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Interactive effects of hydrology and fire drive differential biogeochemical legacies in subtropical wetlands

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Abstract. Fire is an important component of many ecosystems, as it impacts biodiversity, biogeochemical cycles, and primary production. In wetlands, fire interacts with hydrologic regimes and other ecosystem characteristics to determine soil carbon (C) gains or losses and rates of nutrient cycling. However, how legacies of fire interact with wetland hydroperiod to affect soil chemistry is uncertain. We used the Florida Everglades as a model landscape to study how fire regimes, hydroperiod, and soil types collectively contribute to long-term C, nitrogen (N), and phosphorus (P) concentrations and stoichiometric mass ratios (C:N, C:P, N:P) in both short- and long-hydroperiod subtropical wetlands that consist of marl and peat soils, respectively. We used fire records from 1948 to 2018 and hydroperiod from 1991 to 2003, and analyzed these data together with soil chemistry data collected during two extensive field surveys (n = 539) across different ecosystem and soil types throughout Everglades National Park. We also analyzed macrophyte and periphyton P concentrations (n = 150) collected from 2003 to 2016 in fire-impacted wetland sites. Hydroperiod was the main driver of soil C concentration in both marl and peat soils, but fire played a substantial role in nutrient cycling. Particularly in marl soils, soil P concentrations were affected by the absence of fire. In the first decade post-fire, we observed an amplification of P cycling with decreased soil C:P ratios by 95% and N:P ratios by 45%. After more than a decade post-fire, soil P became increasingly depleted (41% lower). Macrophyte P tissue concentration was 50% higher only in the first year post-fire, whereas periphyton P did not change. By recycling nutrients and through removal of litter accumulation, which forms a physical obstacle to photosynthesis, fire likely helps maintain high levels of macrophyte aboveground live biomass as well. Given its substantial effect on nutrient cycling, we advocate for fire management that uses fire return intervals that minimize depletion of soil nutrients and promote positive feedbacks to productivity in wetland ecosystems. In addition, coordinated management of fire return intervals and wetland hydroperiod can be used to set priorities for wetland soil nutrient concentrations and ratios.

Key words: carbon; everglades; nitrogen; peat versus marl; periphyton; phosphorus; time since last fire.

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Introduction

Fire is an important ecological force that regulates biodiversity and other ecosystem characteristics in many areas of the globe (González-Pérez et al. 2004, Bond and Keeley 2005, Bowman et al. 2009, Driscoll et al. 2010, Pressler et al. 2019). In fire-prone regions, over long periods of time, many plant species have developed specific traits that have allowed them to best adapt to fire and associated environmental conditions (Noss 2018). Human-induced fire suppression has altered the composition of fire-adapted plant communities and facilitated encroachment of invasive woody species (Bond and Keeley 2005, Noss 2018). Hence, fire is a fundamental ecological process for maintaining ecosystem structure and function across biomes (Bond and Keeley 2005). In recent decades, prescribed fires that reduce fuel loads to minimize fire hazards and catastrophic wildfires have been widely used for species conservation as well (Driscoll et al. 2010, Noss 2018).

Fire regimes (i.e., fire frequency, seasonality, intensity, and severity) impact ecosystem biogeochemical cycles. For example, in biomes such as oak savannas and broadleaf forests, high fire frequency can cause carbon (C) losses by limiting aboveground vegetation development (Tilman 2000, Pellegrini et al. 2018) or by directly burning the soil with the release of organic matter (Turetsky et al. 2015). In contrast, in grassland biomes fire generally promotes rapid increase in seed germination rates and increases production of aboveground biomass (Knapp and Seastedt 1986, Singh 1993, Ojima et al. 1994, Brys et al. 2005). Fire can also increase ecosystem C storage by stabilizing soil humic substances (González-Pérez et al. 2004) and with the production of biochar, which can persist in the soil on a centennial scale (Singh et al. 2012). In addition, fire may alter the short- and long-term bioavailability of macro- and micronutrients (Smith 1970, Boerner 1982, Wan et al. 2001, Dijkstra and Adams 2015, Schaller et al. 2015, Butler et al. 2018). For instance, in both soil and litter, mineral phosphorus (P) increases, whereas C:P and nitrogen (N):P ratios decrease (Schaller et al. 2015, Butler et al. 2018). Plant N is readily volatilized during fire compared with plant P (Boerner 1982, Hogue and Inglett 2012). Thus, the long-term suppression of fire can increase ecosystem N relative to P (Turner et al. 2008). However, long-term legacy effects of fire or fire suppression on ecosystem nutrient levels, especially in wetlands, are less understood than short-term impacts (Smith 1970, Christensen 1977, Ojima et al. 1994, Smith et al. 2001, Turner et al. 2008).

In wetland ecosystems, the ecological impacts of fire are often unpredictable based on how fire interacts with hydrology (Lockwood et al. 2003, Osborne et al. 2013, Ruiz et al. 2013). In the short term, fire in wetlands can affect soil C, N, and P concentrations (Smith et al. 2001, Liao et al. 2013; J. S. Kominoski, *unpublished data*), surface water P and dissolved organic C concentrations (Miao et al. 2010, Brown et al. 2015; J. S. Kominoski, *unpublished data*), and algal and plant P concentrations (Miao et al. 2010; J. S. Kominoski, *unpublished data*). But how fire regimes interact with hydrologic regimes to affect long-term wetland ecosystem nutrient concentrations and ratios is uncertain. Hence, a comparison of soil chemistry levels among wetlands that vary in hydroperiod and time since fire is needed.

Fire has long been used as a management tool in the southeastern USA natural areas (Christensen 1977, Abrahamson 1984, Noss 2018), including subtropical wetlands of the Florida Everglades (National Park Service 2015). The Everglades serves as a model region to study how fire regimes affect long-term wetland biogeochemistry, given the region's rich history of fire management and extensive biogeochemistry datasets that span wetlands of different hydroperiods (Osborne et al. 2011, FCE-LTER 2019). The Everglades is also a P-limited oligotrophic system where fire plays a primary role in promoting nutrient mobilization, primary production, and dictating vegetation composition (Sah et al. 2007, Miao et al. 2010, Liao et al. 2013).

