

Landscape Pattern- Ridge, Slough, and Tree Island Mosaics (Cooperative Agreement #: W912HZ-15-2-0027) Cycle-2: Year 5 Report (2015-2020)



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General Background

The Water Resources Development Act (WRDA) of 2000 authorized the Comprehensive Everglades Restoration Plan (CERP) as a framework for modifications and operational changes to the Central and Southern Florida Project needed to restore the South Florida ecosystems. Provisions within WRDA 2000 provide for specific authorization for an adaptive assessment and monitoring program. A CERP Monitoring and Assessment Plan (MAP; RECOVER 2004, 2006, 2009) has been developed as the primary tool to assess the system-wide performance of the CERP by the Restoration Coordination and Verification (RECOVER) program. The MAP presents the monitoring and supporting research needed to measure the responses of the South Florida ecosystem to CERP implementation. In addition, the MAP also presents system-wide performance measures representative of the natural and human systems found in South Florida that will be evaluated to help determine CERP success.

The general goals of restoration are to stem, and possibly reverse the degradation of the ridge-slough-tree island landscape by redirecting flows to coastal waters across the surface of this landscape (USACE and SFWMD 1999). The CERP MAP, Parts 1 and 2, presented the overarching monitoring framework for guiding restoration efforts throughout the entire process (RECOVER 2004, 2006). This requires not only a comprehensive assessment of the current state of the ecosystem and assessment of restoration endpoints (targets), but also ongoing monitoring and evaluation throughout the process that will aid the implementing agencies in optimizing operational procedures and project designs. The work described below represents the system-wide landscape monitoring project, entitled *"Landscape Pattern - Ridge, Slough, and Tree Island Mosaics"*, initiated in 2009 with funding from US Army Corps of Engineers (USACE). Until 2012, the study was led by Dr. James Heffernan (PI), and then by Dr. Michael Ross for next three years (2012-2015). Since the Fall of 2015 (Cooperative Agreement # W912HZ-15-2-0027), the study has been led by Dr. Jay Sah (PI), while Dr. Michael Ross is also actively involved as the Co-PI, and Dr. James Heffernan (Duke University) is a collaborator in the study.

This monitoring effort supports the Greater Everglades Wetlands module of the MAP, and it is directly linked to the monitoring or research component identified in that module as number 3.1.3.6. The monitoring work is designed to address the needs identified in the Greater Everglades wetlands performance measures: (1) GE 15: Wetland Landscape Patterns – Ridge-Slough Community Sustainability, and 2) Total System Performance Measures - Slough Vegetation (RECOVER 2011). This study specifically addresses the Greater Everglades Wetland Landscape and Plant Community Dynamics hypotheses: (1) ridge and slough microtopography in relation to organic soil accretion and loss; (2) ridge and slough landscape pattern in relation to microtopography; and (3) plant community dynamics in ridge-slough peatlands along elevation gradients as water depths and hydroperiods change (RECOVER 2006). The working hypothesis is, 'Spatial patterning and topographic relief of ridges and sloughs are directly related to the volume, timing and distribution of sheet flow and related water depth patterns, identified in the hypothesis cluster, "Landscape Patterns of Ridge and Slough Peatlands and Adjacent Marl Prairies in Relation to Sheet Flow, Water Depth Patterns and Eutrophication" (RECOVER 2009).

The primary objective of this monitoring project is to assess the condition of landscapes within the Greater Everglades Wetlands ecosystem. This effort focuses on the condition of wetlands within the historic distribution of the ridge and slough (R&S) landscape, and provides baseline data needed to detect changes/trends in the patterns in microtopography and vegetation communities in response to water management operations, restoration initiatives and episodic events such as droughts, fire and hurricanes. The secondary objective is to integrate knowledge regarding landscape patterning, soil dynamics and community structure and composition with hydrologic data provided by Everglades Depth Estimation Network (EDEN) and other sources.

The specific objectives of the study are:

- To determine extant reference conditions for each of the performance measures described above (including variability of those measures in time and space).
- To establish present status of landscape performance measures throughout the central Everglades, particularly in areas of historic ridge-slough landscape patterning, identify spatial and temporal trends of those performance measures, and quantify their relationships to the present hydrologic regime.
- To detect unanticipated changes in ecosystem structure and processes that result from hydrologic management or manipulation, CERP restoration activities, or climatic variation.
- To provide data in support of scientific studies of inter-relationships among vegetation, microtopography, and hydrologic regime that may provide insight into the causes of unanticipated ecosystem responses.

The work provides indices of system-wide applicability related to the response of the ridgeslough landscape features to the restoration of historic hydrologic conditions, with the goal of informing the adaptive management of Everglades restoration as outlined in the CERP Monitoring and Assessment Plan.

This study takes advantage of the Generalized Random-Tessellation Stratified sampling network (GRTS), an established framework for representative sampling of the entire Everglades landscape (Philippi 2007). The sampling framework divides the Everglades landscape into a grid of 2x5 km landscape blocks (primary sample units; PSUs) of which the 5 km edge is aligned parallel to the historic water flow. Initially, a spatially stratified random sample of 80 PSUs were selected for sampling over a 5-year period (n=16 per year) (Philippi 2007; Heffernan et al. 2009). Those 80 PSUs were drawn to achieve a spatially balanced sample of the modern Everglades compartments (Everglades National Park (ENP), Water Conservation Area 3A North (WCA3AN), Water Conservation Area 3A South (WCA3AS), Water Conservation Area 3B (WCA3B), Water Conservation Area 2 (WCA2), and Water Conservation Area 1 (WCA1)/the Loxahatchee National Wildlife Refuge (LNWR). Sampling design was spatially balanced but was adjusted to have better representation of edges which are likely to change more rapidly than the interior. Also, the design was flexible enough to adjust the sampling rotation of 5-year to 4-year year period, if needed or to monitor certain attributes every 8 or 10 years instead of 4 or 5 years, especially if those are unlikely to change appreciably over short period (Philippi 2007).

Once the project was launched in 2009, after three years (2009-2011) of sampling, including the one during which only 4 PSUs were sampled as a pilot study, because of budget constraints since FY 2012 (Cycle-1, Year 3), the number of PSUs and the number of sites within each PSU sampled in successive years were adjusted. Some PSUs that either were not within the historic R&S landscape or were dominated by woody components were later dropped. During Years 3 and 4, monitoring efforts were also shifted to include additional PSUs or modified primary sample units (M-PSUs) outside the original sampling scheme, with the purpose of documenting pre-restoration reference conditions within wetlands influenced by the construction/ implementation of the DECOMP Physical Model and two Tamiami Bridges. Prior to making these changes, while there has not been any formal evaluation process to determine their consequences on ability to make interferences, it was believed that the retained PSUs cover most of historical R&S landscape and thus would not affect our ability to assess its system-wide condition over time.

Additionally, the monitoring within the modified sampling units (M-PSUs), would provide ecosystem responses to those specific projects over time, and thus would be useful for the adaptive management. Together with these modifications, over six years (2009-2015), including a pilot project year (2009), 67 PSUs were sampled. Among them, five PSUs were within the marl prairie landscape, and the rest were within ridge and slough landscape. These PSU's represent the full range of contemporary hydrologic regimes, and their vegetative and microtopographic structure range from well-conserved to severely degraded ridge and slough landscape (Ross et al. 2016).

During the Cycle-1 (2009-2015) of the project, monitoring efforts consisted of two core components: (1) mapping vegetation features from aerial photographs, and (2) ground surveys of water depth and plant community structure (in both tree islands and surrounding marsh). The data obtained during ground surveys were used to quantify aspects of the hydrologic regime and distribution and spatial structure of peat elevations, determine relationships between vegetation structure and water depth, and ground-truth broader-scale maps based on remote sensing and aerial surveys. While these activities were linked both logistically and analytically (Heffernan et al. 2009; Ross et al. 2013), ground sampling of tree island community was discontinued after the pilot phase (2009) and the first year (2010/2011) of the study, and the vegetation mapping was discontinued after the third year (2012/2013) of the study (Ross et al. 2015a,b, 2016).

With the initiation of the 2nd 5-year cycle (Cycle-2) of monitoring in 2015, the study plan focuses on resampling the plots within the previously sampled 62 PSUs. Five previously sampled PSUs within marl prairie landscape were not included in Cycle-2 sampling schedule. Since researchers have reported that prairie and marsh vegetation may change within 3-5 years in response to hydrologic changes (Armentano et al. 2006; Zweig and Kitchens 2008; Sah et al. 2014), re-sampling the plots 5 years after initial sampling provides an opportunity to assess changes in landscape pattern and plant composition over time. This document summarizes results for all five years (Year 1-5) of the 2nd five-year cycle (Cycle-2: 2015-2020). The report primarily focuses on the changes in metrics of topographic (distribution of soil elevation variance) and community characteristics (community distinctness and the strength of elevation-vegetation associations) between two surveys, Cycle-1 and Cycle-2.

1. Introduction

The Florida Everglades is a large subtropical wetland with diverse hydrologic, edaphic, and vegetative characteristics. Of the eight major historic landscapes that comprised the greater Everglades, the ridge and slough (R&S) landscape - a mosaic of sloughs, sawgrass ridges and tree islands - encompassed slightly over 50% of the total extent (McVoy et al. 2011). Within this landscape, biotic communities occupied distinct elevational niches that were organized in a characteristic elongated pattern parallel to water flow (Figure 1). Ridges, comprised almost entirely of dense stands of sawgrass, were present in areas of higher topographic relief with shallow water depths, whereas sloughs containing white water lily (*Nymphaea odorata*) and other macrophytes, were at lower elevation with relatively deep water (Loveless 1959, Ogden 2005, McVoy et al. 2011). A transitional community, the wet prairie, was comprised of *Eleocharis cellulosa* (spikerush), *Panicum hemitomon* (maidencane), and *Rhynchospora tracyi* (beakrush), and was usually present at the boundary of ridges and sloughs, in areas of intermediate water depths (Loveless 1959, Ogden 2005).



Figure 1: Aerial images and historic distribution of the ridge-slough landscape (Ross et al. 2013, 2016). (Left) Linear, flow-parallel orientation of ridges and sloughs (R&S) under conserved conditions. (Right) Distribution of R&S and other landscape types prior to major hydrologic alteration.

As in all wetlands, the hydrologic regime is a critical factor influencing the distribution and composition of vegetation in the greater Everglades (Gunderson 1994, Ross et al. 2003, Armentano et al. 2006, Zweig and Kitchens 2008, Todd et al. 2010). Local variation in hydrologic conditions resulting from microtopographic differentiation is essential for the maintenance of the distinct vegetation community boundaries that were a feature of the pre-drainage R&S landscape (Loveless 1959, Ogden 2005, McVoy et al. 2011). This landscape, however, has undergone dramatic structural, compositional and functional changes since human modification of the hydrologic regime began in the early 20th century (Davis and Ogden 1994, Ross et al. 2003, Ogden 2005, Bernhardt and Willard 2009, Larsen et al. 2011, McVoy et al. 2011, Nungesser 2011, Harvey et al. 2017). Where hydroperiods have been reduced, ridges have invaded marsh areas (Ogden 2005), and much of the slough component of the landscape has been usurped by both wet prairie and ridge (Davis and Ogden 1994, Olmsted and Armentano 1997, Richards et al. 2011). Woody vegetation might have been uncommon in the ridge community prior to hydrologic modification (Loveless 1959, McVoy et al. 2011), but wax myrtle (*Morella cerifera*) and coastal plain willow (*Salix caroliniana*) now frequently inhabit ridges in drained areas (McVoy et al. 2011).

Hydrologic modification, coupled with flow of phosphorus-enriched water into the system, also had consequences for the landscape-scale structure of the R&S mosaic (Figure 2). Areas of reduced flow have lost the elongated R&S topography, while areas with excessively extended flooding have experienced a decline in the prevalence of ridges and tree islands (Sklar et al. 2004, Ogden 2005). Remaining ridges have lost rigidity, structure, and directionality (or anisotropy; Wu et al. 2006, Watts et al. 2010; Ross et al. 2016), and elevation differences between ridges and sloughs have become less distinct (Figure 3; Watts et al. 2010, Hefferenan et al. 2009; Nungesser 2011; Ross et al. 2016). Moreover, nutrient enriched areas have become dominated by stands of *Typha* with little topographic relief (Urban et al. 1993; Newman et al. 1998).



Figure 2: Present configuration of the greater Everglades, and associated changes in ridge-slough structure (Ross et al. 2013, 2016). (Left) The contemporary Everglades, subdivided into distinct management basins subject to varied uses and management objectives. (Right top) Degraded R&S landscape in the area where hydrologic modification has reduced water levels and hydroperiod. (Right bottom) Degraded R&S landscape in the area where impoundment has raised water levels and lengthened hydroperiods.



Figure 3: Examples of conserved (top) and degraded (bottom) microtopographic structure. Conserved landscapes are characterized by high topographic heterogeneity and bimodal elevation distributions. Degraded landscapes have lost these characteristics (Source: Watts et al. 2010). Shadings indicate vegetation communities, and arrows indicate their median elevation. Solid line indicates best-fit model of density vs. elevation. Dashed line indicates probability of inundation over preceding 10 years at each elevation.

The characteristic R&S mosaic has been theorized to be a self-organized landscape maintained by autogenic processes that balance ridge expansion and slough persistence (Larsen et al. 2007, Givnish et al. 2008, Larsen and Harvey 2010, Watts et al. 2010, Cohen et al. 2011, Heffernan et al. 2013, Acharya et al. 2015). Decoupling of soil elevations from underlying bedrock topography in areas of relatively conserved landscape pattern suggests that historic microtopography and R&S landscape structure have arisen largely from internal feedbacks between vegetation, hydrology, and soil development. Whether local geologic features have acted as nucleation sites for ridge initiation remains unresolved. In either case, plant production provides raw material for the development of peat and may increase as soil elevation allows for high productivity of recalcitrant organic matter by sawgrass (Figure 4). Peat depth is maintained by deposition of root biomass, while peat is lost through aerobic respiration (Craft et al. 1995, Borkhataria et al. 2011). Ridges accumulate biomass faster than sloughs, but shallower water

depths promote more rapid decomposition that roughly balances higher gross peat production (Larsen and Harvey 2010, Cohen et al. 2011). The production-respiration equilibrium is regulated within both community types at nearly equal rates over long time periods, keeping ridges and sloughs from forming mountains and valleys. Vegetation shifts in microtopographic range when the hydrologic regime changes may help maintain plant zonation, and thus potentially feedback on microtopographic structure (Science Coordination Team 2003, Larsen and Harvey 2010, Cohen et al. 2011, D'Odorico et al. 2011). Zweig et al. (2018) suggest that once R&S pattern is established, decomposition is more important than production in maintaining the patterned microtopography and associated vegetation types in Everglades R&S landscape.



Figure 4: Conceptual model showing the relationships among causal factors such as soil microtopography, water regimes and disturbances (fire and nutrient enrichment) and vegetation dynamics within R&S landscape (Modified from Ross et al. (2006)).

The flow-parallel pattern of ridge and sloughs in the Everglades is believed to be the result of spatial feedbacks that act anisotropically (i.e., differently with direction) (Watts et al. 2010), and water flow is an important component of those feedbacks (Heffernan et al. 2013, Achraya et al. 2015, Harvey et al. 2017). However, the specific mechanisms that create flow-parallel ridges remain unresolved, as multiple plausible mechanisms have been suggested, including sediment entrainment and deposition (Larsen et al. 2007, Larsen and Harvey 2010), transpiration-driven nutrient concentration (Ross et al. 2006, Cheng et al. 2011), and hydrologic competence (Givnish et al. 2008, Watts et al. 2010, Cohen et al. 2011, Heffernan et al. 2013, Achraya et al. 2015, Harvey et al. 2017). While the relative importance of and interactions between these mechanisms remains an active area of research, study of pattern loss in response to hydrologic management, nutrient enrichment, and other disturbances suggests that the disruption of those feedbacks is a primary cause of R&S landscape degradation (Sklar et al. 2004).

The combination of microtopography, hydrology, vegetation composition and productivity, and their responses to hydrologic modification and other disturbances (fire and nutrient enrichment) create challenges in disentangling causal relationships and diagnosing trajectories of change. Therefore, one objective of this ongoing monitoring study has been to assess whether microtopographic structure, vegetation community composition, or relationships between these variables serve as leading indicators of pending change in other landscape characteristics. While it is known that altered microtopography affects vegetation structure after hydrologic modification (Ross et al. 2003, Givnish et al. 2008, Zweig and Kitchens 2008, 2009), vegetation changes may also influence microtopography (Cohen et al. 2011, Larsen et al. 2011, Casey et al. 2015, 2016). It has been hypothesized that topographic changes are more rapid than those of vegetation structure, especially in well-drained areas, primarily because drainage and stabilization of the Everglades hydrologic regime leads to more rapid peat loss through aerobic bacterial respiration and/or episodic fire events that consume the substantial peat materials in higher elevation ridges compared to sloughs, flattening landscape scale topography (Watts et al. 2010). Simultaneously, but over much longer timeframes, drained and stabilized hydrologic regimes facilitate ridge expansion into the more drained sloughs, resulting in vegetation structure homogeneity (Larsen and Harvey 2010).

