Episodic disturbances drive nutrient dynamics along freshwater-to-estuary gradients in a subtropical wetland

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Abstract. Wetlands are biogeochemically active ecosystems where primary production and respiration interact with physico-chemical conditions to influence nutrient availability across spatio-temporal scales. The effect of episodic disturbances on water quality dynamics within wetlands is relatively unknown, especially in large oligotrophic wetlands such as the Everglades. We describe a range of episodic disturbance events and their impacts on the spatio-temporal dynamics of surface water total N (TN) and total P (TP) concentrations in the Everglades as a means to understand their effect and legacies. Water quality monitoring along the two principal drainages—Taylor Slough (TS) and Shark River Slough (SRS)—has been ongoing since 2000, spanning myriad disturbances ranging from high-energy storms such as Hurricane Wilma in 2005 to a record cold event in 2010 and large fires. Local events include pulsed rainfall, low marsh stage, and stage recession and recovery (i.e., droughts and subsequent dry-to-wet transitions). The deposition of marine-derived sediment from Hurricane Wilma corresponded with a doubling of TP in SRS mangrove sites (from 0.39 to 0.84 μmol/L) before recovering to pre-disturbance mean after 5–6 yr. A brief increase in TP within one week of the 2010 cold event was followed by delayed spikes in TN (>1000 μmol/L) and TN:TP exceeding 5000 after one month. In 2008, a large fire in upper SRS prior to the wet season caused a lagged TP pulse at downstream locations SRS2, SRS3, and possibly SRS4. TP also varied negatively with depth/stage in marsh sites and positively with salinity in estuarine sites, reflecting physical concentration or dilution effects. In upper TS, TP varied according to extremes such as high rainfall and low stage relative to normal conditions. Although excess P in the Everglades is generally derived from anthropogenic upland or natural marine sources, episodic disturbance mobilizes internal sources of nutrients along an Everglades freshwater-to-estuary continuum, affecting water quality from days to years depending on disturbance type and intensity. The capacity for resilience is high in coastal wetland ecosystems that are exposed to high-energy tropical storms and other episodic events, even in the highly managed Florida Everglades.

Key words: cold spell; disturbance; episodic events; Everglades; fire; high-energy storms; internal loading; mangrove; marsh; nitrogen; peat soil; phosphorus; Special Feature: High-Energy Storms.

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INTRODUCTION

Wetlands are biogeochemical hotspots that serve as sites of intense nutrient uptake or transformation (McClain et al. 2003, Lindau et al. 2008). As periodically flooded or saturated environments, conditions at the interface of aerobic and anaerobic boundaries provide distinct gradients in redox and elemental concentrations that can influence soil–water column exchanges and ultimately the availability of ecologically important elements such as nitrogen (N) and phosphorus (P; see Mitsch and Gosselink 2000 for overview). Combined with plant productivity and capacity for high nutrient uptake and sequestration, these characteristics of wetlands account for their frequent use in the treatment of wastewater, stormwater, and agricultural runoff (Mitsch and Gosselink 2000, Kadlec and Wallace 2009).

The concept of hot moments is also exemplified by wetlands (McClain et al. 2003). Processes that affect nutrient uptake, release, or transformation vary seasonally with temperature and rainfall or runoff (Spieles and Mitsch 2000, Hernandez and Mitsch 2007), chronically over time with presses of land-use change, or episodically with disturbances such as high-energy storms that lead to pulses in nutrient input or transformation (Davis et al. 2004, Shipley et al. 2013, Palta et al. 2014). The net effect is often observed as high spatial and temporal variability in water quality or nutrient fluxes. These effects can be short-lived and local or the signal can persist from weeks to years, spanning an entire ecosystem (McClain et al. 2003), and events or combination of events (e.g., high-energy storms) can account for a significant portion of net annual flux of water and materials to the estuary (Davis et al. 2004).

The concepts summarized by McClain et al. (2003) and advanced by others (Shipley et al. 2013) motivated our questions about disturbance-mediated nutrient dynamics across the Florida Everglades, a large flowing subtropical wetland complex. By combining information about upland and marine end-member contributions with an understanding of the drivers of those contributions and the rates of biogeochemical processing at locations between those end-members, we can then understand water quality variability and its biological consequences over space and time. As an oligotrophic P-limited ecosystem, the Everglades is vulnerable to P enrichment from upland agricultural and canal-derived sources (Noe et al. 2001, Gaiser et al. 2006). Consequences of these nutrient sources on Everglades habitat are loss of periphyton mats (Gaiser et al. 2006), chronic enrichment of soil P (Osborne et al. 2014), and vegetation shifts from sawgrass (Cladium jamaicense) marsh and wet prairies to monotypic stands of invasive yet native cattail (Typha domingensis; Newman et al. 1996, Surrratt et al. 2012).

P is rapidly sequestered in the Everglades by plant, microbial, soil-floc components (Noe et al. 2003), and various biogeochemical processes can result in the return of nutrients to the water column with local or downstream transport (Ensign and Doyle 2006, Leigh et al. 2016). Based on observations of historic surface water quality data, sequestered nutrients in Everglades wetlands are vulnerable to episodic disturbance events such as tropical storms and frontal passages (Sutula et al. 2003, Abtew and Iricanin 2008), seasonal hydrology (Davis et al. 2003, Sutula et al. 2003), short duration, high-volume precipitation (Williams et al. 2008), and shallow water levels (Zapata-Rios et al. 2012). The combination of peat fire and marsh re-hydration is also effective at mineralizing and mobilizing nutrients (Wu et al. 2012).

Given the importance of N and P to the Everglades and its coastal waters (Fourqurean et al. 1992, Childers et al. 2006), there is a need to characterize the role of various drivers in affecting the availability and downstream transport of these ecologically important elements. Routine water quality sampling by the Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) program provides an important dataset for understanding sources of limiting nutrients, particularly from marine-derived surface and groundwater (Childers et al. 2006, Price et al. 2006). These long-term data have been important in understanding intra- and inter-annual patterns in P and N availability (Childers et al. 2006, Koch et al. 2012), net exchange of nutrients from freshwater-to-estuary (Davis et al. 2009), and the potential impact of flow restoration (Koch et al. 2012, Briceño et al. 2014, Dessu et al. 2018).

