

Assessment of vegetation and peat soil characteristics of a fire-impacted tropical peatland in Costa Rica

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Abstract

Tropical peatlands are highly vulnerable to anthropogenic alterations. In Costa Rica, riverine peatlands are understudied, and most are excluded from the protected areas. Aiming to assess the anthropogenic pressure in the Los Robles sector (LRS) of Medio Queso Wetland (MQW), this study evaluates its changes in vegetation cover, productivity, the topsoil, and soil profile. Fires have prevented the LRS from accumulating carbon (C) in the upper layers. Higher density and ash content; and lower C:N ratio in the dark black layers than the lower peat profile without carbonization, point to recurrent fires with a low water table (WT) for many years. To reduce the damage by fires to C accumulation, urgent measures to prevent prescribed fires, avoiding them specially until the beginning of the rainy season when the WT rise to near soil surface level. The species *Eleocharis interstincta* promotes higher C stability during the dry season, has a foliage with lower C:N ratio which make it more palatable for livestock and a more recalcitrant composition of the root system that favors peat formation than the temporally dominant *Scleria melaleuca*. Therefore, conserving *E. interstincta* could promote the recovery of the peatland functionality in the LRS.

Resumen

Las turberas tropicales son altamente vulnerables a las alteraciones antropogénicas. En Costa Rica, las turberas ribereñas han sido poco estudiadas y la mayoría están excluidas de las áreas protegidas. Con el objetivo de evaluar la presión antropogénica en el sector Los Robles (LRS) del Humedal Medio Queso (MQW), este estudio evalúa sus cambios en la cobertura vegetal, la productividad, la capa superior del suelo y el perfil del suelo. Los incendios han impedido que el LRS acumule carbono (C) en las capas superiores. Una mayor densidad y contenido de cenizas; y una relación C:N más baja en las capas de color negro oscuro que en el perfil de turba inferior sin carbonización, apuntan a incendios recurrentes con un nivel freático (WT) bajo durante muchos años. Para reducir el daño de los incendios sobre la acumulación de C, se necesitan medidas urgentes para prevenir los incendios prescritos, evitándolos al máximo hasta el comienzo de la temporada de lluvias cuando el WT alcanza un nivel cercano a la superficie del suelo. En comparación con la especie *Scleria melaleuca* (temporalmente dominante), *Eleocharis interstincta* promueve una mayor estabilidad de C durante la estación seca, tiene un follaje con una relación C:N más baja que la hace más apetecible para el ganado y una composición más recalcitrante del sistema de raíces que favorece la formación de turba. Por lo tanto, la conservación de *E. interstincta* podría promover la recuperación de la funcionalidad de la turbera en el LRS.

1 Introduction

Tropical peatlands are among the most efficient C-sequestering terrestrial ecosystems (Page et al. 2011; Ribeiro et al. 2020) due to the combination of high biomass productivity and low decomposition rates caused by their waterlogged conditions (Leng et al. 2019). The role of these ecosystems in terms of climate feedback depends on whether they are preserved as C sinks or become sources of greenhouse gases (GHG) (Anisha et al. 2020). Although wetlands span around 7% of the territory of Costa Rica (~

307,315 ha), the extent of peatlands in the country has not been systematically accounted (SINAC-PNUD-GEF 2018).

The C dynamics of tropical peatlands is strongly influenced by environmental conditions, with changes in rainfall and temperature acting as key modulators (Leng et al. 2019). As the rainy season is established, soil moisture increases and flooding is more likely to occur. During flooding, the rapid depletion of oxygen (O_2) and changes in soil microbial activity are enabled. Anaerobic and nutrient-poor conditions inhibit the complete decomposition of organic matter (OM) contributing to the formation of peat soils in a slow process that depends on local vegetation cover, temperature, and hydrological conditions (Jauhiainen et al. 2016).

Tropical peatlands are vulnerable to anthropogenic alterations such as drainage, fires, and conversion to cropland and pastures (Lilleskov et al. 2019; Kunarso et al. 2022). Drainages entail the development of a deeper oxic peat profile that enhances aerobic decomposition and results in peat C removal, increased CO_2 fluxes to the atmosphere, organic C leaching in drainage waters, peat surface subsidence and the transformation of the ecosystem (Hooijer et al. 2011; Couwenberg and Hooijer 2013; Jauhiainen et al. 2016). An early study on fire effects and recovery studies on riverine herbaceous wetlands was conducted in the Paraná river delta marshes (Salvia et al. 2012). During drought periods, smoldering fires can combust large peatland C pools (Jauhiainen et al. 2016; Leng et al. 2019; Flanagan et al. 2020; Lupascu et al. 2020) and reduce the SOC stocks of peatlands in the long term (Sommers et al. 2014). The latter affects hydrology through land subsidence, reduction of infiltration and water storage capacity, and the increase of water runoff rates. Furthermore, fires destroy the vegetation cover, which enhances erosion and nutrients loss, inducing a reduction of soil fertility. Such changes enable frequent surface floods that lead to predominant vegetation of flood-tolerant fern and herbaceous plant communities and make it difficult to re-establish trees (González-Pérez et al. 2004; Page et al. 2009; Lupascu et al. 2020). In peatlands, typical wildfires occur as low-severity surface burns when vegetation is desiccated and soil moisture is high. These low-severity fires produce flash heating of surface layers with minimal loss of underlying peat and can increase the pool of stable soil C (Flanagan et al. 2020).

The MQW complex is recognized as the most significant transboundary peatland in Central America (Montes de Oca-Lugo 2006). Livestock and agriculture have disturbed the MQW, resulting in high oxidation and subsidence due to farming practices such as field burning and the construction of small-scale drainage systems (Obando and Malavassi 1993; Peters and Tegetmeyer 2019). In Costa Rica, tropical riverine peatlands like the MQW are understudied, and most are not included in the national protected areas (SINAC-PNUD-GEF 2018). Although conservation of these ecosystems has been suggested as one of the most cost-effective ways to mitigate the national GHG emissions (Joosten et al. 2012); there is a major knowledge gap in the assessment of the local impacts on riverine peatlands, their current state, and potential management strategies for conservation. Only one previous study on peat profiles have been conducted in the MQW, however such record is not available in the Costa Rica's archives (communicated by General Directorate of Hydrocarbons, MINAE, June 2022). Therefore, the objective of this study is advance and evaluate records of the current vegetation cover, productivity, and

soil profile conditions of the LRS within the MQW. By establishing a baseline criterion for anthropogenic impacts, we aim to shed light on the vulnerability of this wetland type to human actions, as it represents one of the most numerous and vulnerable wetlands in the country (Camacho-Navarro et al. 2017).

2 Materials and methods

2.1 Analysis area

The MQW is in the middle and low basin of the Medio Queso river (11°02' 07" 'N, 84° 41' 16" W). It is a transborder wetland with only 2 km wide of protected area along the border with Nicaragua, which correspond to the National Wildlife Refuge North Border Corridor of Costa Rica (Fig. 1a) that adjoins the Nicaraguan Wildlife Reserve Los Guatuzos (Montes de Oca-Lugo 2006).

Climate in the region is characterized by long-term annual accumulated rainfall of 1856 mm (maximum 2584 mm in 2018, minimum 1437 mm in 2015) with a maximum in July (mean 275.4 mm) and a marked rainfall reduction during the dry season that peaks in March (mean 28.2 mm) for the 1995–2020 period. The annual temperature average oscillates between 21.9 °C and 31.5 °C with an average monthly value of 25.5 °C for the 1995–2005 period (National Meteorological Institute, IMN, Automatic Weather Station Los Chiles, Alajuela).

The water supply for MQW is sourced from precipitation, the Medio Queso river and other tributaries, including Hernández, Landeros, and Medio Quesito rivers (Montes de Oca-Lugo 2006). The MQW exhibits significant water level (WL) fluctuations, with occasional floods reaching up to 2 m above surface level during the rainy season and dry soils with few permanent ponds at the end of the dry season (Moreno-Casasola and Warner 2009). In the LRS, a dike was raised over the wetland on both sides of the river when the national Costa Rican Route 1856 was built, forming two permanent channels along the two segments of the central fill (Vega-García and Gómez-Navarro 2012).

For the whole MQW, a maximum peatland area of 3800 ha was reported in 1988 (Peters and Tegetmeyer 2019), containing approximately 1 024 264 MT (dry base) of peat (Obando and Malavassi 1993), most of it formed on the west of the river, with the thickest layer in a trough approximately parallel to the present river (Cohen et al. 1995).

