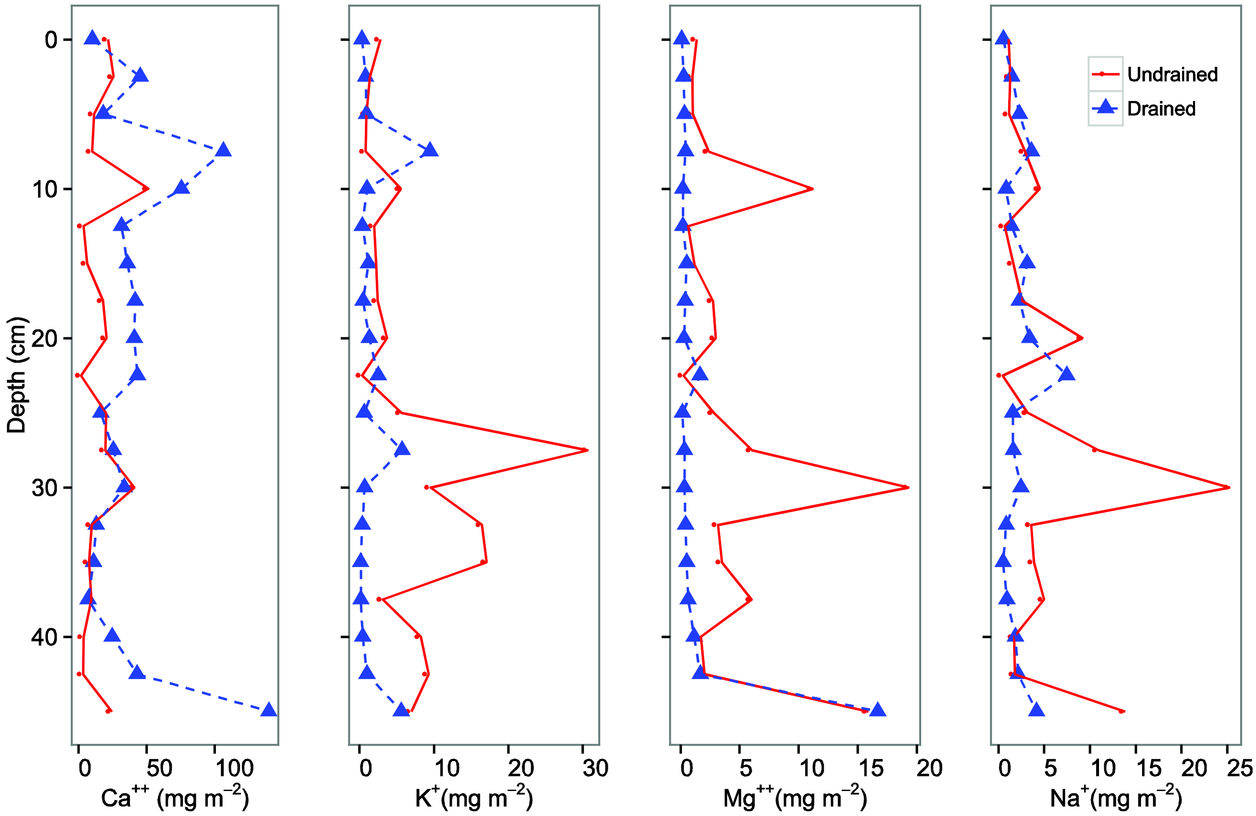

Figure 7. Vertical distributions of the concentrations of Ca^{++}, K^{+}, Mg^{++} and Na^{+} in peat cores from two high-altitude Andean peatlands (one drained, one undrained). The cores were sectioned at 2.5 cm intervals.