The prevalence of large-scale episodic disturbances such as high-energy storms and fire in the
Everglades (Smith et al. 1994, 2015, Davis et al., in press) warrant consideration in terms of effects on nutrient mobilization and transport. Consequently, a synthesis is needed to advance understanding of how Everglades water quality is driven by episodic disturbance events and climatic extremes. We focused on water quality shifts associated with four discrete events: two hurricanes, a record cold spell, and a large upstream wildfire. We also investigated the response of surface water P to seasonal transitions from a drying marsh to re-hydration as well as short duration, high-volume precipitation, and extreme lows in marsh water level (i.e., stage) along a spatial cluster of sampling sites. Our objective was to utilize high frequency, long-term water chemistry data along freshwater-to-estuary gradients to test for the impact of disturbance on water quality change and the capacity for resilience in the highly managed coastal Everglades. We anticipated that episodic disturbance and extreme climatic events would alter nutrient concentrations relative to long-term means for each site and that processes such as rainfall, sediment deposition, and organic matter mineralization would all be important in driving concentration change. However, we were uncertain as to the timing, magnitude, duration, and spatial extent of water quality responses. We anticipated that certain events might elicit differential responses of N relative to P in water quality signals over scales of space and time. Therefore, a more refined goal of this study is to understand whether these events have sustained or far-reaching water quality impacts along the freshwater-to-estuary axis in the Everglades.

**METHODS**

**Site description**

The FCE LTER program was established in May 2000 and primarily occurs within the bounds of Everglades National Park (ENP; Fig. 1), an area of remnant Everglades downstream of the water conservation areas. Water flow is actively managed between these areas,邢

![Fig. 1. Map (left panel) of Everglades National Park (ENP) and water quality sampling sites (open circles) along Shark River Slough (sites SRS1–6) and Taylor Slough (sites TS1–3, 6 & 7), part of the Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) Program. Sites TS1–TS3, TS6, and TS7 are synonymous with TS/Ph1–TS/Ph3, TS/Ph6, and TS/Ph7 in the FCE LTER dataset. Map at right provides close-up views of Taylor Slough including freshwater sites TS1–TS3 and additional ENP sampling stations (TSC, S332, UTS.1, UTS.2, and TSB) in the expanded view of Upper Taylor Slough. Locations of stage and rainfall gages on maps are indicated by shaded triangles and black squares, respectively.](image-url)
ultimately resulting in a free-flowing condition once water is introduced into Shark River Slough (SRS) or Taylor Slough (TS) of ENP. Since its inception, the FCE LTER program has focused research efforts on understanding the interaction between end-member nutrient sources, water management (including Everglades restoration efforts), and climate change in affecting ecological processes such as primary production and carbon exchange along the ecotone spanning from freshwater marshes and sloughs, to the upstream end, to estuarine mangroves and seagrass meadows at the interface of the Gulf of Mexico. These areas are also influenced by differences in flow and water delivery between the wet season (typically lasting from May through October) and dry season (from November to April).

A key component of the FCE LTER program is a water quality monitoring program that tracks changes in surface water total nitrogen (TN) and total phosphorus (TP) over time through the two major flow paths in ENP. SRS is the largest flow path for freshwater through ENP, receiving surface water inflow primarily from the conservation areas and conveying it southwest toward the Gulf of Mexico and western Florida Bay. Sampling sites in SRS are spaced from canal inputs of freshwater at Tamiami Trail to a mangrove site near the mouth of Shark River and the Gulf of Mexico (Fig. 1, Table 1). TS extends from the L31W canal down to Florida Bay. Direct discharges into upper TS (UTS) ceased in 1999, coincident with modifications in the headwater that promote surface and subsurface water movement into the slough, which was linked to downward trends in total phosphorus in UTS (Surratt et al. 2012, Kotun and Renshaw 2014). Presently, the L31W canal and associated retention ponds convey water from more northern portions of the Everglades into the headwater of UTS, and it is part of a canal network supporting a hydrologic barrier on the eastern boundary of the Park with the objective of preventing eastward seepage of water out of the marsh. These management features have also increased hydroperiods in UTS (Surratt et al. 2012).

**Data sources and analyses**

Water quality samples were collected at each site using ISCO auto-samplers containing 24 1-L bottles. Until December 2006, water at all FCE LTER sites was sampled by programming auto-samplers to take composite samples once every

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**Table 1.** List of water quality sampling locations associated with Florida Coastal Everglades Long-Term Ecological Research (FCE LTER) and Everglades National Park–Florida International University (ENP, FIU), including date of sampling initiation and habitat description for each site.

| Site   | Program          | Sampling initiated | Habitat description   |
|--------|------------------|--------------------|-----------------------|
| SRS1†  | FCE LTER         | 1 December 2000    | Freshwater marsh      |
| SRS2   | FCE LTER         | 19 November 2000   | Freshwater marsh      |
| SRS3   | FCE LTER         | 17 November 2000   | Freshwater marsh      |
| SRS4   | FCE LTER         | 31 October 2000    | Estuarine mangrove    |
| SRS5   | FCE LTER         | 31 October 2000    | Estuarine mangrove    |
| SRS6   | FCE LTER         | 31 October 2000    | Estuarine mangrove    |
| TS1†   | FCE LTER/ENP     | 10 December 1999   | Freshwater marsh      |
| TS2    | FCE LTER/ENP     | 29 July 1999       | Freshwater marsh      |
| TS3    | FCE LTER/ENP     | 29 July 2001       | Freshwater marsh      |
| TS6    | FCE LTER/ENP     | 28 May 1998        | Estuarine mangrove    |
| TS7    | FCE LTER/ENP     | 7 April 1996       | Estuarine mangrove    |
| TSC    | ENP, FIU         | 3 October 2010     | Canal                 |
| S332   | ENP, FIU         | 29 March 2003      | Tailwater of structure|
| UTS.1  | ENP, FIU         | 21 July 2011       | Freshwater marsh      |
| UTS.2  | ENP, FIU         | 4 July 2011        | Freshwater marsh      |
| TSB    | SFWMD            | 29 October 1985    | Freshwater marsh      |

**Note:** SRS, Shark River Slough; TS, Taylor Slough.

Sites TS1–TS3, TS6, and TS7 are synonymous with TS/Ph1–TS/Ph3, TS/Ph6, and TS/Ph7 in the FCE LTER dataset. See relative locations on map (Fig. 1).