2.2 Research plots

A study area of 12 500 m² (250 m x 50 m) peat plain was delimited in the LRS of MQW (Fig. 1a) 600 m away from the nearest point of the central fill built for the Route 1856 to protect them from permanent channels effect (Sinclair et al 2018). This area was subdivided into ten plots of 50 m x 25 m, arranged in five pairs along a transect of 250 m in the direction of the river where three WL monitoring wells were installed (Fig. 1b). During flood periods, fishes and seeds and marshy sediments are carried into the area from Medio Queso river, which, like most tropical rivers, is loaded with sediments. The LRS, including the research plots, was fully burnt by fire events on May 12nd, 2019, on May 18th, 2021 and on April 22nd,

2022. Fire events were considered of high severity as the remaining standing biomass and litter was lower than 10% based on visual inspection (Salvia et al. 2012).

The WL was monitored by water-level data loggers (model U20-001-04, Onset Computer Corporation, USA). The WL monitoring period started just after the first fire in May 2019 and ended in November 2021 (Fig. 2). In the soil profile S6 (Fig. 1a, Cuba palm -*Acoelorrhaphe wrightii*- islet) the WL measured punctually with a measuring tape, was 25 cm higher than the rest of the plots. Meteorological data were obtained from the automatic weather station Los Chiles, located 1.3 km from the site and operated by the Costa Rica National Meteorological Institute (IMN).

2.3 Vegetation cover and plant productivity

Digital photographic survey of the macrophyte species and the surrounding landscape was conducted in three transects in the LRS; one transect was oriented from the high ground on west side of the plain to Medio Queso river and the other two transects covered from the channel parallel to the highway to the Cuba palm (*Acoelorrhaphe wrightii*) islet (soil profile S6, Fig. 1a). The species inventory was conducted six months after the first fire (November 22, 2019) and five months after the second one (October 25, 2021), respectively. The aquatic plants were identified using plant guides (Crow 2002; SINAC-PNUD-GEF 2018) and the species were classified as obligate plants (OBL), facultative wetland plants (FACW), facultative plants (FAC), facultative raised ground plants (FACU), and upland plants (UPL), according to the parameters of the Natural Resources Conservation Service (USDA, NRCS 2022) and the Wetlands Project (SINAC-PNUD-GEF 2018).

Six and five months after the 2021 and 2022 fires, respectively, one subplot of 1 m² for each pair of parcels equidistant from the river, denoted as a level within the spatial distribution, were randomly selected (n = 5) and photographed to estimate recovery after one growing season in terms of cover percentage for *S. melaleuca*, *E. interstincta*, and water mirror. The images were adjusted to 600 ppi in the software Inkscape (version 1.2.1). The original images were transformed into RGB color scale and, analyzed in the program ImageJ (version 1.9.0) to estimate the total percentage occupied by each species and the water mirror. In ImageJ, the color threshold, saturation, magnitude, and brightness parameters were adjusted according to the plant species and the water mirror observed in the original image. Each cover percentage was estimated by the number of pixels registered of each color per unit area. Finally, the size of the resulting images was adjusted to a width of 5.3 cm by 5 cm height using software Gimp (version 2.10.32). The photos are shown in Online Resource 1 (Fig. 1S, levels 1–5).

Aboveground primary productivity (APP) was analyzed in four periods. The first two samplings were carried out from May 13rd, 2019 to March 3rd, 2020, and from March 4th, 2020 to April 9th, 2021 when water was at soil level. In this case, plants regrowth was measured into the same sampling square meter, which implied sampling interval of approximately one year that could increase errors on biomass estimates. The last two harvests were carried out from April 10th, 2021 to September 9th, 2021, and from April 23rd, 2022 to September 21st, 2022 under flooding conditions in the peatland (32 ± 3 cm and 92 ± 5

cm). Herbaceous vegetation was harvested in a 1 m² grid at the soil level in each plot. The biomass collected included the foliage within the sampling surface of plants rooted inside or outside the 1 m² frame. Dry and green biomass were separated for each sampling.

From the fresh weight of the dry and green biomass samples registered, 300 g subsamples were cut and dried until constant weight was reached at 70 °C (approximately 72 h) (Santos and Esteves 2004). Total productivity per area was calculated by the equation:

$$APP = \frac{\left\{ \left(\frac{DW_{GB}}{FW_{GB}} \right) \times FW_{GB} + \left(\frac{DW_{DB}}{FW_{DB}} \right) \times FW_{DB} \right\}}{A \times t} \quad (1)$$

where DW_{GB} is dry weight green biomass, FW_{GB} is fresh weight green biomass, DW_{DB} is dry weight dry biomass, FW_{DB} is fresh weight dry biomass, A is the sampled area (m²), and t is the foliage growth period (days). The biomass for each level within the spatial distribution corresponded to the average of the pair of parcels equidistant from the river.

Nine complete plants of *S. melaleuca* and *E. interstincta* were randomly selected and extracted preserving the roots. Then, aerial parts and roots were separated and dried at 70°C until constant weight. For each tissue, three plants were used to prepare a composite sample (n = 3), the composites samples were milled and analyzed by dry combustion (Bertsch and Ostinelli 2019) using a C-N analyzer (Vario Macro cube model, Elementar Analysensysteme GmbH, Germany) to determine the total C and N content.

2.4 Topsoil

Soil samplings took place on May 15th, 2019, just after the first fire, on April 5th, 2021, six weeks before the second fire and on May 3rd, 2022, 10 days after the third fire. In each sampling, two composite soil samples were collected from 10 points of each plot at the surface level (0–20 cm of depth) when WT were at the maximum annual depth.

Total C and N concentrations were determined by dry combustion as described above. The soil was extracted by the KCl-Olsen modified method. The content of calcium (Ca), magnesium (Mg), potassium (K), total phosphorus (P), zinc (Zn), copper (Cu), iron (Fe), and manganese (Mn) were quantified using atomic absorption spectroscopy (novAA 400p, Analytik Jena, Germany).

Soil pH was measured at a soil: water suspension with a 1:2.5 ratio (Hanna Instruments, model HI99121). Additionally, soil temperature and pH were measured *in situ* at 10 cm depth with a handheld pHmeter (model HI99121, Hanna Instruments, USA) on different days from June 2nd, 2019 to November 24th, 2021.

2.5 Soil profile

Six undisturbed soil profiles were extracted with a Russian type peat corer, one of them in the Cuba palm islet that has remained in the LRS, 600 m north of the established plots to target an area less altered by

the fire. Bulk density, total C and N, and ash soil content, as well as $\delta^{13}\text{C}$ isotopic signature were determined every 10 cm in the first-meter depth and every 25 cm until the mineral soil was identified. Total C and N soil content were analyzed by dry combustion, as mentioned before. Ash content was analyzed by gravimetric analysis, in which samples were first heated in a fume hood, and then burned in a muffle at 500 ° C for 6 h (Adapted from NREL 2005). The samples milled to powder and packed in tin capsules were analyzed using a Picarro's Combustion Module-Cavity Ring-Down Spectroscopy (CM-CRDS), and a curve calibration constructed by three standards (USGS77: -30.71, USGS62: -14.79 and USGS41a: +36.55) to determine the $\delta^{13}\text{C}$ isotopic signature.

2.8 Statistical analysis

Numeric data are reported as the mean $\pm$ standard deviation. Productivity measurement and variables of the topsoil and soil profile were tested for normality with the Shapiro-Wilk test. C total, C:N ratio, K, Zn, and P from topsoil samples gave not normal distribution. Equality of variances was tested using the Bartlett test. The *coefstest* function was applied for Ca, Mg, and Cu from topsoil samples and C:N ratio from tissues plants as they did not present homogeneity of variances. APP for dry and rainy season harvests were analyzed with the Student's t-test with paired and unpaired samples, respectively. To compare the C and N content, as well as the C:N ratio of *E. interstincta* and *S. melaleuca* a two-way analysis of variance was made to the root and aerial part. Topsoil composition variables were compared by one way analysis of variance (ANOVA) or Kruskal-Wallis test, in the case of no normality. In the soil profile, to contrast total C content between the conserved fibrous material and the carbonized peat and to compare bulk density between carbonized peat and preserved peat an ANOVA and Kruskal-Wallis test were applied, respectively. Correlations between soil profile properties were evaluated using the Pearson correlation coefficient. The R software (version 3.6.1) was used for statistical analysis.

3 Results

3.1 Vegetation cover and productivity

Fire events on May 12nd, 2019, May 18th, 2021, and April 23rd, 2022, left the LRS devoid of vegetation with a roots layer below an ash layer. Since an earlier prospecting visit (April 2018), the woody vegetation cover was absent in the flooded area, and only a few small islets of Cuba palm northward have resisted the fire impact. The Post-2019 fire vegetation structure included the highly dominant species *E. interstincta*, and the abundant Cyperaceae species, *Cyperus luzulae*, *Eleocharis retroflexa*, *Fuirena umbellata*, *S. melaleuca* and *Rhynchospora corymbosa*. Post-2021 fire, the makeup of the dominant vegetation changed with the Cyperaceae species *S. melaleuca* replacing *E. interstincta* as the dominant species, and the water mirror increased from less than 5% to $43.4 \pm 8.2\%$ in 2021 and $66.9 \pm 8.2\%$ in 2022 (Table 1). A detailed list of vegetation is shown in the Online Resource 2 (Table 1S and 2S).

