



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 not included in protected areas. This study aims to generating information useful to assess the anthropogenic pressure in a riverine peatland in Los Robles Sector (LRS) of Medio Queso Wetland (MQW) complex. Evaluations of impacts of fires on vegetation and surface peat chemistry, and the post-2021 fire, makeup of dominant vegetation changes with the Cyperaceae species *Scleria melaleuca* replacing *Eleocharis interstincta* as the dominant species are presented. The topsoil (0–20 cm) total C content was quantified as lower than 300 g kg⁻¹ with no significant statistical differences in total C and N content between soil shortly after the fires or two years later. The species *E. interstincta* is observed to promote higher C stability during the dry season, and has a more recalcitrant composition of the root system compared to the post 2021-fire dominant *S. melaleuca*. To reduce the impact on C accumulation, measures to prevent grazing-originated fires, especially when the water table is low, are urgent. Hence, this work aims at proving information that can be a baseline for impacts assessment and to inform conservation measures and policies.

Keywords *Eleocharis interstincta* · Fire · Peat chemistry · Riverine peatland · *Scleria melaleuca* · Anthropogenic impact

Introduction

The impact of anthropogenic disturbances on the dynamics of Carbon (C) sequestration in tropical peatlands is higher compared to that of climate variability and change

(Leng et al. 2019; Ribeiro et al. 2020). Tropical peatlands are vulnerable and significantly affected by drainage, fires, and land use change (Jauhiainen et al. 2016; Kunarso et al. 2022). The impact of fire in riverine peatlands is understudied in tropical America with earlier studies in the Paraná River delta marshes (Salvia et al. 2012) and recent megafire records in the Pantanal wetlands (Couto-Garcia et al. 2021), but none in peatlands of Central America. During drought, fire increased frequency exacerbated by peat drainage has been observed to drive vegetation changes in Kalimantan, Indonesia (Page et al. 2009). Low-severity fires occur when vegetation is desiccated and soil moisture is high, a common condition during the transition between dry and rainy seasons. Fires destroy vegetation cover, enhancing erosion, nutrients loss and reducing soil fertility (González-Pérez et al. 2004; Leng et al. 2019). Most studies on the effects of fires on soil chemistry are focused on Malaysia and Indonesia (Kunarso et al. 2022).

In Costa Rica, the national wetland inventory reports an area of 307,315 ha, but peatlands extension has not been systematically quantified and most riverine peatlands are

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not included in the national protected areas (SINAC-PNUD-GEF 2018), despite that their conservation is a cost-effective mitigation action for the national greenhouse gases emissions (Joosten et al. 2012) or would store the larger soil carbon repositories in the country. The Medio Queso Wetland (MQW) complex is a relevant transboundary peatland in Central America (Montes de Oca-Lugo 2006) and one of the most vulnerable wetlands in Costa Rica. The degradation of MQW has increased due to road construction, grazing-recovery fires, and small-scale drainage systems for agricultural farming (Camacho-Navarro et al. 2017). These risk factors contribute to increased soil C losses, compaction, drainage, and desiccation of the peatland (Peters and Tegetmeyer 2019; Rodríguez-Vasquez 2021). There is a major knowledge gap in assessing the local impacts on riverine peatlands, their current state, and potential management strategies for conservation. The objective of this study is to provide a first approximation of short-term effect of fire from human activities on vegetation cover and surface peat chemistry.

Materials and Methods

Medio Queso Wetland

The MQW is in the middle and low basin of the Medio Queso River (MQR, 11°02' 07" N, 84° 41' 16" W) (Fig. 1a). It has a 2 km wide protected area along the border with Nicaragua, known as the Wildlife Refuge North Border Corridor of Costa Rica, that adjoins the Nicaraguan Wildlife Reserve Los Guatuzos (Montes de Oca-Lugo 2006). A peatland area of 3800 ha was reported in 1988 for MQW with most of the peat formed on the west of the river (Peters and Tegetmeyer 2019). Long-term average annual rainfall is 1864 mm and mean temperature is approximately 25.56 °C, based on the 1995–2021 record of Los Chiles meteorological station operated by the Costa Rica National Meteorological Institute (IMN). The rainy season spans from April to November and exhibits a bimodal distribution, and the dry season from December to April. Based on the Köppen-Geiger