† Sites have been re-positioned due to changes in water management or restoration actions.
3 d. These samples were a composite of four 250-mL subsamples drawn every 18 h (a scheme that captures a dawn, noon, dusk, and midnight sample in every three-day composite). Beginning in December 2006, freshwater marsh sites (SRS1, SRS2, SRS3, TS1, TS2, and TS3) were subsampled at 36-h intervals, with four 250-mL samples composited into a single 1-L bottle reflecting 6 d of integrated water quality. Estuarine sites (SRS4, SRS5, SRS6, TS6, and TS7) remain on a 3-d sampling interval, reflecting the higher degree of temporal variability at sites with a tidal influence. TS sites are synonymous with Taylor Slough–Panhandle (TS/Ph) sites in the FCE LTER dataset. We did not consider any FCE LTER Panhandle sites and hence the use of TS only.

A smaller, companion program in UTS tracks the spatial and temporal variability of water quality across a cluster of sites from the canal input source to the Taylor Slough Bridge (TSB) and includes TSC, S332, UTS1, and UTS2 (Fig. 1 and Table 1). The TSB site is a long running station with a history of sampling by the South Florida Water Management District (SFWMD) since the 1980s. Data for this site are stored on DBHYDRO (https://www.sfwmd.gov/science-data/dbhydro). Samples for this station are collected by the ENP staff and analyzed by the SFWMD's laboratory. Samples for the remaining stations were collected and analyzed by the Southeast Environmental Research Center’s Water Quality Laboratory at Florida International University as part of agreements with the ENP. All FCE LTER and ENP-FIU water quality samples are retrieved every 3–4 weeks and analyzed for concentrations of TP, TN, and salinity. TP is analyzed with a modified Solorzano and Sharp (1980) technique. TN is measured with an ANTEK 7000N elemental analyzer (Frankovich and Jones 1998), and salinity is measured with an YSI conductivity meter.

Rainfall and stage data were downloaded from EDEN (see: https://sofia.usgs.gov/eden/) and DBHYDRO. We considered stage data from sites NESRS2 and P33 (see Fig. 1) as a proxy for marsh stages along the freshwater sites of SRS and as an indicator of head-driven flow from the freshwater segment of the SRS transect into the estuarine segment. For characterization of rainfall conditions in UTS, an average of daily rainfall at stations S177 and S18C (Fig. 1) was summed over five days to generate time series. For the purposes of comparison, we define “high” rain as any rainfall event that exceeds 10.2 cm (4 inches) within five days. Rainfall below this was considered to be within the normal range of conditions. Stage data from NP-NTS1 (Fig. 1) were used to represent water levels from across the TS study area. For the purposes of comparison, low stage is less than the 25th percentile of the period of record stage distribution; anything greater is considered to be within a normal range of marsh stage.

Between 1926 and 2014, the coastal Everglades experienced 18 hurricane landfalls, 21 yr with drought, and 15 yr with a severe cold event (as defined by Boucek and Rehage 2014, see Davis et al., in press). The discrete events included were the most extreme or best representations of their type. Two hurricanes affected the Everglades in 2005. Hurricane Wilma struck the southwest coast of Florida near SRS6 on 24 October 2005 as a Category 3 storm bringing both storm surge and a load of marine-derived carbonate sediment (Castañeda-Moya et al. 2010). Two months prior, on 25 August 2005, Hurricane Katrina crossed South Florida as a Category 1 storm. A record cold spell affected all of south Florida in 2010 from January 2 to 13, leading to substantial fish mortality in the marsh and defoliation of many trees, especially mangroves (Boucek and Rehage 2014, Boucek et al. 2016, Danielson 2016). Beginning on 14 May 2008, the Mustang Corner fire ignited, burning nearly 16,000 ha of marsh between SRS1 and SRS2 before the onset of wet season rains helped to subdue the fire one month later (Ruiz et al. 2010). Finally, we have observed a few distinct instances of the transition from continual marsh stage recession to re-wetting in the summer of 2006 and again in the winter of 2015, the latter following an extended drought.

Concentrations of TN and TP (hereafter [TN] and [TP]) at each site were depicted using box and whisker plots. Box and whisker plots were also used to depict year-to-year change in aggregated [TP] from all SRS estuarine sites combined. Means were compared across sites (all sites, [TN] and [TP]) and across years (SRS estuarine sites, [TP]) using analysis of variance (ANOVA) and Tukey's honest significant difference (HSD) to determine significant differences among sites and years, respectively. To document and describe event-driven
changes in [TN] and [TP] in surface water, we plotted time series of water quality relative to the aforementioned events and corresponding hydrologic shifts. We describe deviations in water quality relative to the long-term means for each site.

In our evaluation of TS water quality relative to extremes in rain and stage, we tested the difference between sampling events when episodic events occurred versus conditions when neither of the identified episodic events occurred using Wilcoxon rank sum test. Tests were applied by station between three basic environmental conditions under which samples were collected: high rainfall versus normal rainfall conditions; low stage versus normal stage conditions. In addition, we analyzed differences between two-factor combinations (rainfall × stage) at each station to understand interactions. We performed Spearman's correlation test to quantify associations between station-specific rainfall or stage and surface water [TP].