Table 1

Flood level, water mirror, and vegetation cover percentage six and five months after the 2021 and 2022 fires in the LRS of MQW. Estimates are derived from stratified random sampling of 1 m² subplots per level of spatial distribution on November 21st, 2021 and September 21st, 2022. Mean $\pm$ standard deviation (n = 5)

Level	Flood level (cm)		Water mirror (%)		<i>E. interstincta</i> (%)		<i>S. melaleuca</i> (%)	
	2021	2022	2021	2022	2021	2022	2021	2022
1	39	87	50	53	14	19	36	28
2	40	88	38	71	22	10	40	19
3	43	88	33	71	19	19	48	10
4	47	94	42	65	17	21	41	14
5	50	98	53	68	15	13	32	19
Mean	44 $\pm$ 5	91 $\pm$ 5	43.2 $\pm$ 8.3	65.6 $\pm$ 7.5	17.3 $\pm$ 3.3	16.4 $\pm$ 4.7	39.4 $\pm$ 6.0	18 $\pm$ 6.7

Table 1

Flood level, water mirror, and land cover percentage six and five months after the 2021 and 2022 fires in the LRS of MQW. Estimates are derived from stratified random sampling of 1 m² subplots per level of spatial distribution on November 21st, 2021 and September 21st, 2022. Mean $\pm$ standard deviation (n = 5)

Level	Flood level (cm)		Water mirror (%)		<i>E. interstincta</i> (%)		<i>S. melaleuca</i> (%)	
	2021	2022	2021	2022	2021	2022	2021	2022
1	39	87	50	53	14	19	36	28
2	40	88	38	71	22	10	40	19
3	43	88	33	71	19	19	48	10
4	47	94	42	65	17	21	41	14
5	50	98	53	68	15	13	32	19
Mean	44 $\pm$ 5	91 $\pm$ 5	43.2 $\pm$ 8.3	65.6 $\pm$ 7.5	17.3 $\pm$ 3.3	16.4 $\pm$ 4.7	39.4 $\pm$ 6.0	18 $\pm$ 6.7

In the dry season, aboveground biomass was made up of 72% and 74% of dry biomass and 28% and 26% of green biomass for March 2020 and April 2021, respectively. These percentages were reversed in the rainy season when dry matter reached 19% and 30% and the green one 81% and 70% in September 2021 and September 2022, respectively (See data in Online Resource 3, Fig. 2S). It is worth mentioning that even when the dry seasons were advanced during the biomass samplings, the surface was still damp.

Based on T-test (paired for dry season and unpaired for the rainy season) the harvests in the dry season of the first and second-year post-2019 fire showed non statistically significant differences in the APP of herbaceous vegetation (Fig. 3a). In contrast, in the rainy season, the APP measured in September 2021 was significantly greater ($p = 0.02$) than its value measured in September 2022. Subplots harvested in

September 2021 were cut shortly before the 2021-fire, and unlike those harvested in September 2022, they were not affected by the fire event. On the other hand, no significant differences were found in APP as a function of the distance from the river (Fig. 3b).

The C:N ratio of aerial biomass and roots of *E. interstincta* were lower and higher respectively than those values for *S. melaleuca* (Table 2).

Table 2
Total C and N content (%) and C:N ratio (n = 3) of *E. interstincta* and *S. melaleuca*,
in the LRS of MQW

Species	Plant tissue	Total C (%)	Total N (%)	C:N ratio
<i>E.</i>	Aerial	42.84 ± 0.40a	0.88 ± 0.02a*	48.9 ± 1.1c*
<i>Interstincta</i>	Root	43.86 ± 0.45a	0.66 ± 0.00c**	66.80 ± 0.86a**
<i>S.</i>	Aerial	43.02 ± 0.79a	0.80 ± 0.03b*	54.1 ± 3.8b*
<i>melaleuca</i>	Root	43.68 ± 0.54a	0.81 ± 0.01b*	53.71 ± 0.36b*

**values with a statistical significance a $p < 0.001$

3.2 Topsoil properties

The topsoil (0–20 cm) was characterized by total C content lower than 300 g kg^{-1} (Table 3) with no significant statistical differences in the total C and N content between soil shortly after the fires (2019 and 2022) or two years later (2021). In contrast, C:N ratios of 2019 and 2021 showed a small but significant difference ($p < 0.05$). There was a decrease in Ca (-17% and - 77%), Mg (-20% and - 75%), and K (+ 25% and - 60%) content from 2019 to 2021 and from 2021 to 2022, while the exchangeable soil acidity also decreased. Finally, the metals Fe, Zn, Cu, and Mn concentration decreased sharply after the 2022 fire event.

In the LRS, the soil at 10 cm depth was characterized by a relatively constant mildly acidic pH (4.83 ± 0.22) from October 2019 to April 2021, which slightly increased after the fire on May 18th, 2021 (5.00 ± 0.19 on June 2nd, 2021 and 5.23 ± 0.11 on July 19th, 2021 Fig. 4).

Table 3

Properties of the topsoil (0–20 cm) based on dry soil throughout four years in the LRS of MQW, Los Chiles, Costa Rica, with the following conditions: May 2019, just after the first fire, April 2021, 6 weeks before the second fire and on May 2022, 10 days after the third fire. Mean $\pm$ standard deviation (n = 10)

Chemical properties*	Units	May 2019	April 2021	May 2022
C _{tot}	g kg ⁻¹	253 $\pm$ 26a	241 $\pm$ 13a	249 $\pm$ 18a
N _{tot}	g kg ⁻¹	16 $\pm$ 1a	16 $\pm$ 1a	16 $\pm$ 1a
C:N ratio		16.2 $\pm$ 1.5a	15.1 $\pm$ 0.5b	15.4 $\pm$ 0.8ab
pH		4.75 $\pm$ 0.07a	4.78 $\pm$ 0.10a	4.53 $\pm$ 0.14b
Ca	g kg ⁻¹	10.4 $\pm$ 2.0a	8.6 $\pm$ 1.1b	2.0 $\pm$ 0.3c
Mg	g kg ⁻¹	1.5 $\pm$ 0.3a	1.2 $\pm$ 0.2b	0.3 $\pm$ 0.1c
K	g kg ⁻¹	0.4 $\pm$ 0.04a	0.5 $\pm$ 0.1a	0.2 $\pm$ 0.1b
E A ^a	g kg ⁻¹	6.4 $\pm$ 0.8a	5.4 $\pm$ 0.5a	1.2 $\pm$ 0.5b
Fe	g kg ⁻¹	4.7 $\pm$ 1.1a	5.2 $\pm$ 0.6a	0.8 $\pm$ 0.5b
Zn	mg kg ⁻¹	4.4 $\pm$ 2.6ab	9.7 $\pm$ 7.7a	2.1 $\pm$ 1.0b
Cu	mg kg ⁻¹	289 $\pm$ 99a	181 $\pm$ 45b	26 $\pm$ 16c
Mn	mg kg ⁻¹	188 $\pm$ 29a	160 $\pm$ 20b	29 $\pm$ 19c
P	mg kg ⁻¹	40 $\pm$ 10a	27 $\pm$ 7b	37 $\pm$ 23ab
*Values with a different letter in the same line are significantly different ($p < 0.01$)				
^a Exchangeable acidity				

3.3 Soil profiles

In the upper layers of the plots (0–60/65 cm depth) and in Cuba palm islet (0–40 cm depth), a dark colored matter was observed associated with the occurrence of carbonization processes (Fig. 5).

The top burnt peat layer of LRS showed high variability of total C and N, varying between a minimum of 208 $\pm$ 35 g C kg⁻¹ and 9 $\pm$ 2 g N kg⁻¹ to a maximum of 329 $\pm$ 56 g C kg⁻¹ and 12 $\pm$ 4 g N kg⁻¹ (Fig. 5a and 5b). Total C was 142 mg kg⁻¹ higher in the conserved fibrous material than in carbonized peat ($p < 0.001$). Peat layer thickness varied with the sampling point. Layers with C contents larger than 300 g kg⁻¹ and ash less than 400 g kg⁻¹ (Fig. 5d) were found at different depths depending on the sampling site (S1: -50-150 cm; S2: -60-200 cm; S3: -50-300 cm; S4: -60-150 cm; S5: -60-175 cm and S6: -40-100 cm). In

S3 the peat layer is interrupted by a low soil C layer between 100–125 cm. In S6 (Cuba palm islet) the peat layer showed the least thickness.