A system-wide, simultaneous assessment of microtopographic structure and vegetation community composition over six years (2009-2015) suggests that while substantial portions of the R&S landscape are severely degraded (Heffernan et al. 2009, Ross et al. 2016), ground elevation changes often precede vegetation change during critical transitions from patterned to degraded landscape states in the drained landscapes (Figure 5, Scenario 1). In contrast, vegetation change

(reduction in vegetation distinctness) may serve as a leading indicator of landscape degradation in impounded conditions (Figure 5, Scenario 3; Ross et al. 2016). This degradation process is expected to slow down or even reverse as the result of restoration activities associated with Comprehensive Everglades Restoration Plan (CERP) that are in place. Nonetheless, the relative timescales of changing vegetation and topographic structure in R&S are not well understood yet.



Figure 5: Possible pathways of microtopographic and vegetative degradation in the ridge-slough landscape. In one scenario (uppermost arrow), topographic structure is reduced after modification of the hydrologic regime, followed by a lagged response from the vegetation structure. Alternatively, (lowermost arrow) vegetation patterning may degrade initially in response to modification of the hydrologic regime, followed by a lagged response of topographic patterning. Finally, (middle arrow) microtopographic flattening and vegetation homogenization may occur simultaneously, but both lag behind modification of the hydrologic regime (Source: Isherwood 2013).

In general, vegetation change in the Everglades occurs at different time scales. For instance, in the marl prairie of Taylor Slough, changes in the hydrologic regime over periods as brief as three to four years resulted in concurrent changes in vegetation composition (Armentano et al. 2006, Sah et al. 2014). In the R&S landscape within WCA3A, Zweig and Kitchens (2008, 2009) found that vegetation communities are influenced by both current and historic (up to four years) hydrologic conditions, though vegetation responses to hydrologic modification varied among species. Thus, the current system-wide monitoring of topographic structure and vegetation composition carried out at five-year intervals is expected to capture changes in the composition and spatial patterns of vegetation communities, and to some extent in microtopography, that occur as a result of water management operations, restoration initiatives, and episodic events such as droughts and fire within the Everglades R&S landscape.

2. Methods

2.1 Study Area

The study area includes the historical R&S landscape that currently exists in the Everglades. In general, the R&S landscape encompass the deeper central portion of the Everglades and is a peat-dominated system. This landscape, however, has undergone dramatic structural changes since human modification of the hydrologic regime began in the early 20th century. The most obvious outcome of these changes was the compartmentalization of the landscape into discrete management areas subjected to different water management, resulting in hydrologically independent systems that sharply differ in the hydrological conditions (Science Coordination Team 2003) (Figure 6). In many parts of these areas, prolonged flooding, drainage and/or phosphorus enrichment have led to the deterioration of the R&S landscape pattern (Larsen et al. 2011). Moreover, in some areas of the landscape, including northern WCA3A and WCA3B, widespread drainage has contributed to extreme losses in peat through both oxidation and peat-consuming fires (McVoy et al. 2011; Dreschel et al. 2018).

2.1.1 Water Conservation Areas (WCAs)

In the northern Everglades, Water Conservation Areas 1-3 (WCAs 1-3) are managed as compartments with varying water management strategies to hold water in order to augment water supply demand by the growing population along the east coast and Everglades National Park (Light and Dineen 1994). Among the WCAs, the northernmost one is WCA1, an enclosed area surrounded by canal dikes. The interior portion of this area is mainly fed by rainfall. The regulated water discharge from this area through control structures (S-10s) into WCA2 has caused deterioration of R&S landscape, and changed it from a sheet-flow-driven system to an impounded marsh dotted with tree islands (Brandt et al. 2000).



Figure 6: Study area showing the boundary of remaining ridge and slough landscape system (as mentioned in Ogden 2005), Water Conservation Areas (WCA 1-3) and Everglades National Park. Regions in the ENP and the WCAs were named following RECOVER (2020).

The WCA2, surrounded by levees and canal dikes, has two parts, WCA2A and WCA2B. In the mid- to late-20th century, these areas were impacted by different water management strategies (Light and Dineen 1994) resulting in the loss of typical R&S pattern. In addition, high phosphorus concentrations in water entering those areas have greatly contributed to the deterioration of landscape pattern. Currently, vegetation in WCA2A is a mosaic of sawgrass, cattails, wet prairies and willows with deep sloughs in some areas (Gann and Richards 2015), while WCA2B has relatively high percent of sloughs.

Among WCAs, the WCA3A is the largest unit, and has four indicator zones or hydrologic regions (northern, central, southern and L28-Gap; Figure 6) that are used by some hydrological models to make predictions (RECOVER 2020). These zones differ in hydrologic conditions. For instance, northern WCA3A (WCA3AN), bounded by I-75 to the south and L-38W canal to the east, has been over-drained in recent years. The central WCA3A (WCA3AC), bounded by I-75 to the north and the Miami Canal to the east, receives sheet flow from the Big Cypress region to the west via L28-Gap and through water control structures that connect it to the WCAs to the north and east. Surface water flows in WCA3AC are substantially lower than historic conditions and so are mean water levels (Science Coordination Team 2003, McVoy et al. 2011). In contrast, southern WCA3A (WCA3AS), bounded on the south by the Tamiami Trail, has pooled water north of the roadway levee and restricts the surface flow into the southern Everglades. In this area, impoundment has reduced the strong seasonal and multi-year differences in flow rates and volumes that once characterized the landscape. The impoundment in the WCA3AS and the relatively dry conditions in the upstream sections of the WCA3A have caused the fragmentation of ridges and loss of sloughs, respectively (Larsen et al. 2011, McVoy et al. 2011). Moreover, in the southern WCA3A, management-related highwater levels have also caused severe damage to tree islands. The WCA3B, separated from WCA3A by the L-67s canals is bounded on the east by L-30 and L-33 canal levees. WCA3B, experiences very little surface water flow, virtually making this a rainfed-system. The low water level together with negligible flow in this area has resulted in loss of sloughs and expansion of sawgrass ridges. In fact, this area has largely become a monoculture of sawgrass (Givnish et al. 2008). However, the recent changes, including Decompartmentalization Physical Model (DPM), to degrade some portions of the L-67 levees are underway to allow water flow from WCA3A to the WCA3B.

2.1.2 Shark River Slough (Everglades National Park, ENP)

Within ENP, the R&S landscape is mainly confined to the Shark River Slough (SRS) basin, on both sides of the L-67 Extension canal. Since the early 20th century, the water flow pattern through SRS has changed several times, mainly due to the changes in water management strategies. While the basin received unregulated water from the north as sheet flow before 1925 and through culverts under Tamiami Train during 1925-1960, this region received much less water during the 1960s and 1970s than in the past, resulting in over dryness and increased fire frequency in the area. Later, as plans were initiated for restoration and maintenance of natural Everglades ecosystems, a series of regulatory changes were made. For instance, since 1985, the water delivery to the SRS basin was regulated based on a Rainfall Plan based on rainfall, evaporation, and water level in WCA3A. After the early 2000s, some adjustments in the flow plan were made under the Interim Operation Plan (IOP) and Everglades Restoration Transition Plan (ERTP), but much of the water delivered until most recently remained concentrated west of the L-67 levee, away from its primary pre-development flow-way. These flow patterns resulted in a decrease in water level and flooding duration in the NESRS region while wetter conditions in northern and central SRS. Hence, over more than half century, the water flow regimes within the SRS have remained in deviance resulting in various degree of deterioration of R&S landscape in different regions. Under the recently adopted Combined Operation Plan (COP), water deliveries to the SRS are believed to improve, with an increase in flow to the NESRS (USACE 2020), which will have a significant impact on the R&S landscape.

2.2 Data Collection

This study uses a Generalized Random-Tessellation Stratified (GRTS) sampling network, an established framework for system-wide representative sampling within ENP and WCAs (Philippi 2007). The primary study design divides the Everglades landscape into a grid of 2x5 km landscape blocks (primary sample units, PSUs), of which the 5 km edge is aligned parallel to the historic water flow. Initially, a spatially stratified random sample of 80 PSUs were selected for sampling over a 5-year period (n=16 per year) (Philippi 2007, Heffernan et al. 2009) (Figure 7a). However, owing to budget constraints since FY 2012 (Cycle-1, Year-3), the number of PSUs and the number of sites within each PSUs sampled in successive years were adjusted. Some PSUs that either were not within the historic R&S landscape or were dominated by woody components were

eliminated, whereas several areas within the footprint of the DECOMP Physical Model (DPM), and two Tamiami Bridges (completed or under construction) were added, in the form of modified PSUs (M-PSUs). Elimination of PSUs from some areas might have affected the balanced design by causing under-sampling of those areas such as WCA1, WCA2, and the eastern and southern portions of ENP, but the adjustment was necessary owing to the changes in available budgets. Over six years, (2009-2015), including a pilot phase of the study (2009), 67 PSUs, were sampled (Figure 7b). However, detailed data analyses focused on 62 PSUs that were within the historic distribution of the R&S landscape, and five PSUs, located within the marl prairie landscape in the ENP were excluded from the analysis (Ross et al. 2016).



Figure 7: Map of PSUs for landscape sampling. (A) All 80 PSUs that were originally scheduled for sampling over five years (from Philippi 2007). (B) Sixty-seven, PSUs, including the modified ones within the footprint of DPM and downstream of the Tamiami bridges (completed or under construction) sampled over six years (2009-2015) (Modified from Ross et al. 2016). Colors indicate years for sampling of individual PSUs.

Over the 2015-2020 period, the 2nd 5-year monitoring cycle (Cycle-2), we sampled 58 PSUs: 11 in each of first two years, Years-1 and 2; 12 in Year-3 (2017/2018); 13 in Year-4 (2018/2019); and 11 in Year-5 (2019/2020) (Figure 8). Those PSUs were from ENP (14), WCA3AN (9), WCA3AC (11), WCA3AS (8), WCA3B (6), WCA2 (7), and the WCA1/LNWR

(3) (Table 1). Within the ENP, the sampled PSUs were from Northeast Shark River Slough or northern ENP (NESRS, hereafter 'ENP_N'), western region (ENP_W) and southern ENP (ENP_S). Regions in the ENP and the WCAs were named following RECOVER (2020) (Figure 8; Table 1).

Ten PSUs that were sampled in first two years of the first cycle (2009-2015) of the monitoring work were not sampled during Cycle-2. Those were either within the marl prairie landscape in the ENP (5) or in a recently burned area in WCA3AN (3). Likewise, two previously sampled PSUs, one each in WCA1 and WCA2, were also not re-sampled. In contrast, one PSU in WCA3AN that was not sampled in Cycle-1 because it had burned prior to sampling began was sampled for the first time in Year-4 of the current cycle. Moreover, in Cycle-1, two PSUs (PSU 50 and 54) and the Blue Shanty area within ENP were sampled in Year-5 and Year-4, but they were sampled in Year-4 and Year-5 of this cycle, respectively.



Figure 8: Map showing the PSUs sampled in Year 1-5 (2015-2020) of the current five-year cycle (2015-2020). Regions in the ENP and the WCA3A are according to RECOVER (2020).

PSU	Cycle	Cycle-2 Year	Cycle-1 Sampling Year (WYr)	Cycle-2 Sampling Year (WYr)	Cycle-2 Sampling date	Region*	Historical R&S	X_UTMNAD83	Y_UTMNAD83	Cycle-2 No. of plots
0	2	1	2012	2016	12/11, 12/14/2015; 03/11/2016	ENP_W	Y	532345.5	2842696.3	135
1	2	1	2010	2016	03/02, 03/04, 03/07/2016	WCA1	Y	566677.9	2942982.1	113
2	2	1	2010	2016	09/28, 09/30/2015	WCA3AS	Y	525056.6	2861614.1	129
3	2	1	2010	2016	02/23, 02/25/2016	WCA3AN	Y	532505.3	2910966.9	71
4	2	1	2010	2016	10/12, 11/02, 11/13/2015	WCA3AC	Y	530756.4	2872127.6	121
6	2	1	2010	2016	11/23, 11/25/2015	ENP_S	Y	519649.4	2814585.3	129
7	2	1	2010	2016	01/13, 01/25/2016	WCA3AN	Y	526262.4	2891226.1	135
9	2	1	2010	2016	02/08, 02/10/2016	WCA2A	Y	557549.6	2919280.2	120
11	2	1	2011	2016	01/08, 01/11/2016	WCA3AC	Y	546603.3	2893273.0	135
15	2	1	2011	2016	02/02, 02/03/2016	WCA3AC	Y	544263.6	2888174.1	135
108	2	1	2011	2016	10/02, 10/07/2015	WCA3B	Y	544130.1	2853456.0	117
17	2	2	2010	2017	11/07, 11/14/2016	WCA1	Y	575467.5	2927079.8	120
18	2	2	2011	2017	1/11/2017	ENP_W	Y	523582.5	2837739.8	42
19	2	2	2011	2018	07/26, 08/02/2017	WCA3AN	Y	532020.9	2901747.8	88
20	2	2	2011	2017	01/20, 01/23/2017	WCA3B	Y	541840.2	2858248.3	135
21	2	2	2010	2018	08/04, 08/07/2017	WCA2A	Y	560020.3	2904486.4	135
23	2	2	2012	2017	02/08, 02/10/2017	WCA3AC	Y	527209.6	2876687.7	132
24	2	2	2012	2017	12/19, 12/29/2016	ENP_N	Y	543033.6	2843539.1	130
26	2	2	2011	2017	01/30, 02/01/2017	WCA3AC	Y	519957.4	2866106.0	129
28	2	2	2011	2017	01/25, 01/27/2017	WCA3B	Y	547035.4	2863766.4	135
30	2	2	2012	2017	01/13, 01/18/2017	ENP_S	Y	525597.5	2882440.9	135
31	2	2	2012	2017	02/13, 02/15/2017	WCA3AC	Y	535763.3	2882440.9	135
32	2	3	2013	2018	01/29, 01/31/2018	ENP_N	Y	534894.8	2838347.8	134
34	2	3	2013	2018	11/22, 12/01/2017	WCA3AS	Y	530097.7	2852094.7	135
35	2	3	2013	2018	10/13/2017	WCA3AN	Y	523207.3	2905898.8	30
36	2	3	2013	2018	01/24, 01/26/2018	WCA3AS	Y	540859.6	2873130.6	126
37	2	3	2013	2018	10/09, 10/11/2017	WCA2A	Y	563108.3	2909792.2	111

Table 1: Characteristics of PSUs sampled in Year 1-5 of the current 5-year project cycle (2015-2020).

PSU	Cycle	Cycle-2 Year	Cycle-1 Sampling Year (WYr)	Cycle-2 Sampling Year (WYr)	Cycle-2 Sampling date	Region*	Historical R&S	X_UTMNAD83	Y_UTMNAD83	Cycle-2 No. of plots
39	2	3	2013	2018	10/16, 10/25, 10/27/2017	WCA3AN	Y	520196.3	2890623.0	135
43	2	3	2013	2018	09/25, 09/27/2017	WCA3AN	Y	539077.4	2897449.3	129
44	2	3	2013	2018	01/19, 01/22/2018	WCA3B	Y	545823.9	2858632.9	132
45	2	3	2013	2018	02/07, 02/09/2018	WCA3AS	Ν	550107.7	2883908.2	102
47	2	3	2013	2018, 2019	02/12, 02/14, 08/27/2018	WCA3AC	Y	540134.9	2887740.3	120
513	2	3	2013	2018	02/02, 02/05/2018	ENP_N	Y	547619.4	2846243.2	108
DPM	2	3	2013	2018, 2019	03/16, 03/19, 08/22, 08/24/2018	WCA3B	Y	538203.0	2858189.1	215
50	2	4	2015	2019	01/25, 01/28/2019	ENP_W	Y	528202.2	2833604.6	135
51	2	4	2014	2019	09/24, 09/26/2018	WCA3AN	Y	522037.9	2900773.4	135
52	2	4	2014	2019	02/08, 02/11/2019	WCA3AS	Y	532107.6	2852288.6	117
53	2	4	2014	2019	09/14, 09/17/2018	WCA2B	Y	563079.2	2894981.9	126
54	2	4	2015	2019	01/09, 01/14/2019	ENP_W	Y	517243.7	2825691.9	111
55	2	4	2014	2019	10/03, 10/05/2019	WCA3AC	Y	521064.6	2876059.2	129
56	2	4	2014	2019	11/21/2018; 01/11/2019	ENP_N	Y	538819.5	2843183.1	135
58	2	4	2014	2019	02/15, 02/18/2019	WCA3AS	Y	522023.7	2851319.8	117
59	2	4	-	2019	09/10, 09/12/2018	WCA3AN	Y	547146.9	2908234.8	135
61	2	4	2014	2019	09/05, 09/07/2018	WCA2A	Y	556317.0	2914142.6	129
62	2	4	2014	2019	01/16, 01/23/2019	ENP_S	Y	522506.2	2825415.4	135
63	2	4	2014	2019	10/26, 11/02/2018	WCA3AS	Y	543511.7	2878334.2	135
220	2	4	2014	2019	11/30/2018; 01/18/2019	WCA3B	Y	548070.8	2868866.4	126
65	2	5	2014	2020	08/23, 08/26, 11/25/2019	WCA1	Y	565318.4	2930799.6	122
66	2	5	2015	2020	08/28, 09/13/2019	WCA3AC	Y	523983.1	2866499.2	132
67	2	5	2014	2020, 2021	09/30/2019; 09/04, 09/05/2020	WCA3AN	Y	525201.9	2906093.8	132
68	2	5	2014	2020	09/16, 09/18/2019	WCA3AS	Y	535046.2	2862596.3	136
69	2	5	2014	2020	11/06, 11/08/2019	WCA2A	Y	567098.5	2910181.7	123
71	2	5	2014	2020	09/20, 09/23/2019	WCA3AC	Y	525747.1	2886258.6	126
73	2	5	2014	2020, 2021	11/27/2019; 09/11, 09/19/2020	WCA2A	Y	554872.2	2923975.3	135
79	2	5	2014	2020	09/25, 09/27/2019	WCA3AC	Y	542515.4	2892858.7	126
BS1	2	5	2013	2020	12/05, 12/11/2019	ENP_N	Y	535434.7	2848146.9	120

PSU	Cycle	Cycle-2 Year	Cycle-1 Sampling Year (WYr)	Cycle-2 Sampling Year (WYr)	Cycle-2 Sampling date	Region*	Historical R&S	X_UTMNAD83	Y_UTMNAD83	Cycle-2 No. of plots
BS2	2	5	2013	2020	11/15, 12/11, 12/14/2019	ENP_N	Y	535135.0	2846113.0	129
BS3	2	5	2013	2020	12/16, 12/27/2019	ENP_N	Y	535354.0	2844092.0	135

* ENP = Everglades National Park, WCA1 = Loxahatchee National Wildlife Refuge (Water Conservation Area 1), WCA 2 = Water Conservation Area 2, WCA3AN, S = Water Conservation Area 3A North and South, WCA3B = Water Conservation Area 3B. The suffix 'C', 'N', 'S' and 'W' after ENP and WCA3A represents central, northern, southern and western regions of those management areas (RECOVER 2020).