Our objective was to understand how fire regimes interact with hydroperiod (i.e., number of days in a year with soil inundated) and soil types in shaping long-term soil total C (TC), total N (TN), and total P (TP) pools across a wetland landscape. We analyzed the effects of fire on soil C and nutrients and plant nutrients in wetlands that varied in multiple ecosystem attributes (shorter versus longer hydroperiod, relative P limitation, and soil type [peat versus marl]; Ross et al. 2006, Osborne et al. 2011). Specifically, we tested how time since fire impacts (1) soil C and nutrient concentrations (N, P), in subtropical wetlands that differ in hydroperiods and soil types, (2) soil C:N, C:P, and N:P stoichiometric ratios that drive differences in nutrient limitation among oligotrophic subtropical wetlands, and (3) plant tissue P and periphyton mat P concentrations. We predicted that, with time, as sites were left unburned, independent of hydroperiod and soil type, soil N concentrations would increase (Turner et al. 2008), and soil P concentrations would decrease (Butler et al. 2018). We also predicted that with more recent burns we would observe decoupling of C, N, and P cycling, since fire disproportionately releases mineralized P and therefore causes a decrease in soil N:P and C:P ratios. In contrast, we predicted that soil C:N ratios would increase with more recent burns, primarily due to the loss of ecosystem N through volatilization (Boerner 1982, Hogue and Inglett 2012). Finally, we predicted an increase in both plant and periphyton P concentrations in the first year post-fire due to the uptake/absorption of the mineralized P released. We did not predict how long-term soil C concentrations would be affected by fire because we believed that soil C loss (i.e., peat burn) or increase (i.e., charred C deposition) with fire would strongly depend on fire intensity and severity, which vary based on several factors such as water levels and fuel loads at the time of burning. Although we could not estimate fire severity due to limited data, the large scale of this analysis of time since fire across wetlands that vary in hydroperiod will enhance our understanding of the role that management of fire and water can have in wetland C and nutrient storage.

Materials and Methods

Study region

The study was conducted in freshwater subtropical wetlands within the Everglades National Park (ENP), South Florida, USA (Fig. 1). While sawgrass (*Cladium jamaicense* Crantz.) is the dominant species in the Greater Everglades System (Todd et al. 2010), freshwater marshes inside the ENP can be divided into distinct ecosystem types (hereafter "ecotypes") because of marked differences in hydrology and soil, which consequently impact vegetation composition and productivity (Osborne et al. 2011). The main ecotypes identified by Osborne et al. (2011) were the Shark River Slough, Taylor Slough, eastern marl prairies, western marl and wet prairies, and the mangrove interface. For this study, we adopted the same ecosystem subdivisions, focusing on the deep peat soils (PS) of Shark River Slough, eastern marl soils (MS), and western wet prairies, which constitute an intermediate typology with transition soils (TS), from marl to medium-depth peat.

Shark River Slough drains the water entering ENP from the North and is characterized by low elevation and long hydroperiod (saturated or inundated 95–100% of the year; U.S. Geological Survey 2018). Longer hydroperiods within Shark River Slough promote accumulation of organic matter mostly derived from macrophytes and the formation of deep peat soils with high C content, as well as high P concentrations due to higher contributions from canal sources and Water Conservation Areas (Osborne et al. 2011). Marl prairie is an ecosystem type with shallow soils (often 10 cm depth or less), hence shorter hydroperiod, completely drying down in part of the landscape during winter and spring. Because of relatively short hydroperiod, marl prairies do not accrete peat and have low-C soils, which are mostly derived from calcareous periphyton and limestone parent material. Marl prairies are also the most oligotrophic ecotype in the Everglades and are severely P-limited (Osborne et al. 2011). Wet prairies have intermediate characteristics between Shark River Slough and marl prairies, transitioning from marl soils to peat accumulating soils with intermediate C concentrations (Osborne et al. 2011). Sawgrass is the dominant or a co-dominant species in all of these ecotypes, and, although it is tall and dense in long-hydroperiod areas like PS, its density and size diminish gradually through TS and MS. In MS, important co-dominant species are muhly grass (*Muhlenbergia capillaris* (Lam.) Trin. var. *filipes* (M. A. Curtis) Chapm. ex Beal.), little bluestem (*Schizachyrium spontaneum* L.), and/or black-top sedge (*Schoenus nigricans* L.). A summary of the vegetation types found in PS, TS, and MS is presented in Table 1.

Periphyton, an association of algae, bacteria, fungi, and microfauna, forming thick mats which cover limestone sediments, coat the submerged stems of macrophytes, or form rafts floating in the water, is an abundant and ubiquitous feature of these ecotypes as well, particularly of the marl prairies (Gaiser et al. 2011). Periphyton is known to rapidly respond to environmental changes (Gaiser et al. 2011) and owns a high capacity of uptaking P both biotically and abiotically (Scinto and Reddy 2003), and could therefore, together with macrophytes communities, play a major role in post-burn nutrients cycling.