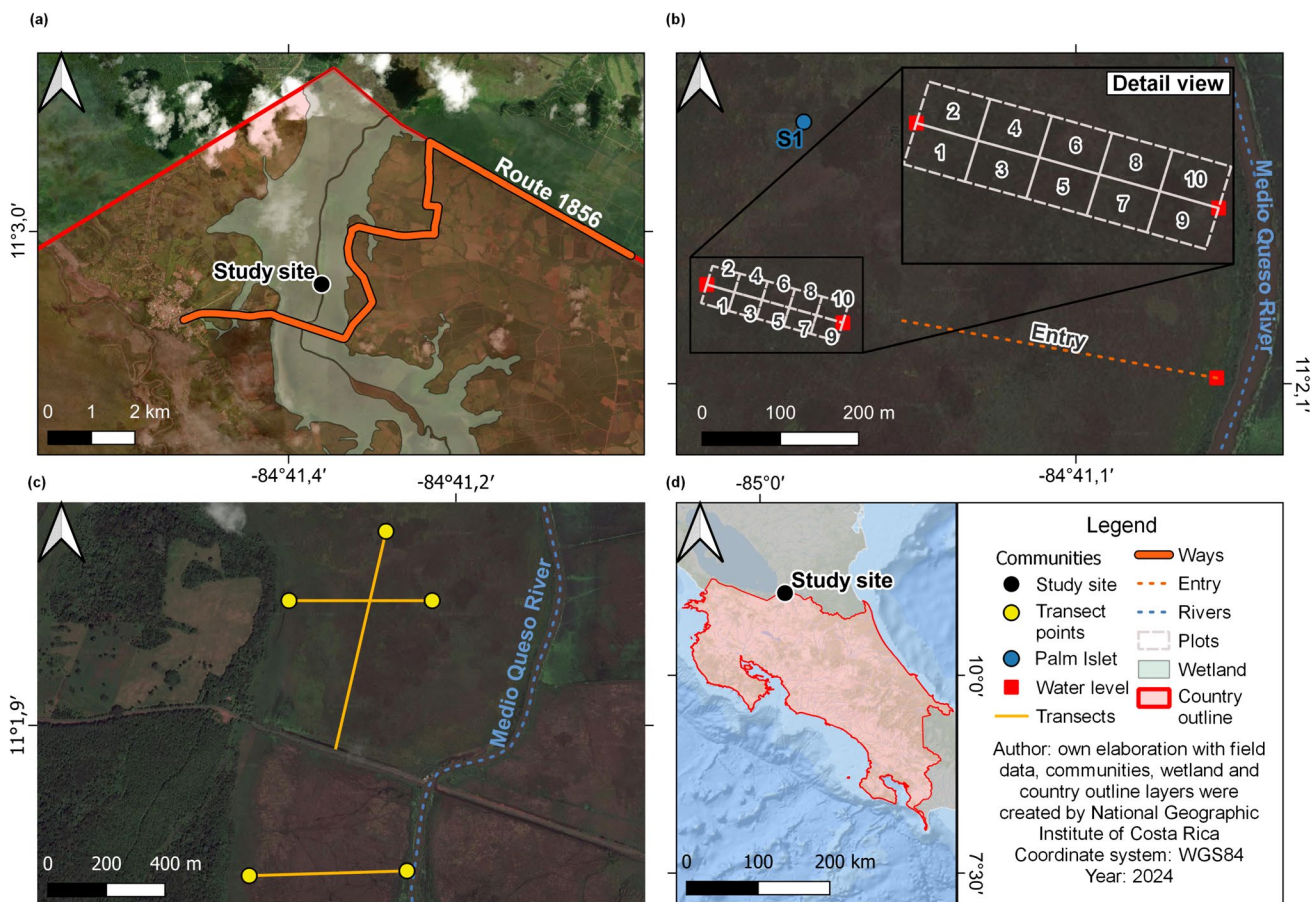


Fig. 1 Location of area of study and details of plot distribution. (a) MQW's area in light green shade along with the location of the LRS and Route 1856. (b) Experimental area set up with plots, and wells in

LRS. (c) Transects conducted for LRS Digital photographic survey of macrophyte species and surrounding landscape (d) Study site location in Costa Rican map

classification, the climate of the region is defined as Tropical Montane Forest. MQW is a topogenous peatland where water is sourced from precipitation, the MQR, and other tributaries (Montes de Oca-Lugo 2006; Flores 2014). It exhibits significant water level (WL) fluctuations, with flooding 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).