**RESULTS**

Long-term patterns of [TN] and [TP] along the SRS transect are inversely related to one another (Fig. 2). At the freshwater end, [TN] was highest at SRS2 (averaging 71.3 μmol/L ± 57.9 SD) and [TP] lowest at SRS2 (averaging 0.24 μmol/L ± 0.26 SD). At SRS6, [TN] declined significantly to 37.3 μmol/L ± 18.1 SD, while [TP] increased to

![Fig. 2](image-url)
1.01 μmol/L ± 0.92 SD—more than four times the long-term mean at SRS2. Along the TS transect, no inverse correlation exists between [TN] and [TP], and much less variation characterizes long-term mean concentrations from the freshwater end-member to marine end-member, with only a slight increase in both [TN] and [TP] noted at sites TS6 and TS7 relative to the freshwater TS sites. In fact, TS6 exhibited significantly higher [TN] and [TP] relative to the freshwater sites along the TS transect. However, the range of [TN] and [TP] at TS7 fell in between the ranges observed at TS3 and TS6 and was not significantly different from either (Fig. 2). When considering each event’s impact on water quality (in sections below), we used long-term averages for both SRS and TS sites as reference points.

**High-energy storms**

Hurricane Katrina crossed over South Florida from east to west on 25 August 2005, producing a 3-d rainfall total of 23.7 cm in ENP. The resulting effect on water quality at most FCE LTER sites was minimal, aside from increased runoff into the mangrove ecotone that lowered salinity at TS6 from 19 ppt to 0 ppt, [TN] from 37.8 to 18 μmol/L, and [TP] from 0.19 to 0.09 μmol/L between August 25 and October 3. A similar effect was observed at TS7, where salinity declined 26 ppt over the same timeframe, and [TN] and [TP] declined from 42.6 to 20.2 μmol/L and 0.22 to 0.18 μmol/L, respectively.

Hurricane Wilma, a considerably stronger storm that approached from the southwest, was associated with a significant and sustained increase in surface water [TP] at SRS estuarine mangrove sites (SRS4, SRS5, and SRS6; Castañeda-Moya et al. 2010, Davis et al., in press). Based on combined data from sites SRS4–SRS6, mean annual [TP] increased significantly from 2005 to 2006, more than doubling from 0.39 μmol/L in 2005 to 0.84 μmol/L in 2007 and subsequently declined to an approximate pre-disturbance mean of 0.44 μmol/L in 2011 (Fig. 3).

**Cold event**

The 2010 cold event, lasting from January 2 to 13 and having daily low air temperatures <5.4°C and a low water temperature of 6.2°C (Boucek and Rehage 2014), affected water quality at all sites in SRS, with a sharp increase in [TP] immediately following the event (Fig. 4). At SRS1, SRS2, and SRS3, [TP] increased a minimum of threefold (with highs ranging from 0.39 to 1.16 μmol/L) as the event subsided and remained high until January 25. This occurred as [TN] declined at all sites (Fig. 4). This period was followed by a rapid decline in [TP] to pre-disturbance levels at all sites and a concomitant five- to sixfold increase in [TN] to the highest concentrations recorded at FCE LTER sites (ranging from 1006 to 1326 μmol/L; Fig. 4). TN:TP, which is typically just over 100 at these freshwater sites, increased to more than 5000 at SRS1, SRS2, and SRS3. [TN] remained high until March 3, 49 d after the cold event subsided. For [TP] and [TN], the most rapid and dramatic increases or decreases were at SRS1, the most upstream site.

Despite the strong marine influence at the mangrove sites, a similar trend was noted at sites SRS4, SRS5, and SRS6. However, [TN] increased 15–35% at all sites, whereas [TP] remained low (between 0.13 and 0.61 μmol/L; TP), resulting in TN:TP highs of 692 at SRS4 (January 8), 328 at SRS5 (January 10) and 259 at SRS6 (January 10).
Similar to the freshwater sites, [TP] increased and [TN] decreased at all estuarine SRS sites as the cold event was waning or immediately after it subsided (Fig. 4). During this period, [TP] increased from <1 μmol/L at SRS6 to more than 3 μmol/L by January 20, from an average of about 0.5 to 1.81 μmol/L at SRS5, and from <0.2 to 0.79 μmol/L at SRS4—all reflecting the general decline in surface water [TP] with distance from the marine end-member. [TN] dropped during the ensuing two weeks as [TP] increased (Fig. 4). Beginning February 6, [TN] increased sharply at sites SRS4-SRS6 and generally decreased through the remainder of the month (Fig. 4).

The region-wide influence of the cold event was evident at TS sites, although the pattern was somewhat different from that observed at SRS (Fig. 5). At all TS sites, [TN] was either decreasing or low and stable immediately following and for almost one month after the cold event. Beyond that period, [TN] increased more than twofold at all TS sites by February 20 (TS1, TS2, and TS3) and February 21 (TS6 and TS7), remaining high for at least the next month. [TP] at TS2 and TS3 also exhibited dramatic increases on February 20 and remained high for the next 2 weeks. At TS6 and TS7, [TP] increased more than threefold in the days immediately following the cold event and declined by the end of January, only showing an increase again in mid-March, nearly two months following the cold event (Fig. 5).
Mustang Corner fire

Despite a high frequency of fire inside ENP (mean = 28.3 per yr for period 1948 to 2010), many fires are small and do not occur in the deeper sloughs that represent the primary flow paths (Smith et al. 2015). The Mustang Corner fire burned in northeast SRS from 14 May to 14 June 2008. By the end of May 2008, marsh stages in SRS reached the lowest level for the year. Water sampling at SRS3 was suspended on April 22 due to low marsh stages; however, SRS2 still remained sufficiently wet for sample collection (Fig. 6). Marsh stage began increasing by early June with the onset of wet season rains. At this time, [TP] at SRS2 increased from a pre-fire low of 0.18 to 0.78–0.82 μmol/L as stages were increasing, and peaking with stage at 1.65 μmol/L (nearly seven times greater than the long-term average for the site of 0.24 μmol/L TP) on June 19, five days after the fire was extinguished. Nearly one month later on July 18, [TP] at SRS3 (approximately 11.3 km downstream of the SRS2 site) peaked at 0.94 μmol/L from a low of 0.45 μmol/L, and then returned to a near-mean [TP] for this site of 0.4 μmol/L by August 9. As stages continued to increase with advancement of the wet season, [TP] increased at SRS4 (12.9 km...
downstream of the SRS3 site) from 0.54 to 0.94 μmol/L on August 6, although this was not as high relative to its long-term mean (0.6 μmol/L TP) as the signals identified at the other sites (Fig. 6).