The N content remained between 10 and 18 g kg⁻¹ (Fig. 5b). The soil C:N ratio variability was higher in the top layers and showed values lower than 25 when the underlying mineral soil was reached at the bottom of the profiles (Fig. 5c). The correlation Pearson (r) between total C and N in the soil profile was positive at the Cuba palm islet (0.59), moderate at S1 (0.40) and weak in the S2 (0.20), S3 (0.22), S5(0.18). On the other hand, the correlation Pearson was negative and weak in S4 (-0.05) (See data in Online Resource 4, Fig. 3S).

The bulk density was significantly higher ($p < 0.001$) for the dark burnt peat layers compared to the peat profile that did not show carbonization processes. In the plot area, the bulk density profile was 0.169 ± 0.039 g cm⁻³ (range from 0.13 to 0.22 g cm⁻³) for burnt peat layers and 0.095 ± 0.040 g cm⁻³ (range from 0.6 to 0.15 g cm⁻³) for the conserved peat. The bulk density profile from the Cuba palm islet (S6) decreased from 0.193 ± 0.028 g cm⁻³ with carbonization evidence present to 0.085 ± 0.040 g cm⁻³ where the peat was conserved. Moreover, there was a strong negative correlation coefficient between bulk density and total C content in soil profiles ($r = -0.74$).

The isotopic shift of ¹³C ($\delta^{13}\text{C}$) throughout the depth profiles showed similar patterns (Online Resource 5, Fig. 4S) and distinct differences between aerobic and anaerobic peat layers. Soil profiles signal of ¹³C from the LRS showed a very stable value ($-27.77 \pm 0.57\text{‰}$) from -85 cm to -200 cm depth (Fig. 6). The most noticeable differences in $\delta^{13}\text{C}$ values between degraded peat, preserved peat, and mineral layers was observed when evaluated against C:N ratios.

4 Discussion

4.1 Current anthropogenic pressures

MQW is highly vulnerable due to the lack of protection, construction of recent road, fires set up to recover grazing areas in the dry season, and small-scale drainage systems, being those risk factors for peatlands also identified for other regions (Lilleskov et al. 2019). Human interventions have strong impacts as reported previously in MQW; namely construction of canals and dikes, small-holding agriculture, and community set-up fires (Obando and Malavassi 1993; Vega-García and Gómez-Navarro 2012). Such interventions increase the risk of soil C losses, compaction, drainage, and eventually desiccation of the wetland (Lupascu et al. 2020; Rodríguez-Vasquez 2021). The opening of Route 1856 has not only restricted the water flow but has also led to an increase in the influx of people and therefore, the anthropogenic pressure on the wetland (Vega-García and Gómez-Navarro 2012). The latter might have contributed in the very short fire turnover of the LRS in recent years (three fires in the last four dry seasons). However, it is difficult to validate this hypothesis due to the site's lack of available historical fire frequency information.

Beyond the influence of WL on the plant's development, other studies have noted that ash and C fine particles produced during fires are associated with reduced infiltration rates (Larsen et al. 2009, Woods and Balfour 2010). Such infiltration changes directly affect the soil water holding capacity and WL, creating a connection between fire dynamics and surface hydrology in this type of ecosystem. The impact of smoldering fires on the local hydrology could increase the sensitivity of the area to overland flow during heavy rainfall events (González-Pérez et al. 2004; Lupascu et al. 2020). Considering that heavy rainfall events are expected to increase due to global warming (Papalexiou and Montanari 2019), the increasing frequency of smoldering fires could amplify flood risk in the LRS.

4.2 Vegetation cover and productivity is severely affected by fire

Since at least 1993, the LRS has been devoid of trees except along the river's edge and its vegetation has been characterized primarily by reeds, sedges, bushes, a few underdeveloped palms, and other small plants (Obando and Malavassi 1993). This contrasts with the Costa Rican Atlantic coast peat deposits, where the *Raphia* palm is the predominant species, and with Caño Negro Wetland, where *Yoliales* (*Raphia taedigera*) are present (SINAC-PNUD-GEF 2018). A source of this difference are likely the recurrent fires that produced open areas favoring the domination of grasses and sedges, which are fire-adapted species with a C pool more labile than woody plant residues (Noble et al. 2019; Flanagan et al. 2020; Lupascu et al. 2020). Results on vegetation lost are comparable with high severity fires at the Paraná river delta marshes; in both cases remaining plant cover was less than 10% with almost no plants in some sites (Salvia et al. 2012). The high degree of flammability of dominant secondary vegetation and the pressure of livestock production for grassland suckers probably boost short fire return periods, reducing the size of the few Cuba palm islets since 2019. On the other hand, the risk of recurrent fire in the LRS is increased by the absence of forest, which raises the temperature and contributes to the decrease of soil moisture, and by the channels formed on both sides of the dike that promote drying thus decreasing the water level artificially (Boehm et al. 2001; Siegert et al. 2001; Jauhiainen et al. 2016).

The color threshold, magnitude, and brightness of each color using ImageJ software showed a better separation for water mirror area than between vegetation species. After 2021-fire, most of the site showed a lower recovery following one growth season than what was observed in the Paraná river delta marshes based on plant cover (around 57% or 44% against 87%) (Salvia et al. 2012). This difference in vegetation recovery could be linked to a higher severity or frequency of fires in MQW, which may have left patches of rhizomes burnt and slow down the recovery process (Salvia et al. 2012). Nevertheless, frequent fire return, areas with a better water supply and water-saturated soil due to microtopography had let the survival of a few Cuba palm islets (Sandi et al. 2020).

After the fire on May 21, 2021, along with the recovery in the plant cover, there was a notorious shift in the dominant species from *E. interstincta* to *S. melaleuca* that could indicate changes in the C dynamics of the LRS (Mitsch and Gosselink 2007; Bernal and Mitsch 2012; Leroy et al. 2017). High-frequency fire return and variations on WL are likely the main factors that drive the change in the dominant species. Fire

events might produce changes in species dominance because of species-specific responses (Salvia et al. 2012) which can be supported or neutralized by variability of WL between years, as observed in LRS. Here WL was above 50 cm for a shorter period during the rainy season of 2021 compared to that of 2019 (Fig. 2). It must be mentioned that the coverage of *E. interstincta* reached a cover visually over 90% on March 9th, 2023. This recovery was likely due to the unexpected high flood level that exceeded 100 cm in the dry season because of the increase of rainfall as result of the influence of the cold phase of ENSO (La Niña), which causes wetter conditions in the region.

Changes in the dominant species within peatlands can pose a significant threat to peat formation. The vegetation composition plays a central role in the peatland ecology as it impacts the timing and extent of inundation due to their hydrodynamic resistance (Sandi et al. 2020) and soil temperature that alters C losses as CO₂ or dissolved C (Noble et al. 2019). Compared to *S. melaleuca*, *E. interstincta* could contribute to soil saturation and the reduction of oxygen concentration as its phenology left a layer of dry plant material, (among 761 ± 174 and 827 ± 67 g biomass m⁻²) in the driest months of the year. This layer can result in a less exposed peat soil with reduced temperature increases and atmospheric oxygen exchange (Agus et al. 2019). Therefore, the loss of the dry material layer probably will affect peat formation significantly as organic matter quick decomposition by oxidation rather than productivity is the principal factor that diminishes peat accumulation in tropical wetlands (Chimner and Ewel 2005; Franzluebbers et al. 2001; Bernal and Mitsch 2013). The behavior of the fires is a concern because it was observed that a shorter burning rotation length resulted in a water mirror increment (Table 1), suggesting the changes in the dominant graminoid could generate a faster overland flow, which can lead to higher erosion vulnerability as shown by Noble et al. (2019).

The comparison of the C:N ratio of the tissues of *E. interstincta* and *S. melaleuca* plants (Table 2) suggests that the foliage of *E. interstincta* is more palatable for livestock (Moretto and Distel 2002), whereas its root has a more recalcitrant composition which is favorable for peat formation (Chimner and Ewel 2005; Sonnier et al. 2020). This result has direct implications for policymakers concerned with conservation, as it provides evidence on the relevance of *E. interstincta* for environmental functioning and sustainable socioeconomic development of MQW. It is worth mentioning that local producers have noticed livestock consumes *E. interstincta* (spikerush) but no *S. melaleuca* (locally known as navajuela).

High seasonal variations among dry and green biomass are in line with the variability reported previously for other ecosystems as Lower Paraná River (Villar et al. 1996) and Macaé, Rio de Janeiro (Santos and Esteves 2004). The significant difference in the APP between September 2021 and September 2022 ($p = 0.02$), could be either attributed to changes in the WL by interannual differences in precipitation (Gordon-Colón and Velásquez 1989; Santos and Esteves 2002), the negative effect produced by the removal of plant material by the fire on April 2022, that could affect rhizome -the responsible tissue for rapid growth of herbaceous vegetation as it supplies the demand for N and P after a fire event in a P poor environment (14 ± 4 mg kg⁻¹) (Amado et al. 2005; Snyder and Rejmankova 2015)-, or the combination of both factors.