Study Area

A study area of 12 500 m² (250 m × 50 m) was delimited in LRS of MQW (Fig. 1a), 600 m away from the central fill built for Route 1856 road to protect the plots from the effect of permanent channels. The area was subdivided into ten plots of 50 m × 25 m, arranged in five pairs along a 250 m transect in the direction of the river. Three WL monitoring wells were installed at 26 m, 442 m and 840 m from the river (Fig. 1b).

The WL was monitored using water-level sensors (model U20-001–04, Onset Computer Corporation, USA) between May 2019 and May 2022 (Fig. 2a). In absence of a WL sensor for the Cuba palm *Acoelorrhaphe wrightii*- islet (S1, Fig. 1b) WL measured with a scale was found to be 25 cm higher than the rest of the plots. Meteorological data used was from IMN station Los Chiles, located 1.3 km from the site.

The LRS was devoid of trees except along the edge of the river and its vegetation was characterized primarily by reeds, sedges, bushes, few underdeveloped palms, and other small plants, condition reported by Obando and Malavassi (1993).

In the rainy season, LRS area is flooded, and fishes, seeds and marshy sediments are transported from the MQR. From January to August, dry season and first leg of the rainy season, extensive cattle grazed in the LRS with similar livestock charge during the study period. Grazing-recovery fires had been reported by Obando and Malavassi in 1993, however, fire frequency has increased since 2019 according to local newspapers. Fires that affected the study area in the last nine years are shown in Fig. 3.

In LRS, the dike built for National Route 1856 restricted the water flow, formed two permanent channels along the two segments of the central fill, and increased people transit, leading to higher anthropogenic pressure (Vega-García and Gómez-Navarro 2012). Impact of Route 1856 to a shorter fire turnover in recent years (four fires between 2019–2023) might exist but is difficult to confirm due to lack of historical fire information.

Fire and State of Vegetation

Digital photographic survey of macrophyte species and surrounding landscape was conducted in three transects in LRS (Fig. 1c). The species inventory was compiled six and five months after the 2019 and 2021 fires, respectively (Fig. 3). The inventory is provided in Online Resource 1 (Table 1S and 2S). In response to an observed change in the dominant species, nine complete plants of *S. melaleuca* (navajuela) and *E. interstincta* (spikerush) were randomly selected and extracted preserving the roots to analyze their differences in their biomass C:N ratio. Aerial parts and roots were separated and dried at 70 °C until constant weight. For each

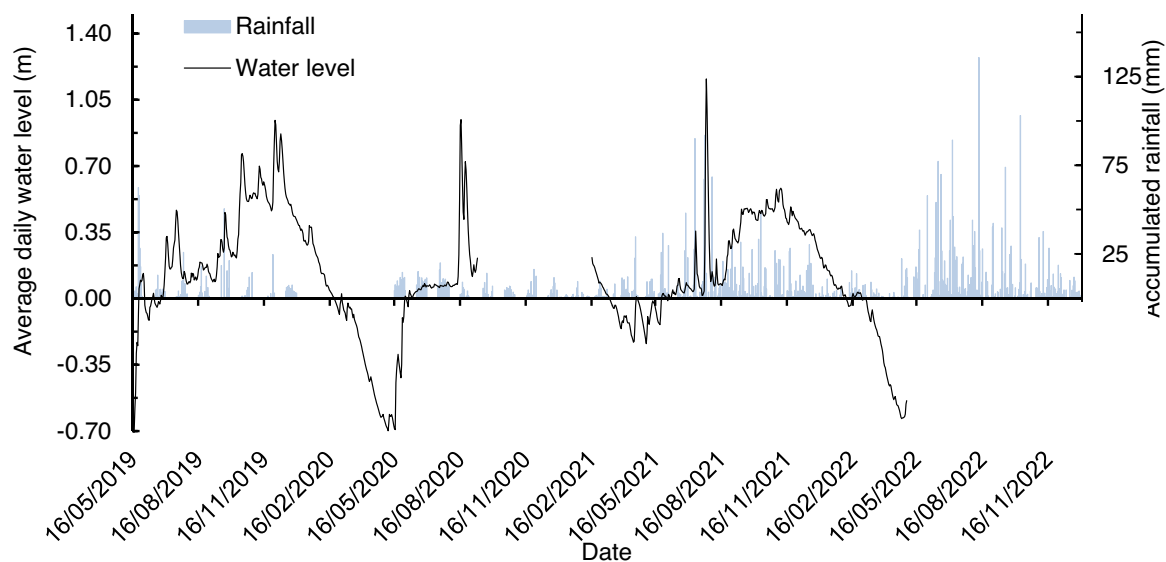


Fig. 2 Daily rain and average water level (WL) in LRS in the MQW (n=3). WL data from September 7, 2020 to February 20, 2021 were lost because of Covid-19 pandemic restrictions and after May