**Stage and freshwater flow recovery**

In the dry season of 2006, an uninterrupted decline in marsh stage at freshwater SRS sites persisted from March 24 to May 16, when early wet season rains increased stage by 22 cm (0.72 feet) in two days (Fig. 7). As marsh stage receded, [TP] substantially increased from near the long-term means of these freshwater sites (0.2–0.4 μmol/L TP) to highs of 1.59 μmol/L (SRS1), 1.51 μmol/L (SRS2), and 1.87 μmol/L (SRS3). Matching the inflection points in stage decline, noticeable increases in [TP] corresponded to NESRS2 stages around 1.49 m (4.9 feet) relative to North America Vertical Datum of 1988 (NAVD88) and again at 1.37 m (4.5 feet NAVD88). Upon stage reversal, [TP] decreased to 0.26 μmol/L (SRS1), 0.43 μmol/L (SRS2), and to 0.59 μmol/L (SRS3; Fig. 7).

Following a drought that persisted over the Everglades from mid-2014 through the summer of 2015, El Niño-driven rainfall in late 2015 brought substantial freshwater flows through both SRS and TS. In the TS mangrove ecotone, where salinity levels can become hypersaline during drought years, the effect of El Niño rains was most pronounced, lowering salinity at TS6 from >45 ppt in mid-August 2015 to <1 ppt by the end of the 2015 (Fig. 8). TP data at TS6 tracked fluctuations in salinity during this same period, regularly exceeding the long-term mean for the site (0.37 μmol/L) and peaking twice at 0.62 μmol/L. [TP] dipped below the long-term mean for the site during freshets associated with rainfall and more P-depleted runoff from upstream freshwater marsh (Fig. 8).

**Extreme rainfall and stage in upper Taylor Slough**

[TP] at four sites in upper TS differed between periods of high rainfall and normal rainfall ($P < 0.1$ or 0.05, respectively; Wilcoxon rank sums test; Table 2). Of these, TSC, TS1, and TSB had lower [TP] coincident with high rainfall relative to normal rainfall conditions, whereas S332 exhibited higher [TP] during high rainfall conditions.
periods (Table 2). Also, sites UTS.1, UTS.2, and TSB had higher [TP] at low stage conditions relative to normal stage conditions ($P < 0.05$; Wilcoxon rank sums test; Table 2).

We found significant differences in [TP] at each upper TS site when considering the combined effects of rainfall and stage. Representing the source of managed inflow, the normal rainfall/normal stage scenario at TSC had higher [TP] than the high rainfall/normal stage or normal rainfall/low stage scenarios (Table 3). Immediately downstream at the S332 site (i.e., canal tailwater), a similar normal rain/high stage difference was observed relative to normal rain/low stage; however, this site typically had higher [TP] under most scenarios involving high rainfall (especially during low stage periods). Further downstream in the marsh area and throughout the rest of upper TS, lower [TP] was associated with normal stage and often in combination with high rainfall (Table 3). Conversely, higher [TP] generally occurred during periods of low stage, independent of rainfall intensity (Table 3). However, data from UTS.1, UTS.2, TSB, and even S332 indicate that the extreme combination of high rainfall and low stage corresponds with the highest [TP] in the water column.

**DISCUSSION**

Temporal and spatial phenomena that lead to biogeochemical hotspots and hot moments are
Table 2. Significant differences in total phosphorus (TP) concentrations (μmol/L) along Taylor Slough during extremes in rainfall (HR, high rainfall) or stage (LS, low stage) versus normal rainfall (NR) or normal stage (NS) conditions, respectively.

| Site ID | Scenario 1 TP GM (IQ range) | Scenario 2 TP GM (IQ range) | Scenario comparison | Significance |
|---------|-----------------------------|-----------------------------|---------------------|--------------|
| TSC     | HR = 0.25 (0.16–0.35)       | NR = 0.29 (0.16–0.34)       | HR < NR             | **           |
| S332    | HR = 0.30 (0.19–0.48)       | NR = 0.27 (0.19–0.38)       | HR > NR             | **           |
| TSI     | HR = 0.20 (0.13–0.29)       | NR = 0.24 (0.16–0.35)       | HR < NR             | **           |
| TSB     | HR = 0.12 (0.10–0.16)       | NR = 0.14 (0.10–0.19)       | HR < NR             | *            |
| UTS.1   | NS = 0.26 (0.20–0.34)       | LS = 0.41 (0.25–0.50)       | NS < LS             | **           |
| UTS.2   | NS = 0.26 (0.19–0.34)       | LS = 0.32 (0.20–0.45)       | NS < LS             | **           |
| TSB     | NS = 0.11 (0.10–0.13)       | LS = 0.19 (0.13–0.29)       | NS < LS             | **           |

Notes: See definitions in text. Geometric means are presented with inter-quartile (IQ) ranges for each distribution in parentheses. Significant differences were determined using Wilcoxon rank sums test (*0.10 ≥ P > 0.05; **P ≤ 0.05).

Table 3. Taylor Slough sites exhibiting significant differences in total phosphorus (TP) concentrations (μmol/L) across combined scenarios of rainfall (NR, normal rainfall; HR, high rainfall) and stage (LS, low stage; NS, normal stage) as defined in text.

