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LETTER

Widespread carbon-dense peatlands in the Colombian lowlands

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Abstract

Peatlands are some of the world's most carbon-dense ecosystems and release substantial quantities of greenhouse gases when degraded. However, conserving peatlands in many tropical areas is challenging due to limited knowledge of their distribution. To address this, we surveyed soils and plant communities in Colombia's eastern lowlands, where few peatlands have previously been described. We documented peat soils >40 cm thick at 51 of more than 100 surveyed wetlands. We use our data to update a regional peatland classification, which includes a new and possibly widespread peatland type, 'the white-sand peatland,' as well as two distinctive open-canopy sub-types. Analysis of peat bulk density and organic matter content from 39 intact peat cores indicates that the average per-area carbon densities of these sites (490–1230 Mg C ha^{-1}, depending on type) is 4–10 times the typical carbon stock of a (non-peatland) Amazonian forest. We used remote sensing to upscale our observations, generating the first data-driven peatland map for the region. The total estimated carbon stock of these peatlands of 1.91 petagrams (Pg C) (2-sigma confidence interval, 0.60–4.22) approaches that of South America's largest known peatland complex in the northern Peruvian Amazon, indicating that substantial peat carbon stores on the continent have yet to be documented. These observations indicate that tropical peatlands may be far more diverse in form and structure and broadly distributed than is widely understood, which could have important implications for tropical peatland conservation strategies.

1. Introduction

Tropical peatlands are among the world's most carbon dense ecosystems[1–3], and their ongoing degradation and destruction is exacerbating the climate crisis [4–8] and impacting peoples' livelihoods [9, 10]. Peatland protection is regarded as one of the more cost-effective natural climate solutions [11, 12], but despite their importance to global climate, the extent and distribution of peatlands throughout many parts of the global tropics remains highly uncertain 13, 14].

One of the more enigmatic peatland regions is the Colombian lowlands in northern South America [15]. In Colombia, peatland accounting is extremely uncertain with published estimates of peat volume and area differing by orders of magnitude. At one extreme, the algorithmic Global Wetland Map product predicts roughly 50 000 km^2 of peatlands throughout the country's climatically and geologically diverse lowland regions, with peat thicknesses of up to 10 m, representing approximately 200 km^3 of peat [16]. In contrast, a synthesis based on soil maps shows only a few modest areas of mapped Histosols (710 km^2) accounting for just 0.3 km^3 of peat [1]. Colombia is emerging from five decades of civil conflict and many rural areas have been inaccessible for scientific investigation until recently [17], so it is possible that extensive peatlands have eluded field detection. Furthermore, the region is facing acute environmental degradation [18], raising the prospect that peatland loss may be outpacing peatland detection. Field investigations are therefore crucial to determine whether peatlands are scarce or ubiquitous in Colombia's lowlands, how much carbon they hold, and more generally, to assess the accuracy of global peatland mapping products [16, 19, 20] in under-surveyed tropical regions.

Tropical peat soils often occur beneath distinctive wetland-adapted plant communities [21–23] and thus peatland ecosystem classification serves as a foundation for understanding peatland spatial distributions necessary for carbon stock estimations. Such ecosystem-peat soil linkages have not yet been established for Colombia; in fact, nearly all studies of tropical South American lowland peatland ecology to date have been conducted in Peru. Ecological peat classification systems for Peru [24] may not apply to parts of Colombia's lowlands where climate, soils, and geology are dramatically different, such as in the highly seasonal savanna region of the Orinoco basin (the Llanos Orientales), or among the nutrient-poor white sand forests of the Guiana shield—two ecoregions with little Peruvian analogue. An ecological classification of Colombian peatlands based on vegetation surveys and soil sampling is needed because, as in similarly inaccessible locations, the high cost of collecting field data in lowland Colombia means that peat accounting must depend upon remotely sensed ecosystem information in order to upscale from scarce field data and infer peatland distributions on a regional scale [25, 26].

To advance our empirical understanding of the distribution, ecology and carbon stock of peatlands in the Colombian lowlands, we embarked on a series of field campaigns in search of potential peatlands. We used multispectral Landsat imagery to identify prospective peat-forming wetlands [27, 28] and in the field, when peat was encountered, we sampled soils and plant communities to support classification into different types. We analyzed 39 extracted peat cores for organic matter (OM) content to estimate belowground ecosystem carbon densities. Finally, to generate a peat map and estimates of total peat area and carbon stock, we used remote sensing products and a random forest (RF) machine learning algorithm [29] to predict the distributions of peat-forming ecosystems throughout the region.

2. Materials and methods

2.1. Field campaigns

We undertook a series of field campaigns in Colombia's Eastern lowlands between October 2020 and February 2023 to search for peatlands among a variety of wetland types. The Global Wetlands Map V3 [16] helped us identify regions of interest, which were further investigated using Landsat false color imagery of infrared and near-infrared bands and digital elevation models to look for wetland areas similar in appearance to known peatland sites in Peru (figure S1). Security and logistical limitations prevented us from visiting some promising regions, such as the middle and lower Rio Caquetá. Within our regions of interest, we visited the sites with the most convenient access by road or boat to efficiently visit wetlands and sample as many distinct potential peatland sites as possible. Altogether we assessed more than 100 discrete wetland sites across seven Colombian departments.

At each wetland site we first determined whether peat was present, with a depth of 40 cm as a minimum following the USDA histosol definition [30].

If we determined a site to be a mineral soil wetland, we carried out a rapid survey of vegetation (noting dominant species and classifying the community type), hydrologic indicators and soil texture and color before moving on to search elsewhere. If we encountered at least 40 cm of peat, we established a transect up to 600 m long through the site taking rapid surveys with measurements of peat thickness, canopy height and density, and hydrologic and plant community observations every 100 m. At a central point on each transect we completed one detailed survey of a peatland that included a 0.1 ha floristic inventory, identifying and measuring all trees of at least 10 cm diameter at breast height (DBH), as well as extraction of an intact peat core in 50 cm sections using a Russian style peat auger until a core section overlapped with underlying mineral material (figure S2).