2022 because sensors were damaged. Rainfall data were obtained by Instituto Meteorológico Nacional (IMN) station Los Chiles, located 1.3 km from the site

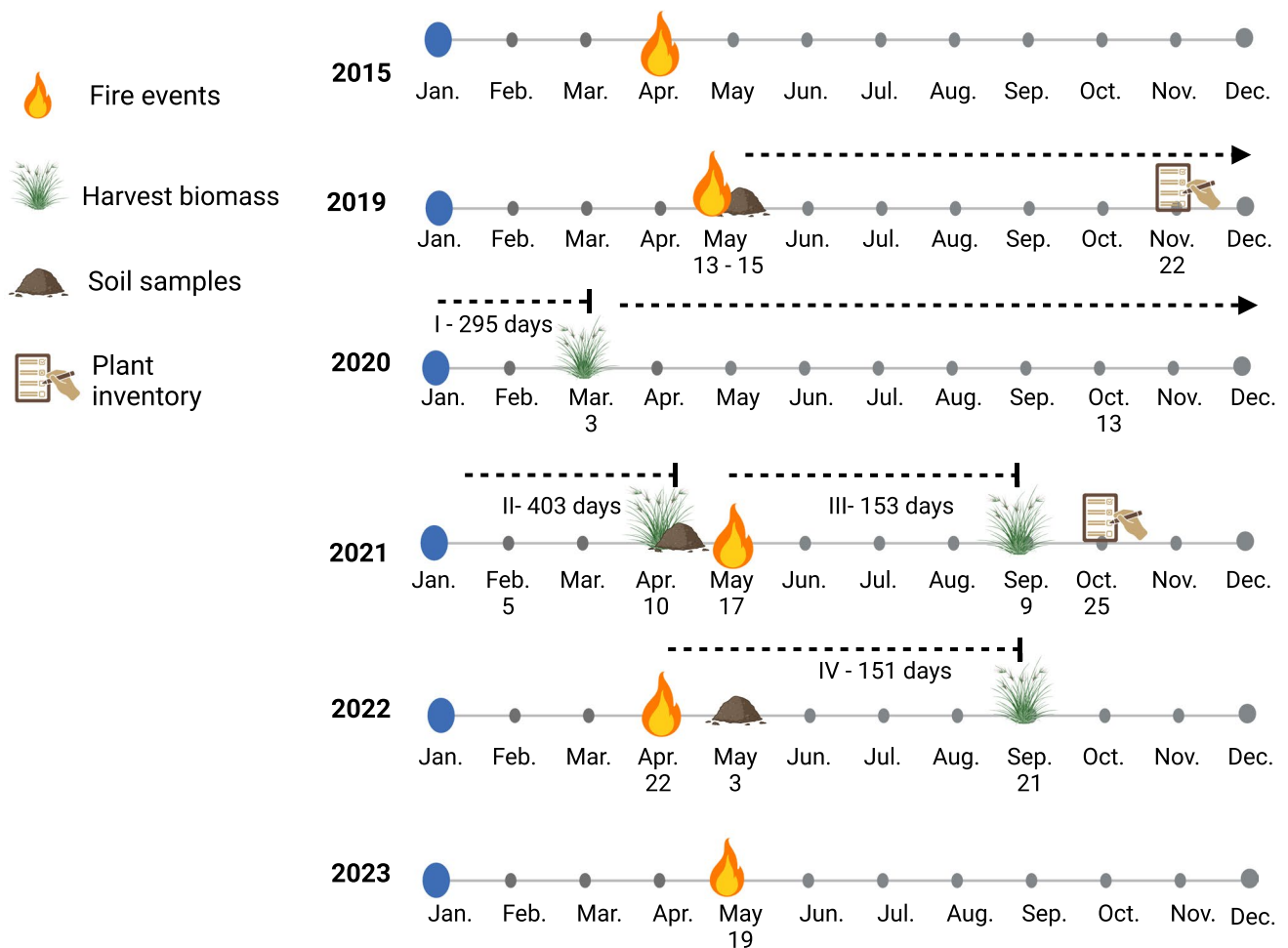


Fig. 3 Fires occurred in LRS from 2015 to 2023 (sources: local newspaper reports and 2019–2022 monitored registers), and samplings events dates from May 15, 2019 to September 21, 2022. Post-2021

fire, *S. melaleuca* replaced *E. interstincta* as the dominant species. Created with BioRender.com

tissue, three plants were used to prepare a composite sample ($n=3$), these samples were milled and analyzed by dry combustion for total C and N content (Bertsch and Ostinelli 2019) using a C-N analyzer (Vario Macro cube model, Elementar Analysensysteme GmbH, Germany).