2.2.1 Field Survey

The approach for field sampling adopted during this study was the same as described in Ross et al. (2016). In the beginning of the first cycle of the study (2009-2015), the 2x5 km area in each PSU was subdivided in 80 equal area zones (250 m x 500 m) and a sampling cluster was located at a random location in those grid cells (Figure 9). At each cluster, samples were then collected using 1m² quadrat, placed at the center and at two randomly selected distances between 3 and 35 m in two cardinal directions, east and north. Thus, there were 240 sample quadrats in each PSU. However, after 2012 (i.e., after two years of study during the first cycle), the number of clusters for sampling was reduced to 45 clusters, resulting in maximum of 135 quadrats in each PSU, and they were located at a random location in 40 500 m x 500 m grid cells. Therefore, in Year-1 and 2 PSUs during the current cycle, we did not revisit all the 80 clusters that were previously sampled. Instead, we sampled the sites at a maximum of 45 clusters (i.e., 135 quadrats) in each PSU, resulting in a lower number of sampling quadrats during this study than in the Year-1 and 2 PSUs of Cycle-1. However, in each PSU over next three years (Year-3, 4 and 5) of the Cycle-2, the number of sampling quadrats were more or less the same as in Cycle-1.



Figure 9: Locations of sampling clusters (red dots) within 2x5 km primary sampling units (PSUs); the location of clusters within 500 x 500 m zone is assigned randomly. At each cluster, 3 sampling locations are visited; sites are situated at the center of each cluster, and at a random distance between 3 and 35 m in the direction of the PSU azimuth and in the orthogonal direction.

Within each quadrat, water depth was measured using a meter stick. Field training of sampling personnel ensured that a standardized amount of pressure was applied so that the measurement of water depth was uniform across time and space. Water depths were measured with a precision of 0.5 cm. In addition, we determined soil depth, i.e., depth to bedrock at each node, using 1 cm diameter metal rod. At some sites, however, the soil depth was much deeper than the metal rod we used, and thus we were not able to reach to bedrock. Soil depth at those sites was recorded as >160 and >270 cm, i.e., the effective length of the metal rod used at the time.

Vegetation characterization within each quadrat consisted of identifying all taxa present to species level and estimating the abundance of each species as percentage cover of the plot area, in either 1%, 5% or 10% intervals. Based on visual observation associated with these vegetation measurements, the vegetation within a 25 m radius of each sampling location was assigned to a community category (ridge, slough, tree island vegetation, wet prairie, and cattail). Where study site spanned a transition from one community type to another, we assigned points to mixed categories (e.g., ridge/wet prairie or transition). The field classifications of vegetation type were also adjusted so that they are better and more directly related to community classifications adopted by Rutchey et al. (2006) and Sah et al. (2010), and the types recently used in mapping from aerial imagery (Ruiz et al. 2017).

Field sampling of the ridge-slough landscape was done via airboat, during periods when sufficient water was present to obtain a reliable measure of water depth at all locations. As such, no dry weather sampling was conducted. For PSUs situated in Everglades National Park, sites were accessed by airboat or helicopter, as allowed by permitting and budgetary constraints.

2.2.2 Fire Data

To quantify fire occurrences within each PSU, we obtained fire data for the Park from 1948 to 2019 (Source: ENP), and for WCAs from 1997 to 2019 (Source: US Fish and Wildlife Commission), and a comprehensive fire history geodatabase detailing the location and attributes of fires was created. However, for consistency purposes, only fire data between the years 1997 and 2019 were used for both areas. The shapefiles for each year were merged into one fire history dataset, resulting in overlapping polygons from different years whilst maintaining the spatial integrity and attributes of all original fire data.

Fire frequency was calculated for every polygon in the fire history dataset. We started with the original vector files that contained data for fire occurrence in a single year only. A column was

created in each vector file (called count) and a number one (1) was entered for every record (row) in that vector file to indicate the presence of a fire event. All vector files from 1997 through 2019 were then joined together using the 'Union' command in ArcMap, which has the effect of combining overlapping polygons into singular polygons that contain the attributes of all source polygons. A column was created (frequency) within which the occurrences of fire were summed for each row to determine the number of fires that had occurred in that polygon between 1997 and 2019. The PSU vector layer was then used to extract the fire data that fell within each PSU boundary. The resulting vector layer was dissolved by PSU ID and fire frequency. Thereafter, using the information for fire frequency and percent of PSU area burned in each frequency category, for each PSU, we calculated Frequency*Area index (from here Fire Frequency Index or abbreviated as 'FF Index') using following expression:

$$FF \ Index = \frac{\sum_{1}^{i} (Area * Fire \ Frequency)}{Total \ Area \ of \ PSU}$$

Where, Area = the area with a particular fire frequency; i = Number of fires, (0, 1, 2, ...8)

2.3 Data analysis

2.3.1 *Site/Point Hydrology*

Since water depths in the field were measured over several months in different hydrological conditions, we established site hydrologic conditions by coupling our synoptic measurements of water depths with water surface elevation obtained from Everglades Depth Estimation Network (EDEN) based on the geographic location of PSU centroid. For each sampling point, we established a hydrologic history spanning from the day of sampling back to 1991, by benchmarking measured water depth and EDEN-estimated water elevation at the center point of each PSU. Because PSUs were not spatially situated to maximize proximity to sites where water level is directly recorded, we relied on spatially-interpolated EDEN water surfaces to estimate water depths on the day of sampling and to reconstruct point-scale hydrologic history. We evaluated the assumption of negligible water slope by examining relationships between UTM coordinates (easting, northing) and water elevation. For PSUs with significant relationships between water elevation and coordinates, we divided PSUs into 4 north-south bands and benchmarked points within each band to water elevations at the center point of that band.

To determine the particular hydrologic conditions at a site requires first that soil (ground) elevation be determined from EDEN estimates of water elevation on the day of sampling and water depths. Then, using the daily water surface elevation data, we calculated mean water depth and inundation frequency at each point over the preceding 0.25, 0.5, 1, 2, 5, 10, 20 and ca. 25-29 years (i.e., the complete hydrologic record). Because of strong correlation among these measures within PSUs, we used measures derived from 20-year hydrologic record as predictors of vegetative and microtopographic condition (Ross et al. 2016).

2.3.2 *Microtopography*

To assess microtopographic variation and hydrologic regime, we calculated summary statistics of soil elevation and water level, including mean, standard deviation, skew and kurtosis following Heffernan et al. (2009). Standard deviation of water level describes the temporal variability of water level, while standard deviation of water depth (or soil elevation) describes the magnitude of spatial variation in microtopography. To test for bimodality in the peat elevation distributions, we used the R package 'mclust' to assess goodness-of-fit between the observed histogram of peat elevations, and 1) a single normal, and 2) a mixture of two normal distributions:

$$P_s = N\left(\mu_{\rm i}, \, \sigma_{\rm i}\right) \tag{1}$$

$$P_{m} = q \cdot N(\mu_{l}, \sigma_{l}) + (1 - q) \cdot N(\mu_{2}, \sigma_{2})$$
(2)

where *q* represents the probability of falling within the first normal distribution, and *N* is a normal distribution with mean μ_i and standard deviation σ_i . Model goodness of fit was compared using Bayes' information criterion (BIC). The best-fit model was considered to have the lowest BIC score. Moreover, to evaluate how microtopographic structure responds to hydrologic regime, we examined the relationship between mean annual water depth and the elevation difference between modes of bimodal distributions, where present.

2.3.3 Vegetation structure and composition

In the R&S landscape, vegetation communities are generally separated in ridge and slough by clear topographic boundaries in areas with relatively well-maintained hydrologic regimes. However, as the hydrologic regime degrades, this patterning is lost. We assessed variation in community distinctness in response to hydrologic and topographic changes using dissimilarity between R&S vegetation community composition, defined as the distance (in multivariate space) between two vegetation clusters (Isherwood 2013). First, using the species cover data from all PSUs sampled over five years (Year 1-5) from the current cycles, we generated Nonmetric multidimensional scaling (NMDS) ordination plot. This single global NMDS ordination plot enabled us to 1) obtain a global estimate of the clustering of sampling points containing a set of species among all PSUs; and 2) standardize the among-PSU data. For the global NMDS ordination, we decided to retain five dimensions (5-d) solution as was done in analysing first two-years data of Cycle-1 (Ross et al. 2013) but differed from the four-dimension (4-d) solution used in analysis of five-year data by Ross et al. (2016). Each individual PSU was then isolated from the global NMDS ordination plot and coerced into two distinct clusters using k-means clustering. The sum of squares distance between the two cluster centres (BSS) based on their Voronoi sets was calculated for each PSU to obtain a test statistic that we used as a description of vegetation community distinctness (Isherwood 2013). A higher BSS value (greater distance between the two clusters) indicated a more distinct vegetation community structure, whereas more overlapping clusters (smaller BSS) would indicate less distinctness between sites, and a more degraded landscape structure (Isherwood 2013, Ross et al. 2013, 2016).

Since the sample points in ordination space were artificially grouped into only two clusters, rather than allowing them for multiple clusters, several approaches were used to assess the rationality of using R&S community distinctness (Isherwood 2013, Ross et al. 2013, 2016). Those included analysis of the distribution of key indicator taxa (*Cladium, Eleocharis, Nymphaea*, and *Utricularia* species) in the two global clusters, agreement between cluster assignments in the global analysis and within individual PSUs, analysis of the covariation among characteristic species of each community in NMDS space, and the distribution of sample points along individual axes of the global NMDS. The rationale for using these approaches and detailed interpretation is given in Isherwood (2013) and Ross et al. (2016). The global NMDS plot was created using the 'metaMDS' function in the *vegan* package (Oksanen et al. 2020). The dissimilarity matrix for the NMDS was calculated using the 'vegdist' function in *vegan* using the metric Jaccard index, as implemented in the analysis of first five years of the study (Ross et al. 2016). All the statistical analyses, including k-means clustering, were performed using the R program (R Core Team 2021).

Landscape scale co-variation between elevation and vegetation community composition was assessed by different metrics: bivariate regression between sawgrass abundance and elevation within each PSU, a Mantel test between matrices of between-site dissimilarities in elevation and in community composition, and the difference in elevation between points assigned to the two clusters in the k-means analysis (Isherwood 2013; Ross et al. 2016). This suite of measures provides a more integrated view of vegetative and microtopographic structure of R&S landscapes.

Diversity indices, including species richness, evenness, and beta diversity, were calculated at both plot and PSU level using PC-ORD v. 6.22 (McCune & Mefford 2011). We explored the relationship of species diversity indices with hydrology and fire variables by analysing the effects of LTMWD, standard deviation of mean long-term water depth and FF Index on species richness using Generalized Linear Models, and on beta diversity and evenness, both continuous variables, with General Linear Models. These analyses were run in R v.4.1.1 (R core team 2021).

Finally, we examined the changes in both topographic and community metrics between Cycle-1 and Cycle-2 across all the study PSUs, and assessed the relationship between those changes and hydrologic conditions and FF Index using both linear and non-linear regressions.

3. Results

3.1 Hydrologic conditions & Microtopography

In the PSUs sampled during 2015-2020, long-term mean water depth (LTMWD: averaged over all points sampled within each PSU) varied from 10.1 cm in PSU-3 to 93.2 cm in PSU-45. The lowest water depths were in units within the northern water conservation area 3A (WCA3AN), whereas moderately-high to high water depths were in southern, central and northeastern portions of WCA 3A. (Table 2; Figure 10). In these PSUs, LTMWD was reasonably consistent across cycles (n = 56; r = 0.91; p < 0.001), with few exceptions (Figure 11). One was the DPM area, which had the highest difference (30.5 cm) in LTMWD between the two sampling periods. In this PSU, the value of LTMWD during the Cycle-2 was lower than in the Cycle-1. In general, there was a slight bias toward greater depths in Cycle-2, though 64% of PSUs differed by < 4 cm, while less than one-fifth of PSUs had differences >8 cm (Figures 11, 12). There was no consistent pattern across the regions. Difference in LTMWD between periods was small in WCA3AC (RMSE = 3.6 cm), while the PSUs in WCA3B had the highest difference (RMSE = 12.7 cm) in LTMWD between two periods. Eight PSUs (one in each of 4 regions, WCA3AN, WCA3AS, WCA3B and ENP, and 4 PSUs in WCA2) had relatively high (>10 cm) differences in water depth (Figure 13).

Table 2: Hydrologic and microtopographic characteristics of Cycle-2 Year 1-5 PSUs. Additional hydrologic descriptors at the p	point scale are included in data
reports for each PSU.	

Water Elevation Statistics Elevation Cluster Analysis										nalysis						
P50-	·identiii		Water H	Elevation		Peat	Surface			Mode 1			Mode 2		*Best Model	Notes
PSU	Cycle	Cycle-2 Year	Mean (cm asl)	[§] St. Dev. (cm)	MWD (cm)	[†] SD (cm)	Kurtosis	Skew	Depth (cm)	[†] St. Dev. (cm)	^{††} Mode Wt (q)	Depth (cm asl)	[†] St. Dev. (cm)	^{††} Mode Wt (q)	wiouei	
0	2	1	181.18	25.03	39.92	7.47	0.02	0.34	39.92	7.44	1.00	-	-	-	1	Large difference in WD on DoS b/w Cy1 and Cy2 ; delta EV for 2E is similar to cycle 1 (~10 cm)
1	2	1	450.58	15.84	17.47	5.39	0.33	0.35	17.47	5.37	1.00	-	-	-	1	
2	2	1	253.15	23.68	52.60	8.78	-0.51	-0.57	42.69	4.89	0.35	57.91	4.89	0.65	2E	
3	2	1	304.62	24.21	10.10	4.22	0.19	-1.00	6.32	1.94	0.49	13.75	1.94	0.51	2E	
4	2	1	261.20	25.18	41.39	11.30	-0.45	1.13	34.50	5.04	0.64	52.53	5.04	0.36	2E	
6	2	1	34.98	21.67	37.21	5.12	-0.84	1.52	23.98	4.11	0.05	37.90	4.11	0.95	2E	q<0.25
7	2	1	286.24	21.53	35.02	6.27	-0.07	-0.97	29.80	3.65	0.49	39.95	3.65	0.52	2E	
9	2	1	355.74	24.20	14.91	9.15	0.26	-1.08	8.75	4.99	0.61	24.36	4.99	0.39	2E	HUGE difference in MWE on (DoS); N-S gradient in WD
11	2	1	269.81	31.68	58.66	9.52	0.76	0.86	58.66	9.49	1.00	-	-	-	1	-
15	2	1	269.48	30.87	79.47	8.71	-0.22	-0.04	79.47	8.67	1.00	-	-	-	1	q<0.25
108	2	1	176.72	22.22	31.30	5.20	-0.05	-0.70	31.30	5.18	1.00	-	-	-	1	q<0.25
17	2	2	448.71	19.36	32.14	11.28	0.54	-0.31	26.77	7.14	0.72	46.14	7.14	0.28	2E	
18	2	2	153.50	24.13	34.11	4.32	-0.68	-0.04	34.11	4.26	1.00	-	-	-	1	limited sampling
19	2	2	288.90	21.92	22.51	9.16	0.83	1.27	12.70	1.74	0.24	25.53	8.28	0.77	2V	
20	2	2	184.98	15.45	32.54	4.69	-1.24	2.97	18.71	3.56	0.05	33.21	3.56	0.95	2E	q<0.25
21	2	2	328.88	28.14	53.55	14.98	0.79	-0.03	43.49	4.43	0.42	60.76	15.61	0.58	2V	HUGE difference in MWE DoS; delta EV for 2E is similar to cycle 1 (~11 cm)
23	2	2	265.42	21.72	33.25	10.73	-0.23	-1.21	25.09	6.82	0.56	43.45	3.43	0.44	2V	
24	2	2	157.84	20.54	33.36	6.19	-1.04	2.00	12.24	5.18	0.02	33.89	5.18	0.98	2E	q<0.25
26	2	2	259.57	23.97	44.91	9.64	-0.09	-0.95	36.26	5.46	0.46	52.13	5.46	0.55	2E	
28	2	2	186.44	17.46	36.44	4.64	-0.86	1.16	25.35	3.50	0.07	37.26	3.50	0.93	2E	q<0.25
30	2	2	124.75	20.66	30.96	8.70	-0.18	-0.27	30.96	8.67	1.00	-	-	-	1	
31	2	2	267.94	26.07	38.08	11.77	0.46	-0.39	38.08	11.72	1.00	-	-	-	1	