2.2. Laboratory analysis

All peat core sections were transferred to 4 cm PVC half tubes and wrapped in plastic wrap in the field, labeled, stored immediately in coolers and then transferred to freezers in the nearest town until the end of the regional campaign. At the end of each campaign cores were transferred frozen to Pontificia Universidad Javeriana in Bogota for processing. Each core was thawed and then sliced into 10 cm sections before being oven dried at 80 °C and weighed for calculation of dry bulk density (dry weight (g)/volume (cm^3)). We performed loss on ignition assays from 39 cores at 10 cm intervals along each peat profile for a total of 1046 analyses in a muffle furnace for 4 h at 450 °C. Since conversion factors from soil OM to soil organic carbon vary substantially between soil types [31, 32], we analyzed a subset of 42 samples for total carbon at the Environmental Measurements Facility at Stanford University using a ThermoScientific Flash elemental analyzer to generate a conversion factor specific to our data set.

2.3. Carbon calculations

We found a strongly linear relationship between % OM from loss on ignition and %C from elemental analysis (figure S3; $r^2 = 0.98$, p-value < 0.001) and used the slope of the regression line (%C = %OM * 0.5591 − 1.64) to estimate carbon content of samples for which we only had % OM data [32]. To calculate ecosystem belowground carbon density we summed carbon in each 10 cm layer of each of 39 fully processed peat cores using the following equation:

$$\mathrm{EBCD} = \sum_{n=1}^{N} (10 \times D_n \times \rho_n \times C_n)$$

Where EBCD is ecosystem belowground carbon density in Gg C ha^{-1}, D_n is thickness of the nth peat layer in cm (usually 10 cm except in case of missing data, in which case we interpolated linearly), ρ_n is dry bulk density of the nth peat layer in g cm^{-3}, and C_n is carbon content of the nth peat layer in %. For peat thickness, we defined the peat core bottom as the deepest sample containing at least 45% OM, the threshold recommended by a systematic review of peat classification systems in the context of extensive organic-rich valley soil observations from tropical Asia [30]. Because belowground ecosystem carbon densities were non-normally distributed, we used a bootstrap resampling with replacement approach to generate 100 000 simulated bootstrapped distributions from which we extracted mean values and 95% confidence intervals. This is a slightly different approach than in prior carbon estimates from Peru where authors had non-overlapping observations of peat bulk density, carbon content and thickness and treated these as independent measurements [24, 33]. In this study we instead calculated the peat column carbon of an intact core from each site and treated those as independent measurements. This is preferable in a setting where peat columns contain high levels of mineral intrusions because the three variables of carbon content, thickness and bulk density tend to be correlated rather than independent with higher bulk densities associated with lower carbon content and deeper peat columns.

To estimate peat carbon stock for each ecosystem we used a Monte Carlo method of randomly selecting a value from bootstrap simulated distributions of mean belowground ecosystem carbon density and our two distributions of estimated area (as described below) to multiply together to generate carbon stock values. We repeated this process 10^7 times to generate mean carbon stocks and 95% confidence intervals for each peatland type.

2.4. Floristic analysis

We compared the floristic composition of the 53 0.1 ha Colombian plots to a wide range of RAINFOR forest plots established in different ecosystem types in north-western Amazonia [34–36]. The RAINFOR dataset contains 116 forest plots of 0.1–1.0 ha in size, with small plot sizes (0.1–0.5 ha) generally established on low diversity ecosystems including peatland ecosystems, such as open peatlands, palm swamps and pole forests. Large plot sizes (1 ha) were generally used on more diverse ecosystems such as white-sand forests, seasonally flooded forests, and Terra Firme forests. Identification of all individuals with DBH $\geqslant$ 10 cm was done by comparing botanical specimens collected in each plot with herbarium vouchers [34]. Only plots with at least 75% of stems identified to species level were selected.

We built a matrix of the species abundance of the combined 169 plots. Scientific names of species were standardized using the Taxonomic Name Resolution Service online (Boyle *et al* [37], [38]). After removal of unidentified individuals, the matrix remained with 1698 species and 40 618 individuals. We transformed the dataset using the Hellinger method and constructed the floristic distance matrix using the Euclidean distance in the 'vegan' package in R (Dixon [39]). This distance matrix was used to create non-metric multidimensional scaling ordinations optimized for three axes to visualize floristic dissimilarity among ecosystem types (figure S4). This ordination provides a way of assessing how similar plots are to one another based on the abundance of tree species.

2.5. Mapping and upscaling

To map peatlands, we took two steps. First, to leverage known linkages between ecosystem types and peat presence in the tropics [24], we generated a land cover classification to identify areas corresponding to ecosystems with the potential for peat formation and those not known to support peat soils. Second, to capture spatial uncertainty of peat presence among potentially peat-forming ecosystems [28], we assessed the probability of peat soil presence within potentially peat-forming ecosystems. For both classifications, we trained a RF classifier [29, 40] on 70% of the samples (of those directly collected for this study as well as some addition reference field samples from [41–44]) using a stratified group k-fold cross-validation (5 folds; see figure S5) and a maximum depth of 300 estimators. Maximum features per split were set to the square root of total number of features. The remaining 30% of the samples were used for independent validation. All spatial modeling was performed using the python scikit-learn package [45]. For both classifiers we removed redundant variables from a larger group of potential variables to avoid overfitting, based on an assessment of partial dependency and comparison of classifier results using different variables. While some of the selected variables still show a cross-correlation, for example the wet and dry season HH and HV backscatter products (table S2), we used them in the classifier as they were crucial in the separation of specific land cover classes [46].