As fires develop at the end of the dry season, the effect of seasonality can be assessed from dry and green biomass, which were harvested in a 1 m^2 grid protected from grazing, at the soil level, in each plot. Biomass collected included foliage within the sampling surface of plants rooted inside or outside the 1 m^2 frame. Dry and green biomass fresh samples were weighed and quartered to obtain 300 g subsamples, which were cut and dried at 70°C until constant weight was reached (Santos and Esteves 2004).

Aboveground primary productivity (APP) was analyzed to evaluate the effect of fire. The four periods sampled are shown in Fig. 3. The samplings at the end of the dry season (March 2020 and April 2021) were conducted

in the same area when water was at the soil surface level, enabling plant regrowth. In April 2022, sampling was not carried out because fire just happened the week, we planned to harvest biomass. The sampling in the middle of the rainy season were randomized in each plot and conducted under flood conditions (WL on September 9th, 2021: $32 \pm 3\text{ cm}$ and on September 21st, 2022: $92 \pm 5\text{ cm}$). In September 2020, biomass harvest was not carried out due to Covid-19 pandemic restrictions.

Aboveground primary productivity per area (APP) was calculated as

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

where DW_{GB} is dry-weight green biomass, DW_{DB} dry-weight dry biomass, A the sampled area (m^2), and t the foliage growth period (days).

Surface Peat Chemistry

Soil samplings were conducted during the dry season of each year. Since fire occurrence escapes the control of this study, samplings were conducted after the 2019 fire, six weeks before the 2021 fire, and 10 days after the 2022 fire (Fig. 3). In each sampling, one composite soil sample was collected from 10 points of each plot at the surface level (0–20 cm) when the water table (WT) was the lowest. Total C and N concentrations were determined by dry combustion and pH was measured at a soil water suspension with a 1:2.5 ratio. The content of calcium (Ca), magnesium (Mg), potassium (K), and total phosphorus (P) was determined by KCl-Olsen modified method; and zinc (Zn), copper (Cu), iron (Fe), and manganese (Mn) were quantified using atomic absorption spectroscopy (novAA 400p, Analytik Jena, Germany). To analyze the medium-term effect of fire on pH, it was also measured *in situ* at 10 cm depth with a handheld pH meter (model HI99121, Hanna Instruments, USA) from June 2019 to November 2021.

Statistical Analysis

Data are reported as the mean $\pm$ standard deviation. Normality was tested with the Shapiro–Wilk test and outliers of topsoil variables were corrected. Homogeneity of variances was tested using Levene’s test. APP for dry and rainy season harvests were analyzed with the Student’s *t*-test with paired and unpaired samples, respectively. Two-way analysis of variance (ANOVA) was conducted to compare a) C and N content, the C:N ratio of *E. interstincta* and *S. melaleuca* for the root and aerial part, and b) topsoil composition variables. Tukey’s HSD test was used to find difference between means, with significantly different values at $p < 0.05$.

Results

Fires and State of Vegetation

Fires left the LRS devoid of vegetation with roots beneath an ash layer. Based on visual inspection, over 90% of vegetation cover was lost after each event, and the decline of Cuban palm islets has been observed since 2019. The post-2019 fire vegetation structure included the highly dominant species *E. interstincta* with less than an estimated of 5% of open water area. Post-2021 fire, makeup of dominant vegetation changed with the Cyperaceae species *S. melaleuca* replacing *E. interstincta* as the dominant species and a visually observed increment of open water area (Fig. 4).

The C:N ratio of aerial biomass and roots of *E. interstincta* were lower and higher respectively compared to *S. melaleuca* (Table 1). The percentage of green and dry biomass was observed to depend on rainfall seasonality. During the dry season, when *E. interstincta* was highly dominant, aboveground dry biomass varied between 827 ± 67 and 761 ± 174 g biomass m^{-2} (See data in Online Resource 2, Fig. 1S).