PSU-Identification				Wate	r Elevati	on Stat	istics			El	evation C	luster A				
150-	Iucitiii		Water Elevation			Peat	Surface			Mode 1	!		Mode 2		*Best Model	Notes
PSU	Cycle	Cycle-2	Mean	[§] St. Dev.	MWD	†SD	Kurtosis	Skew	Depth	[†] St. Dev.	††Mode	Depth	[†] St. Dev.	^{††} Mode	WIUUCI	
		Year	(cm asl)	(cm)	(cm)	(cm)			(cm)	(cm)	Wt (q)	(cm asl)	(cm)	Wt (q)		
32	2	3	161.18	19.39	34.72	7.68	-0.80	0.31	20.63	5.18	0.14	36.97	5.18	0.86	2E	q<0.25
34	2	3	246.74	22.59	52.51	16.76	-1.36	7.95	33.46	45.39	0.07	53.93	10.78	0.93	2V	q<0.25
35	2	3	312.55	22.61	11.85	4.61	-0.29	-0.28	11.85	4.53	1.00	-	-	-	1	
36	2	3	256.30	29.81	79.61	9.85	-0.83	0.18	73.44	9.22	0.53	86.68	3.94	0.47	2V	
37	2	3	337.56	23.88	30.98	9.53	1.28	1.86	28.26	6.13	0.88	50.28	6.13	0.12	2E	q<0.25
39	2	3	290.60	23.36	20.93	6.41	-0.09	-0.82	20.93	6.38	1.00	-	-	-	1	
43	2	3	276.30	25.63	27.69	4.06	-1.02	3.36	17.78	3.42	0.05	28.16	3.42	0.96	2E	q<0.25
44	2	3	179.99	18.78	31.21	4.93	-0.70	0.60	31.21	4.91	1.00	-	-	-	1	
45	2	3	264.38	33.98	93.18	9.15	-0.49	0.44	93.18	9.09	1.00	-	-	-	1	
47	2	3	271.84	28.35	53.44	18.47	0.90	-0.53	45.16	8.74	0.80	86.56	2.99	0.20	2V	q<0.25
513	2	3	155.29	23.46	30.68	4.27	-0.57	0.49	30.68	4.25	1.00	-	-	-	1	
DPM	2	3	187.21	14.63	35.45	12.08	-0.02	-0.61	26.33	6.91	0.54	46.14	6.91	0.46	2E	
50	2	4	149.40	19.04	33.27	10.63	0.35	-0.51	33.27	10.59	1.00	-	-	-	1	
51	2	4	302.23	22.76	16.92	6.24	0.22	-0.10	16.92	6.22	1.00	-	-	-	1	
52	2	4	242.07	24.85	51.93	17.33	1.67	3.64	47.49	10.39	0.91	94.56	10.39	0.094	2E	q<0.25
53	2	4	257.92	28.61	59.99	16.33	-0.12	-0.30	43.50	9.83	0.38	70.17	9.83	0.618	2E	
54	2	4	79.37	19.30	28.15	7.50	-0.13	-0.45	28.15	7.47	1.00	-	-	-	1	
55	2	4	267.47	20.93	37.57	10.26	-0.25	-0.57	37.57	10.22	1.00	-	-	-	1	
56	2	4	163.67	17.85	35.99	8.50	1.94	7.81	34.56	5.54	0.94	56.43	14.5	0.065	2V	q<0.25
58	2	4	244.45	22.47	56.21	12.63	-0.45	-0.26	56.21	12.57	1.00	-	-	-	1	
59	2	4	273.95	33.93	13.54	4.59	0.37	1.04	13.54	4.57	1.00	-	-	-	1	
61	2	4	344.53	21.10	25.03	6.62	-0.29	0.06	25.03	6.59	1.00	-	-	-	1	
62	2	4	100.32	20.11	29.65	7.94	-0.26	-0.53	20.39	4.87	0.31	33.85	4.87	0.688	2E	
63	2	4	258.99	30.74	77.46	7.69	-0.47	0.58	77.46	7.66	1.00	-	-	-	1	
220	2	4	187.27	16.85	34.07	3.67	-0.17	-0.45	34.07	3.66	1.00	-	-	-	1	
65	2	5	455.27	14.97	30.45	12.28	-0.53	0.30	17.25	3.42	0.343	37.3	9.1	0.657	2V	
66	2	5	257.31	23.81	43.90	11.28	-1.32	-0.02	36.84	7.27	0.64	56.47	3.24	0.35944	2V	
67	2	5	306.87	20.92	10.20	7.09	6.05	0.51	7.82	4.08	0.25	10.99	11.87	0.75	2V	q<0.25
68	2	5	250.98	26.84	67.93	12.27	-0.27	-0.66	51.83	7.48	0.26	73.74	7.48	0.74	2E	q<0.25
69	2	5	338.33	25.24	34.55	9.22	2.15	0.78	32.91	7.19	0.92	54.53	7.19	0.80	2E	q<0.25
71	2	5	278.52	21.60	33.24	7.80	-0.77	-0.41	24.54	4.24	0.36	38.11	4.24	0.64	2E	

DSU Identification				Wate	r Elevati	on Stat	istics		Elevation Cluster Analysis							
PSU-Identification		Water E	Elevation	Peat Surface					Mode 1			Mode 2			Notes	
PSU	Cycle	Cycle-2	Mean	[§] St. Dev.	MWD	†SD	Kurtosis	Skew	Depth	[†] St. Dev.	††Mode	Depth	[†] St. Dev.	††Mode	litiouci	
		Year	(cm asl)	(cm)	(cm)	(cm)			(cm)	(cm)	Wt (q)	(cm asl)	(cm)	Wt (q)		
73	2	5	366.41	26.65	37.80	18.97	0.70	1.19	28.02	4.25	0.57	52.84	20.4	0.43	2V	
79	2	5	272.42	28.49	43.51	6.02	-0.53	0.47	40.41	3.57	0.71	50.99	3.57	0.29	2E	
BS1	2	5	169.99	18.13	28.20	7.13	0.19	0.12	28.2	7.1	1	-	-	0	1	
BS2	2	5	169.07	18.12	30.78	10.05	3.74	1.34	29.8	8.14	0.97	65.99	8.14	0.03	2E	q<0.25
BS3	2	5	167.91	17.89	33.86	9.19	0.42	-0.33	33.85	9.15	1	-	-	0	1	

[§]Standard Deviation of water elevation describes the temporal variability of water level at the centre point of each PSU.

*Standard Deviation of water depth describes the spatial variability of soil elevation across all points sampled within each PSU.

^{††} Mode weight describes the proportion of data that occur within each mode, allowing for imbalance in mode prevalence

* Best fit model selected based on Bayes' Information Criterion; number refers to the number of modes, E and V denote whether variances of the two modes are equal (E) or unequal (V). Where the best fit model included more than 2 modes, data presented are from the best fit model among 1 and 2 mode models.

'q' represents the weight of the modes of water depth (or soil elevation), and so reflects the relative prevalence of the high- and low-elevation points within the landscape. When q<0.25 was in any of two modes, unimodal distribution is preferred (see Table 3).



Figure 10: Spatial patterns in Long-term (20+ years average) mean water depth (LTMWD) in 58 PSUs sampled over five years (Year 1-5; 2015-2020) of the current five-year cycle.



Figure 11: Relationship between long-term mean water depth (cm) in PSUs between Cycle-1 and Cycle-2.



Figure 12: Number of PSUs with a range of difference in long-term mean water depth between Cycle-1 and Cycle-2. About 71% of 45 PSUs sampled over five years (Year 1-5) had < 4 cm difference in water depth. Among 58 PSUs sampled over five years, PSU-35 was not included in analysis, and PSU-59 was sampled only in Cycle-2.

The magnitude and structure of microtopographic relief also varied considerably among 58 PSUs (Table 2; Figures 13-15). Standard deviations of soil elevation (water depth) ranged from 3.7 to 19.0 cm (Table 2), with most values falling between 5.0 and 10.0 cm (Figure 13). As reported in Ross et al. (2016) for PSUs sampled during Cycle-1, the magnitude of topographic relief during Cycle-2 was generally highest in PSUs in the central WCA3A. In contrast, PSU 220 in WCA3B had the least topographic relief.



Figure 13: Spatial patterns of elevation variance across historic ridge-slough landscape represented 58 PSUs sampled over four years (Year 1-5: 2015-2020) of Cycle-2. Colours indicate the amount of microtopographic relief (measured as the standard deviation of elevation within each PSU).

The standard deviation of LTMWD, which reflects variation in soil elevation, was correlated (r = 0.83) across cycles, but with higher uncertainty in Cycle-2 (Figure 14), and with a strong bias toward greater variability in Cycle-2. Uncertainty in microtopographic variation was tied to hydrologic conditions at the time of sampling, and differences in microtopography between cycles were greatest when the sites were sampled under very different hydrologic conditions. For instance, even though the number of PSUs with bimodal distribution in soil elevation (water depth) was equal in both Cycle-2 and Cycle-1 (19 PSUs) (Table 3), wet conditions during Cycle-2 may have inflated standard deviation of water depths of some PSUs (Table 2).



Figure 14: Relationship between microtopography variation (long-term water depth standard deviation (cm)) in 56 PSUs between Cycle-1 and Cycle-2. PSU-35 was not included in analysis, and PSU-59 was sampled only in Cycle-2.
In general, more PSUs exhibited statistically significant bimodality in Cycle-2 than was observed in Cycle-1 (Table 2). However, more PSUs in Cycle-2 had also the q<0.25 or >0.75 than in Cycle-1. The parameter q represents the weight of the modes of water depth (or soil elevation), and so reflects the relative prevalence of the high- and low-elevation points within the landscape. Because the historic and conserved ridge-slough landscape has an approximately equal proportion of ridges and sloughs (McVoy et al. 2011), the PSUs with q<0.25 or >0.75 were not considered to exhibit conserved microtopography, even if water depth distributions were best fit statistically with a bimodal rather than a unimodal model. When the PSUs with q<0.25 or >0.75 were discounted, almost equal number of PSUs had the bimodality fit in both cycles (Table 3). However, the PSUs with b-modality fit were not all the same in both Cycles. Only twelve of nineteen PSUs in which strong bimodality was observed during Cycle-2 sampling also had conserved topography in Cycle-1 (Table 3). These include PSUs 4, 23, 26, 66 and 71, all located within the WCA3AC, as well as PSU 17 in WCA1, 3 and 19 in WCA3AN, and three PSUs (21, 53 and 73) in WCA2. The DECOMP PSU (DPM) had the greatest elevation separation between ridges and sloughs in Cycle-1, and was again found to have bimodal soil elevations with an elevation difference of about 20 cm. In seven PSUs bimodality that was not detected in Cycle-1 was present in Cycle-2. Among PSUs in which bimodality was detected in both cycles, elevation differences between the modes were similar in both, generally around 15-25 cm.

Four PSUs (PSUs 0, 18, 54 and BS1) within ENP that had bimodal soil elevations in Cycle-1 did not have statistically detectable bimodality during Cycle-2. All these have microtopographic variation of <10 cm (Table 2; Figure 13). Other PSUs in which previous bimodality was not detected include PSU 39 (WCA3AN), PSU 108 (WCA3B), and PSU 37 (WCA2). These PSUs in which bimodality was observed initially but not in the subsequent cycle generally had relatively small mode elevation differences (5-13 cm) during Cycle-1. Among the seven PSUs that had bimodal soil elevations in Cycle-2, after exhibiting a unimodal distribution in Cycle-1, one PSU had the observed Cycle-2 elevation difference of ~20 cm, while the rest six PSUs had of the elevation difference between 10 and 15 cm. In contrast, PSUs 37 and 39, located in WCA3AS and WCA2, respectively, were not shown to have bimodal distributions in Cycle-2, after exhibiting bimodal soil elevation distributions in Cycle-1. In both cases, statistical distributions were best fit by 3 modes (data not shown), rather than 1 or 2, indicating microtopographic structure that deviates from the simple conceptual model of ridges and sloughs.



Figure 15a: Soil elevation (SD of water depth) distributions in PSUs sampled over five years (2015-2020) in different regions of the WCAs. Bimodality and high variability in elevation (e.g., PSU 4 in WCA3AC) are characteristics of relatively conserved conditions, while low variability and unimodality (e.g., PSU 43 in WCA3AN) are characteristics of degraded conditions. PSUs are grouped by regions, defined in Table 1.



Figure 15b: Soil elevation (SD of water depth) distributions in PSUs sampled over five years (2015-2020) in different regions of the ENP. Bimodality and high variability in elevation (e.g., PSU 54 in ENP_S) are characteristics of relatively conserved conditions, while low variability and unimodality (e.g., PSU 56) are characteristics of degraded conditions. PSUs are grouped by regions, defined in Table 1.

	Area [†]	С	ycle-1***	Cycle-2		
PSU		Bimodal in Cycle-1?	Elevation Difference between two modes (cm)	Bimodal in Cycle-2?	Elevation Difference between two modes (cm)	
0	ENP_W	Yes	11.61	No†	-	
1	WCA1	No	-	No	-	
2	WCA3AS	No*	-	Yes	15.10	
3	WCA3AN	Yes	5.78	Yes	7.43	
4	WCA3AC	Yes	20.08	Yes	18.04	
6	ENP_S	No	-	No*	-	
7	WCA3AN	No	-	Yes	10.15	
9	WCA2	No	-	No†	15.61	
11	WCA3AC	No	-	No	-	
15	WCA3AC	No	-	No	-	
108	WCA3B	Yes	12.35	No	-	
17	WCA1	Yes	12.72	Yes	19.13	
18	ENP_W	Yes	12.25	No	-	
19	WCA3AN	Yes	13.59	Yes	13.34	
20	WCA3B	No*	-	No*	-	
21	WCA2	Yes	16.10	Yes†	17.76	
23	WCA3AC	Yes	18.31	Yes	18.36	
24	ENP N	No	-	No*	-	
26	WCA3AC	Yes	18.17	Yes	15.87	
28	WCA3B	No	-	No*	-	
30	ENP S	No	-	No	-	
31	WCA3AC	No	-	No	-	
32	ENP N	No	-	No*	-	
34	WCA3AS	No	-	No*	-	
35	WCA3AN	No	_	No	_	
36	WCA3AS	No*	-	Yes	13.24	
37	WCA2	Yes	16.86	No*		
39	WCA3AN	Yes	9.91	No	-	
43	WCA3AN	No	-	No*	-	
44	WCA3B	No*	-	No	-	
45	WCA3AS	No*	_	No	_	
47	WCA3AC	No	-	No*	-	
513	ENP N	No	_	No	_	
DPM	WCA3B	Yes	23 44	Yes	19.81	
50	FNP W	No	-	No	-	
51	WCA3AN	No	_	No	_	
52	WCA3AS	No*	-	No*	-	
53	WCA2	Yes	22.88	Ves	26.67	
54	FNP W	Yes	13 69	No	-	
55	WCA3AC	No*	-	No	-	
55	FNP N	No		No*		
58	WCA3AG	No	-	No	-	
50**	WCA3AN	110	-	140	-	
61	WCA?	No*	-	No	-	
62	ENP S	No	-	Yes	13.46	

Table 3: Summary of difference in mean elevation (water depth) between two modes for the PSUs, which were sampled during both Cycle-1 and Cycl-2.

		C	ycle-1***	Cycle-2		
PSU	Area [†]	Bimodal in Cycle-1?	Elevation Difference between two modes (cm)	Bimodal in Cycle-2?	Elevation Difference between two modes (cm)	
63	WCA3AS	No*	-	No	-	
220	WCA3B	No	-	No	-	
65	WCA1	No	-	Yes	20.05	
66	WCA3AC	Yes	18.73	Yes	19.63	
67	WCA3AN	No	-	No*	-	
68	WCA3AS	No	-	No*	-	
69	WCA2	No	-	No*	-	
71	WCA3AC	Yes	12.73	Yes	13.57	
73	WCA2	Yes	54.16	Yes	24.82	
79	WCA3AC	No	-	Yes	10.57	
BS1	ENP_N	Yes	0.77	No	-	
BS2	ENP_N	No	-	No*	-	
BS3	ENP N	No	-	No	-	

* indicates high unevenness in cluster weight (q<0.25 was in any of two modes: See Table 2), on which basis a unimodal model was deemed the more appropriate fit.