MQW showed a higher APP (3.56 and $2.79 \text{ g m}^{-2} \text{ d}^{-1}$ harvested in April 2020 and March 2021, when *E. interstincta* was the dominant species), than two other riparian regions like El Burro lagoon (Guarico, Venezuela), whose mean daily productivity was $1.67 \text{ g m}^{-2} \text{ d}^{-1}$ (minimum $1.27 \text{ g m}^{-2} \text{ d}^{-1}$ and maximum $2.27 \text{ g m}^{-2} \text{ d}^{-1}$), and the Jurubatiba lagoon (Rio de Janeiro, Brazil), where *E. interstincta*'s APP varied from 0.6 to $1.8 \text{ g m}^{-2} \text{ d}^{-1}$ (Gordon-Colón and Velásquez 1989; Santos and Esteves 2002). This difference in *E. interstincta* dynamics is likely due to lower WL value and a shorter flood period in MQW (maximum 1.05 m) compared to El Burro lagoon (maximum 1.24 m) and Jurubatiba lagoon (maximum 1.35 m). (Gordon-Colón and Velásquez 1989; Santos and Esteves 2002).

4.3 Fire and topsoil characteristics

In tropical peatlands, there are few studies on the effects of land fires on soil chemistry (Salvia et al. 2012; Wasis et al. 2019; Sulaeman et al. 2021; Marcotte et al. 2022), most of them concentrated on Selangor, Malaysia and Central Kalimantan, Indonesia (Kunarso et al. 2022). Therefore, more information on this subject is necessary to promote sustainable peatland management. In MQW topsoil, a low capacity of organic material sequestration was shown by no statistical differences in total C and N content between soil just after the fires (2019 and 2022) and two years later (2021). This result is consistent with previous findings by Salvia et al. (2012), who observed no recovery of C and N following one growing season, and the small values reported for C sequestration ($0.05 - 3 \text{ mm year}^{-1}$) (Bernal and Mitsch 2008; Dommain et al. 2011; Warren et al. 2017; Agus et al. 2019) in areas with more extended flooding periods. Additionally, the stability of the C and N in the topsoil caused by previous fire events contrasted with the significant decrease in SOC and N content observed in new peatland areas affected by fire (Salvia et al. 2012; Sulaeman et al. 2021). In the case of MQW, changes in C and N by fire could be restricted to the top centimeters soil layer due to the low thermal conductivity of relatively low C content of the LRS soil and the water-saturated soil condition where evaporation of water prevents soil temperatures from surpassing the water boiling point (Salvia et al. 2012). On the other hand, the quick vegetation recovery of pioneer species such as *E. interstincta* can lower the C:N ratio just two years after a fire due to the formation of a layer of necromass with a more labile C pool in the topsoil (Lupascu et al. 2020).

While increments of calcium (Ca) and magnesium (Mg) have been identified as indicators of fire impact on Indonesian peat soil (Wasis et al. 2019) and a possible factor for the improvement of soil fertility, our results showed that during the monitoring period, fires reduced the availability of these macronutrients. The latter could be attributed to rain washing off elements to water courses after fires left the LRS devoid of vegetation (Salvia et al. 2012) or due to low ash production in the parts where organic compounds are highly oxidized as suggested by the presence of dark charcoal.

High intensity wildfires not only lead to a substantial reduction of the SOM content but also transforms it into new aromatic compounds (Terzano et al. 2021). The increase in humic acids leads to a decrease in pH along with a reduction in exchangeable bases because the H^+ ions released into the soil solution are replaced by cation salts (Ali and Mindari 2016; Yang and Antonietti 2020). As a result of peat burning, the

structure of humic acids would lose hydrogen and oxygen, thereby increasing the carbon proportion in their structure and their cation-complexing ability (Yustiaawati et al. 2014; Ali and Mindari 2016). This is why not only a reduction in exchangeable acidity but also in Fe and Mn content was observed.

Although fire events have been found to increase the availability of phosphorus, prescribed fires for cattle grazing are an unsustainable practice because this increase is short-lived, as demonstrated by the decrease observed in April 2021 and the findings of Sulaeman et al. (2021).

The topsoil analysis (0–20 cm) showed a decrease in soil pH (Table 3). This observation is consistent with earlier studies that demonstrated no variation or an elevated soil pH in areas that had not been smoldered or burnt compared to those affected by fire (Salvia et al. 2012; Sulaeman et al. 2021; Marcotte et al. 2022). This may indicate that there was not enough ash present at the field site to change the peat pH or the rapid recovery of pH after the removal of ash by the leaching process. On the other hand, the increase in pH at 10 cm depth in June and July 2021 is in line with previous reports that indicate that peatland fires can decrease soil acidity (Wasis et al. 2019; Sulaeman et al. 2021; Marcotte et al. 2022) by combusting soil organic matter. As it generates losses of organic acids and contributes to increasing carbonates and oxides released from ash (Wasis et al. 2019; Lupascu et al. 2020; Sulaeman et al. 2021). Both measurements showed that the time it takes for the peat pH returns to pre-fire conditions after the addition of ash is shorter than the one reported for other soils and ecosystems (Marcotte et al. 2022), likely due to the high base neutralizing capacity of the peat during the post-fire period.

4.4 Effect of fire on soil profile

The sum of smoldering and low-severity fires events reported by SINAC in the area during the dry season (Matamoros et al. 2006) is likely responsible for the drop of C content to below 300 g kg^{-1} in the upper layers of LRS and the biggest fluctuations in total C and N soil content in the first 60 cm depth. This hypothesis is supported by the black coloration of these upper strata, which is associated with a mix of strongly oxidized and carbonized peat with clay from Medio Queso river (Obando and Malavassi 1993) and its correspondence with the level of the water-saturated conditions during the dry season that reach a depth of approximately – 60 cm. The SOC depletion is most likely due to peat oxidation that leads to organic matter losses in fire events (Wasis et al. 2019; Sulaeman et al. 2021). In addition, after low-severity fires, stable soil C stock might increase due to C condensation and aromatization of functional groups on the surface of peat, reducing the following degradation rates of soil organic matter (SOM) (Flanagan et al. 2020).

In contrast to the drops in the C content in the LRS, peatlands not affected by fire or drainage, like the EARTH campus site (Costa Rica) and an undrained peat swamp forest in Central Kalimantan (Indonesia) are characterized by a constant increment in the C content throughout the soil profile depth (Mitsch et al. 2008; Novita et al. 2021). We suggest that the variations observed in the vertical profile at which the C content steadily enhances above 30 g kg^{-1} can be attributed to distinct fire or WT impacts on each peat profile rather than differences in the decomposition of shallow peat (Warren et al. 2017).

The observed C:N ratio decrease in the upper layers suggests that the LRS has been drained or affected by multiple fires, as peat decomposition causes a reduction in C:N ratios due to a fast-oxidizing effect on the organic matter content (Itoh et al. 2017; Leifeld et al. 2020). Conversely, water saturation in the unburnt peat led to high C:N ratios, which is a characteristic of the highly recalcitrant organic matter accumulated in deep layers, similar to other tropical peatlands profiles (Bernal and Mitch 2013). At deeper layers, the degradation rate of compounds is lower, as the activity of the phenol oxidase enzyme is restricted by anaerobic conditions, resulting in a greater accumulation of phenolic compounds such as humic acids (Velásquez-Betancur 2018).

Another aspect that probably reflects a high oxidation in the experimental site is the low correlation between total C and N, which only reaches a coefficient of $r = 0.59$ in the Cuba palm islet. This contrasts with the significant Pearson's correlation found in other preserved peatlands such as the EARTH site ($R^2 = 0.99$, a permanent tropical floodplain) (Bernal and Mitsch 2013) and Xianghai wetland ($R^2 = 0.931$, permanent and temporal floodplain areas in China's continental monsoon climate) (Bai et al. 2020). Therefore, we hypothesize that the greater C:N correlation in S6 compared to the rest of the sampling points could be attributable to its more extended periods of flooding that limited the severity of surface burns.

The high ash content of the peat, from less than 25% to more than 50%, was also reported by Obando and Malavassi (1993). This peat characteristic can be caused by a few mechanisms including the entry of inorganic material into the peat deposit from the high areas along the outer edge of the floodplain (Obando and Malavassi 1993) or the SOC partially transformed to ash when it is burnt (Sulaeman et al. 2021). The last factor could explain why the ash pattern in the soil profile appears as a negative mirror of C content.