| Site ID | Scenario 1 TP GM (IQ range) | Scenario 2 TP GM (IQ range) | Scenario comparison | Significance |
|---------|-----------------------------|-----------------------------|---------------------|--------------|
| TSC     | NR/NS = 0.31 (0.18–0.45)    | HR/NS = 0.25 (0.16–0.32)    | NR/NS > HR/NS       | **           |
| TSC     | NR/NS = 0.31 (0.18–0.45)    | NR/LS = 0.25 (0.16–0.37)    | NR/NS > NR/LS       | **           |
| S332    | NR/NS = 0.29 (0.22–0.35)    | NR/LS = 0.23 (0.17–0.30)    | NR/NS > NR/LS       | **           |
| S332    | NR/NS = 0.29 (0.22–0.35)    | HR/LS = 0.50 (0.35–0.69)    | NR/NS < HR/LS       | **           |
| S332    | HR/NS = 0.28 (0.18–0.40)    | HR/LS = 0.50 (0.35–0.69)    | HR/NS < HR/LS       | **           |
| S332    | HR/NS = 0.28 (0.18–0.40)    | HR/LS = 0.50 (0.35–0.69)    | HR/NS < HR/LS       | **           |
| TSI     | NR/NS = 0.25 (0.18–0.36)    | HR/NS = 0.19 (0.13–0.27)    | NR/NS > HR/NS       | **           |
| TSI     | NR/NS = 0.25 (0.18–0.36)    | HR/LS = 0.20 (0.14–0.33)    | NR/NS > HR/LS       | **           |
| TSI     | HR/NS = 0.19 (0.13–0.27)    | HR/LS = 0.24 (0.17–0.32)    | HR/NS < HR/LS       | **           |
| UTS.1   | NR/NS = 0.26 (0.19–0.35)    | NR/LS = 0.40 (0.23–0.49)    | NR/NS < HR/LS       | **           |
| UTS.1   | NR/NS = 0.26 (0.19–0.35)    | HR/LS = 0.45 (0.34–0.54)    | NR/NS < HR/LS       | **           |
| UTS.1   | HR/NS = 0.26 (0.20–0.33)    | HR/LS = 0.45 (0.34–0.54)    | HR/NS < HR/LS       | **           |
| UTS.1   | HR/NS = 0.26 (0.20–0.33)    | HR/LS = 0.45 (0.34–0.54)    | HR/NS < HR/LS       | **           |
| UTS.1   | HR/NS = 0.40 (0.23–0.49)    | HR/LS = 0.45 (0.34–0.54)    | HR/NS < HR/LS       | *            |
| UTS.2   | NR/NS = 0.29 (0.20–0.39)    | HR/NS = 0.24 (0.18–0.30)    | NR/NS > HR/NS       | **           |
| UTS.2   | NR/NS = 0.29 (0.20–0.39)    | HR/LS = 0.35 (0.27–0.46)    | NR/NS < HR/LS       | **           |
| UTS.2   | HR/NS = 0.24 (0.18–0.30)    | HR/LS = 0.35 (0.27–0.46)    | HR/NS < HR/LS       | **           |
| UTS.2   | HR/NS = 0.31 (0.18–0.42)    | HR/LS = 0.35 (0.27–0.46)    | HR/NS < HR/LS       | **           |
| TS2     | NR/LS = 0.16 (0.11–0.22)    | HR/LS = 0.20 (0.15–0.28)    | NR/LS < HR/LS       | **           |
| TSB     | NR/NS = 0.12 (0.09–0.13)    | NR/LS = 0.20 (0.16–0.30)    | NR/NS < HR/LS       | **           |
| TSB     | NR/NS = 0.12 (0.09–0.13)    | HR/LS = 0.17 (0.10–0.28)    | NR/NS < HR/LS       | *            |
| TSB     | HR/NS = 0.11 (0.10–0.13)    | HR/LS = 0.17 (0.10–0.28)    | HR/NS < HR/LS       | **           |

Notes: Geometric means for each scenario combination are presented with inter-quartile (IQ) ranges for each distribution in parentheses. Significant differences were determined using Wilcoxon rank sums test (*0.10 ≥ P > 0.05; **P ≤ 0.05).

strongly influenced by disturbance events and site-specific differences in nutrient availability. Along freshwater-to-estuary gradients, we illustrate how the timing, location, type, and magnitude of disturbance events interact to affect pulses of N and P in oligotrophic Everglades wetlands. Everglades freshwater marshes can be seasonal sources of TN (Sutula et al. 2003, Childers et al. 2006), whereas upstream canal inputs and the Gulf of Mexico are considered anthropogenic and natural sources of TP, respectively (Childers et al. 2006). Biogeochemical hot moments occur as temporal and spatial lags from the origin of episodic disturbance as mediated by
these marine versus freshwater forcings. Furthermore, compartmentalization in the Everglades has influenced the degree of connectivity and drivers affecting water quality across this managed landscape (Childers et al. 2006, Dessu et al. 2018).

That the disparity in [TP] between freshwater and estuarine mangrove sites along SRS is growing with increasing concentrations at the marine end is noteworthy. Anthropogenic sources are often the driver of elevated TP concentrations in the Everglades (Surratt et al. 2012, Osborne et al. 2014). Although SRS1 [TP] was more elevated relative to downstream freshwater sites, high [TP] at this site is linked to gate closure or low flow events, suggesting an internal source of TP at SRS1 (Childers et al. 2006). Incorporating 13 additional years of water quality data at these sites relative to that analyzed by Childers et al. (2006) indicates that the marine influence on [TP] is increasing in the SRS estuarine mangrove sites, while the central tendency of [TP] in the freshwater sites (especially at SRS2 and SRS3) has remained relatively constant. In particular, where Childers et al. (2006) noted median [TP] <0.25 μmol/L at SRS4, <0.35 μmol/L at SRS5, and <0.45 μmol/L at SRS6, median values of [TP] are near or above 0.5 μmol/L at these three sites. Interestingly, median [TP] at TS6 and TS7 has remained approximately the same over this period of time, perhaps reflecting the influence of Florida Bay in attenuating naturally higher Gulf of Mexico-sourced TP (Childers et al. 2006).

**High-energy storms**

Rainfall and runoff from Hurricane Katrina had nearly a 1-month dilution effect on water quality at TS mangrove sites, which are less tidally influenced than SRS mangrove sites. By comparison, the multiyear legacy of Hurricane Wilma on [TP] at SRS mangrove sites was primarily associated with Wilma's 3–5 m storm surge and corresponding deposition of nearly 10 cm of marine-derived carbonate sediment (Krauss et al. 2009, Smith et al. 2009, Castañeda-Moya et al. 2010). Since the TP content of this sediment was on average 1.6 times higher than that in native mangrove soils, soil TP enrichment ranged from 20% to 54% in the SRS mangrove sites (Castañeda-Moya et al. 2010). Over time, this deposited layer was flushed by tides, yet some of the sediment and TP was retained, contributing to soil elevation at SRS6 (Whelan et al. 2009). Released TP from this sediment was apparent over a period of 5–6 yr, attenuating to pre-storm levels around 2011. The more recent and gradual increase in [TP] at these mangrove sites may be attributable to sea level rise and more of a landward encroachment of marine-derived P into this oligotrophic, P-limited environment (Dessu et al. 2018).