** this PSU was not sampled in Cycle-1.

*** Cycle-1 information is based on (Ross et al. 2016)

† Indicates large differences in Water Surface Elevation on Day of Sampling between cycles 1 and 2. Results should be interpreted cautiously.

'-' Not available, as unimodal fit was considered more appropriate fit.

3.2 Fire frequency and time since last fire

Fire is an integral component of Everglades ecosystem, including the R&S landscape. An analysis of fire frequency within the studied PSUs revealed that burn frequency across the landscape was not consistent. For instance, between 1997 and 2019, while 47 of 58 PSUs, burned at least once in part or whole, 11 PSUs did not burn. The unburned PSUs were mostly in WCA1 and WCA3S (Figure 16). In contrast, in WCA3AN and northern portion of WCA2A, R&S landscape burned more frequently than the landscape in other management areas. Likewise, total burned area varied among PSUs, and it ranged between 0 and 100%. The PSUs with highest percent of burned area were in WCA3AN, WCA3B and ENP_N (Figure 16, Appendix 1). In these regions, >80% of area within each PSU had burned at least once. The results are not surprising as these are the areas within the Everglades that had been relatively dry in recent decades.

The FF Index that combines the areas burned with different frequencies within each PSU was negatively correlated with long-term mean water depth (Figure 17). PSUs with LTWD between 25 and 50 cm had wide range of FF Index, whereas the PSUs with impounded water (LTWD > 55 cm), mostly within southern WCA3A had the lowest index value. Since most PSUs had burned multiple times, surveyed plots within a PSU, differ in time since last fire (TSLF).



Figure 16: Fire frequency (# of fires/decade) in the sampled PSUs. Fire frequency for the PSUs in both ENP and WCAs was calculated using fire data for 23 years (1997-2019).



Figure 17: Relationship between long-term mean water depth (LTMWD) and fire frequency index for all PSUs grouped by region.

3.3 Soil depth

Soil depth varied greatly among PSUs throughout the R&S landscape. Mean (\pm SD) soil depth ranged between 32.9 (\pm 14.9) cm in PSU 18 and 312 (\pm 26.7) cm in PSU 65. In general, soils are much deeper in WCA1 (LNWR) than in other areas, whereas most of PSUs in northern WCA3A had shallow soil depths (Figure 18; Appendix 2).



Figure 18: Spatial patterns of mean soil depth in 58 PSUs surveyed over five years (Year 1-5) of Cycle-2.

Mean (\pm SD) soil depth in WCA1 was 260.3 (\pm 54.9) cm, and the values were relatively uniform across all PSUs within that region. In WCA2, the mean soil depth was 155.0 (\pm 52.2) cm, and the depths decreased from north to south. In contrast, within WCA3A, soil depths increased from north to south. The mean depths in WCA3AN, WCA3AC and WCA3AS were 67.2 (\pm 49.4)

cm, 99.3 (\pm 33.1) cm and 108.1 (\pm 47.8) cm, respectively. While the mean soil depth in WCA3B was relatively high (128.7 \pm 38.0), the values were lower in different regions of ENP than other regions, except WCA3AN. Within the PSUs of ENP, the mean soil depths were 75.9 (\pm 39.6) cm, 78.4 (\pm 44.4) cm and 61.3 (\pm 32.5) in ENP_N, ENP_S and ENP_W, respectively. Across all the studied PSUs, soil depths did not have a significant relationship with LTMWD and FF Index, suggesting that within the existing R&S landscape, soil depths are not only the result of recent ecological processes, but they also represent the historical legacy.

3.4 Vegetation characteristics

3.4.1 Vegetation composition and community distinctness

Vegetation composition varied greatly within and across the PSUs sampled over five years (2015-2020) of Cycle-2 (Table 4). The abundance of major taxa followed expected trends with water depth at the scale of system-wide PSUs, a pattern that was also observed in Cycle-1 (Figure 19). The mean percent cover of sawgrass was the highest in PSUs with lower long-term mean water depth, while the characteristic species of sloughs, water lily and bladderworts (Nymphaea odorata and Utricularia spp.) were most abundant in PSUs with high long-term mean water depths. Sawgrass showed high variability in relative cover at low to intermediate water depths, while its mean cover sharply declined when mean water exceeded 50 cm (Figure 19a). Spikerush (Eleocharis spp.) were most abundant in PSUs with intermediate water depths (Figure 19b). Relative cover of major species across PSUs were fairly correlated between Cycle-1 and Cycle-2. However, percent cover of three major taxa, sawgrass, spikerush and waterlily were higher in Cycle-2 than Cycle-1 (Figure 20). In contrast, relative cover of bladderworts (Utricularia spp.) decreased in five years. Shift in relative cover of major taxa followed a pattern. For instance, relative cover of sawgrass in twelve PSUs (2 in WCA3AN, 4 in WCA3B, including DPM, and 6 in ENP) was >30% higher in Cycle-2 than Cycle-1. In contrast, PSUs in WCA3AS, had much less increase in sawgrass cover, whereas in one PSU in this region, sawgrass cover decreased over the period. In three PSUs in WCA3AN and one in LNWR, sawgrass relative cover decreased by >15%. The relative cover of sawgrass in one PSU (PSU45) in WCA3AN decreased by 42% over 5 years.

PSU-Identification			Vegetation cl	naracteristics		Vegetation composition-Elevation Relationships				
			Species M	Iean Relative C	over (%)	Community	k-means WD		\mathbf{r}^2	
PSU	Cycle	Cycle (Year)	Cladium jamaicense	Nymphaea spp.	Utricularia spp.	Eleocharis spp.	Distinctness (cluster distance)	difference (cm)	Mantel's r	Cladium- WD
0	2	1	62.68	0.70	9.13	16.05	0.642	10.9	0.244	0.2030
1	2	1	17.23	11.71	35.45	4.94	0.524	18.7	0.244	0.4182
2	2	1	34.03	40.64	10.47	7.90	1.143	13.7	0.532	0.5528
3	2	1	70.56	0.00	0.00	0.00	0.594	2.1	0.121	0.0248
4	2	1	41.80	32.52	8.17	7.31	1.209	14.1	0.498	0.3150
6	2	1	56.12	0.00	16.86	22.19	0.299	0.4	0.101	0.0001
7	2	1	51.39	10.99	17.72	8.62	0.936	5.1	0.284	0.0266
9	2	1	65.86	4.65	23.74	2.95	0.181	6.8	0.118	0.3180
11	2	1	47.14	27.13	6.17	2.00	0.593	2.2	0.158	0.1067
15	2	1	27.16	29.55	36.36	0.83	0.536	3.4	0.166	0.0121
108	2	1	66.24	7.17	0.66	8.95	0.584	5.0	0.141	0.1999
17	2	2	43.84	21.25	11.06	12.13	0.827	9.7	0.313	0.1567
18	2	2	28.36	0.86	3.05	56.34	0.327	1.3	0.205	0.1492
19	2	2	37.55	3.22	1.05	0.09	0.764	11.2	0.316	0.1615
20	2	2	72.12	4.21	2.30	7.30	0.269	0.4	0.023	0.0041
21	2	2	55.99	0.00	6.66	31.34	1.033	20.8	0.455	0.4679
23	2	2	28.92	31.59	6.22	7.86	1.095	17.8	0.668	0.5018
24	2	2	64.15	0.22	17.36	8.64	0.383	1.1	0.246	0.0004
26	2	2	25.93	28.25	8.59	9.72	0.886	14.4	0.521	0.4403
28	2	2	51.85	13.53	15.94	6.73	0.358	0.8	0.056	0.0003
30	2	2	56.66	3.57	3.54	21.23	0.824	9.7	0.349	0.2660
31	2	2	49.75	25.02	4.15	6.05	0.819	11.2	0.325	0.3801
32	2	3	76.58	5.59	4.17	7.86	0.565	10.0	0.173	0.2946
34	2	3	27.93	43.73	8.96	3.85	0.83	15.5	0.338	0.0679
35	2	3	5.85	0.26	5.11	27.66	0.446	3.0	0.246	0.1977
36	2	3	20.57	50.71	19.49	0.46	0.66	9.5	0.071	0.1426
37	2	3	53.93	12.53	8.82	1.89	0.602	7.2	0.477	0.1779
39	2	3	36.04	8.75	3.31	16.28	0.977	8.2	0.390	0.3812
43	2	3	70.44	1.03	1.78	2.87	0.553	0.4	0.057	0.0144

 Table 4: Vegetation characteristics of Cycle-2 Year 1-5 PSUs.

PSU-Identification			Vegetation cl	naracteristics		Vegetation composition-Elevation Relationships				
			Species Mean Relative Cover (%)				Community	k-means WD		\mathbf{r}^2
PSU	Cycle	Cycle (Year)	Cladium jamaicense	Nymphaea spp.	Utricularia spp.	Eleocharis spp.	Distinctness (cluster distance)	difference (cm)	Mantel's r	Cladium- WD
44	2	3	62.75	7.80	3.51	20.25	0.323	1.5	0.021	0.0077
45	2	3	39.13	15.71	10.42	5.54	1.07	3.7	-0.069	0.0530
47	2	3	52.59	21.12	3.07	2.07	0.65	8.4	0.101	0.1187
513	2	3	82.07	0.00	6.66	4.22	0.202	0.9	0.216	0.0097
DPM	2	3	74.86	2.54	2.51	13.80	0.862	8.3	0.053	0.0547
50	2	4	74.06	4.56	2.55	14.74	0.634	16.3	0.391	0.3588
51	2	4	13.71	0.19	0.00	27.78	1.226	2.8	0.102	0.0289
52	2	4	33.75	19.33	7.15	17.61	0.958	21.0	0.233	0.1412
53	2	4	35.58	23.36	31.99	6.33	0.817	19.3	0.366	0.3832
54	2	4	64.72	0.06	1.35	28.07	0.581	7.3	0.178	0.1743
55	2	4	31.55	27.50	7.38	17.16	1.094	15.5	0.489	0.5022
56	2	4	77.77	0.15	7.46	9.44	0.38	8.1	0.254	0.2687
58	2	4	33.68	1.41	5.86	42.62	0.867	14.1	0.232	0.2571
59	2	4	91.59	0.00	0.02	0.60	0.169	0.0	0.070	0.0254
61	2	4	54.56	33.18	6.21	2.21	0.833	6.1	0.124	0.1967
62	2	4	76.49	0.01	0.40	16.44	0.478	6.5	0.203	0.0964
63	2	4	12.15	54.72	27.72	1.80	0.356	4.9	0.152	0.0537
220	2	4	87.03	4.53	1.17	3.03	0.331	1.2	0.076	0.0039
65	2	5	19.0	26.4	13.7	13.5	0.654	13.3	0.458	0.2788
66	2	5	40.3	27.9	12.3	5.1	1.155	17.3	0.601	0.5460
67	2	5	8.3	0.0	0.5	14.3	0.807	7.1	0.139	0.0074
68	2	5	19.8	47.8	15.0	9.9	0.65	12.3	0.215	0.2053
69	2	5	55.2	15.4	16.9	3.9	0.543	7.2	0.208	0.1473
71	2	5	32.3	15.1	8.0	18.4	0.954	12.6	0.663	0.7430
73	2	5	61.0	0.5	0.1	0.0	1.02	23.3	0.512	0.3619
79	2	5	38.6	18.8	8.1	9.2	0.598	0.5	0.047	0.0041
BS1	2	5	53.3	0.1	23.7	8.7	0.326	0.4	0.233	0.0105
BS2	2	5	52.1	0.2	24.5	12.6	0.266	5.0	0.243	0.0736
BS3	2	5	61.4	0.4	21.9	8.1	0.262	5.3	0.227	0.0984





Figure 19: Relationship between long-term mean water depth and relative cover of major species that are characteristics of ridge, slough and wet prairie based on 57 PSUs sampled over five years (Year 1-5) of Cycle-2. The PSU 35 in WCA3AN had very few plots sampled, and thus was excluded from the analysis.



Cycle 1 & Cycle 2: Major Species Relative Cover (%)

Figure 20: Cycle-1 and Cycle-2 PSU level major species relative cover in 57 PSUs sampled over five years (Year 1-5; 2015-2020) in both Cycle 1 and 2. PSU 35 in WCA3AN had very few plots sampled, and thus was excluded from the analysis.

In non-metric multidimensional scaling (NMDS) ordination, sites were primarily arranged along hydrologic gradients. Likewise, species in the ordination space also followed the same pattern (Figure 21). Sawgrass, ferns, and other species common on ridges were clearly separated from slough species along Axis 1, while wet prairie species were intermediate along this axis, and somewhat differentiated along Axis 2.



Figure 21: Distribution of major ridge-slough plant species in ordination space. Note coherent clustering of species by community type, which indicates relatively strong fidelity of species to their associated communities across the landscape. Species names are given in Appendix 3.

The global k-means clustering analysis for classifying the sites in two groups identified ridges dominated by sawgrass as one dominant cluster, and communities including both wet prairies and sloughs as a second dominant cluster. These groups were somewhat separated on the first ordination axis. Since Cycle-1 data analysis had shown that k-means clustering within individual PSUs mostly corresponded to the global k-means clustering (Ross et al. 2016), cluster distance within individual PSUs were used as a measure of community distinctness in this study as well. In the sampled PSUs, the community distinctness varied from 0.169 to 1.226, while 60% of the sampled PSUs had the values less than 0.80, representing the less distinct to almost indistinct ridge and slough features. One third of the sampled PSUs had the community distinctiveness values <0.50, which represented uniform vegetation, an indication of deteriorated condition of R&S landscape. Those PSUs are mostly in WCA3B and NESRS areas which have been relatively dry in recent decades. Spatially, community distinctness showed similar geographic patterns to

those observed for microtopographic variability. For instance, PSUs within WCA3AC had relatively high community distinctness (Figure 22), suggesting that the R&S pattern are well conserved in that area. In contrast, the PSUs with less distinct communities in WCA3AN, WCA3B and ENP suggested various degree of degradation in R&S landscape in those areas.



Figure 22: Spatial patterns of vegetation community distinctness measured as a distance between two clusters (k-means clustering) in 58 PSUs sampled over five years (Year 1-5) of Cycle-2.

In the studied PSUs within R&S landscape, community distinctness, represented by the distance between clusters, was not significantly correlated with long-term mean water depth (Figure 23). Rather, with a few exceptions, maximal community distinctness (value >0.8) generally occurred within PSUs with LTMWD between 20 and 55 cm. Most of those PSUs are within WCA3AC, and some are in WCA3AS and WCA2. PSUs in ENP_N, ENP_W and WCA 3B clustered closely on both the LTMWD and the community distinctiveness axes. Among them, the ENP_N and WCA3B PSUs were notably indistinct on both axes. In contrast, WCA3AS PSUs showed high variability in both LTMWD and community distinctness; a decrease in distinctness with an increase in LTMWD beyond 55 cm. The community distinctness was positively correlated ($r^2 = 0.24$; p<0.001) with heterogeneity in microtopographic variation, represented by the LTMWD standard deviation. PSUs with high distinctiveness also had higher separation of those communities in water depth (Figure 23b). The exceptions were some PSUS in WCA2 and WCA3A which had high topographic variability but relatively low community distinctness.



Figure 23: Relationship of community distinctness with (a) long-term mean water depth (LTMWD) and (b) topographic relief, measured as standard deviation of LTMWD.

In general, differences in elevation between two clusters within each PSU represents the status of R&S landscape within the area. Spatially, the distribution of the differences in elevation between two k-means clusters mirrored the distribution of community distinctness and topographic variability; PSUs with more than 10 cm difference in elevation between two clusters were mostly present in WCA3AC and WCA3AS (Figure 24).



Figure 24: Spatial patterns of difference in long-term mean water level between two clusters (k-means clustering) in 58 PSUs sampled over five years (Year 1-5; 2015-2020) of Cycle-2.

Community distinctness was consistent across cycles (r = 0.75; RMSE = 0.227), though there was a slight bias toward greater distinctness in Cycle-1 (Figure 25). Most of PSUs with higher difference ($\Delta > 0.25$) in distinctness between Cycle-1 and Cycle-2 were in WCA3AN (3) and WCA2 (3) than in other regions suggesting high level of uncertainties in those areas. The PSU-21 in WCA2 had the highest difference (decrease) in distinctness. In this PSU, the community distinctness was much less in Cycle-2 than in Cycle-1. Seventeen PSUs, (5 PSUs in WCA3AC, 3 in WCA3S, 5 in ENP, 2 in WCA2, and one in each of WCA3AN and WCA3B) had <0.05 difference in community distinctness between the two sampling events. However, in general, the decrease in distinctness was negatively correlated ($r^2 = 0.37$; p < 0.001) with the community distinctness values in Cycle-1, suggesting that PSUs with low distinctness had high level of variation in differences between two cycles (Figure 26).