The land cover model was trained on a variety of earth observation products and derivatives conventionally used in digital peat mapping, including mean wet-season and mean dry-season backscatter of ALOS2 PALSAR2 L-band ScanSAR HH and HV data; Copernicus Sentinel-1 VV multi-temporal 5th percentile and standard deviation; Harmonized Landsat Sentinel-2 (HLS) shortwave-infrared (SWIR) and SWIR 2 bands [47], the normalized difference vegetation index [25], and the normalized difference wetness index [48]. We also used the Copernicus GLO30 digital elevation model. To complement our field data with additional samples of the other land cover types (water, barren soil, urban, grassland, palm plantation), we inferred random samples from the satellite data or stratified by the Global Surface Water product [49] and the World Settlement Footprint [50]. We then applied this model to predict the land cover and ecosystem classes for the entire study area. We applied a two-fold post-classification morphological closing to filter for a minimum size of 5 ha per classified object.

We grouped the land cover classes of potential peat (palm swamp, wet white-sand ecosystems, herbaceous/shrub wetland, and floodplain forest) together for peat probability predictions. We included floodplain forest in this second analysis because of high misclassifications with the potential peat classes in the land cover prediction and because it is likely that peatlands of this ecosystem type exist in Colombia (AGB and JCB personal observations) and it has been reported in Peru [24].

The second model, the peat classifier, constrained to potential peat classes (figure S6), utilized the ecosystem type and peat presence/absence reference data described in figure 1 as well as additional reference points from other sources (figure S7). The peat classifier model was trained using the ALOS2 PALSAR2 dry season HH and wet season HV backscatter and a flood fraction product derived from the HH backscatter time-series. We further included the Sentinel-1 VH multi-temporal standard deviation and the HLS NDVI and NDWI. The output generated a peat probability for each pixel of peatland landcover types.

From this output we generated two estimates of peatland area by ecosystem type following different assumptions that create more inclusive or more conservative estimates. For the first, our 'inclusive area estimate,' we multiplied the area of each pixel by the peat probability (e.g. $0.30 \times 900\ \text{m}^2 = 270\ \text{m}^2$ of likely peat area, for a 30×30 m pixel with an assigned probability of 30%). This generates a large estimate because of large areas with low probability for peat cover, especially in the floodplain forest class. Additionally, we generated an alternative more conservative estimate of peatland area, which discounts areas with low probability to 0. For this 'conservative area estimate,' we grouped the peatland probabilities result into four modal categories (very low probability, low probability, medium probability and high probability) as defined by local minima of the distribution function of probabilities. The conservative estimate of peat area assumes peat is present within the more probable modes of predicted peatland cover (medium and high probability) and absent from the low and lowest probability areas.

For each of these approaches to estimating area, we generated 95% confidence intervals from the confusion matrix of the classification to estimate map estimation error and 95% confidence intervals of each ecosystem type [51]. We used these 95% confidence intervals to simulate a distribution of 1000 values of area for each peatland type.

To estimate peat volume, we used a similar bootstrap resampling approach as described above

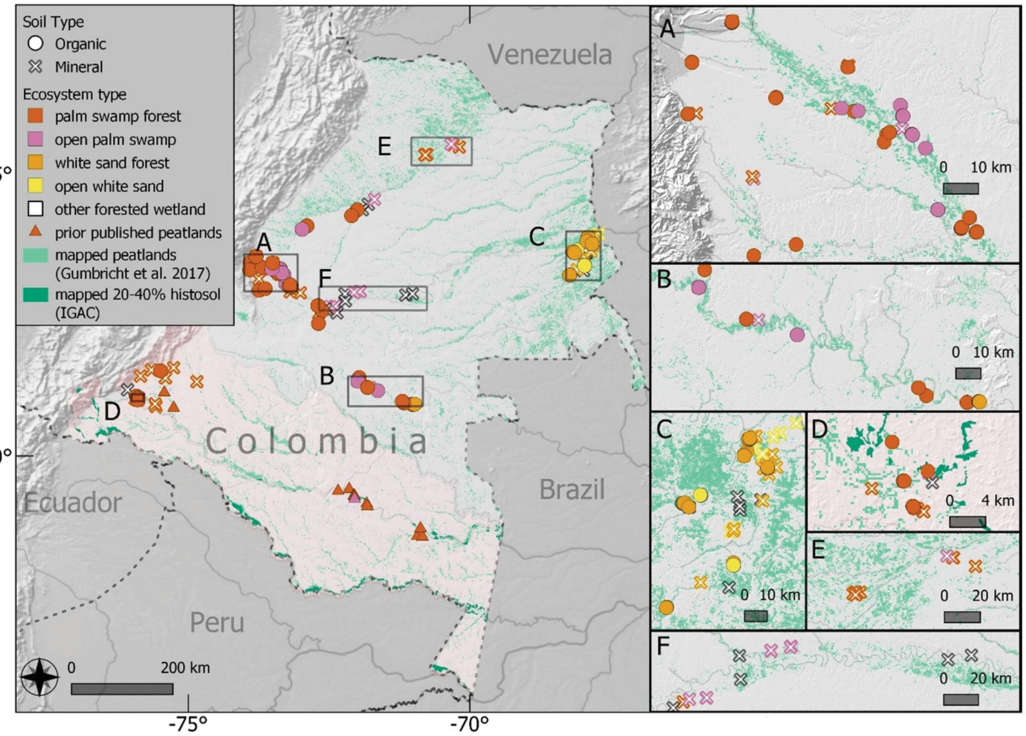

Figure 1. Map of new field observations of wetland soils from this study as well as prior information on predicted and confirmed peatland locations in the eastern Colombian lowlands. Insets detail clusters of peatland-rich regions we identified: Rio Ariari catchment in the Andean piedmont of the Amazon-Llanos ecological transition (A); the Rio Vaupés floodplain, a blackwater Amazonian river that feeds the Rio Negro (B); lower Rio Inirida blackwater catchment near the confluence with the Rio Orinoco (C); upper Rio Caquetá catchment in the Andean piedmont of the Amazon basin (D). Insets also detail regions with concentrations of predictively mapped peatlands, but where we were unable to detect any peatlands: palm swamps and riparian wetlands near the Rio Meta in the Llanos Orientales (E); upper Rio Guaviare floodplain, an Andean whitewater river tributary of the Orinoco (F). Red-tinted regions in the south cover the only three Colombia departments within the study area (Amazonas, Putumayo, Caquetá) with mapped histosols [1] or prior published peatland observations [43, 44] (figure S7). Base map is public domain provided by Natural Earth (www.naturalearthdata.com/). Reproduced with permission from [https://www.naturalearthdata.com/].