The harvests in the dry season, both after fire on May 15, 2019, showed non-statistically significant differences for APP of herbaceous vegetation. The sampling interval of approximately one year could induce errors on biomass estimates (Online Resource 2, Fig. 2Sa).

In the rainy season, APP measured in September 2021, unaffected by the fire event as plots had been cut at soil level just few days before the fire, was significantly larger ($p = 0.02$) than in September 2022 (Online Resource 2, Fig. 2Sb).

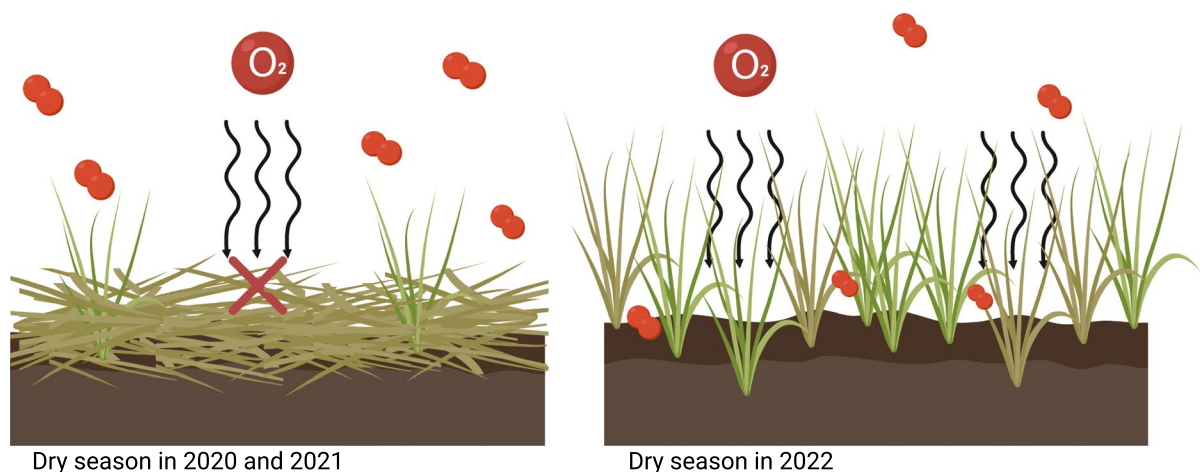


Fig. 4 Scheme contrasting the condition in the LRS of MQW in the dry season of 2020 and 2021 when the dominant species was *E. interstincta*, and in the 2022 dry season when the dominant species was *S. melaleuca*. Created with BioRender.com

Table 1 Differences of total C and N content (%) and C:N ratio (n=3) in the structural composition between *E. interstincta* and *S. melaleuca*, in the LRS of MQW

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

Values with a different letter in the same column are significantly different at $p < 0.05$ (*) or at $p < 0.001$ (**)

Surface Peat Chemistry

A dark-colored matter associated with the occurrence of carbonization was observed in the surface layer of LRS. The total C content of the topsoil (0–20 cm) was lower than 300 g kg⁻¹ (Table 2) with no significant statistical differences in total C and N content shortly after the fires (2019 and 2022) or two years later (2021). However, C:N ratios of 2019 (post-fire) and 2021(pre-fire) showed a statistically significant difference ($p < 0.05$). Exchangeable soil acidity and Ca (-17% and -77%), Mg (-20% and -75%), and K (+10% and -63%) content decreased from 2019 to 2021 and from 2021 to 2022. Metals (Fe, Zn, Cu, and Mn) concentration decreased sharply after the 2022 fire. Other results of composite samples are shown in Table 2.

In the LRS, the medium-term effect of fire on pH at 10 cm depth was characterized by a relatively constant mildly acidic pH (in situ) (4.83 ± 0.22) from October 2019 to April

2021. There was a slight increase after the May 2021 fire (5.00 ± 0.19 on June 2nd, 2021, and 5.23 ± 0.11 on July 19th, 2021, which had already returned to the mean value on September 7th, 2021 (Online Resource 3, Fig. 3S).

Discussion

Fire and State of Vegetation

Based on visual inspection of vegetation lost, the fires can be classified of high severity according to Salvia et al. (2012). The short fire turnover (annual frequency) caused Cuban palm islets to decline, although microtopography enabled some to survive in areas with more water supply and saturated soil (Sandi et al. 2020). The pressure from livestock production for grassland suckers, high flammability of dominant secondary vegetation, and channels on both sides of the dike that decreased the water level, have likely boosted short fire turnover (Siegert et al. 2001; Jauhiainen et al. 2016).