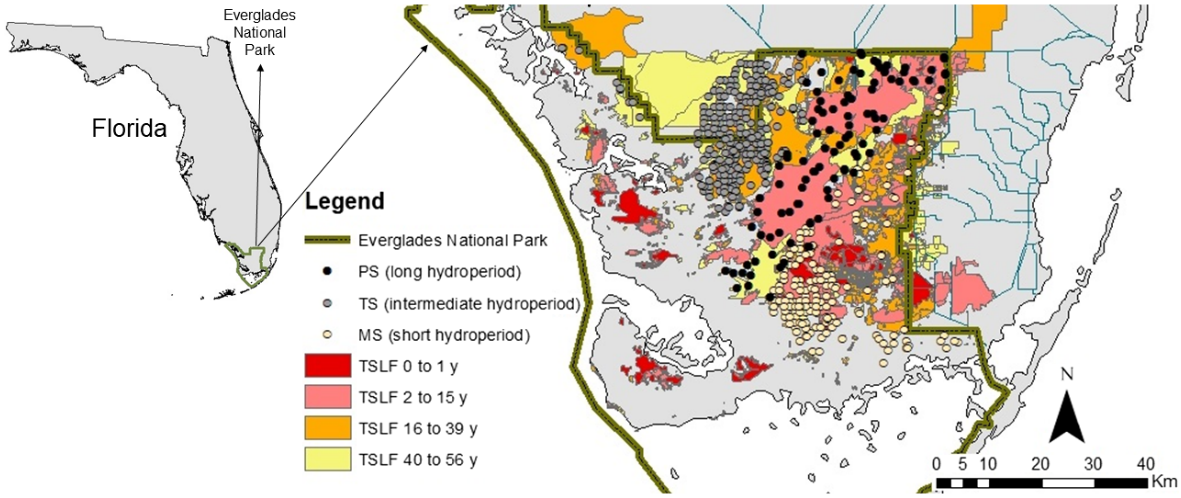

Fig. 1. Map of Everglades National Park (ENP) showing the points sampled for soil chemistry data grouped by soil type (abbreviations are PS, Peat Soils; TS, Transition Soils; MS, Marl Soils), and the fire regimes estimated from fire records for the period 1948–2018 and expressed as time since last fire (TSLF). Note that TSLF in the figure was calculated as the difference in years between the last fire occurrence and the year 2003, which is the sampling year for the soil chemistry data used in the study.

Fire history and wetland hydroperiod

To quantify differences in fire regimes, we used fire history data recorded from 1948 to 2018 by the ENP (Smith III et al. 2015; fire data for the most recent years were unpublished and were provided to us by ENP) and summarized into GIS (Geographic Information System) maps. The database included the following information: location, fire perimeters, burned area, and date and type (wildfire, prescribed fire, etc.) of fires.

Surface water depth data were obtained from the Everglades Depth Estimation Network (EDEN) database (U.S. Geological Survey 2018). Daily water depth maps from EDEN were computed by subtracting the ground elevation from the daily water surface elevation for each grid cell (400×400 m). Water depth data for all sites were extracted from the EDEN water depth maps using a script in R version 3.4.3 (R Core Team 2018). Hydroperiod was calculated based on daily water depth at each site for each year. Water depths of ≤0 cm were considered dry, and water depths >0 cm were considered wet. Total wet and dry days for each site were summed for a particular year at each site to calculate hydroperiod. Hydroperiod was calculated as the sum of days within a year with water depth >0 cm. Although water depth has been recorded in the Everglades prior to 1991, we used EDEN data from 1991 to 2003 to calculate hydroperiod, given the much higher spatial resolution of the EDEN data compared with the prior data from gauges. Our exclusive use of EDEN data increased spatial uniformity in analysis throughout our study area. We also calculated a drought score for each sampling point as the ratio between the number of days with water level ≤0 cm and the total number of days between 1991 and the sampling year.

Soil, macrophyte, and periphyton chemistry

For soil chemistry data, we used two extensive surveys carried out inside ENP (Sah et al. 2007, Osborne et al. 2011). In Osborne et al. (2011), all soil types inside ENP were sampled (n = 309 sampling locations) in December 2003. Soil cores were collected, down to 20 cm, and samples (only the top 10 cm) were analyzed in laboratory for TC, TN, and TP (Appendix S1). Total C and TN were measured using a Carlo-Erba NA 1500 CNS analyzer (Haak-Buchler Instruments, Saddlebrook, New Jersey, USA), and TP was measured spectrophotometrically following acidification of combusted (500°C for 4 h) soil subsamples using standard methods (Solórzano and Sharp 1980). In Sah et al. (2007), soil samples in only MS and TS were collected (n = 298 sampling locations)

Table 1. Vegetation types characterizing the sampling sites considered in the study (Sah et al. 2007, Osborne et al. 2011).

Vegetation type	PS (%)	TS (%)	MS (%)	All soil types (%)
Bayhead Shrubland	1			<1
Bayhead Swamp Scrub	3	<1		<1
Beakrush Marsh		<1		<1
Black Sedge Prairie		1	3	2
Cypress Scrub			2	<1
Cypress Woodland		<1		<1
Graminoid Freshwater Prairie	5	21	56	29
Mixed Graminoid Freshwater Marsh	9	41	7	23
Pine Rockland			<1	<1
Red Mangrove Scrub	2	<1	10	4
Sawgrass Prairie			1	<1
Sawgrass Marsh	68	35	17	35
Spikerush Marsh	11		<1	2
Transitional Bayhead Shrubland		<1	<1	<1
Tropical Hardwood Hammock			<1	<1
Upland Hardwood Scrub-Graminoid Prairie			<1	<1
Mixed Mangrove Scrub		<1		<1
Willow Scrub	1			<1
Willow Shrubland		<1	<1	<1

Notes: Percent of each specific vegetation type within each soil type was calculated as the ratio between the number of sites characterized by that vegetation type and the total number of sampling sites within the soil type. Marsh vegetation types were dominant in peat soils (PS), whereas prairie vegetation types were dominant in marl soils (MS). Transition soils (TS) were characterized by a mix of marsh and prairie vegetation.

between 2003 and 2005, and the samples (0-10 cm) were analyzed in laboratory for TC, TN, and TP (Appendix S1). Also in Sah et al. (2007), TC and TN were measured by combustion using an elemental analyzer, and TP was measured following Solórzano and Sharp (1980). Both databases reported the coordinates of each sampling point. We calculated all stoichiometric ratios as mass ratios.

We only included the soils of Shark River Slough, eastern marl prairies, and western marl and wet prairies, for the following reasons: (1) They represent a large portion of the landscape, (2) Taylor Slough was excluded from the analysis due to few data points (n = 22) available compared with the other ecotypes, and (3) the mangrove interface is not affected by fire as the other ecotypes inside ENP.