Community Distinctness

Figure 25: Relationship between Cycle-1 and Cycle-2 PSU community distinctness. Only the PSUs that were sampled over five years (Year 1-5) of both cycles were considered.



Figure 26: Relationship between Cycle-1 PSU community distinctness and change in community distinctness between Cycle-1 and Cycle-2. Only the PSUs that were sampled over five years (Year 1-5) of both cycles were considered. PSU 35 in WCA3AN had very few plots sampled, and thus was excluded from the analysis.

The PSUs with high community distinctness also showed strong relationships between local water depth and vegetation community composition (as measured by Mantel's r) (Figure 27). An exception was PSU 45, located in WCA3AN, which had high community distinctness, but very low Mantel's r, showing some anomaly in vegetation structure. The relationship between Mantel's r and LTMWD was polynomial, suggesting that the vegetation-elevation association tended to be stronger at the medium range of water depth, usually between 25 and 55 cm (Figure 28a). The vegetation-environment association was also significantly related ($r^2 = 0.25$) with microtopographic variation (Figure 28b). Spatial distribution of the vegetation-elevation association followed similar patterns to those observed for microtopographic variability and vegetation community distinctness, as the vegetation-elevation correlation (Mantel r) is strongly correlated across cycles (r=0.77, p<0.001), and with moderate variability (rmse = 0.122; Figure 30). The differences in community distinctness and Mantel's r between two cycles were negatively correlated with change in PSU-level LTMWD, though the relationship was not significant.



Figure 27: Relationship between community distinctness and mantel r (association between vegetation composition and water depth). PSU 35 in WCA3AN had very few plots sampled, and thus was excluded from the analysis.



Figure 28: Relationship of Mantel-r with (a) long-term mean water depth (LTMWD) and (b) topographic relief, measured as standard deviation of LTMWD.



Figure 29: Spatial patterns of elevation-vegetation associations (as measured by Mantel's correlation coefficient [r]) in 58 PSUs sampled over five years (Year 1-5; 2015-2020) of Cycle-2.



Figure 30: Cycle-1 and Cycle-2 Mantel r (relationship between vegetation composition and water depth (elevation)). PSU 35 in WCA3AN had very few plots sampled, and thus was excluded from the analysis.

3.4.2 Species richness and evenness

The total number of species recorded within the PSUs during Cycle-2 survey was 114, ranging between 6 species in PSU-73 and 39 species in PSU-17 and PSU-65 (Appendix 4). Within each PSU, the average species richness, number of species per $1m^2$ plot (defined here as alpha diversity, α) also varied. Across all 58 PSUs, 1.0% of sampled plots did not have any species present, whereas the highest number of species in a plot was 13. The alpha diversity (α) varied greatly across all ranges of LTMWD, and maximal number of species per plot occurred in the areas with LTMWD ranging between 15 and 50 cm (Figure 31). The plots with mean water depth >55 cm tend to have low (<7 species) species richness. Generalized Linear Model results revealed that both LTMWD and fire frequency (FF Index) had significant effects on plot-level species richness. Frequently burned plots tend to have higher number of species (Appendix 5). However, interaction between LTMWD and FF Index also was significant (p < 0.001), suggesting that the effects water depth could modify the effects of fire. The effects of time since last fire (TSLF) was only marginally significant.



Figure 31: Long-term mean water depth (cm) vs species richness (# of species m⁻²) in 58 PSUs surveyed over five years (2015-2020)

Total species richness in each PSU, here defined as 'gamma diversity, γ ', was significantly related with LTMWD, but the relationship was polynomial (Generalized Linear Model, p = 0.019; Appendix 5). Species richness tends to be higher at intermediate water depth (<55 cm), and richness was far low when water depth increased beyond 70 cm (Figure 32a). The results of Generalized Linear Model revealed that species richness had significant (p < 0.001) hump-shaped relationship also with microtopography, expressed as standard deviation of long-term average water depth (LTWD-SD). Species richness tended to be higher at intermediate microtopographic variation (Figure 32b; Appendix 5). In contrast, effect of FF Index on species richness exhibited an inverted hump-shaped curve showing that species richness was higher in both unburned and most frequently burned areas. However, effects of interaction between microtopography (LTMWD-SD) and FF Index on species richness was also significant (p = 0.004), suggesting that water level could modify the effect of fire.



Figure 32: Relationships of species richness (# of species/PSU) and beta diversity (β) with long-term mean water depth (LTMWD) and fire frequency index (FF Index) across 58 PSUs studied over five years (2015-2020).

Beta diversity (β), expressed as γ/α for each PSU (Whittaker 1960; Tuomisto 2010a), was significantly affected by mean water level (General Linear Model (GLM), p = 0.002; Figure 32d) but the beta diversity did not respond to water depth variation and fire frequency (Figure 32e, f). Beta diversity decreased steadily as water level increased.

The results of General Linear Model (GLM) also revealed that effects of LTMWD on evenness was only marginally significant (p = 0.056). However, a significant interaction between LTMWD and FF Index on evenness (GLM, p = 0.002) would indicate that water level could modify the effect of fire. Most PSUs with LTMWD higher than the average and low fire frequency showed high evenness. Among the rest of PSUs, the group with LTMWD lower than the average and higher fire frequency had a greater range of evenness (Figure 33; Appendix 5).



Figure 33: Relationship of species evenness (Shannon's diversity/Species richness) with long-term mean water depth (LTMWD, cm) and fire frequency index across 58 PSUs studied over five years (2015-2020).

4. Discussion

In the Ridge and Slough landscape, microtopography is one critical component of historic landscape structure, characterized by dense sawgrass ridges >30 cm higher than the adjacent sloughs (McVoy et al. 2011). However, human modification of the hydrologic regime that began in the early 20th century has resulted in significant reduction in topographic variation, particularly, a loss of elevation differences between ridge height and slough depths throughout the historical R&S landscape (Ogden 2005, Bernhardt and Willard 2009, Larsen et al. 2011, Harvey et al. 2017). Such a flattening of microtopography together with a loss of distinct ridge and slough vegetation has been a focus of concern for maintaining Everglades ecosystems (NRC 2003; Ogden et al. 2005). Thus, the maintenance and re-establishment of distinct modes of soil elevation (associated with sawgrass ridges and open water sloughs, respectively) is a central goal of Everglades conservation and restoration (USACE and SFWMD 1999). Previous monitoring of landscapes throughout the historic R&S landscape has identified bimodality of soil elevations as a key measure of this microtopography (Watts et al. 2010, Ross et al. 2016). The presence of bimodal soil elevations was found to be largely restricted to PSUs within central WCA3A (Ross et al. 2016). In these most conserved landscapes, the elevation difference between the high and low elevation mode was generally between 15 and 25 cm, and occurred in PSUs with long-term mean water depths between 30 and 50 cm. The present study, which was the continuation of the landscape monitoring efforts, reiterates that R&S landscape condition varies among different regions, and relatively conserved R&S with distinct bimodality in soil elevations and vegetation communities is mostly confined within central WCA3A, while PSUs in WCA3AN, WCA3B and ENP_N have unimodal soil elevation distributions and are in varied degrees of degradation.

The R&S mosaic is considered a self-organized landscape, and several mechanisms involving feedbacks between vegetation, hydrology, and soil development have been proposed for its formation and the stabilization of ridge and slough at elevations in quasi-equilibrium (Larsen et al. 2007, Givnish et al. 2008, Larsen and Harvey 2010, Watts et al. 2010, Cohen et al. 2011, Larsen et al 2011; Heffernan et al. 2013, Acharya et al. 2015). In this study, the presence of distinct elevation modes associated with ridges and sloughs was detected by measuring water depths at randomized points within representative 2×5 km landscape blocks, which themselves are distributed randomly throughout the Everglades. These water depths were converted into soil elevation measurements by benchmarking water depths on the day of sampling to the multi-annual

mean water level. The statistical analysis of bimodality involved comparing the goodness-of-fit of a single normal distribution with the fit of two normal distributions, which might have equal or unequal variances and equal or unequal weighting. PSUs in which modes had extremely unequal weights (i.e., 75% or more points fall within the higher weighted mode) were not considered to have conserved microtopography, both because such uneven modes are more likely to arise as statistical artifacts, and because the historic ridge-slough landscape was composed of approximately equal areas of ridge and slough (McVoy et al. 2011).

Over the five years of Cycle-2, the same number of PSUs exhibited statistically significant bimodality as was observed in Cycle-1 (Table 3). However, the PSUs with statistically significant bimodality in soil elevations were not the same in both cycles. For instance, 7 PSUs that displayed bimodality in Cycle-1 did not show bimodality in Cycle-2, and the reverse was also true. The PSUs in which a shift from detection of bimodal soil elevations in Cycle-1 to their non-detection during the Cycle-2 were mostly in areas that have experienced dry conditions in recent decades, including ENP and WCA3B. Since the interval between the two sampling events is short (5 years), this shift may not necessarily indicate ongoing degradation of remnant pattern in ENP and WCA3B, although this possibility should be a cause for concern. However, several factors might have contributed to this change. First, in many PSUs, fewer points were sampled during Cycle-2 than were sampled in Cycle-1, owing to logistical and budgetary constraints. Detection of bimodality requires substantial statistical power. While ~135 points in a PSU in Cycle-2 are also a considerable number typically adequate for distribution modeling, among seven PSUs that showed non-bimodality in Cycle-2, four PSUs had sampling points <135. Such a reduction in sampling intensity between two samplings might have impacted the power to detect subtle bimodality. Moreover, the shift from statistically significant to non-significant bimodality does not necessarily indicate a substantial loss of microtopographic relief. For example, in PSU 0, the1-mode model had stronger fit than 2-mode model, and thus was selected, but the 2-mode model yielded an estimate of elevation differences (10.3 cm) that was like what we observed in Cycle-1. The same was true for other two PSUs (PSUs 2 and 36) that had 2-mode model in both Cycle-1 and 2 with approximately 18 cm and 14 cm in elevation differences, but those PSUs in Cycle-1 had elevation modes with unequal weights (i.e., one mode >75%), and thus were considered as having unimodal (Table 3). Finally, relatively wet hydrologic conditions through Year-5 of the Cycle -2 sampling period may have influenced the estimates of soil elevation, as we observed substantial differences

in estimates of mean water depth and the standard deviation of water depth in PSUs sampled during wet conditions.

In the ridge and slough landscape, the distinct zonation of plant communities is shaped by abrupt differences in elevation between ridges and sloughs (Ogden 2005, McVoy et al. 2011). Ridges with relatively high topographic relief and shallow water depth consist of dense stands of sawgrass, whereas sloughs with low elevation and deep water deep have white water lily and other macrophytes (Loveless 1959, McVoy et al. 2011, Ross et al. 2006). A transitional community comprised of spikerush, maidencane and beakrush is usually present in the areas of intermediate water depths. In this study, the distinctness between ridge and slough communities was represented by a test statistic "community distinctness" which was measured using dissimilarity between R&S vegetation community composition, defined as the distance (in multivariate space) between two forcefully imposed vegetation clusters (Isherwood 2013; Ross et al. 2016). Our approach to measuring community distinctness is a novel measure based on measurements of distances between two clusters of plant communities in ordination space (Isherwood 2013). However, the robustness of representation of ridge and slough features by those two clusters have been vigorously tested, and community distinctness has been found to be a robust measure of the status of ridge and slough communities (Ross et al. 2016). During Cycle-2, high community distinctness values representing highly distinct sawgrass-dominated ridges and Nymphea- and Utriculariadominated sloughs observed in conserved landscapes of WCA3AC are consistent with the findings during Cycle-1 of this ongoing monitoring study (Ross et al. 2016) and in other studies (Watts et al. 2010; Nungesser 2011). Likewise, in areas subject to increased or decreased water levels due to water management or altered infrastructure, this distinctness is reduced. For instance, the degraded ridge and slough community pattern observed in WCA3AN, the southeastern portion of WCA3AC, WCA3B and ENP_N during both Cycle-1 and 2 was consistent with loss of characteristic microtopography variability in those areas, suggesting that this metric is appropriate to assess the system-wide status of the ridge and slough landscape.

While community distinctness was consistent across both cycles (RMSE = 0.23), several PSUs had reduced distinctness in Cycle-2 compared to Cycle-1. The reduction in community distinctness was observed in all areas, but was most prevalent in PSUs within WCA1, WCA2, ENP_W (Figure 25), where ridge and sloughs have long disintegrated and topographic variation is very patchy. Two PSUs within well conserved R&S landscape in WCA3AC regions and one in

WCA3AS also had reduction in community distinctness of >0.20. In contrast, three PSUs in WCA3AN, two in WCA3AS, and one in WCA3AC and WCA3B showed an increase in community distinctness by >0.2. Several studies have documented rapid shifts (within 3-5 years) in prairie and marsh plant community composition in response to changing hydrologic regimes (Armentano et al. 2006; Zweig and Kitchens 2008; Sah et al. 2014). Hence, the difference in community distinctness might have resulted from a shift in species composition at a local scale. In general, hydrologic conditions during Cycle-2 were slightly wetter than in Cycle-1, and in some PSUs the difference in mean water depth was greater than 4 cm, which might have extended the hydroperiod as well. During Cycle-1 (2009-2015), relatively high distinctness values were observed in PSUs that had mean water level between 20 and 50 cm (Ross et al. 2016). Shift in hydrologic conditions outside this range might have caused decreases in distinctness. It becomes a matter of concern, especially when the change in distinctness between two cycles is negatively correlated with the Cycle-1 distinctness (Figure 26). For instance, PSU 21, which showed a much wetter condition in Cycle-2 (LTMWD = 53.5 cm) than in Cycle-1 (LTMWD = 39.5), exhibited the highest decrease in community distinctness. Similarly, PSU 68 that had an increase in LTMWD from 46.9 cm in Cycle-1 to 67.9 cm in Cycle-2 also decreased by 0.35 in community distinctness.

In degraded areas, where loss in microtopography has primarily been attributed to relatively dry conditions resulting in peat loss (Watts et al. 2010), the reduction in community distinctiveness observed in the last five years might be related to extreme drought conditions that were prevalent in two of 5 years between the two surveys. South Florida witnessed extreme droughts in 2011 and 2014, during which excessive peat decomposition might have occurred, affecting the microtopography of the area. This is somewhat consistent with the pattern observed in microtopography in Cycle-1 and 2. As bimodality in soil elevations is a key measure of microtopography in this landscape, several PSUs that had bimodal elevation distributions during Cycle-1 did not display bimodality during Cycle-2. While many of them also showed much reduced ($\Delta \sim 0.3$) community distinctness in Cycle-2, there were some PSUs that showed similar shift in microtopography between two cycles but had slightly improved community distinctness. Moreover, a PSU (PSU 21 in WCA2) that exhibited bimodality in both cycles showed the greatest reduction in community distinctness between two cycles. Thus, the reduction in community distinctness might be a concern, especially when it is hypothesized that in drained areas, loss of microtopography precedes the degradation of R&S plant community distinctness.

Several other factors might have contributed to the observed changes in microtopography and community distinctness. Among them, fire, an integral component of Everglades ecosystem (Robertson 1962; Wade et al. 1980; Gunderson and Snyder 1994; Osborne et al. 2013), is also believed to have an important role in R&S landscape dynamics. An analysis of fire frequency over 23 years (1997-2019) suggests that the northern WCA3A and some part of WCA3B, which have experienced dry conditions in recent decades, have burned more frequently than other areas (Figure 16). Since the fire severity data were not available, we were unable to assess whether those fires consumed peat and affected topography or not. However, it is logical to assume that if a relatively dry area burns frequently, especially during the dry seasons when there is no standing water, the fires are likely to consume peat materials and affect topography, thereby impacting water regions and vegetation communities in the area (Gunderson 1994; Ogden 2005). Among the PSUs that burned more than three times over 10 years (2010-2019), 6 PSUS (3, 7, 19, 35, 43, 67) were within WCN3AN, and one in WCA2 (PPSU 9), WCA3AC (PSU 71) and WCA3B (PSU 220). Most of those PSUs burned between March and early July when the areas were dry. In many of these PSUs, soil depths were also relatively low (Figure 16; Appendix 2), probably due to peat loss caused by oxidation due to excessive dryness. In contrast, six PSUs in NESRS (PSUs 24, 56, 513, BS1, BS2 and BS3) also burned three or more times during the same period, but most of those burns occurred during the wet season. The discrepancy in burn season in those two regions (WCAs and ENP) might have affected vegetation communities differently. For instance, four of nine burned PSUs in WCAs decreased in community distinctness by >0.2, whereas in the burned PSUs within ENP, a change in distinctness between the two surveys was much less, usually >0.1.

Effects of fire on vegetation would also depend on post-fire hydrologic conditions (Wu et al. 2012; Sah et al. 2014). For instance, re-growth of sawgrass in the R&S landscape is also severely impeded by deep water after a surface-burn (Wu et al. 2012). Moreover, regardless of season, fire usually consumes standing vegetation, and thus it not only affects vegetation composition in subsequent years but may also have effects on organic matter production and deposition, at least in the short term after fire (Watts 2013). For instance, Ponzio et al. (2004) found a temporary increase in *Typha* density for two years after fire. Thus, while it is apparent that fires might have played some role in changes in topography and vegetation pattern observed during this study in the R&S landscape, a detailed analysis of hydrology and fire regimes would help to clarify their interactive effects on vegetation within the PSUs throughout the system.