Bulk density tended to decrease with fiber content, like most peats in Costa Rica (Cohen et al. 1986) and their values are into the range reported for peatlands of Southeast Asia (Kunarso et al. 2022). The reduction of the peat layer bulk density by 49% with respect to the upper layer (0–60 cm) was associated with a higher total C content (Page et al. 2011) and lower oxidation of the organic matter as indicated by the absence of the black color in peat. The highest densities of the upper strata could be due to subsidence, considering that the WT was 60 cm below the peat surface when the fire occurred in May 2019 (Wösten et al. 2008; Warren et al. 2017). A condition probably recurrent due to El Niño-Southern Oscillation (ENSO), which generates reduced rainfall and a prolonged dry season in the study area (Durán-Quesada et al. 2020).

The $\delta^{13}\text{C}$ at similar depth profiles might reflect a similar degree of peat degradation (Drollinger et al. 2019). Based on the WT and visual depth of black C, the peat cores can be divided into peat layers strongly degraded or flooded conserved, the second ones characterized by a ^{13}C signal more negative and stable. The increase in the $\delta^{13}\text{C}$ values observed in the upper peat profile could be due to low WT, especially during fire events, that could generate a selective loss of ^{13}C depleted C as observed by Nykänen et al. (2020) in a drained boreal bog. In aerobic layers, microbial respiration would have induced

the selective ^{12}C losses and could lead to signatures of $\delta^{13}\text{C}$ less depleted in degraded peat layers (Drollinger et al. 2019). On the other hand, in waterlogged periods, the preferential substrate utilization of residual enriched ^{13}C OM could justify drops in $\delta^{13}\text{C}$. The approximately constant stable isotope ratios in the layers deeper than 70 cm support the hypothesis that anaerobic conditions entail negligible ^{13}C fractionation (Drollinger et al. 2019).

5 Conclusions

Observational evidence of changes in land and vegetation cover, productivity, topsoil chemical properties variability, and oxidation in the soil profile can be used to inform about the impacts of recurrent grazing fires on riverine peatlands and raise awareness of the necessity to implement public policies to preserve the functionality of the ecosystem given its relevance as a major C sink. Soil profiles monitored shown that fires prevented the LRS from accumulating C in the layers below the surface leading to the observed sharp decreases in the C content of shallow layers. The soil profile reveals the influence of smoldering fires during periods in which the WT is deeper than 60 cm from the surface level. Such impacts are reflected as changes in density, ash, and C:N ratio with respect to the preserved peat layers usually at 60 cm depth. The latter implies the variability of rainfall which modulates the WT depth which is strongly linked to the sensitivity of the ecosystem to the impact of fires.

It was observed that fire occurrence during years with precipitation deficit and shallow WL favor the dominance of *S. melaleuca* over *E. interstincta*, which promotes C stability during the dry season. Furthermore, this species is palatable for livestock, which is not the case for *S. melaleuca*, according to local farmers. The known impact of El Niño events on the occurrence of drought episodes in the region must be considered as a relevant factor in the role of MQW vegetation to reduce the impact of fires on soil C pools.

This study concludes that increasing awareness and promoting efforts by authorities and communities to prevent prescribed fires and monitor water level is key to reduce the fire damage to the dry aerial biomass and contribute to reducing the impacts on C, N, and soil nutrient pools. The results of this study provide evidence to support the discussion about the need of protecting the MQW while assisting the community that live in the area with the development of sustainable exploitation practices to reduce the loss of soil C. It is important to inform the communities on the benefits of the conservation of MQW, as actions to reduce the soil C loss also contribute to improve the growth of vegetation that is more favorable for sustainable livestock.

Declarations

Statements and Declarations

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Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

Author contributions

Ana Gabriela Pérez-Castillo, Ana María Durán-Quesada and Hinsby Cadillo-Quiroz designed the study. Ana Gabriela Pérez-Castillo, Mayela Monge-Muñoz and Weynner Giraldo-Sanclemente conducted the field work with essential contributions from Ana Cristina Méndez-Esquivel and Néstor Briceño. Laboratory and isotopic analyses were performed by Ana Gabriela Pérez-Castillo and Mayela Monge-Muñoz. Weynner Giraldo-Sanclemente supported the field image and statistical analysis. Ana Gabriela Pérez-Castillo, Mayela Monge-Muñoz and Ana María Durán-Quesada performed the data analysis. Ana Gabriela Pérez-Castillo, Mayela Monge-Muñoz, Ana María Durán-Quesada and Hinsby Cadillo-Quiroz wrote the manuscript, and all co-authors contributed to the final version of the paper.

Data availability

The datasets generated during sampling and laboratory analysis throughout this study are available from the corresponding author by request.

Compliance with ethical standards

This research was approved by National System of Conservation Areas (SINAC) of the Ministry of Environment and Energy of Costa Rica (MINAE).

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Figures

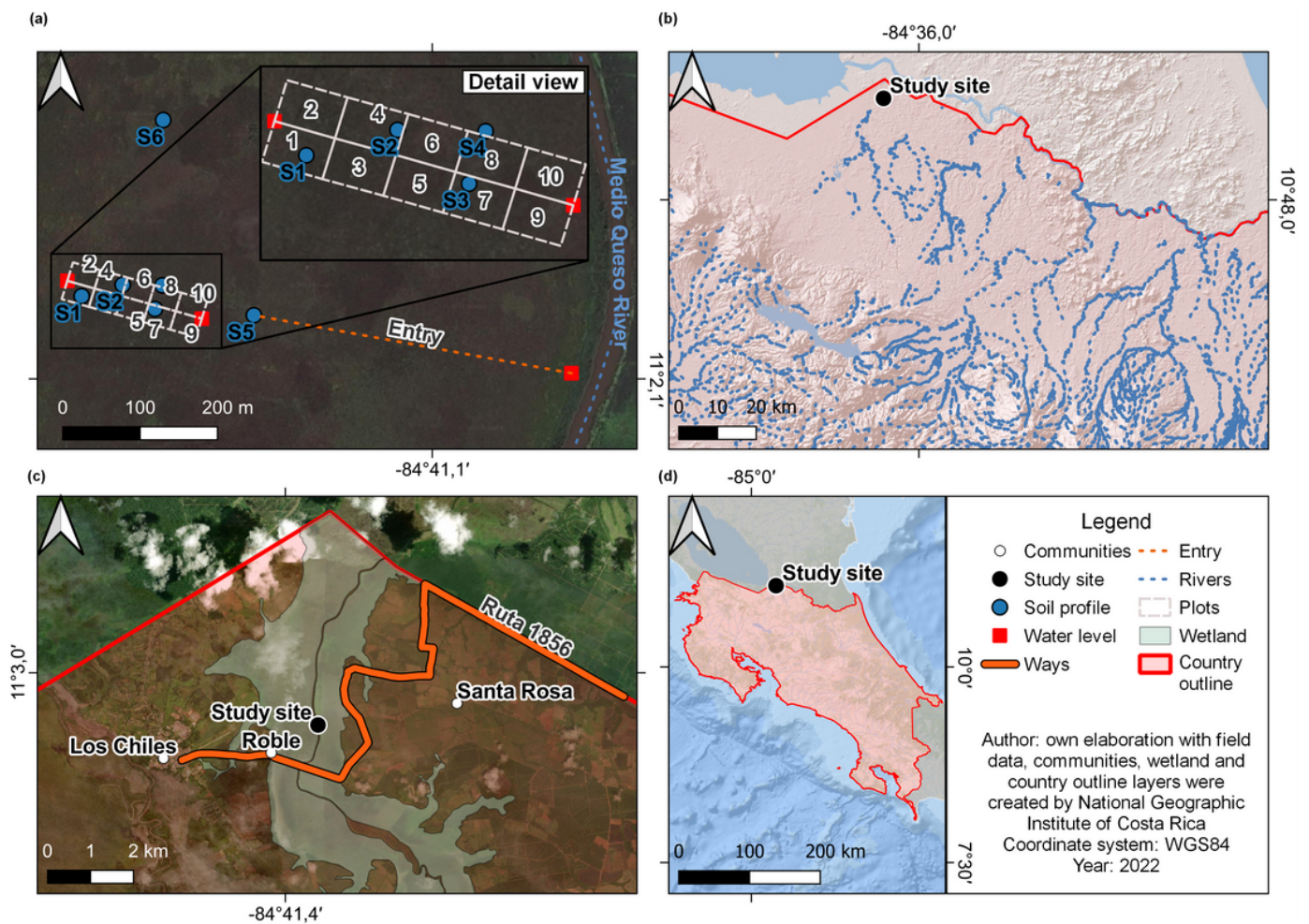


Figure 1

Location of area of study and details of plot distribution. (a) Experimental area set up with plots, wells, and soil profiles sampling points in LRS (b) Location of the study site and the north region of Costa Rica (c) MQW's area in light green shade along with the location of the LRS and Route 1856 (d) Inset of Costa Rica map that shows where the study site is