Gaiser et al. (2014) recorded macrophytes and periphyton TP concentrations annually in transects (n = 14) located in a portion of the eastern marl prairies (MS) from the year 2003 to 2016 (data from recent years, not included in Gaiser et al. 2014, are unpublished). Total P concentration was analyzed on aggregated periphyton subsamples from associated substrates (plants, soil, and/or bedrock) and plant leaf (center and tip) samples, after combustion of dried material following Solórzano and Sharp (1980). A part of these sites experienced fires during the sampling window (specifically, in the years 2007, 2008, 2011, and 2012), giving us the opportunity to analyze pre-fire and post-fire macrophyte and periphyton P data (Appendices S2 and S3). We identified 15 sites on four transects that burned during the sampling period.

We tested differences between pre- and post-fire TP concentrations in plant tissues and periphyton mats to provide greater understanding of post-fire P cycling (Butler et al. 2018). Consistent data were available for all 15 sites only for the four years post-fire as some of the burns occurred in 2012 (i.e., four years before the end of the macrophytes and periphyton TP data time series). For this reason, the analysis included pre-fire and the first four years post-fire.

Vegetation types

We extracted data on vegetation types from each sampling site used in the study from high-resolution maps. In the vegetation mapping project (Ruiz et al. 2017, 2018, 2019), ENP and Big Cypress National Preserve were divided into six regions. Although not published yet, maps of region 1 and 4 were provided to us by the authors. Vegetation type data were collected to further characterize the considered soil types. Marsh vegetation types were dominant in PS, whereas prairie vegetation types were dominant in MS. A mix of marsh and prairie vegetation characterized TS instead (Table 1).

Data analyses

We used time since last fire (TSLF) as the variable to assess the short- and long-term effects of fire on wetland soil chemistry (Turner et al. 2008, Dijkstra and Adams 2015, Santos et al. 2019). We obtained TSLF for each sampling point by overlaying the referenced sampling points on fire maps (1948–2018; Fig. 1) using ArcMap 10.5 (Esri, Redlands, California, USA). For each sampling point, TSLF was expressed as the number of years elapsed between the last fire event and year of sampling. If a sampling point had not burned since 1948, TSLF for that point was calculated as if the last fire had occurred in 1947. In addition, we calculated fire frequency as the mean number of fires occurred per decade at a specific sampling point between 1948 and the sampling year.

To see whether our decision to analyze separately the effect of fire and hydrology on soil chemistry based on ecosystem and soil characteristics, as defined in Osborne et al. (2011), was supported, we performed a Welch's one-way ANOVA, testing for significant differences in hydroperiod and soil chemistry purely based on soil type. Welch's one-way ANOVA was chosen as variance was not homogeneous among soil type groups (Levene's test $P \leq 0.001$). The one-way ANOVA was followed by Games-Howell post hoc test for pair-wise comparisons.

We performed a multiple regression analysis to test how the covariates fire and hydrology are shaping soil chemistry within the distinct soil types of the studied wetland. Therefore, the soil chemistry variables were set as response variables, whereas TSLF and hydroperiod as explanatory variables. The analysis was separately run for the distinct soil types considered (PS, MS, and TS).

We applied a generalized linear mixed-effect model using the glmmTMB package in R, which included time as a fixed effect and site as random effect, to test for differences between pre- and post-fire TP concentrations in macrophyte tissues and periphyton mats.

For all statistical analyses, we used R version 3.4.3 (R Core Team 2018).

Results

Wetland hydroperiod and fire history

Hydroperiod varied among the three ecotypes, PS, TS, and MS ($F_{2,266} = 161.7$, $P < 0.001$). Mean hydroperiod was 322 ± 35, 276 ± 49, and 185 ± 88 d·yr^{-1} in PS, TS, and MS, respectively. Mean calculated drought score was 0.12 ± 0.1, 0.27 ± 0.2, and 0.47 ± 0.2 in PS, TS, and MS, respectively.

Between 1948 and 2018, on average, 127.5 km^2 of wetlands in ENP burned every year. Land surface area burned by wildfires decreased nonlinearly over time, whereas land surface area burned by prescribed fires increased exponentially in the last two decades (Fig. 2). In all soil types, TSLF ranged between 0 and 55 yr. Median values of TSLF were similar in PS and MS (14 and 16 yr, respectively) and higher in TS (29 yr). Although fire frequency reached maximum values of 1.1 or 1.3 fires per decade in TS and PS, respectively, it peaked at 2.2 fires per decade in MS.

Soil, macrophyte, and periphyton chemistry

Soil TC, TN, and TP concentrations varied substantially among the three soil types (Fig. 3). Soil TC was different ($F_{2,223} = 122.9$, $P < 0.001$) among soil types, and the value in PS (341 ± 108 mg/g) was up to 2 × higher than in TS (181 ± 67.4 mg/g) or MS (164 ± 34.7 mg/g). Soil TN (24.1 ± 9.3, 12.9 ± 6.5, and 8.9 ± 4.2 mg/g in PS, TS, and MS, respectively; $F_{2,229} = 124.1$, $P < 0.001$) followed the same trend as soil TC. Soil TP also differed among soil types ($F_{2,248)} = 69.9$, $P < 0.001$), and it was about 40% lower in MS (202 ± 114 μg/g) than in PS and TS (332 ± 148 and 344 ± 146 μg/g, respectively). Soil TP was not different between PS and TS (Games-Howell post hoc test: $P = 0.77$).