The change in the dominant species from *E. interstincta* to *S. melaleuca*, after May 2021 fire, was likely caused by high-frequency fires and enhanced by WL variations. Fire events might produce changes in species dominance because of species-specific responses (Salvia et al. 2012) which are supported or neutralized by interannual variability of WL, as observed in LRS. In this case, WL was above 50 cm for a shorter period during the 2021 rainy season compared to 2019 (Fig. 2), meaning that lower WL may have enhanced the impact of the fires on *E. interstincta* dominant distribution. The relationship between fires and WL on vegetation is relevant to assess the impact precipitation anomalies may have on the fire-vegetation dynamics under ENSO impact and warming climate conditions.

Changes in the dominant peatland's species can indicate alterations in LRS C dynamics (Leroy et al. 2017) threatening peat formation. The composition of vegetation impacts flooding duration through hydrodynamic resistance (Sandi et al. 2020), and soil temperature which alters C losses as CO₂ or dissolved C (Noble et al. 2019). For instance, compared to *S. melaleuca*, *E. interstincta* phenology left a layer of dry plant material, in the driest months. This layer can contribute to soil saturation, mitigate temperature increases,

Table 2 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 in May 2022, 10 days after the third fire. Mean ± standard deviation (n=10)

Chemical properties	Units	May 2019	April 2021	May 2022
C _{tot}	g kg ⁻¹	246 ± 13a	241 ± 13a	249 ± 18a
N _{tot}	g kg ⁻¹	16 ± 1a	16 ± 1a	16 ± 1a
C:N ratio*		15.8 ± 1.1a	15.1 ± 0.5b	15.4 ± 0.8ab
pH **		4.75 ± 0.07a	4.78 ± 0.10a	4.53 ± 0.14b
Ca**	g kg ⁻¹	10.4 ± 2.0a	8.6 ± 1.1b	2.0 ± 0.3c
Mg**	g kg ⁻¹	1.5 ± 0.3a	1.2 ± 0.2b	0.3 ± 0.1c
K**	g kg ⁻¹	0.39 ± 0.04a	0.43 ± 0.05a	0.16 ± 0.06b
E A ^{a**}	g kg ⁻¹	6.4 ± 0.8a	5.4 ± 0.5b	1.2 ± 0.5c
Fe*	g kg ⁻¹	4.7 ± 1.1b	5.2 ± 0.6a	0.8 ± 0.5c
Zn*	mg kg ⁻¹	4.4 ± 2.6ab	9.7 ± 7.7a	2.1 ± 1.0b
Cu**	mg kg ⁻¹	289 ± 99a	181 ± 45b	26 ± 16c
Mn**	mg kg ⁻¹	188 ± 29a	160 ± 20b	29 ± 19c
P	mg kg ⁻¹	40 ± 10a	27 ± 7a	37 ± 23a

Values with a different letter in the same line are significantly different at $p < 0.05$ (*) or significantly different at $p < 0.01$ (**)

^aEA: exchangeable acidity

and reduce atmospheric oxygen exchange (Agus et al. 2019). The loss of the dry material layer can affect peat formation, SOM fast decomposition by oxidation, rather than productivity, is the principal factor reducing peat accumulation in tropical wetlands (Chimner and Ewel 2005; Bernal and Mitsch 2013).

Local producers have noticed livestock consumes *E. interstincta* but not *S. melaleuca*. The comparison of the C:N ratio of these plants tissues suggests *E. interstincta*'s foliage may be more palatable for livestock (Moretto and Distel 2002). While its root composition, being more recalcitrant, favors peat formation (Chimner and Ewel 2005; Sonnier et al. 2020). This study emphasizes the role of *E. interstincta* in the ecosystem functionality and suggests fire occurrence during years with precipitation deficit and shallow WL to favor the dominance of *S. melaleuca* over *E. interstincta* in MQW.

Seasonal variations among dry and green biomass coincide with reported variability for other ecosystems (Villar et al. 1996; Santos and Esteves 2004). APP difference between rainy seasons ($p=0.02$), could be either attributed to changes in WL by interannual differences in precipitation (Santos and Esteves 2004), the negative effect of plant material removal by the fire on April 2022, that could affect rhizomes which supply N and P after a fire event (Amado et al. 2005; Snyder and Rejmankova 2015), or the combination of both.