for estimating carbon stocks, except instead of calculating ecosystem carbon densities, we simply generated mean values and 95% confidence intervals of depth for each peatland type. To estimate carbon stock (as described above) for the floodplain forest peatland class for which we lack soil cores, we substitute palm swamp soils data since these ecosystems are most closely related ecologically.

3. Results and discussion

3.1. Wide distribution of peatlands

Our results demonstrate that peatlands are widely distributed throughout Colombia's eastern lowlands. During 8 field campaigns spanning five Colombian departments, we visited 104 potentially peat-forming wetlands, finding 51 sites with peat soils >40 cm thick (figure 1, table S1). These peatlands exist within a variety of hydrogeochemical, geomorphologic and climatic settings, occurring on both whitewater and blackwater/clearwater floodplain terraces; in the Andean piedmont as high as 400 m elevation; and overlying gray clayey sediment and white-sand soils derived from the Guiana Shield formation. We find peatlands to be present hundreds of kilometers away from any previously published locations [43, 44] or mapped Histosols [52] and within regions and biomes not recognized to be conducive to peat formation, such as riparian vegetation within savannas or shrublands and in white-sand forests (figure S8). In addition to their wide spatial distribution, peatlands in the Colombian lowlands are ecologically diverse, occurring among seven different ecoregions [53].

3.2. Classification

We classified the surveyed lowland Colombian peatlands into two types based on our field observations of vegetation (figure 2) and subsoils (figure 3): palm swamp peatlands and white-sand peatlands. The two types differ in their hydrogeomorphic setting and geologic context, and their peats differ in their typical ranges of OM content and thickness. Each type can occur as a closed-canopy 'forest' or as a sparsely-treed 'open' ecosystem with a dense herbaceous cover