The multiple regression results revealed that hydroperiod was strongly related to soil TC, TN, and TC:TN and TN:TP ratios in PS ($P < 0.01$; Table 2). Soil TC, TN and TN:TP ratio increased with increasing hydroperiod, whereas soil TC:TN ratio decreased with hydroperiod. However, in MS, only soil TC seemed to be correlated with hydroperiod ($P < 0.001$; directly proportional). The variable TSLF, which did not correlate to soil nutrients concentrations in PS, was correlated to soil TP, and TC:TN, TC:TP, and TN:TP ratios in MS (Table 2; Fig. 4; $P < 0.05$). Although soil TP was highest between 2 and 15 yr post-fire, it decreased afterward with increasing TSLF (Fig. 4). Soil TC:TP and TN:TP ratios showed an opposite trend (Fig. 4). In deviation from PS and MS, in TS, only the interaction between TSLF and hydroperiod was correlated with soil TC:TP and TN:TP ratios (Table 2; $P < 0.05$).

Using a generalized linear mixed-effect model, we were able to test for differences in

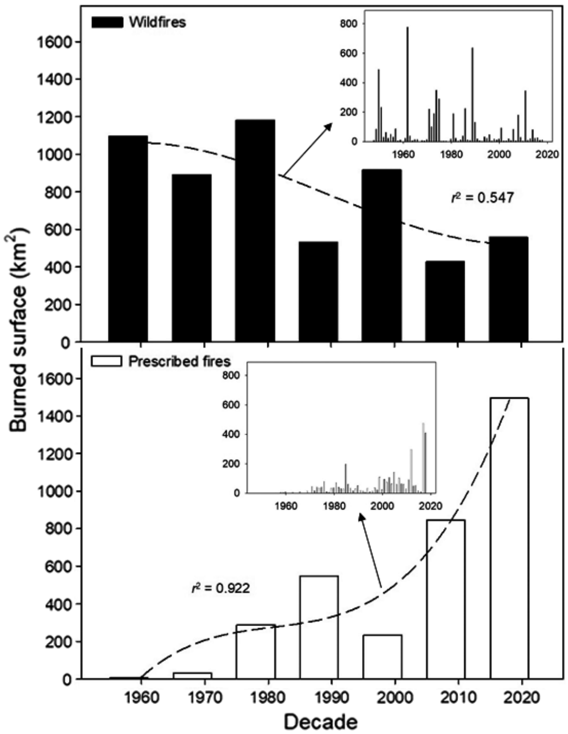

Fig. 2. Cumulative burned surface area per decade by wild versus prescribed fires inside Everglades National Park, from 1948 to 2018. In time, the surface area burned by natural fires has decreased while, on the opposite, the surface area burned by prescribed fires has increased. Annual surface area burned is shown in inset graphs.

macrophytes and periphyton TP concentration in time, before fire and at different time steps post-fire (1, 2, 3 or 4 yr post-fire). Macrophyte TP was substantially higher one year post-fire than pre-fire (50% increase; Fig. 5), but it decreased again after the first year post-fire ($P < 0.001$; residual df = 86; $y = -29.4\times + 370.4$). In contrast, periphyton TP concentration did not change between pre- and post-fire samplings ($P = 0.44$; residual df = 99; $y = -7.87\times + 194.3$).

Discussion

Soil nutrient concentrations varied among subtropical wetlands with different hydroperiods, characterized by distinct soil types (Osborne et al. 2011) and vegetation communities (Todd et al. 2010). In this study, we observed that soil TC, TN, and TP were greater in longer- than shorter-hydroperiod wetlands, as longer inundation creates anoxic conditions that result in higher accumulation of rich peat soils (Moore 1987, Craft and Richardson 1993, Hohner and Dreschel 2015).

Our study depicts the different roles of hydrology and fire in regulating wetland biogeochemistry. Time since last fire was deemed as the most ecologically appropriate variable of fire regimes for the present study compared with fire frequency, which is never high within ENP; fire frequency peaked at 2.2 fires per decade in MP, much less than 5–10 fires per decade, which is generally considered high fire frequency (Johnson and Knapp 1995, Beckage et al. 2005). In our study, hydrology was undoubtedly the regulator of soil TC concentrations, irrespective of soil type, whereas fire was an important factor in relocating nutrients in wetlands (Table 2). By analyzing the effects of TSLF on soil chemistry parameters, we were able to detect legacy effects of recent fires as well as of long-term (decadal scale) fire absence on soil TP concentration and stoichiometric ratios. In contrast to our predictions, where we hypothesized that the long-term absence of fire would affect both TN and TP soil concentrations irrespective of soil or hydroperiod type, we found a net divergence between the peat and the marl soils. In PS, hydrology explained C and N cycling in the soil. In contrast, in MS, apart from soil TC, fire was prevalent in explaining the variation in nutrient concentrations. In TS, however, it was the interaction between hydroperiod and fire that was strongly related to soil chemistry (Table 2).

In many ecosystems, fire-induced nutrient release is positively correlated with fuel load. Fire occurs where there is sufficient vegetation to serve as fuel and, once the fuel burns, ashes are produced, from which nutrients are released. So, why are we detecting a clear effect of fire on surficial soil nutrients only in the drier marl soils? We hypothesize that in MS the effect of fire remains more detectable due to the drier conditions, thus reduced lateral transport of nutrients, and to lower macrophyte biomass (mean macrophyte aboveground biomass is 728 ± 88 and 576 ± 246 g/m^2 in PS and MS, respectively; Troxler et al. 2013, Sah et al. 2015) and subsequent reduced nutrients uptake by the roots, whereas in PS post-fire nutrient mineralization