We did not see the same effect of Hurricane Wilma in TS sites, as the Florida Bay-derived mud deposited in this area was much lower in TP content than that derived from the Florida Shelf and deposited at SRS6 (Castañeda-Moya et al. 2010). In 1999, Hurricane Irene had a similar southwest approach toward the coastal Everglades, depositing a layer of carbonate sediment near TS7 and resulting in a sharp increase in soluble reactive P and [TN] but little change in [TP] (Davis et al. 2004). As one of the strongest storms to affect South Florida over the past century, Hurricane Andrew brought a substantial storm surge and high winds on 24 August 1992 as it passed over ENP from east to west—a path similar to that of Hurricane Katrina. In the weeks following this Category 5 storm, neither TP nor ammonia changed significantly in Everglades marsh sites (Roman et al. 1994).

**Cold event**

The historic cold event of early 2010 had a region-wide effect on vegetation and faunal mortality in the coastal Everglades. At all SRS sites, a near-term rise in [TP] occurred immediately following the cold event and a delayed increase in [TN], the former likely related to contributions from rapidly senesced litter and the latter likely attributable to faunal (i.e., fish) mortality and decay. At the TS freshwater sites, no immediate response occurred with respect to [TP], but the mangrove sites (TS6 and TS7) exhibited a similar near-term rise indicating a potential mangrove litter-derived source of P. The longer term increases in surface water [TN] and [TP] possibly reflect a source from faunal decay; however, this was not directly quantified.

The cold event produced substantial mangrove mortality and canopy defoliation at SRS mangrove sites (Danielson 2016). Mangrove litterfall rates were 2.7 (SRS4), 2.1 (SRS5), and 3.2 (SRS6)
times higher immediately following the cold event with recovery to pre-disturbance levels shortly thereafter (Danielson 2016). Litter production is not measured at the freshwater sites; however, significant browning and defoliation characterized Chrysobalanus icaco that occupy many of the tree islands in upper SRS (S. Davis, personal observation). Pulses in leaf litterfall can represent a rapid source of nutrients and labile carbon that can be leached, mineralized, taken up by plants, retained in the soil, or exported to adjacent coastal waters (Tanner et al. 1991, Davis et al. 2006, Lugo 2008). Such inputs following a disturbance are associated with the magnitude of litterfall and timing of the event (Michener et al. 1997), and carbon and nutrient pools could be two to five times higher relative to the average annual litterfall input (Frangi and Lugo 1991). Terrestrial studies have reported increased C, N, and P concentrations on the forest floor after hurricanes. Litterfall from Hurricane Hugo (1989) had 1.3–3.4 times more N and two to five times more P than did the mean annual litterfall in a coastal pine forest in South Carolina and a subtropical montane forest of Puerto Rico (Blood et al. 1991, Frangi and Lugo 1991, Lodge et al. 1991). In addition, the total mass of fine litterfall resulting from Hurricane Hugo was 1.2 to 2.0 times higher than mean annual litterfall input in tabonuco and elfin montane forests in the Luquillo Forest of Puerto Rico (Lodge et al. 1991). Litterfall pulses also contributed to increased soil ammonium pools several months later in tabonuco forests, five times higher than reference plots (Steudler et al. 1991). Our findings suggest a similar effect of disturbance on litterfall dynamics and nutrient availability.

Fish mortality and decomposition also represent an important source of nutrients. N and P comprise about 15% and 3–5% of fish biomass, respectively. N-rich protein structures in fish decompose at a more rapid rate, with nearly 100% of N being released from fish carcasses within 30 d of death. In contrast, only 40% of P is mobilized 100 d after death, in the absence of scavenging (Johnston et al. 2004). In the Everglades, fish mortality can represent an input of 43 µg P/m² to the total P budget (Stevenson and Childers 2004).

As a result of the 2010 cold event, there was an almost complete loss of tropical fish species, which represent 29% of total freshwater fish abundance in SRS. Tropical non-native fishes, including Mayan cichlids, blue and spotted tilapia, and peacock eels, which represented 10% of total fish abundance, declined by 95–100% (Boucek and Rehage 2014, Rehage et al. 2016). Similarly, a dominant estuarine large-bodied piscivore, common snook, decreased by over 90% (Stevens et al. 2016). Lastly, tropical native euryhaline species (i.e., striped mojarra, tidewater mojarra, and striped mullet) decreased by at least 90% following the event, and tidewater mojarras seemed most affected (Boucek and Rehage 2014). Given these observed mortalities, the TN increase we observed within 30 d following the event suggests a contribution from decomposing fish. Weber and Brown (2013) demonstrated that pulsed fish mortality resulted in a non-linear, three- to fivefold increase in N availability 2–3 weeks following disturbance. By comparison, we observed a five- to sixfold spike in [TN] and increasing TN:TP at upstream SRS sites approximately 2–3 weeks after the 2010 cold event.

**Mustang corner fire**

The Mustang Corner fire burned a large area of vegetation and soil in northeast SRS, where soils are calcitic marls <15 cm thick, underlain by limestone of the highly porous Miami oolite formation (Randazzo and Jones 1997). These soils are relatively low in organic C, ranging between 2.3% and 21.0%, with soil TP values ranging between 100 and 358 µg/g (Sah et al., 2007). Following fire, soil nutrient levels can increase (Wu et al. 2012, Liao et al. 2013) or decrease over time through volatilization and subsequent leaching or export of ash particles by fire updrafts and wind (Qian et al. 2009, Hogue and Inglett 2012). In low-P calcareous wetlands, soil N and P availability may increase immediately after fire (Liao et al. 2013). However, other studies have shown that up to 99% of C and N can be lost through volatilization, while P is retained in high concentrations (Baird et al. 1999, Hogue and Inglett 2012). This mineralized P can contribute to the soil pool or be mobilized as bioavailable P (Galang et al. 2010), affecting wetland water quality (Bitner et al. 2001, Battle and Golladay 2003, Tian et al. 2010, Xu et al. 2011).