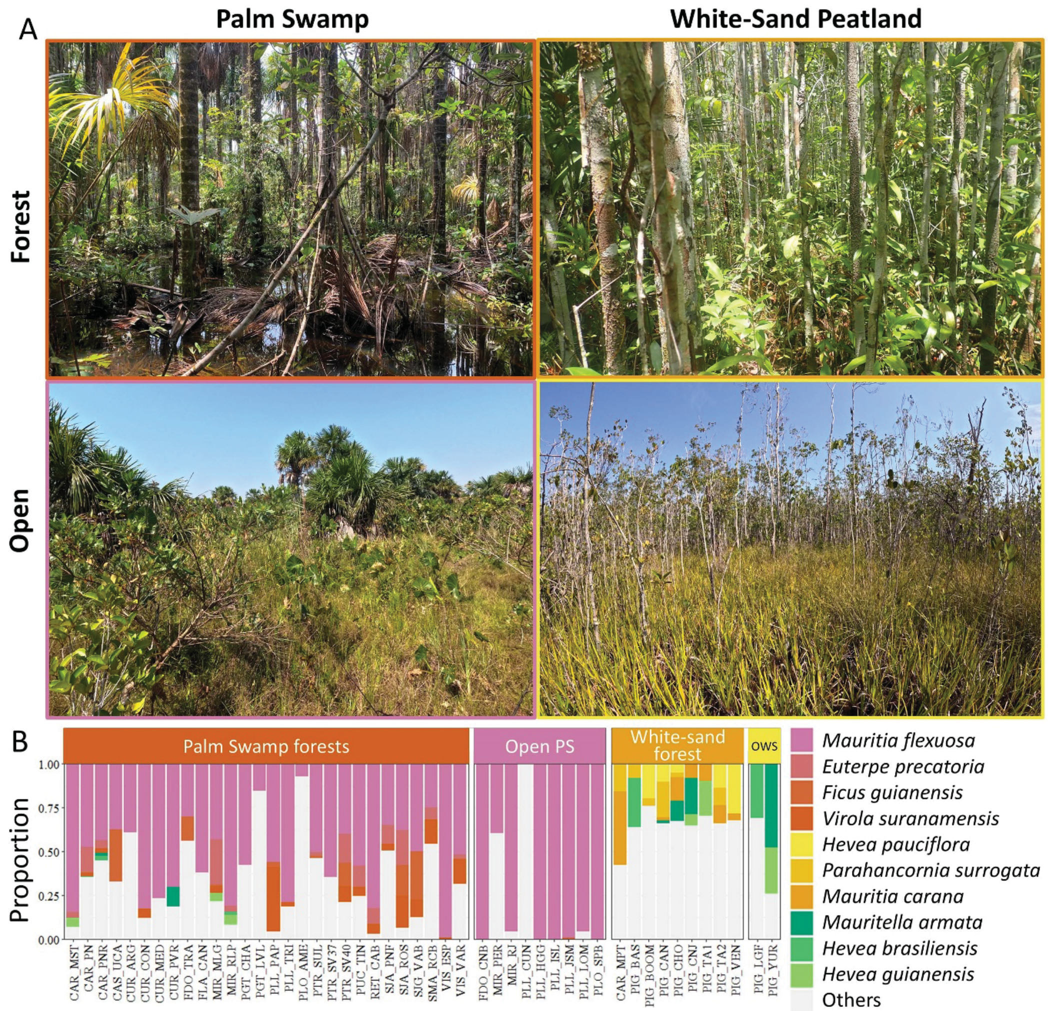

Figure 2. We describe two types of peatlands in the Colombian lowlands based on plant community with two sub-types based on physiognomy (A). Palm swamps with dominance of the *Mauritia flexuosa* palm and white-sand peatlands with a distinctive pole forest community of thin, short trees often including latex (*Hevea* sp.) among other characteristic taxa (B). Both types are commonly closed-canopy forests but may also be encountered as herbaceous/shrub swamps or 'open' ecosystems. PS is an abbreviation for Palm Swamp and OWS is an abbreviation for Open White-Sand. Note that site PLL_CUN contains four species which are not abundant in the dataset (*Enterolobium schomburgkii, Calophyllum brasiliense, Macrolobium acaciifolium* and *Montrichardia arborescens*) and is placed tentatively within the Open PS class due to its structural similarity and the observation of *M. flexuosa* present at the site outside the 0.1 ha plot. We also note that Hevea species encountered in white sand peatland plots lacked reproductive parts, making species level determinations tentative (see SI for further comment).

of grass/sedge. This ecosystem classification system extends and overlaps with a previously developed system for Peruvian Amazonia [24].

3.2.1. Vegetation

Palm swamps peatlands are the most readily encountered and widely distributed peatland type in lowland Colombia. Although they are easily recognized by the dominance of the *Mauritia flexuosa* palm (figure 2), many sites (38 out of 68 surveyed) did not support peat soils, despite having forest structures and plant communities indistinguishable from those of palm swamp peatlands. Non-peat-forming mineral soil palm swamps are known from perennially humid Peru [54], but in Colombia they appear to be more prevalent, especially in the seasonally flooded savannas of the Llanos Orientales where a highly seasonal climate with low precipitation creates less favorable hydrologic conditions for peat formation.

We also found peat in inundated white-sand ecosystems, named for their white sandy substrates [55], which we refer to as 'white-sand peatlands' from hereon. This finding was unexpected as peat has not been previously reported in these South American ecosystems. Floristically and structurally, white-sand forests—whether peat-forming or not—differ markedly from palm swamps, exhibiting a pole forest structure of dense, thin-stemmed and often stunted trees. Although structurally similar, Colombian white-sand peatlands are floristically distinct from 'peatland pole forests' described from Peru [23] (figure S4) and are typically dominated

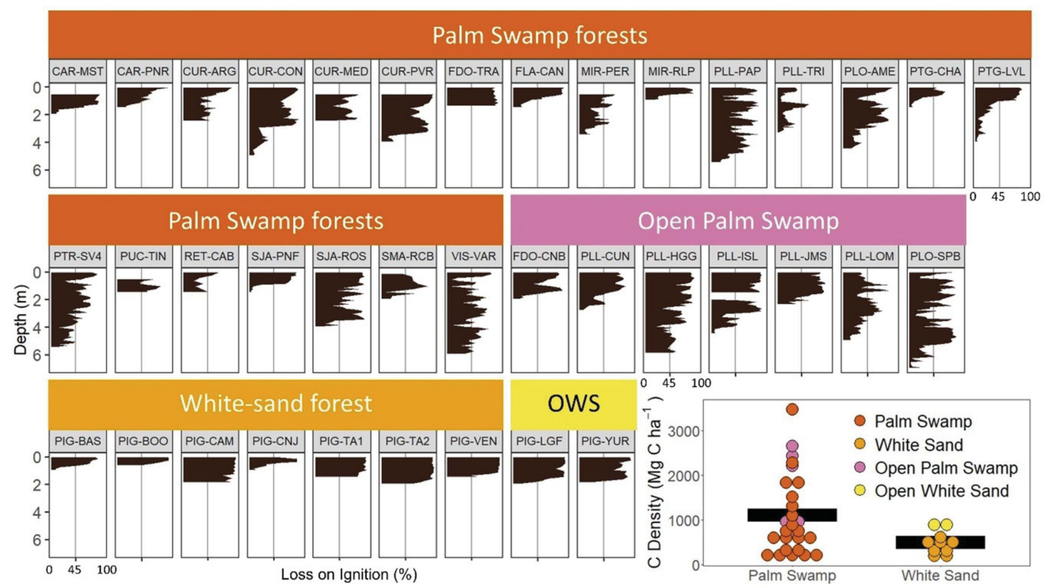

Figure 3. Profiles of organic matter (OM) content from loss on ignition sampled at 10 cm intervals from peat cores of the Colombian lowlands sorted by plant community (A). The vertical lines at 45% OM indicate our threshold for delimiting peat for the purposes of defining the core bottom and mineral intrusions [30] following Wust *et al* [30]. Inset B shows ecosystem carbon density as calculated by organic matter content and bulk density for each site's peat column. Horizontal black bars indicate mean. Core gaps (e.g. open palm swamp site PLL-ISL) represent water filled horizons at sites with floating peat mats. OWS is an abbreviation for Open White-Sand. Site details are listed in table S1.

by latex-producing *Hevea* sp. (figure 2). The presence of a white-sand substrate beneath up to two meters of peat soil is counterintuitive since sandy soils should have a poor water holding capacity and be unlikely to support peatland hydrology. Although we were unable to directly observe deep soil layers, we suspect the presence of an impermeable bedrock or cement ortstein layer beneath the white-sand as is present in hydromorphic spodosols to which Amazonian white-sand ecosystems are often mapped [55]. Interestingly, peat soils atop white sandy substrates have been described in Kerangas heath forests of Southeast Asia [56–58] and a few studies describe thick humus or organic soil layers in inundated white sand ecosystems from other tropical South American countries [59–61], suggesting this may be an under-recognized, but broadly distributed peatland type.

The herbaceous/shrub or 'open' peatlands we encountered, although structurally alike, share a primary affinity with their principal forest type, rather than each other, in terms of both species composition (figure 2(B)) and soil profiles (figure 3). The distinction between forested and open canopy types is often a gradient or patchwork within structurally heterogeneous peatland complexes and may reflect successional trajectories [21]or local disturbance regimes from fire or other yet-to-be studied mechanisms.