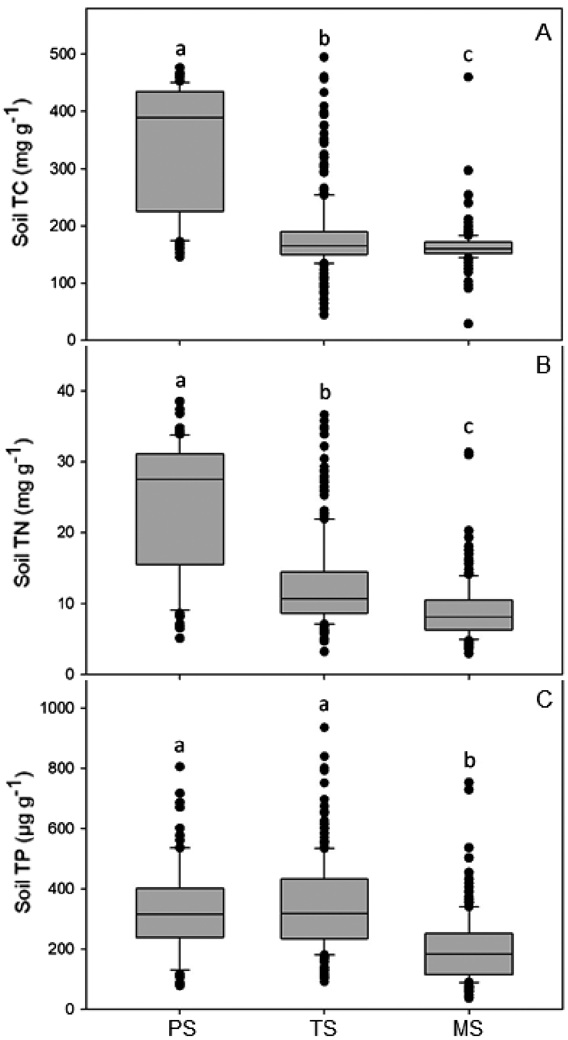

Fig. 3. Soil total carbon (TC; A), total nitrogen (TN; B), and total phosphorus (TP; C) concentrations in the top layer of the different soil types inside Everglades National Park. Abbreviations are PS, Peat Soils (long hydroperiod); TS, Transition Soils (intermediate hydroperiod); MS, Marl Soils (short hydroperiod). Letters placed above the box and error bars denote the significance groupings determined using Games-Howell post hoc test ($P < 0.05$).

becomes locally non-detectable, due to high water levels for a long period in a year and consequent lateral transport and dispersion (Ross et al. 2006, Troxler et al. 2013), to more significant nutrients uptake by macrophytes vegetation, and to higher rates of peat accretion (20-fold; Hohner and Dreschel 2015) that likely bury post-fire products in a shorter time. We also hypothesize that fires in long-hydroperiod wetlands (PS) are likely less severe than fires in short-hydroperiod wetlands (MS), thus resulting in lower nutrient mineralization. Furthermore, Boerner (1982) argues that, in contrast to nutrient-rich eutrophic ecosystems, nutrient-poor oligotrophic ecosystems have developed post-fire mechanisms to retain nutrients, which are vital to their conservation. In the more oligotrophic MS of the Everglades, fire reloads the soil P inventories available for plant regrowth, but, as more seasons and plant cycles go by, concentrations become eventually again low and the system probably becomes fire-starving (Fig. 4). Nonetheless, Fig. 4 shows how soil TP concentrations were 33% lower in the first year post-fire than in the following 14 yr. Nutrients are probably slowly incorporated into the soil in post-fire years, as, in this oligotrophic wetland, the P released post-fire may be readily uptaken by macrophyte communities or absorbed by periphyton mats. Nonetheless, periphyton appears to only hold excess P for a limited amount of time post-fire, and this was observed in nutrient enriched, peat wetlands of the Everglades (Miao et al. 2010), whereas most of the recently mineralized P is used for rapid plant regrowth in the first year post-fire (Fig. 5). Interestingly, a differential effect of fire between distinct wetland types has already been observed: In extremely oligotrophic wetlands, post-burn enzymatic activity and soil nutrient levels were shown to be substantially higher than in P-enriched wetlands (Liao et al. 2013).

In Everglades subtropical wetlands, we found that hydroperiod was a stronger determinant of soil C concentrations than fire regime. No effect of TSLF on soil TC concentrations was detected; thus, we infer that probably, even if there is a production of black C upon fire occurrence, this is not substantial to significantly change TC concentrations, or that larger fragments of char float upon inundation and get exported through lateral transport. However, while fire absence corresponded to lower soil TC in PS, in MS the opposite trend was observed (Table 2). This might suggest that longer-hydroperiod wetlands do not lose C following fire due to inundation and lower soil redox conditions, may produce black C, and promote a rapid regrowth with increased dead root and juvenile fine root C

Table 2. Results from the multiple regression analysis performed using soil chemistry data (total carbon, TC; total nitrogen, TN; total phosphorus, TP; and stoichiometric mass ratios) from the peat soils (PS; n = 98), transition soils (TS; n = 280) and marl soils (MS; n = 161) as response variables, and time since last fire (TSLF) and hydroperiod as covariates.