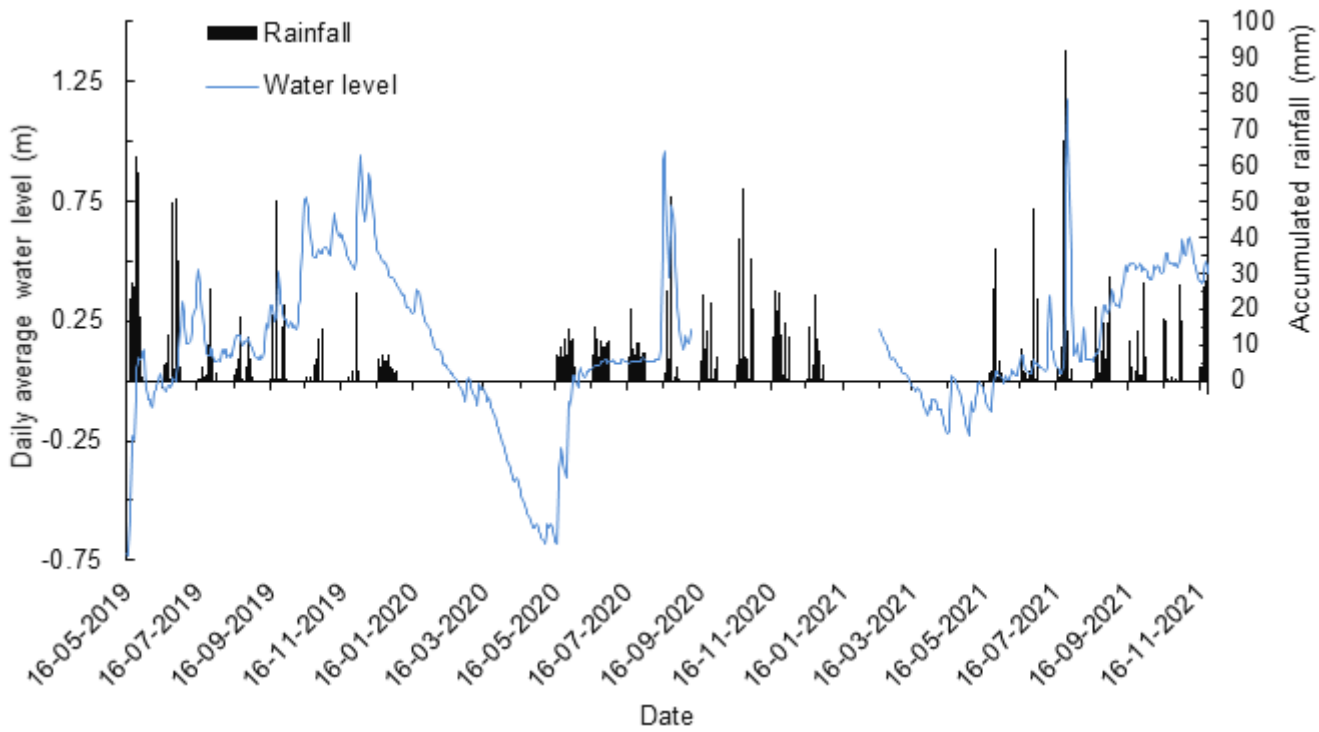


Figure 2

Daily rain (mm) and daily average water level in LRS in the MQW (n=3). Water level data from September 7, 2020 to February 20, 2021 were lost because of Covid-19 pandemic restrictions

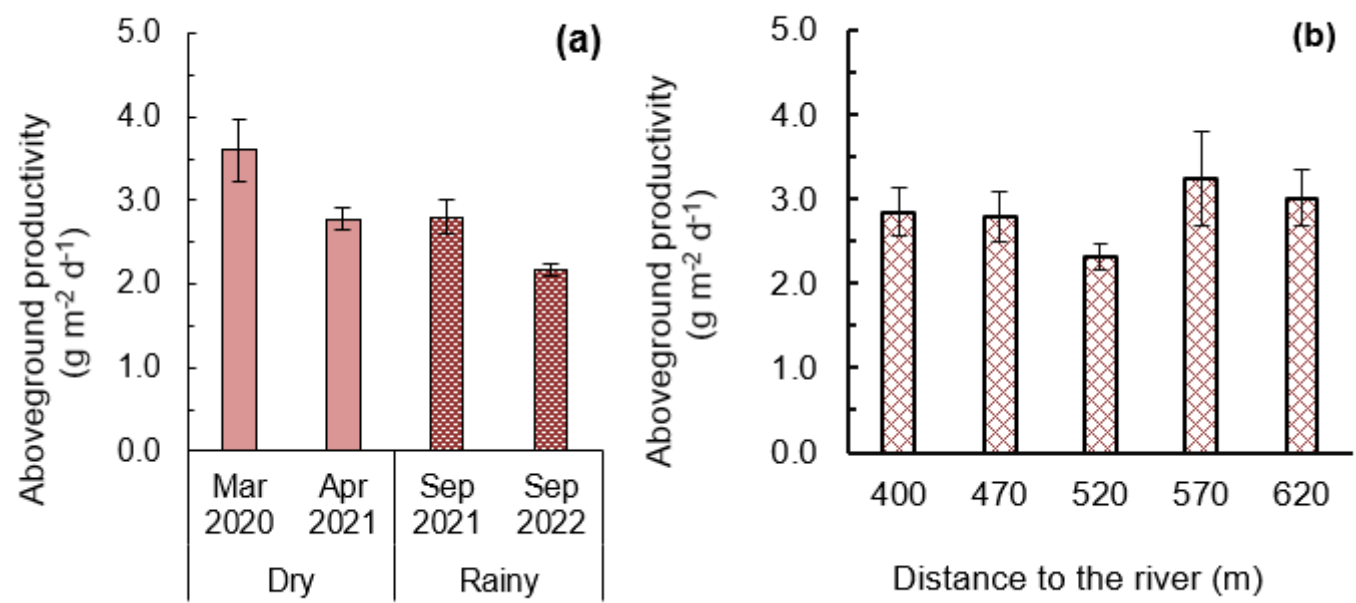


Figure 3

Aboveground primary productivity (APP) measured in the LRS of MQW. (a) Harvests during dry season (March 2020 and April 2021) corresponded to growing periods of 295 and 403 days. On the other hand,

harvests during rainy season (September 2021 and September 2022) corresponded to 153 and 151 days, respectively (n=5 with 2 replicates). and (b) Spatial variation of APP as a function of the distance from the river (n=8, 2 per sampling). Error lines represent the standard error.

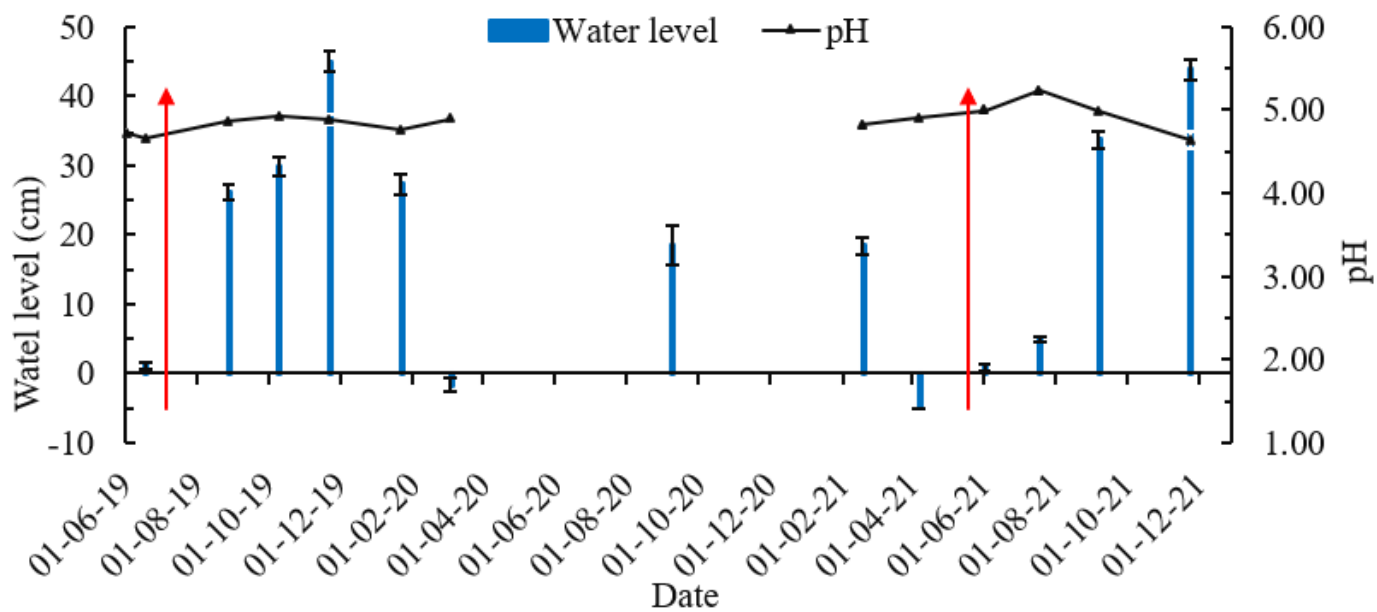


Figure 4

Average water level and pH values (n=10) non-continuously measured in the research plots from June 2nd, 2019 to November 24th, 2021 in LRS of MQW, Los Chiles, Costa Rica. Data between April 2020 and February 2021 were lost because of Covid-19 pandemic restrictions. Error lines represent the standard error (n=10). Arrows mark fire events