The peatland community typology we describe may be expanded in the future, as there are still regions in which wetlands have not been well-surveyed, especially in the southern part of the Colombian Amazon. Two types of peatlands described in Peru, 'open peatlands' and hardwood swamp forested peatlands, have not yet been catalogued in Colombia (though one site, PLL_CUN may be a candidate for a non-palm 'open peatland'). Initial fieldwork in the flooded savannas of the Guiana Shield and in flooded forests of the Orinoco basin (JCB and AGS, personal observation) suggests that these may also constitute distinctive, undescribed peatland ecosystems, with characteristic flora and soil properties, or perhaps end-members of poorly studied ecological gradients.

3.2.2. Soil profiles

Our analysis of peat column OM reveals a wide range of peat depths and patterns of organic content among Colombian peatlands, with clear differences between palm swamp peatlands and white-sand peatlands (figure 3). Because palm swamp peatlands are often associated with abandoned branches or floodplain terraces of whitewater rivers [21, 62, 63], historical flood pulses have deposited mineral material episodically [64, 65], leading to dramatically fluctuating OM content down core. In contrast, white-sand peatlands lack mineral intrusions and maintain extremely high OM content throughout most of their profiles, a difference that reflects settings where blackwater flood waters carry little to no mineral sediment.

Palm swamp peats have a mean belowground ecosystem carbon density that is more than double that of white sand peatlands (1230 versus 490 Mg C ha^{-1}) because of their deeper peat depths (mean of 2.40 versus 1.38 m) and higher bulk density (mean

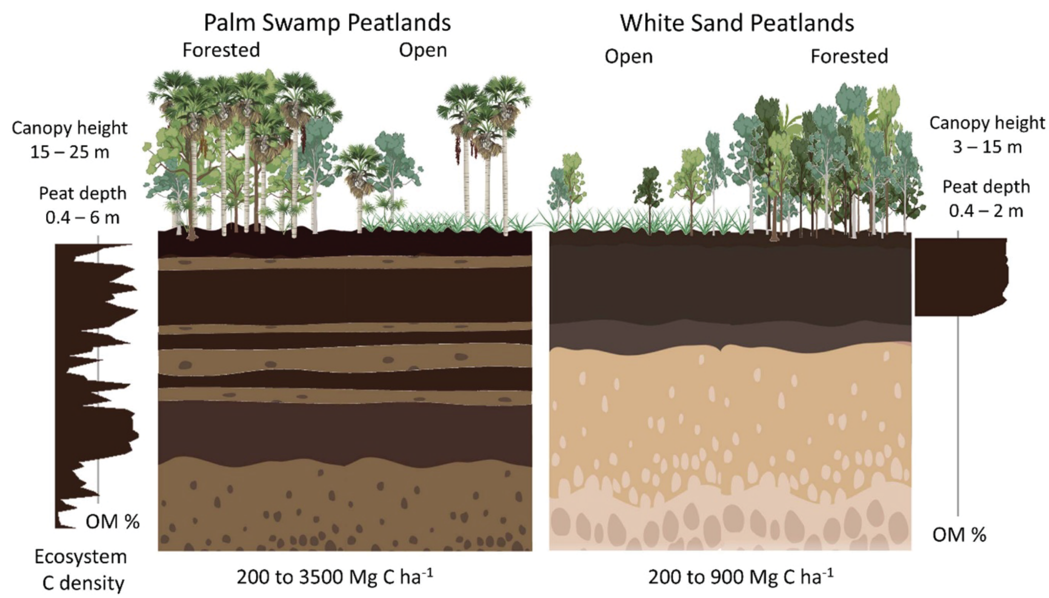

Figure 4. Summary of peatland types in Colombia's eastern lowlands with associated plant communities, vegetation structure, soil organic matter content and ecosystem carbon density based on field observations of 51 peatland sites and lab analyses of 39 intact peat cores in the region. Palm swamp and white sand peatlands may be closed-canopy forests or open-canopy ecosystems with scattered trees and herbaceous cover. Soil profiles reflect the tendency of palm swamps to occur on whitewater floodplains and receive mineral intrusions, whereas white sand peatlands lack mineral inputs and have high concentrations of organic matter throughout their peat profiles. Profiles shown are examples from site PLO-SPB near Puerto Lopez, Meta and site PIG-TA2 near Puerto Inirida Guainía (figure 3).

of 0.19 versus 0.09 g cm^{-3}). For context, these peatland belowground carbon densities are four to ten times greater than aboveground carbon density of Amazonian Terra Firme forests (roughly 125 Mg C ha^{-1}) [24]. Although these relationships between peat depth and ecological community help constrain regional carbon stocks (figure 4), variability and uncertainty remain substantial and further field investigations will yield further improvements in peat carbon accounting within and beyond Colombia.

3.2.3. Mapping and extrapolation

We upscaled our field observations from Colombia's eastern lowlands to build a map of peatland coverage (figure 5) and generate a 'best guess' of peatland areal coverage of 19 230 km^2. This 'best guess' is the mean of two separate estimates (9391 and 29 069 km^2) of area generated using more 'conservative' or more 'inclusive' handling of large areas of wetlands with low predicted peat probabilities, respectively (see methods). We suggest that the true peatland area for the study area likely lies somewhere between 7370 and 36 200 km^2, which includes the 95% confidence intervals of both conservative and inclusive estimates. These area estimates are more than an order of magnitude greater than one based on mapped histosols (638 km^2) [1], but substantially less than estimates from some global peatland models (up to 58 000 km^2) [16, 20] (table 1). Our estimate of 46 km^3 of peat volume (mean of volumes calculated from conservative and inclusive areal estimates multiplied by mean depth of each peatland type) and of 1.91 Pg carbon (from mean of conservative and inclusive volume, mean bulk density and mean % carbon for each type [24]) also fall between widely divergent prior estimates for the region (0.32–214 km^3 and 0.02–10.8 Pg) [1, 16, 19, 20].