	PS		TS		MS	
Covariates	P-value	LM equation	P-value	LM equation	P-value	LM equation
Soil TC						
TSLF	ns	$y = -5.856x - 156.9$	ns	$y = -0.774x + 110.9$	ns	$y = 0.282x + 137.2$
Hydroperiod	<0.001	$y = 1.755x - 156.9$	ns	$y = 0.329x + 110.9$	<0.001	$y = 0.183x + 137.2$
Interaction	ns	$y = 0.009x - 156.9$	ns	$y = 0.0004x + 110.9$	ns	$y = -0.002x + 137.2$
Soil TN						
TSLF	ns	$y = -0.21x - 21.3$	ns	$y = 0.063x + 5.3$	ns	$y = -0.069x + 9.2$
Hydroperiod	<0.001	$y = 0.159x - 21.3$	ns	$y = 0.030x + 5.3$	ns	$y = 0.007x + 9.2$
Interaction	ns	$y = -0.0002x - 21.3$	ns	$y = -0.0003x + 5.3$	ns	$y = 0.00005x + 9.2$
Soil TP						
TSLF	ns	$y = -2.826x + 25.8$	ns	$y = 4.259x + 383.9$	<0.05	$y = -2.958x + 240.9$
Hydroperiod	ns	$y = 1.120x + 25.8$	ns	$y = -0.012x + 383.9$	ns	$y = 0.184x + 240.9$
Interaction	ns	$y = 0.001x + 25.8$	ns	$y = -0.019x + 383.9$	ns	$y = 0.001x + 240.9$
Soil TC:TN						
TSLF	ns	$y = -0.048x + 28.8$	ns	$y = -0.127x + 16.7$	<0.001	$y = 0.303x + 36.4$
Hydroperiod	<0.01	$y = -0.047x + 28.8$	ns	$y = -0.0004x + 16.7$	ns	$y = 0.005x + 36.4$
Interaction	ns	$y = 0.0004x + 28.8$	ns	$y = 0.0003x + 16.7$	ns	$y = -0.0006x + 36.4$
Soil TC:TP						
TSLF	ns	$y = 22.6x + 294.0$	ns	$y = -10.2x + 336.2$	<0.001	$y = 31.6x + 499.0$
Hydroperiod	ns	$y = 2.368x + 294.0$	ns	$y = 0.853x + 336.2$	ns	$y = 0.154x + 499.0$
Interaction	ns	$y = -0.056x + 294.0$	<0.05	$y = 0.037x + 336.2$	ns	$y = -0.054x + 499.0$
Soil TN:TP						
TSLF	ns	$y = 0.784x - 28.5$	ns	$y = -0.500x + 20.4$	<0.001	$y = 0.585x + 36.4$
Hydroperiod	<0.01	$y = 0.339x - 28.5$	ns	$y = 0.054x + 20.4$	ns	$y = -0.002x + 36.4$
Interaction	ns	$y = -0.003x - 28.5$	<0.05	$y = 0.002x + 20.4$	ns	$y = -0.0005x + 36.4$

Note: Significance at $P < 0.05$, ns indicates not significant.

deposition. In addition, long-term absence of fire in PS, which are characterized by considerably high primary productivity rates (Troxler et al. 2013), may cause an enormous accumulation of dead biomass with a consequent substantial reduction in photosynthetic rates and relative C contributions to the soil (Knapp and Seastedt 1986). On the other hand, surface soils in shorter-hydroperiod wetlands have high probability of being negatively impacted by fire and losing C since they normally remain dry for a longer portion of the year. In ecosystems drier than wetlands, frequent fire causes in fact losses of soil C (Pellegrini et al. 2018).

Fire carries P-rich biogeochemical and stoichiometric signatures. As shown by a recent global meta-analysis (Butler et al. 2018) and our study, soil TP, and TC:TP and TN:TP ratios were strongly related to fire. Nonetheless, fire signatures vary depending on vegetation types, soil types, and other environmental factors and are especially evident where fire eases P limitation (Butler et al. 2018). On the other side, we did not find a strong N signature of fire in the soil. Although we expected to see an increase in soil TN with the absence of fire in all soil types (Turner et al. 2008), as with soil TP, higher TSLF generally corresponded to lower soil TN in MS (Table 2). However, soil TC:TN ratio significantly increased with increasing TSLF, suggesting an additional effect of fire on MS soil stoichiometry. Although soil TN decreased with TSLF, one likely explanation for the weak N signature of fire is that, during fire, plant N volatilizes at moderately low temperatures (~200°C) and, commonly, 33–100% can be lost to the atmosphere (Boerner 1982). Fire impacts on soil N are often not detected, while volatilized plant N was estimated at 60% and 71% for grassland and shrubland ecosystems, respectively (Wan et al.

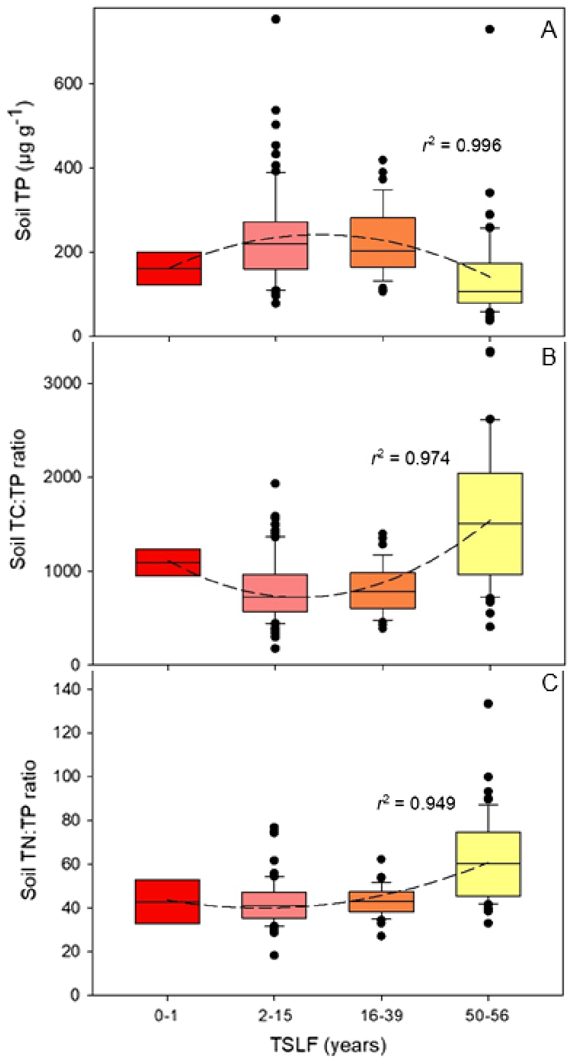

Fig. 4. Variation in (A) soil total phosphorus (TP) concentrations, (B) total nitrogen to total phosphorus (TN:TP), and (C) total carbon to total phosphorus mass ratios (TC:TP) with increasing time since last fire (TSLF) in the marl soils (MS) inside Everglades National Park.

2001). Finally, although live aboveground biomass of TS and MS macrophytes can increase for many years post-fire, declines occur after 20 yr post-fire (Sah et al. 2007). Dynamics of post-fire aboveground biomass may vary depending on fire behavior and/or post-fire hydrologic conditions. So, with increasing TSLF, not only does soil become P-depleted, but P may be accumulating in dead macrophyte biomass which forms a physical obstacle for shoot regrowth, reducing light near the soil surface (Knapp and Seastedt 1986). Therefore, maximum photosynthetic rates steadily decrease year after year with TSLF, eventually reducing live plant biomass stocks after many years. Likewise, differences in macrophytes biomass with TSLF could also be explained by a change in vegetation composition that could occur in time with the absence of fire (Driscoll et al. 2010, Sah et al. 2015, Noss 2018).