Surface Peat Chemistry

SOC depletion below 300 g kg^{-1} can occur due to peat oxidation in fire events resulting in organic matter losses (Wasis et al. 2019; Sulaeman et al. 2021). This hypothesis is supported by the black coloration of the topsoil strata, which is associated with an oxidized and carbonized peat mixed with clay from MQR and its correspondence with the WT during the 2019 and 2020 dry seasons (approximately -60 cm). In MQW topsoil, no statistically significant differences in total C and N content between soil after the fires (2019 and 2022) and two years later (2021) suggests a low capacity of organic material sequestration by this fire degraded peatland. This result is consistent with Salvia et al. (2012), who observed no recovery of C and N following one growing season, and the small C sequestration values ($0.05\text{--}3 \text{ mm year}^{-1}$) reported by Bernal and Mitsch (2008); Dommain et al. (2011) and Warren et al. (2017) in areas with more extended flooding periods. Post-fire stability of C and N content can reflect the relatively C-poor nature of LRS soil caused by previous fires and its lower thermal conductivity compared to preserved peatlands, as these experiment a notable decrease in SOC and N content when burned for the first time (Salvia et al. 2012; Sulaeman et al. 2021).

The low value of C:N ratios observed also can be associated with the fast oxidation of organic matter by fire, which is known to reduce C:N ratio (Itoh et al. 2017; Leifeld et al. 2020). This contrasts with the high C:N ratios observed in preserved tropical peat soils, a feature associated with recalcitrant organic matter, such as humic acids, formed under water saturation (Bernal and Mitch 2013). On the other hand, the lower C:N ratio two years after a fire can reflect the input of a labile C pool in the topsoil necromass layer through the quick vegetation recovery of pioneer species like *E. interstincta* (Lupascu et al. 2020).

The impact of fire on peat soils has been linked to increases in calcium (Ca) and magnesium (Mg), making it a potential factor for enhancing fertility (Wasis et al. 2019). However, our results show fires reduce the availability of these macronutrients during the monitoring period in LRS. This reduction 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 regions with highly oxidized organic compounds.

The observed reductions in exchangeable acidity and Fe and Mn content can be explained by the reduction of SOM content and its transformation into new aromatic compounds as peat is burned (Terzano et al. 2021) which alters the structure of humic acids, reducing hydrogen and oxygen, increasing the carbon proportion in their structure and their cation-complexing ability (Yustiwati et al. 2015). In addition, it is known that peat burning related increased in humic acids leads to pH decrease along with a reduction in exchangeable bases because the H^+ ions released into the soil solution are replaced by cation salts (Yang and Antonietti 2020).

The topsoil analysis revealed a decrease in soil pH 10 days after the fire in 2022 (Table 2), consistent with previous studies (Salvia et al. 2012; Sulaeman et al. 2021). This may suggest a lack of sufficient fresh ash at the field site or a rapid pH recovery after the ash removal by leaching (Marcotte et al. 2022). Conversely, the medium-term pH increased at a 10 cm depth in June and July 2021 may highlight a decrease in soil acidity due to the combustion of SOM, resulting in organic acids losses and carbonates and oxides released from ash in peatland soil (Wasis et al. 2019; Lupascu et al. 2020; Marcotte et al. 2022). The medium-term pH measurements showed that the increase in peat pH after the addition of ash is transient, due to leaching and the fact that aged ash is more acid than fresh ash owing to its neutralization (Marcotte et al. 2022).

Conclusions

Evidence of changes in vegetation, topsoil chemical properties variability, and the black coloration of the topsoil strata can inform about the impacts of grazing fires on

riverine peatlands and raise awareness of the need for public policies to preserve the functionality MQW as a C sink.

The sensitivity of the ecosystem to the impact of fires is strongly linked to the WT depth. Increasing awareness and promoting efforts by authorities and communities to prevent fires and monitor WL are key to reducing fire damage to the dry aerial biomass and contributing to the reduction of impacts on species dominance, C, N, and soil nutrient pools.

Preliminary evidence on changes in species dominance driven by fire events and the influence of interannual variability of WL in this impact is presented. In MQW topsoil, total C and N soil content between soil after the fires (2019 and 2022) below 300 g kg⁻¹ suggests a low capacity of organic material sequestration by this fire degraded peatland.

Contrasting with findings reporting that fire on peat soils may be related to increases in calcium (Ca) and magnesium (Mg), our results suggests that recurrent fires reduce the availability of these macronutrients in the long term.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13157-024-01797-5>.

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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.

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

Declarations

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

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

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