Environmental heterogeneity (EH) is usually positively correlated with species diversity (MacArthur 1965; Stein et al. 2014). In this study, microtopographic heterogeneity within each PSU was represented by the standard deviation of long-term water depth, which exhibited a significant hump shaped relationship with plant species richness across all PSUs (Figure 32b). Microtopography in PSUs is affected by hydrologic conditions and variation in fire regimes. In this study, both plot-level and PSU-level species richness (α and γ diversity, respectively) tended to be higher in mid-range of water depth (20-55 cm; Figures 31, 32a), which is prevalent in conserved PSUs with relatively distinct ridge and slough features. In contrast, PSU-level species richness had inverted hump-shaped relationship with fire frequency index. This is plausible, since relatively high fire frequency tends to burn the peat on the high ground (here, 'ridge') and reduce the microtopographic variation in the area, which can have negative effects on species richness. Nevertheless, to our surprise, beta (β) diversity, was not significantly related to microtopographic variation or and one of its potential drivers: fire frequency (Figure 32). However, a negative relationship of beta diversity with water depth is as expected. We have defined beta diversity simply as γ/α and explored its relationship with environmental variables at the PSU-scale. In fact, there is a whole family of beta diversities, defined in different ways and at different scales (Tuomisto 2010a, 2010b). Moreover, the relationship between beta diversity and environmental heterogeneity and its drivers depends on the scale of study and several other factors (Stein et al. 2014 and others). Hence, more detailed analysis is planned during the next phase of the ongoing monitoring to understand the true nature of variation in beta diversity and its relationship with environmental drivers in the R&S landscape throughout the system.

Summary

Measures of both microtopography and plant community distinctness in 58 PSUs revealed a spatial pattern of R&S conditions consistent with system-wide findings based on much large number of PSUs sampled in previous cycle (2009-2015), suggesting that both metrics are the robust measure of R&S condition in the Everglades. Some PSUs have experienced shifts in microtopographic variability, changing from bimodality to unimodality, and experiencing a reduction in community distinctness (especially in WCA2, WCA3AN, ENP_W) over the five-year period. This pattern may be a cause for concern, especially when two of five years during the first study witnessed extreme drought conditions that possibly had adverse effects on peat soils and microtopography. Several other factors, including fires might also have contributed to the observed changes in microtopographic variability and community characteristics. Finally, despite reduced sampling and power of analysis during Cycle-2, the correspondence in results between the two Cycles in assessing the system-wide status of R&S suggests that the current sampling design with analytical techniques is a robust method to characterize the R&S at a coarse scale. Finer scale (e.g., "fast-twitch") responses of ridge and slough features that may reveal the mechanisms underlying change may require a sampling design that also incorporates measurement of ground elevations and vegetation composition at short intervals along multiple transects that encompass ridge, slough, and transient communities.

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Appendix

Cycle-2			PSU	Fi	re frequ	iency (#	of fires	betwee	en 1997	and 20	19)	Area	FF*A
Year	PSU	PSUID	Area (ha)	1	2	3	4	5	6	7	8	burned (%)	Index
1	0	P000	999.8	18.21	65.29	12.02	0.51					96.0	1.869
1	1	P001	1000.7									0.0	0.000
1	2	P002	1000.6									0.0	0.000
1	3	P003	659.6	0.53	1.11	11.74	49.27	27.42	9.75	0.17		100.0	4.319
1	4	P004	1000.0	52.16	3.32	16.28						71.8	1.076
1	6	P006	1000.0	55.87								55.9	0.559
1	7	P007	999.9	46.99	33.59	0.97						81.6	1.171
1	9	P009	999.6	0.12	7.69	75.23	16.95					100.0	3.090
1	11	P011	1000.0	31.26	47.59							78.9	1.264
1	15	P015	1000.0									0.0	0.000
1	108	P108	999.2	95.01	4.42	0.56						100.0	1.055
2	17	P017	1000.0									0.0	0.000
2	18	P018	999.9	80.48	18.92	0.56						100.0	1.200
2	19	P019	999.9			0.07	24.48	49.44	23.17	2.83	0.001	100.0	5.042
2	20	P020	999.2	11.29	15.56	67.29	5.86					100.0	2.677
2	21	P021	1000.0	37.99								38.0	0.380
2	23	P023	1000.0	10.22	49.77	38.35	0.22					98.6	2.257
2	24	P024	999.9	64.70	15.31	0.47						80.5	0.967
2	26	P026	998.9									0.0	0.000
2	28	P028	1000.5		69.01	30.99						100.0	2.310
2	30	P030	1000.4	55.46	4.54	0.07						60.1	0.647
2	31	P031	1000.1	66.56	0.12							66.7	0.668
3	32	P032	1000.8	68.51	11.20	0.001						79.7	0.909
3	34	P034	1000.0									0.0	0.000
3	35	P035	1000.0	11.84	7.77	8.56	13.25	16.58	29.04	12.95		100.0	4.539
3	36	P036	1000.0	14.58								14.6	0.146
3	37	P037	999.9	35.52	0.36							35.9	0.362
3	39	P039	1000.0	5.11								5.1	0.051
3	43	P043	999.9		8.56	14.83	4.32	31.88	40.41			100.0	4.807
3	44	P044	999.3	19.41	21.33	59.26						100.0	2.398
3	45	P045	1000.3									0.0	0.000
3	47	P047	998.9	19.38								19.4	0.194
3	513	P513	1008.6	30.55	50.65	11.96	5.40					98.6	1.893
3	DPM	PDPM	2250.0	13.41	64.95	21.64						100.0	2.082
4	50	P050	1001.0	40.02	38.09	0.0002						78.1	1.162
4	51	P051	999.9	92.01	7.99							100.0	1.080
4	52	P052	999.9	14.15	0.53							14.7	0.152
4	53	P053	1000.1	45.96	47.12	0.58						93.7	1.420

Appendix 1: Area (%) burned in studied PSUs over 23 years between 1997 and 2019.

Cycle-2			PSU	Fi	re frequ	ency (#	of fires	s betwee	n 1997	7 and 20	19)	Area	FF*A
Year	PSU	PSUID	Area (ha)	1	2	3	4	5	6	7	8	burned (%)	Index
4	54	P054	1000.0	67.63								67.6	0.676
4	55	P055	1000.1									0.0	0.000
4	56	P056	1000.0	48.67	51.01							99.7	1.507
4	58	P058	1000.7	1.43	0.06							1.5	0.016
4	59	P059	1000.0	0.29	2.53	14.47	26.91	55.68				99.9	4.348
4	61	P061	1000.1	96.57	3.43							100.0	1.034
4	62	P062	999.5	50.93	1.07							52.0	0.531
4	63	P063	999.8	6.92								6.9	0.069
4	220	P220	999.9	4.02	27.32	42.42	25.91	0.28				100.0	2.910
5	65	P065	1000.0									0.0	0.000
5	66	P066	1000.5									0.0	0.000
5	67	P067	1000.0	1.57	3.32	15.50	1.70	48.53	16.58	12.80		100.0	4.932
5	68	P068	1001.1									0.0	0.000
5	69	P069	1000.0	36.34	6.28	0.40						43.0	0.501
5	71	P071	1000.0	32.83	14.14	14.24	7.45					68.7	1.336
5	73	P073	973.1	2.48	27.37	40.45	18.28	11.43				100.0	3.088
5	79	P079	1000.6	4.87	63.29	1.84						70.0	1.370
5	BS1	PBS1	1103.8	75.75	21.56	0.38						97.7	1.200
5	BS2	PBS2	1064.8	96.61	2.23	0.23						99.1	1.018
5	BS3	PBS3	1000.0	91.82	4.67	1.20	0.09					97.8	1.052

Cycle-2	DCII	DCI ID	Dogiona		Soil Dep	oth (cm)	
Year	PSU	rsu_in	Regions	Mean	SD	Minimum	Maximum
1	0	P000	ENP_W	83.4	29.7	11.0	156.0
1	1	P001	WCA1	250.0	17.6	226.0	275.0
1	2	P002	WCA3AS	145.5	27.4	104.0	244.0
1	3	P003	WCA3AN	203.4	29.6	101.0	237.0
1	4	P004	WCA3AC	116.1	11.6	94.0	147.0
1	6	P006	ENP_S	45.4	16.5	9.0	124.0
1	7	P007	WCA3AN	70.1	26.7	23.0	170.0
1	9	P009	WCA2	194.1	18.9	159.0	239.0
1	11	P011	WCA3AC	112.9	42.7	55.0	245.0
1	15	P015	WCA3AC	103.2	30.4	50.0	212.0
1	108	P108	WCA3B	171.4	26.9	82.0	234.0
2	17	P017	WCA1	212.3	22.6	155.0	275.0
2	18	P018	ENP_W	32.9	14.9	8.0	70.0
2	19	P019	WCA3AN	41.4	20.6	13.0	99.0
2	20	P020	WCA3B	96.4	24.4	52.0	171.0
2	21	P021	WCA2	135.1	57.7	59.0	280.0
2	23	P023	WCA3AC	87.0	16.0	47.0	137.0
2	24	P024	ENP_N	43.2	21.8	6.5	127.0
2	26	P026	WCA3AC	81.2	42.9	1.0	227.0
2	28	P028	WCA3B	95.2	13.9	65.0	143.0
2	30	P030	ENP_S	114.5	50.1	25.0	263.0
2	31	P031	WCA3AC	124.4	24.8	85.0	280.0
3	32	P032	ENP_N	59.9	39.8	3.0	300.0
3	34	P034	WCA3AS	105.2	34.6	26.0	179.0
3	35	P035	WCA3AN	45.7	32.1	7.0	123.0
3	36	P036	WCA3AS	122.6	19.6	89.0	173.0
3	37	P037	WCA2	142.3	28.6	94.0	208.0
3	39	P039	WCA3AN	51.2	24.7	0.0	126.0
3	43	P043	WCA3AN	65.8	21.9	17.0	153.0
3	44	P044	WCA3B	128.1	23.7	0.0	188.0
3	45	P045	WCA3AS	73.7	32.6	0.0	188.0
3	47	P047	WCA3AC	97.3	21.5	72.0	188.0
3	513	P513	ENP_N	74.6	24.8	28.0	185.0
3	DPM	PDPM	WCA3B	152.8	27.0	0.0	235.0
4	50	P050	ENP_W	60.7	28.6	9.0	149.0
4	51	P051	WCA3AN	48.3	37.5	0.0	187.0
4	52	P052	WCA3AS	105.9	42.2	0.0	169.0
4	53	P053	WCA2	96.9	37.5	0.0	200.0
4	54	P054	ENP_W	45.4	27.5	0.0	135.0

Appendix 2: Soil depth (cm) in 58 PSUs surveyed during Year 1-5 (2015-2020).

Cycle-2	DCU	DCU ID	Destaur		Soil De	oth (cm)	
Year	PSU	PSU_ID	Regions	Mean	SD	Minimum	Maximum
4	55	P055	WCA3AC	88.6	29.7	42.0	164.0
4	56	P056	ENP_N	83.7	39.7	10.0	204.0
4	58	P058	WCA3AS	41.1	24.4	2.0	143.0
4	59	P059	WCA3AN	71.8	26.3	35.0	210.0
4	61	P061	WCA2	159.1	38.3	0.0	208.0
4	62	P062	ENP_S	73.3	25.2	0.0	146.0
4	63	P063	WCA3AS	98.3	44.4	0.0	269.0
4	220	P220	WCA3B	102.7	31.4	0.0	195.0
5	65	P065	WCA1	312.0	26.7	256.0	375.0
5	66	P066	WCA3AC	120.0	18.2	82.0	171.0
5	67	P067	WCA3AN	41.2	34.7	8.0	243.0
5	68	P068	WCA3AS	158.8	23.8	122.0	242.0
5	69	P069	WCA2	141.4	35.4	75.0	312.0
5	71	P071	WCA3AC	66.6	23.1	26.0	130.0
5	73	P073	WCA2	211.4	32.3	145.0	358.0
5	79	P079	WCA3AC	91.9	28.0	59.0	223.0
5	BS1	PBS1	ENP_N	94.8	31.0	16.0	184.0
5	BS2	PBS2	ENP_N	65.0	32.1	11.0	152.0
5	BS3	PBS3	ENP_N	111.3	38.1	29.0	195.0

SPCODE	Species						Year-1					
SICODE	Species	0	1	2	3	4	6	7	9	11	15	108
AESPRA	Aeschynomene pratensis	0.04						0.02				0.06
AGALIN	Agalinis linifolia											
ANNGLA	Annona glabra											
BACCAR	Bacopa caroliniana	0.27	0.22	0.39	0.15	0.06	0.04	1.61				0.33
BLESER	Blechnum serrulatum	0.03		0.02		0.02		0.03				0.15
CENASI	Centella asiatica				3.61							
CEPOCC	Cephalanthus occidentalis	0.01	0.05	0.20		0.26	0.02	0.61				0.14
CHARA	Chara sp.							0.02	2.26			
CHRICA	Chrysobalanus icaco	0.15										
CLAJAM	Cladium jamaicense	15.28	6.18	13.84	24.93	14.78	9.64	35.04	22.82	29.98	11.69	26.66
CRIAME	Crinum americanum	0.36		0.23	0.13	0.33	0.05	1.18		0.01		0.52
DICDIC	Dichanthelium dichotomum		0.04									
DICSPP	Dichanthelium sp.				5.70							
DIOVIR	Diodia virginiana											
ELECEL	Eleocharis cellulosa	3.16		0.97		1.10	2.33	7.02	1.37	1.39	1.01	1.76
ELEELO	Eleocharis elongata			2.20		2.69				0.01		2.29
ELEINT	Eleocharis interstincta		0.02							0.01		
ELESPP	Eleocharis sp.		1.16									
ERISPP	Eriocaulon sp.		0.24									
FUIBRE	Fuirena breviseta	0.01			0.03							
FUISCI	Fuirena scirpoidea											
HYDCOR	Hydrolea corymbosa					0.02						
HYMLAT	Hymenocallis latifolia	0.10			0.21			0.38				
HYMPAL	Hymenocallis palmeri					0.02						0.07
ILECAS	Ilex cassine											
IPOSAG	Ipomoea sagittata	0.03		0.02		0.02		0.04				0.02
JUSANG	Justicia angusta	0.15		0.34		0.32	0.02	0.71		0.01		0.20
LEEHEX	Leersia hexandra		0.01	0.02	0.01	0.03		0.13		0.29		0.02
LUDALA	Ludwigia alata	0.01										
LUDREP	Ludwigia repens				0.03	0.08						
LYGMIC	Lygodium microphyllum		0.03									
MIKSCA	Mikania scandens	0.01			0.72	0.02						
MORCER	Morella cerifera		0.12		1.54			0.04				
NEPBIS	Nephrolepis biserrata											
NYMAQU	Nymphoides aquatica	0.04		0.65		0.39		0.43				0.07
NYMODO	Nymphaea odorata		2.51	18.21		15.82		9.18	2.23	17.81	18.26	3.32
OSMREG	Osmunda regalis				0.28							
OXYFIL	Oxypolis filiformis							0.11				
PANHEM	Panicum hemitomon	0.16	0.39	0.72	0.03	0.65	0.05	0.64		1.52	0.70	0.36
PANTEN	Panicum tenerum											
PASGEM	Paspalidium geminatum	0.11	0.18	0.11		0.03	0.02	0.33		0.12	0.21	0.02
PELVIR	Peltandra virginica	0.19	0.17	0.24	0.15	0.15	0.03	0.16		0.05		0.24
PERHYD	Persicaria hydropiperoides	0.01	0.01		0.10					0.58		0.01
PERSET	Persicaria setaceum											

Appendix 3: Mean species cover (%) in PSU sampled during Year 1-5 (2015-2020). Only the species that were present in more than 5 plots (among 5429 plots sampled in four years) are listed. The number of 1x1 m plots sampled in each PSU is given in Table 1.