3.2.4. Implications and controlling factors

Our field peatland observations resolve the orders of magnitude discrepancy between estimates for peat area based on soils maps and those of more recent model outputs in Colombia. Although we find that peatlands are much scarcer and shallower throughout the study area than the Global Wetland Map predicts [16], we are able to corroborate its authors' general conclusion–that peatlands are more widespread in the interior of tropical South America than is widely understood. Peatlands were previously documented in the Amazon of Colombia [43, 44] and Peru [24, 62, 67, 68], but the occurrence of peatlands in the highly seasonal savanna ecoregion of the Llanos Orientales greatly extends our understanding of geographic range and environmental conditions under which peatlands can form and persist in the neotropics (though we note savanna peatlands from Venezuela, Brazil and Bolivia documented in the paleoecology literature [69–71]). The many wet white-sand peatlands we encountered near the Venezuelan border in the Guainía department (figure 1(C)) confirms peat presence in a region where peatlands have been predicted but had not been previously documented

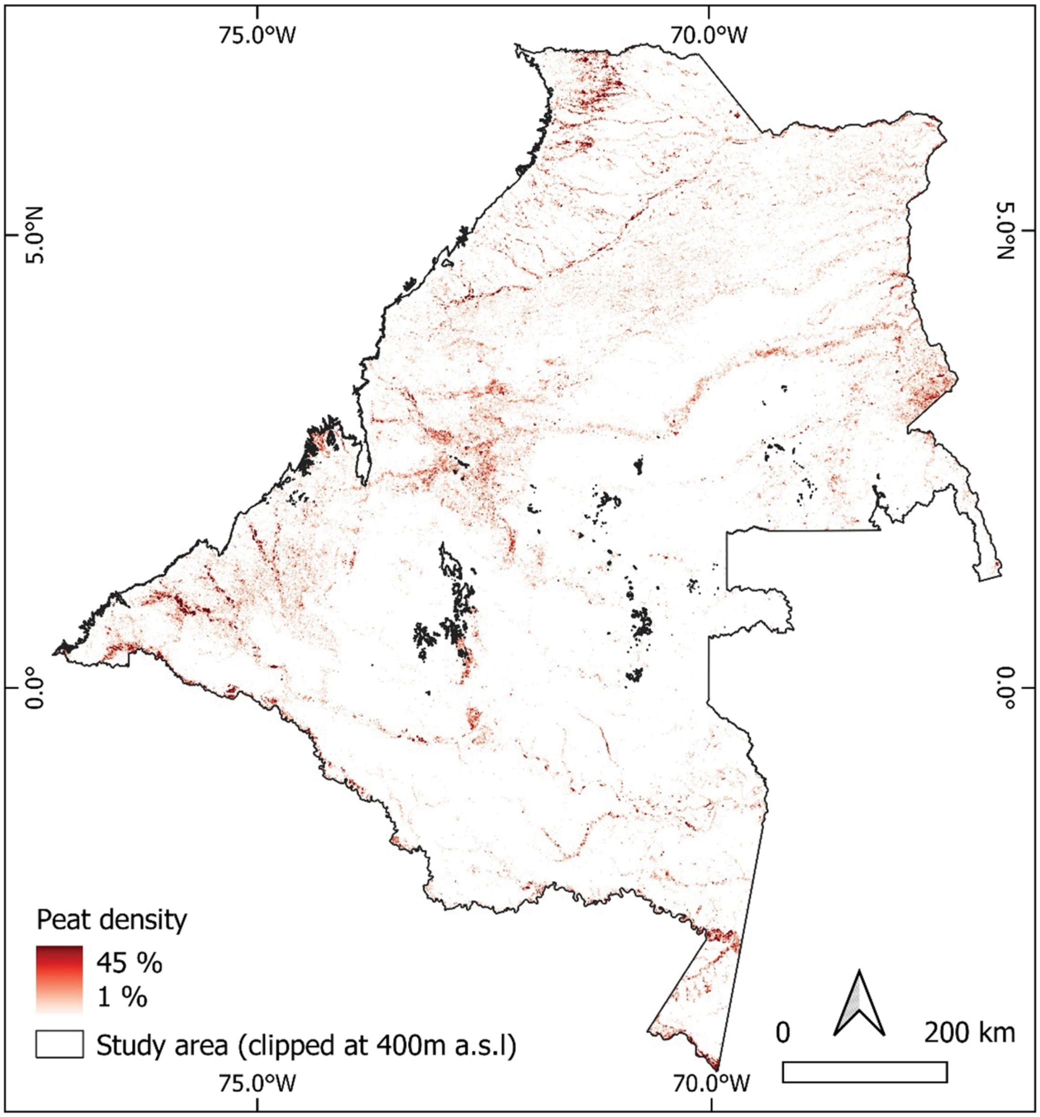

Figure 5. Map of peatland density in the Colombian lowlands as predicted by a Random Forest algorithm trained with our field observations as well as other previously published observations of peat and non-peat soils (figure S7) and using multiple remote sensing products, such as Copernicus Sentinel-1 and −2 and PALSAR2 (see Methods). The map has been upscaled from 30 × 30 m to 1 × 1 km to improve visibility at the scale of the study area, with peat density representing the percentage of 30 × 30 m peat sub-pixels within each 1 × 1 km pixel. Black dots and polygons in the interior of the study region are table mountains exceeding 400 m elevation, which might support peat soils [66], but which we exclude from our predictive mapping since we lack field data from Colombia for such ecosystems.

Table 1. Estimates of peatland area, peat volume and carbon stock for the eastern lowlands of Colombia from this and previous studies. Reported estimates of area for this study are (or are calculated from) means of 'conservative' and 'inclusive' approaches to areal estimation (see Methods). Ranges in parentheses span 95% confidence intervals for both approaches.