Fire has a profound effect on ecosystem biogeochemistry. In wetlands, fire legacies are mainly concentrated on impacts to nutrient cycling. In fact, compared with other ecosystem types where fire can greatly affect soil organic C (Turetsky et al. 2015, Pellegrini et al. 2018), direct impacts of fire to wetland peat and soil organic C are minimized as the soil is often wet or inundated. Moreover, in the last decades, a strict control on wildfires has been adopted, shifting the balance toward prescribed fires (Fig. 2), which in wetlands, like the Everglades, are usually not applied when soils are dry. Particularly, fire amplifies P cycling and a long-term absence of fire seems to bring the ecosystem to a fire-starving condition. Thus, fire is needed, but how frequently should fire occur is uncertain. An excessively high fire frequency might, for example be detrimental for biodiversity rather than of support (Noss 2018). Also, it has been shown that high fire frequency can lead ecosystems to nutrient losses, stoichiometric imbalance and, subsequently, to the disruption of fundamental soil processes (Butler et al. 2019). Designing long-term experiments that evaluate the effects of varying fire frequencies on wetland biogeochemistry would therefore be a valuable step forward for properly managing these regions. So far, our analysis seems to indicate that short-hydroperiod wetlands with oligotrophic soils should not be left unburned for more than 15–20 yr, that is, before soil P starts declining (Fig. 4). While the maximum fire return interval recommended here is solely based on our observation of soil TP that may vary when other aspects of ecosystem characteristics are considered. For instance, the short-hydroperiod MS is primary habitat of Cape Sable seaside sparrow (CSSS; *Ammodramus maritimus mirabilis*), and its habitat is adversely affected if the area is left unburned for longer period (Pimm et al. 2002), as CSSS population has been found

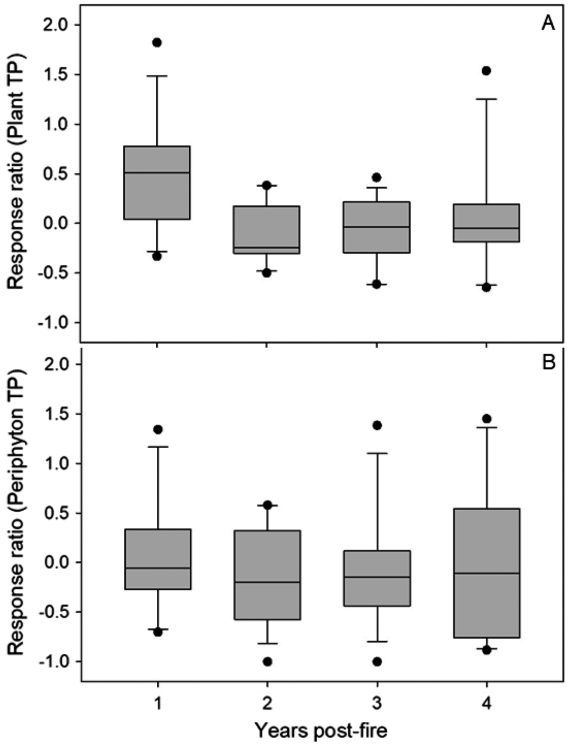

Fig. 5. Response ratio, defined as the ratio between the phosphorus concentration post-fire and pre-fire subtracted by 1, calculated for 4 yr post-fire for both (A) plant (aboveground) total phosphorus (TP) and (B) periphyton TP. The data derived from time series recorded in marl soils of the eastern Everglades since the year 2003 (Gaiser et al. 2014).

highest at a fire return interval of 5–8 yr (Benscoter et al. 2019). We believe that fire is also beneficial for the other soil and hydrologic types analyzed (i.e., richer soils with intermediate or long hydroperiod), which, in our opinion, should not be left unburned for long periods of time either. In addition, if we look at this study's results altogether, there is a clear indication that hydrologic and fire managements complement each other by impacting with relative magnitude the distinct soil constituents. Increasing water delivery and wetland inundation length will benefit, not only C storage, but also provision of soil N, whereas increasing burning frequency will help maintaining the necessary soil P levels.

On a global scale, the increasing frequency and severity of wildfires due to climate change is raising concerns because of the related direct hazards for the human population and C losses (Bowman et al. 2009, Pellegrini et al. 2018). On the other hand, in regions with active fire management we can observe an opposite trend toward less severe, controlled fires (Fig. 2), which can and should be used as an opportunity to achieve not only biological conservation, but also nutrient reload in oligotrophic landscapes. Nonetheless, in the scenario of shifting disturbance regimes in a time of climate change, ecosystem managers should carefully consider the outcomes and ensure to preserve the ecosystem's safe operating space (i.e., maintaining its resilience; Johnstone et al. 2016). Studying the effects of fires with high and low severity on nutrients cycling will increase our understanding of the possible outcomes of shifting the balance to less severe, prescribed fires in managed ecosystems, as compared to an increase in severe wildfires occurring in many regions where climate is becoming hotter and with prolonged, drier seasons (Bowman et al. 2009). Higher frequency of less severe fires (Hurteau et al. 2008) might also achieve to deposit amounts of charred material in wetland soil systems (i.e., black C; Knicker 2007), differently from what seen in the present study, enough to significantly affect soil C accumulation and quality in the long term. This hypothesis is however yet to be tested. Finally, if prescribed fires represent an opportunity for managing nutrients cycling, it should also be recognized that their wide application might not produce the same ecological effects of natural fires (Arkle and Pilliod 2010) and result in ecosystem imbalances, especially if burns are applied in a different season from the natural occurring one.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3408/full