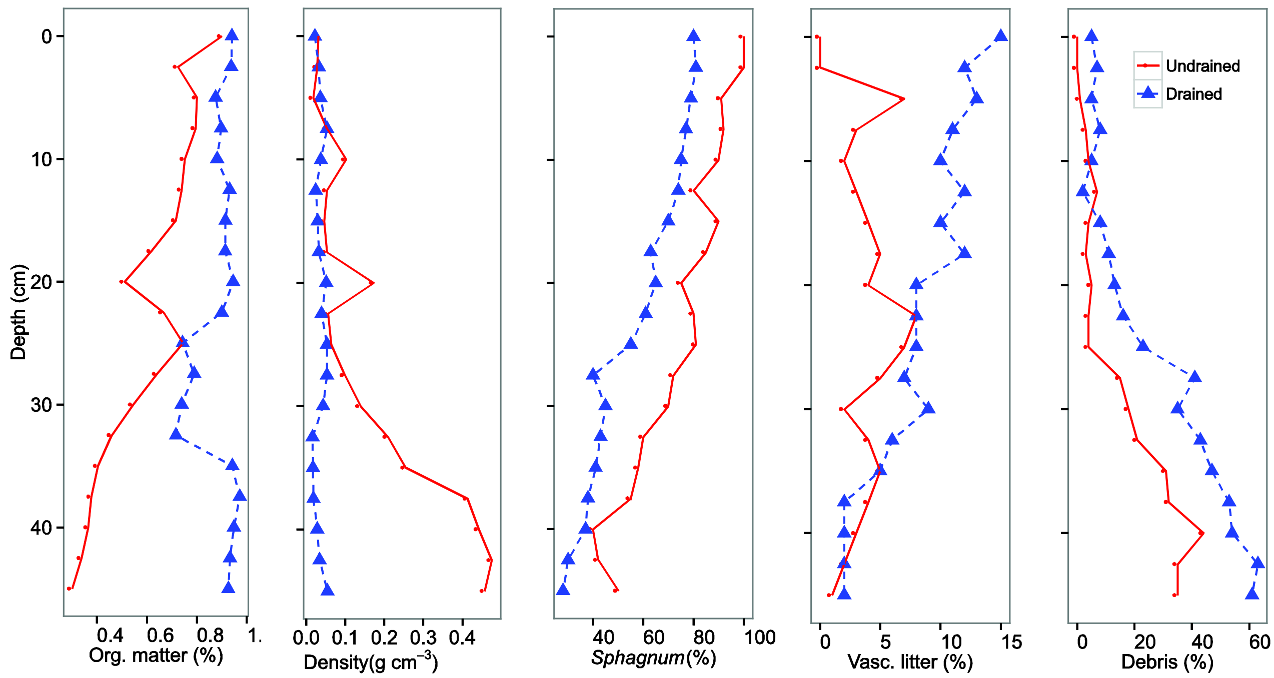

Figure 8. Vertical distributions of percentage organic matter (Org. matter), dry bulk density (Density), proportion of *Sphagnum* macrofossils (*Sphagnum*), vascular plant remains (Vasc. litter), and unidentifiable organic debris (Debris) in peat cores from an undrained and a drained high-altitude Andean peatland.

DISCUSSION

The smaller number of species in the undrained peatlands contrasts with the idea that conservation of tropical areas is equivalent to maximising diversity (Hobbs & Huenneke 1992). In peatlands, diversity has been related to environmental stress, with fewer species occurring at sites with extreme climate or limiting chemical characteristics (Glaser 1992). The smaller number of species found in the undrained sites reflects competition by *Sphagnum* plants, which acidify the peat soil and make most of the nutrients unavailable for vascular plants. *Sphagnum* acidification or water acidity has been found to reduce species richness in boreal peatlands (Gunnarsson *et al.* 2000). The greater number of species in the drained sites is mostly due to colonisation by vascular plant species from the nearby upland páramo including *Calamagrostis* grasses, herbs such as *Lachemilla orbicularis* (Rosaceae), and the ericaceous dwarf shrubs *Disterigma alaternoides* and *Pernettya postrata*. The vascular plants invading the peatlands are also found in the high-altitude ridge peatlands, which are usually small and have large contact zones with nearby upland.

The variation in species composition among the different disturbance and topographical categories indicates the possible trajectories of change in species composition. The premise that vegetation was similar in the drained and undrained sites before disturbance is supported by the similarity in their macrofossil compositions before 1960. The increased water table fluctuations in drained peatlands have since favoured colonisation by graminoids and eriocoid species over *Sphagnum* and bryophyte species. Water table fluctuations have a negative effect on the productivity of most of the *Sphagnum* species (Breeuwer *et al.* 2009). *Sphagnum magellanicum*, a common species of hummocks and drained peatland sites, was the only *Sphagnum* species reported here that has been found to be favoured by increased water table fluctuations (Breeuwer *et al.* 2009).

The difference in plant composition between the drained and undrained sites is as large as the difference between the valley and ridge peatlands. The ridge peatlands are small, up to 400 m^2, and dominated by typical hummock species such as *Sphagnum magellanicum* and *Sphagnum oxyphyllum*. Thus, drained peatlands form a novel human ecosystem not observed elsewhere in the landscape, with large bulk densities but less total carbon due to the high concentration of mineral constituents in the soil. The studied peatlands receive sediments and runoff from the surrounding mountains. The small cover of vegetation and low soil permeability in drained peatlands reduces the hydro-buffering capacity and favours the accumulation of mineral deposits towards the centre (Chimner & Karberg 2008).

Remarkably, drained and undrained peatlands had similar rates of vertical peat accumulation, even though the quality of the peat accumulated differed in both carbon proportion and dry bulk density. Vertical accumulation rates of 30 cm in 100 years are equivalent to the accumulation rates that have been observed in the *Sphagnum*-dominated rich fens of continental Canada, although the quantity of organic matter accumulated in the same 100 years was less, at 15 kg m^{-2} as opposed to 20 kg m^{-2} (Vitt *et al.* 2009). The lower organic matter proportion of the drained peatlands is possibly a consequence of the increased decomposition rates observed when peat soil is exposed to air. Drainage of tropical peatlands has a clear effect on emissions of the two most important greenhouse gases, carbon dioxide and methane (Murray *et al.* 1989, Hillman 1992, Hooijer *et al.* 2010).

The drainage of Andean peatlands has clear impacts on their ecological services. The small sizes of Andean peatlands make them negligible in the global context. However, the strong control of hydrology and the water provided to marginal agrarian communities makes them invaluable, and measures to prevent their destruction should be taken (Holden 2005, Buytaert *et al.* 2006). How peatland drainage affects the variability of the outflow has not been investigated. Nor do we know the ability of the peatland system to recover after halting the disturbance. Protection measurements for the tropical Andean peatlands require a better understanding of the resilience of the systems, their recovery ability and the economic effects that such disturbances have on a strategic ecosystem.

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