	Page *et al* [1]	Gumbricht *et al* [16]	Xu *et al* [20]	Melton *et al* [19]	This study
Area (km^2)	638 (427–1263)	52 915	57 879	27 260	19 230 (7370–36200)
Volume (km^3)	0.32	214	124[b]	58[b]	46 (16–94)
Carbon (Pg)	0.02	10.8[a]	6.2[a]	2.9[a]	1.91 (0.60–4.22)

[a] Carbon stock estimated from volume using mean percent carbon and bulk density from Page *et al* [1]

[b] Volume estimated from area using this study's mean peat depth of 2.14 m

[16, 19, 72]. This updated understanding of peatland biogeography has important implications for conservation planning and Earth system modeling, which rely on accurate spatial distributions of critical wetland ecosystems.

3.2.5. Controls of peatland distribution

We found that peatlands in lowland Colombia can form and persist well away from active river floodplains, which expands the scope of potential peat distribution on the South American continent to interfluvial regions where they may occur in association with springs, seepages or isolated depressions and remain largelyoverlooked. Many of these peatlands are likely to be groundwater-dependent, with shallow water tables difficult to detect via satellite and which might be excluded by global maps, in contrast to regularly flooded wetlands with more readily detected standing surface water [73]. In the absence of consistent year round rainfall or coastal tides, tropical peatlands need natural depressions and/or a source of groundwater to maintain the consistently saturated soil conditions required for peat formation in perennially warm settings [74]. Thus, a combination of rainfall patterns and hydrogeomorphology, along with potential OM recalcitrance factors [75], together impose fundamental constraints on where tropical peatlands can form. In Colombia it is evident that groundwater allows for a wide distribution of peatlands and the same is likely to be true for many other tropical regions where peatlands have evaded scientific detection.

Although global predictive maps show promise, our data suggest that without field observations they may have limited applicability. We find that some of the larger wetland areas in the study area unanimously classified to be peatlands in predictive maps [16, 19, 20] may be largely, if not entirely, peat free. Although such areas are flat and receive high annual rainfall, peat formation is likely inhibited by extreme hydrological seasonality. A long dry season (figure S9) that exposes wetland soils to atmospheric oxygen likely prevents peat accumulation because of rapid decomposition, a phenomenon observed in artificially drained peatlands globally [7, 76]—this is likely the case in the climatically-extreme core of the Llanos Orientales, which experiences little rainfall from December to March in most years (figure 1(E)) [77]. In this very flat area of savanna landscape, a lack of topographic gradients to support groundwater aquifers that could maintain spring-fed swamps explains the lack of peat observations, in this study and previously [78]. Another limit to peat formation is that some river floodplains may be too dynamic for peat formation. Overbank flooding may bury peatlands under mineral silts and clays faster than peat can accumulate [79], and river meandering may excavate and reprocess floodplain sediments more rapidly than the peat can form. River dynamics may explain the apparent scarcity of peatlands along some whitewater rivers, such as the upper Rio Guaviare (figure 1(F)). The apparent absence of peatlands in some areas likely reflects regional climatic or local hydrologic and topographic limits that render these areas largely free of peat.

Further research is needed to more fully assess the occurrence of white-sand peatlands. Of the 29 inundated white-sand ecosystems we surveyed, just 9 supported surficial peat layers of >40 cm, suggesting that white-sand peatlands may not be common; we caution that all but one of these observations stem from a single region (Inirida, Guainia) and may not reflect patterns across the broader domain of white-sand ecosystems in Amazonia. Despite their apparent rarity, white-sand peatlands may be widely distributed, as descriptions of thick (>40 cm) organic horizons atop white-sand soils from Brazil [60], Suriname [61] and Venezuela [59], meet tropical peatland criteria [30] and span a wide swath of northern South America [72]. Also in need of further research are hardwood floodplain forest peatlands, which are poorly known, difficult to detect, and have rarely been recorded. Nonetheless, about three-quarters of the forested wetlands in our study area are covered in hardwood floodplain forest, so it is important to determine precisely what proportion of this large area of forest holds peat.

4. Outlook for conservation

Although our estimate of peatland carbon stocks for the Colombian lowlands remains highly uncertain, our central estimate of 1.91 Pg (mean of inclusive and conservative estimates) is more than one-third of that of the Pastaza-Marañon Foreland Basin (4.36 [26] to 5.4 Pg [33]), the largest known peatland complex in South America, and roughly equivalent to 70 years of emissions from fossil fuels and industry in Colombia [80]. This finding emphasizes the need for further peatland research and carbon-motivated conservation efforts in Colombia, as well as in other global peatland hotspots identified by models, but which lack field data. An important and urgent [18] next step in Colombia will be an assessment of peatland threats, degradation and carbon losses, as has recently been carried out in Peru [8, 33, 81, 82]. Anecdotally, we observed examples of palm swamp felling and many of the open palm swamp peatlands in the Llanos Orientales showed evidence of charring on tree trunks, indicating a history of peatland fires. It is possible that these peatlands may be well-adapted to withstand anthropogenic fire regimes [83, 84] but, given the history of catastrophic peat fires elsewhere [2, 5, 85], their sensitivity to fire should be investigated.

Further socio-ecological research is needed to systematically assess evidence for past destruction and analyze ongoing threats. People that live among

Colombian peatlands include farmers and ranchers as well as indigenous communities, which place a special cultural importance on water bodies [86]. Socio-ecological research should be *a priori*ty to assess interactions between local communities and peatlands, and to identify potential threats as well as opportunities for their protection under an umbrella of community-led sustainable development [87–89].

Data availability statement

All field data described in this manuscript as well as codes used to generate figures will be archived in the open access Dryad database. Plant specimens collected as part of this research are at the Herbario del Orinoquia (Herbario LLANOS).

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.3929/ethz-b-000520816 [90].

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Conflict of interest

Authors declare that they have no competing interests.

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