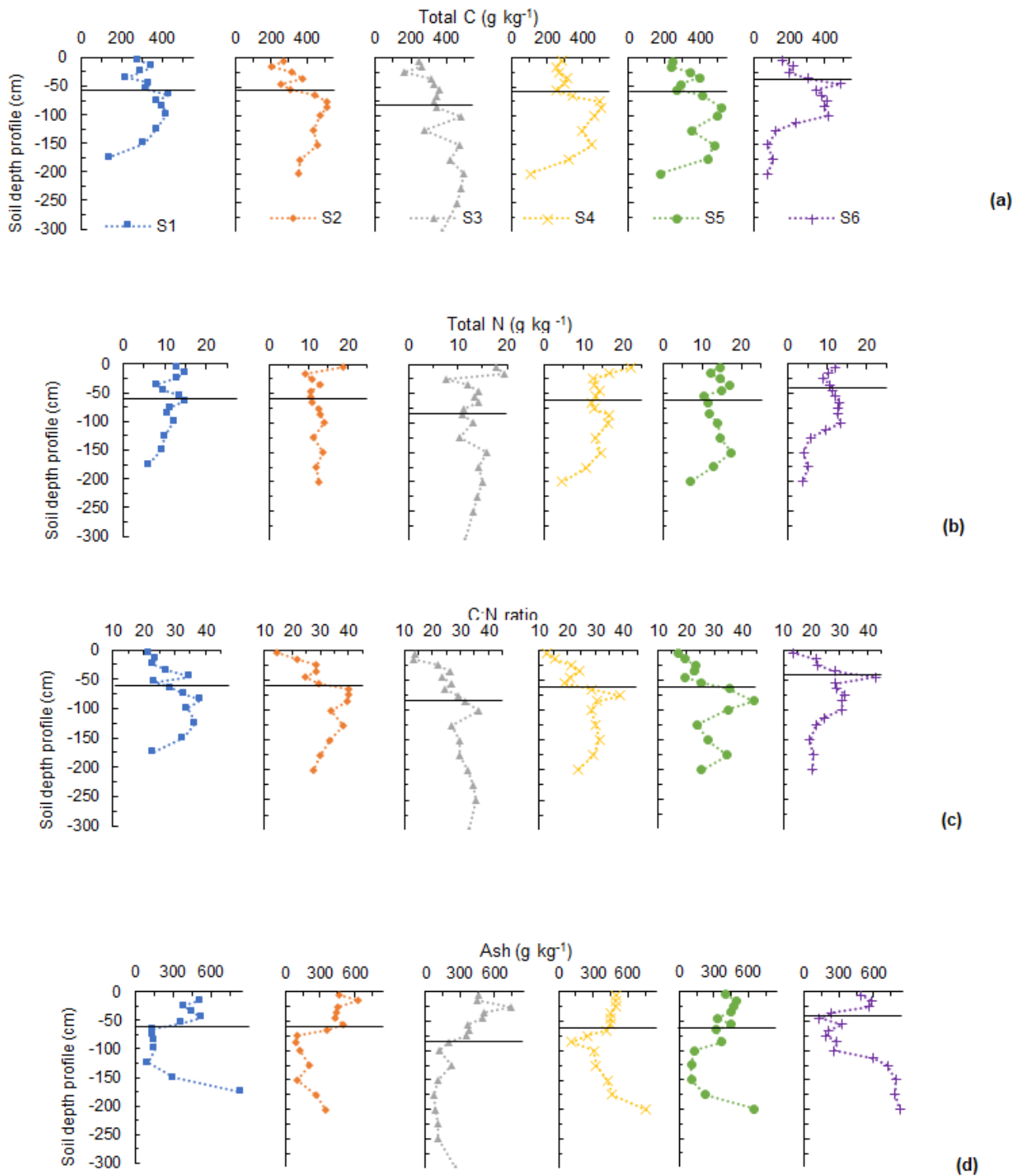


Figure 5

Total C content, total N content, C:N ratio and ash content of six soil profiles (S1-S6). Soil profiles were sampled between October 13, 2020 (S1, S2 and S3) and February 5, 2021 (S4, S5 and S6) in LRS. Black line denotes the lower level at which black matter (charcoal) is not noticeable from soil surface

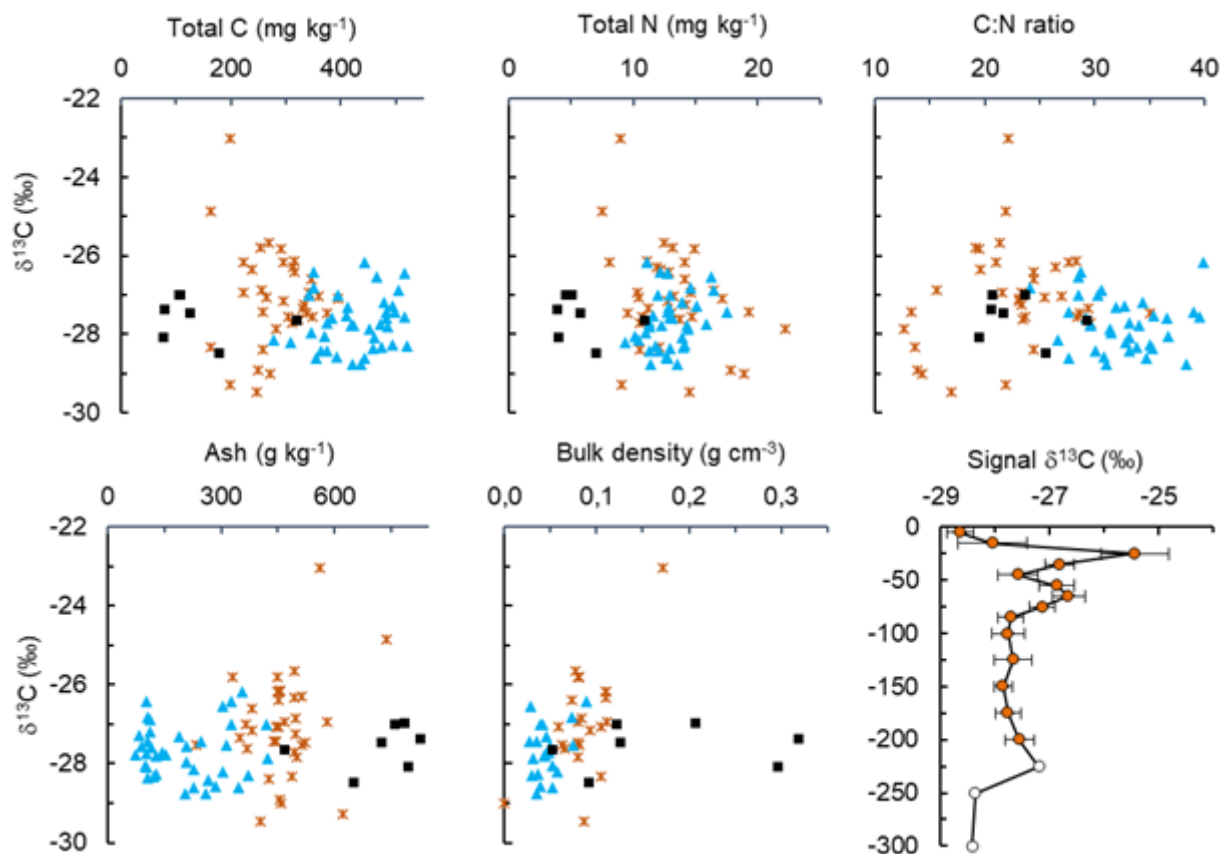


Figure 6

The isotopic shift of ^{13}C ($\delta^{13}\text{C}$) of carbonized peat (x), preserved peat () and mineral soil (■) against (a) total C, (b) total N, (c) C:N ratio, (d) ash and (e) bulk density. (f) ^{13}C signal of soil profiles from LRS (n=6), sampled between October 13, 2020 (S1, S2 and S3) and February 5, 2021 (S4, S5 and S6) in the LRS of MQW. Open circles correspond data only from S3 (n=1) and error bars represent standard error

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