In Everglades peat marshes, surface water [TP] can increase dramatically in burned areas, and
the SRS2 peak of 1.65 \( \mu \text{mol/L} \) TP following the Mustang Corner fire is similar to the mean of 1.68 \( \mu \text{mol/L} \) TP observed by Wu et al. (2012). With the onset of the 2008 wet season and initiation of flow, TP at SRS2 was likely carried to SRS3, approximately 12.3 km downstream. Using a one-month travel time for the signal between SRS sites, this would amount to mean current velocities in the slough of about 0.44 cm/s, which is within the range of velocities reported for SRS (Leonard et al. 2006). The appearance of the TP signal at SRS4 was over a shorter duration (20 d) but may reflect increased velocities down-slough.

**Stage and freshwater flow recovery**

The inverse relationship between [TP] and stage reflects a physical concentration of elements in the water column with dry-down and dilution through rainfall and stage increase. However, we cannot discount the potential contribution of prey concentration and foraging fauna in affecting surface water [TP] as marsh stage recedes (Kushlan 1976). Complete marsh dry-down or reduced hydropertiod can accelerate peat soil oxidation, leading to mineralization of soil TP and flux from the soil to the water column upon re-hydration (Dunne et al. 2010, Zak et al. 2010). In the mangrove ecotone, such as site TS6, where [TP] often shows a positive correlation with salinity in the dry season (Childers et al. 2006, Koch et al. 2012), physical concentration plus the contribution of P-rich groundwater discharge (as described by Price et al. 2006) may explain the increasing [TP] we observed in the transition from a dry to a wet period. This has implications for P inputs to a P-limited Florida Bay that may be mitigated to some extent through restoration of freshwater flow (Koch et al. 2012, Briceño et al. 2014). Moreover, recent studies have focused on saltwater-induced peat collapse at the top of the mangrove ecotone (Chambers et al. 2014), suggesting that this process may contribute to a chronic source of P to the water column, particularly as sea level rise advances saltwater intrusion further inland into brackish and oligohaline peatlands.

**Extreme rainfall and stage in upper Taylor Slough**

Extensive high rainfall and low stage yielded important insights to the interaction of climatic and physical forcings on [TP] in upper TS. [TP] was generally suppressed under high rainfall conditions in the canal and the upper TS marsh sites, likely due to dilution effects. Periods of high rainfall often correspond to lower temperatures that also relate to [TP] reductions in surface waters of wetlands (Kadlec and Reddy 2001). An exception to this pattern was the S332 (i.e., tailwater) site that exhibited higher [TP] during high rainfall and presumably when more water was flowing into the slough from the adjacent canal and agricultural area. However, it is difficult to differentiate the effects of a canal source from re-suspension of TP given that managed discharge enters a previously dry marsh. In general, [TP] in upper TS was elevated in low stages, reflecting a concentration of elements during dry-down, and dilution when low stages return to normal. Smith and McCormick (1999) illustrated a long-term inverse relationship between surface water [TP] and water depth in Everglades marsh. The suppression of surface water [TP] is also associated with long-term rainfall patterns in Everglades marsh (Childers et al. 2006). In upper TS, downstream of L31W, where a water control structure historically discharged directly into the slough, a soil P gradient has grown from the discharge source to more than 6 km downstream (Osborne et al. 2014). A corresponding gradient in surface water [TP] exists. Since May 2012, average annual flow-weighted mean [TP] in UTS was 0.16 \( \mu \text{mol/L} \) and ranged from 0.14 to 0.18 \( \mu \text{mol/L} \) (Mo et al. 2015, 2017). At about 2.75 km downstream of the L31W, five-year average geometric mean [TP] was 0.11 \( \mu \text{mol/L} \) and ranged from 0.09 to 0.13 \( \mu \text{mol/L} \) (Julian 2017). Along this zone, conversion of desirable emergent vegetation to Typha domingensis is indicative of P enrichment (Surrett et al. 2012) and representative of a P hotspot that is vulnerable to re-suspension under low stage and high rainfall conditions or mineralization with soil dry-down and oxidation.

**Conclusions**

Large ecosystems such as the Everglades integrate episodic disturbance events and impacts across the landscape, resulting in differential responses that are often context-dependent. Hydrologic connectivity from freshwater wetlands to the estuary should be balanced by biological fragmentation so as to manage for...
disturbance events that lead to unintended negative impacts (Jackson and Pringle 2010, Rahel 2013). Shifts in the direction, magnitude, and characteristics of ecological state changes (e.g., water quality) are difficult to predict, requiring monitoring and adaptive management during and after disturbances. In the case of this study, the magnitude and duration of water quality change reflected characteristics of disturbance events that were of varying severity and spatial scale.

A long-range goal is to forecast changes in nutrient concentration with episodic events. Given the importance of nutrients (especially P) in affecting marsh habitat quality and functioning in the Everglades as well as the legal framework for ensuring protection of resources, tools to understand the interactions between end-member sources (Dessu et al. 2018) as well as the internal loading of nutrients brought about by episodic disturbances are needed. These interactions are influenced to some extent by climate but also by water management. Although relationships and patterns in water quality do not necessarily suggest cause-and-effect, it is clear that episodic disturbances are linked to temporal changes in TN and TP. To fully understand the magnitude, duration, and scale of disturbance effects, a more refined and targeted approach to water quality sampling is needed during or immediately following a pulsed or episodic event, perhaps including higher frequency sampling for inorganic nutrients (e.g., ammonium, soluble reactive P). Moreover, controlled experiments in the field or in mesocosms will enhance our understanding of source contributions (e.g., fish versus litter) and rates of change, as they pertain to disturbance effects on water quality.

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