SPCODE	Species					Y	lear-1					
SPCODE	Species -	0	1	2	3	4	6	7	9	11	15	108
PLUBAC	Pluchea baccharis				0.45			0.04				
PONCOR	Pontederia cordata	0.04	0.14	0.28	0.31	0.21	0.04	0.28		1.96	0.14	0.36
POTILL	Potamogeton illinoensis											
PROPAL	Proserpinaca palustris				0.62							
RHYINU	Rhynchospora inundata		0.14	0.05	0.07	0.07		0.04				1.29
RHYMIC	Rhynchospora microcarpa		0.06		0.30							
RHYTRA	Rhynchospora tracyi	0.01	6.04				0.13					4.01
SAGLAN	Sagittaria lancifolia	0.04	0.04		0.38		0.04	0.33		0.70	0.01	0.49
SALCAR	Salix caroliniana					0.01						0.50
SALSPP	Salvinia Sp.											
THEINT	Thelypteris interrupta		0.02		0.11							
TYPDOM	Typha domingensis	0.19		0.08		0.47	0.04	1.26	0.78	4.26	2.23	0.10
UTRFOL	Utricularia foliosa	0.41	0.37	1.28		1.02	0.08	3.07	5.79	3.33	4.09	0.01
UTRGIB	Utricularia gibba		0.02	0.02		0.03			0.03	0.33		
UTRPUR	Utricularia purpurea	1.31	14.68	2.84		2.95	2.51	12.48	4.76	0.67	29.44	0.17
XYRCAR	Xyris caroliniana											
XYRSPP	Xyris sp.		0.01									

SPCODE	Species						Year-2					
SPCODE	species	17	18	19	20	21	23	24	26	28	30	31
AESPRA	Aeschynomene pratensis		0.38					0.12	0.12			
AGALIN	Agalinis linifolia											
ANNGLA	Annona glabra		0.02								0.04	
BACCAR	Bacopa caroliniana	0.02	2.26	0.47	2.35		2.43	0.54	6.59	0.82	2.46	2.37
BLESER	Blechnum serrulatum	0.23					0.15		0.20		0.01	
CENASI	Centella asiatica											
CEPOCC	Cephalanthus occidentalis	0.08		0.28			1.85		1.86	0.07		0.46
CHARA	Chara sp.			0.18		1.02	0.08		0.12		0.01	0.01
CHRICA	Chrysobalanus icaco	0.03										
CLAJAM	Cladium jamaicense	24.17	11.81	12.70	18.96	13.49	9.08	14.88	9.37	16.33	23.34	21.27
CRIAME	Crinum americanum			0.54	0.96	0.03	1.04	0.24	1.09	0.44	0.70	0.56
DICDIC	Dichanthelium dichotomum	0.01										
DICSPP	Dichanthelium sp.											
DIOVIR	Diodia virginiana											
ELECEL	Eleocharis cellulosa	0.29	21.98	0.03	1.63	0.87	1.84	1.68	2.99	1.40	5.69	0.69
ELEELO	Eleocharis elongata	3.88				0.37	1.58		1.98		1.33	1.92
ELEINT	Eleocharis interstincta	0.09										
ELESPP	Eleocharis sp.											
ERISPP	Eriocaulon sp.											
FUIBRE	Fuirena breviseta										0.01	
FUISCI	Fuirena scirpoidea	0.13							0.01			
HYDCOR	Hydrolea corymbosa						0.08		0.33			0.01
HYMLAT	Hymenocallis latifolia											
HYMPAL	Hymenocallis palmeri				0.18		1.62	0.39	1.34	0.59	0.04	0.36
ILECAS	Ilex cassine	0.01										

SPCODE	Spacios -						Year-2					
SPCODE	species	17	18	19	20	21	23	24	26	28	30	31
IPOSAG	Ipomoea sagittata						0.11	0.01	0.01		0.04	
JUSANG	Justicia angusta		0.26	0.22	0.19		0.44	0.12	0.95	0.09	0.56	0.05
LEEHEX	Leersia hexandra	0.12		0.04	0.02		0.11		0.05	0.05		0.04
LUDALA	Ludwigia alata			0.02					0.01		0.01	
LUDREP	Ludwigia repens	0.02										
LYGMIC	Lygodium microphyllum	0.03										
MIKSCA	Mikania scandens			0.06			0.04					
MORCER	Morella cerifera	0.24					0.04				0.01	
NEPBIS	Nephrolepis biserrata											
NYMAQU	Nymphoides aquatica	0.11	0.26				2.30	0.05	1.65	0.19	0.76	0.69
NYMODO	Nymphaea odorata	8.19		1.89	1.89		12.20		14.92	6.22	0.52	9.71
OSMREG	Osmunda regalis	0.13					3.03		0.01			
OXYFIL	Oxypolis filiformis						0.31	0.04			0.01	
PANHEM	Panicum hemitomon	0.16	0.64	0.11	0.10	0.06	0.57	0.58	0.66	0.04	0.78	0.19
PANTEN	Panicum tenerum		0.24					0.08		0.03		0.01
PASGEM	Paspalidium geminatum	0.02	0.60		0.07		0.80	0.12	0.41	0.05	0.45	0.13
PELVIR	Peltandra virginica	0.91	0.02	0.12	0.21		0.15		0.94	0.04	0.36	0.13
PERHYD	Persicaria hydropiperoides	0.01										
PERSET	Persicaria setaceum			0.64								
PLUBAC	Pluchea baccharis				0.01			0.01				
PONCOR	Pontederia cordata	1.11		1.26	0.01		0.08	0.25	0.91	0.11	0.39	0.44
POTILL	Potamogeton illinoensis										0.04	0.04
PROPAL	Proserpinaca palustris										0.04	
RHYINU	Rhynchospora inundata	0.10										
RHYMIC	Rhynchospora microcarpa	0.16										
RHYTRA	Rhynchospora tracyi	0.02						0.52				0.02
SAGLAN	Sagittaria lancifolia	0.08		5.12	0.10		0.16	0.02	0.21	0.24	0.47	0.12
SALCAR	Salix caroliniana			0.51								
SALSPP	Salvinia Sp.											
THEINT	Thelypteris interrupta											
TYPDOM	Typha domingensis	0.38		15.28		0.37	0.39	0.27	0.27	1.56	0.11	0.44
UTRFOL	Utricularia foliosa	2.29	1.24	0.26	0.24	0.60	2.02	1.36	3.76	1.15	0.67	1.10
UTRGIB	Utricularia gibba											
UTRPUR	Utricularia purpurea	1.67			0.46		1.06	2.54	1.95	6.52	0.40	0.62
XYRCAR	Xyris caroliniana											
XYRSPP	Xyris sp.	0.02										

SPCODE	Spacios						Yea	r-3					
SPCODE	species	32	34	35	36	37	39	43	44	45	47	513	DPM
AESPRA	Aeschynomene pratensis						0.01						
AGALIN	Agalinis linifolia												
ANNGLA	Annona glabra												
BACCAR	Bacopa caroliniana	0.14	0.13	1.41			1.49	0.98	0.63		0.49	0.02	0.39
BLESER	Blechnum serrulatum		0.26										
CENASI	Centella asiatica												
CEPOCC	Cephalanthus occidentalis	0.07	0.49		0.01	0.11	0.71				0.05	0.03	0.33
CHARA	Chara sp.	0.02		31.45		3.65		0.02	0.02				0.21
CHRICA	Chrysobalanus icaco												
CLAJAM	Cladium jamaicense	35.80	11.19	1.79	11.20	18.44	15.31	20.74	24.89	6.25	19.82	17.16	54.26
CRIAME	Crinum americanum	0.09	0.06	0.38	0.01	0.03	0.54	0.50	0.05		0.03	0.12	0.30
DICDIC	Dichanthelium dichotomum												
DICSPP	Dichanthelium sp.												
DIOVIR	Diodia virginiana												
ELECEL	Eleocharis cellulosa	1.56	1.73	4.45	0.01	0.22	1.60	0.35	4.47	0.31	0.52	0.23	3.82
ELEELO	Eleocharis elongata		0.58			0.03		0.12			0.15		2.26
ELEINT	Eleocharis interstincta	0.10								0.14			
ELESPP	Eleocharis sp.												
ERISPP	Eriocaulon sp.												
FUIBRE	Fuirena breviseta												
FUISCI	Fuirena scirpoidea												
HYDCOR	Hydrolea corymbosa		0.01				0.01	0.03					
HYMLAT	Hymenocallis latifolia												
HYMPAL	Hymenocallis palmeri	0.32		0.38					0.11		0.07	0.03	0.16
ILECAS	Ilex cassine												
IPOSAG	Ipomoea sagittata		0.01			0.02	0.17		0.02			0.08	0.01
JUSANG	Justicia angusta	0.06	0.04	0.07			0.19	0.12	0.05			0.01	0.01
LEEHEX	Leersia hexandra	0.03	0.11	0.21			0.06	0.02	0.10		0.49	0.01	0.00
LUDALA	Ludwigia alata												
LUDREP	Ludwigia repens												
LYGMIC	Lygodium microphyllum												
MIKSCA	Mikania scandens												
MORCER	Morella cerifera												
NEPBIS	Nephrolepis biserrata												
NYMAQU	Nymphoides aquatica	0.20	0.49					0.02	0.05		0.01		0.11
NYMODO	Nymphaea odorata	1.07	21.53	0.07	27.71	7.35	1.63	0.23	2.20	5.45	9.10		1.11
OSMREG	Osmunda regalis		0.01										
OXYFIL	Oxypolis filiformis												
PANHEM	Panicum hemitomon		0.01	0.41			0.74	0.46		0.08			
PANTEN	Panicum tenerum		0.11				0.19		0.02			0.02	0.08
PASGEM	Paspalidium geminatum	0.29	0.12		0.64		0.19		0.09	0.24	0.16	0.05	0.79
PELVIR	Peltandra virginica	0.07	1.08	0.10	0.01		0.10	0.03	0.04	0.2	0.69	0.00	0.17
PERHYD	Persicaria hydropiperoides	0.07	1.00	5.10			5.10	0.05	0.04		0.07	0.02	5.17
PERSET	Persicaria setaceum					0 39						0.02	
PLUBAC	Pluchea baccharis					0.57							
PONCOR	Pontederia cordata	0 00	1 70	1.00	0.28	0.04	0.04		0.01	0.24	1 64	0.06	0.12
PASGEM PELVIR PERHYD PERSET PLUBAC PONCOR	Paspalidium geminatum Peltandra virginica Persicaria hydropiperoides Persicaria setaceum Pluchea baccharis Pontederia cordata	0.29 0.07 0.09	0.12 1.08 1.79	0.10	0.64	0.39 0.04	0.19 0.10 0.04	0.03	0.09 0.04 0.01	0.24	0.16 0.69 1.64	0.05 0.02 0.06	0.79 0.17 0.12

SPCODE	Species						Yea	r-3					
SICODE	Species	32	34	35	36	37	39	43	44	45	47	513	DPM
POTILL	Potamogeton illinoensis	0.17						0.04					0.01
PROPAL	Proserpinaca palustris							0.01					
RHYINU	Rhynchospora inundata						0.01						
RHYMIC	Rhynchospora microcarpa						0.01		0.01				
RHYTRA	Rhynchospora tracyi							0.01				0.06	
SAGLAN	Sagittaria lancifolia	0.06	0.04	3.03	0.05	0.23	0.09	1.83	0.08		0.49	0.03	0.19
SALCAR	Salix caroliniana					0.83		0.03			0.27	0.44	
SALSPP	Salvinia Sp.												
THEINT	Thelypteris interrupta		0.15										
TYPDOM	Typha domingensis	0.23	1.60	0.31	1.70	11.69	0.97	0.58	0.18	3.18	5.92	0.15	0.34
UTRFOL	Utricularia foliosa	0.64	3.48	0.62	1.65	1.32	0.42	0.16	0.13	0.17	0.69	0.08	1.21
UTRGIB	Utricularia gibba												
UTRPUR	Utricularia purpurea	0.29	2.56		17.38	1.33	0.07	0.06	0.60	3.25	0.75	0.83	0.53
XYRCAR	Xyris caroliniana		0.01										
XYRSPP	Xyris sp.												

SPCODE	Spacios							Year-4	Ļ					
SICODE	species	50	51	52	53	54	55	56	58	59	61	62	63	220
AESPRA	Aeschynomene pratensis	0.04	0.01			0.03	0.02	0.04	0.02			0.12		
AGALIN	Agalinis linifolia													
ANNGLA	Annona glabra	0.15		0.09		0.09			0.47			0.19		
BACCAR	Bacopa caroliniana	0.82	2.93		0.04	1.25	1.46	0.84	2.79			0.98		1.07
BLESER	Blechnum serrulatum	0.30		0.09		0.09	0.19		0.04			0.02		
CENASI	Centella asiatica		0.16											
CEPOCC	Cephalanthus occidentalis	0.04	1.84	1.66	0.05		0.36	0.03	0.67	0.46		0.08		
CHARA	Chara sp.		0.04					0.10	0.01		0.62			
CHRICA	Chrysobalanus icaco	0.59							0.09					
CLAJAM	Cladium jamaicense	58.74	11.64	24.79	31.99	53.75	24.74	60.84	24.64	64.81	41.96	67.10	9.78	72.70
CRIAME	Crinum americanum		0.52	0.09		0.02	0.71	0.20	0.53	0.08		0.40		0.04
DICDIC	Dichanthelium dichotomum													
DICSPP	Dichanthelium sp.													
DIOVIR	Diodia virginiana													
ELECEL	Eleocharis cellulosa	7.99	16.24	3.44	2.60	20.46	7.94	2.84	18.53	0.52	1.37	9.08	1.13	1.65
ELEELO	Eleocharis elongata	0.93		11.38	3.17	0.37	2.11	3.02	13.03			1.92		
ELEINT	Eleocharis interstincta								0.13					0.24
ELESPP	Eleocharis sp.													
ERISPP	Eriocaulon sp.													
FUIBRE	Fuirena breviseta													
FUISCI	Fuirena scirpoidea													
HYDCOR	Hydrolea corymbosa						0.02							
HYMLAT	Hymenocallis latifolia													
HYMPAL	Hymenocallis palmeri		0.06			0.05	1.47	0.25	0.04	0.66		0.17		0.22
ILECAS	Ilex cassine													
IPOSAG	Ipomoea sagittata	0.01		0.02			0.11	0.05				0.02		
JUSANG	Justicia angusta	0.13	0.21			0.19	0.22	0.13				0.10		0.16

SPCODE	YPCODE Species Year-4													
SPCODE	Species	50	51	52	53	54	55	56	58	59	61	62	63	220
LEEHEX	Leersia hexandra	0.04	0.54	0.05	0.04	0.07	0.26	0.28	0.03			0.24		0.02
LUDALA	Ludwigia alata									0.02				
LUDREP	Ludwigia repens													
LYGMIC	Lygodium microphyllum													
MIKSCA	Mikania scandens													
MORCER	Morella cerifera													
NEPBIS	Nephrolepis biserrata													
NYMAQU	Nymphoides aquatica	0.14		0.63			3.22	0.10	0.21		0.01		0.11	0.14
NYMODO	Nymphaea odorata	2.25	0.02	15.11	20.40	0.05	13.14		0.90		18.02	0.01	33.84	2.16
OSMREG	Osmunda regalis													
OXYFIL	Oxypolis filiformis		0.10											
PANHEM	Panicum hemitomon	0.21	1.55	0.22	0.17	0.63	2.77	0.60	0.62	0.10		0.82	0.04	0.02
PANTEN	Panicum tenerum													
PASGEM	Paspalidium geminatum	0.18	0.16	0.09	0.42	0.16	0.43	0.24	1.74			0.17	0.40	0.09
PELVIR	Peltandra virginica	0.09	0.02	0.75	0.02	0.20	0.04	0.02	0.63	0.10		0.24		0.08
PERHYD	Persicaria hydropiperoides		0.02					0.01		0.04				
PERSET	Persicaria setaceum									0.60				
PLUBAC	Pluchea baccharis	0.01	0.20			0.01				0.10				
PONCOR	Pontederia cordata		0.07	1.48	0.16	0.06	0.02	0.33	0.52	0.11		0.07		
POTILL	Potamogeton illinoensis	0.07	0.29					0.02	1.77			0.09		
PROPAL	Proserpinaca palustris							0.02		0.01				
RHYINU	Rhynchospora inundata						0.09							
RHYMIC	Rhynchospora microcarpa		0.01											0.02
RHYTRA	Rhynchospora tracyi		1.73				0.29			0.01				
SAGLAN	Sagittaria lancifolia	0.04	1.88	0.15	0.21	0.61	0.02	0.04	0.16	2.26	0.06	0.44		
SALCAR	Salix caroliniana		0.60	0.04			0.97		0.23	0.63	0.05			
SALSPP	Salvinia Sp.													
THEINT	Thelypteris interrupta													
TYPDOM	Typha domingensis	0.30	2.66	8.83	1.15	1.14		0.62	0.68	0.02	2.07	0.88	0.84	0.46
UTRFOL	Utricularia foliosa	0.44		0.09	0.71	0.69	0.74	1.51	0.26		1.94	0.23	4.70	0.42
UTRGIB	Utricularia gibba													
UTRPUR	Utricularia purpurea	1.00		5.85	27.96	0.37	4.42	2.14	4.15	0.01	1.40	0.08	10.81	0.28
XYRCAR	Xyris caroliniana													
XYRSPP	Xyris sp.													

SPCODE	Emosion	Year-5										
	Species	65	66	67	68	69	71	73	79	BS1	BS2	BS3
AESPRA	Aeschynomene pratensis		0.02							0.01	0.04	
AGALIN	Agalinis linifolia		0.75	0.07	0.02	0.06	0.10					
ANNGLA	Annona glabra									0.02	0.20	
BACCAR	Bacopa caroliniana	1.04	0.43	3.43			6.83		3.18	1.03	0.73	1.24
BLESER	Blechnum serrulatum	1.73					0.02			0.04	0.06	0.08
CENASI	Centella asiatica			0.26								
CEPOCC	Cephalanthus occidentalis	0.86	1.77	0.21	0.36	0.33	0.85		0.20	0.13	0.02	
CHARA	Chara sp.	0.02	0.11	3.15	0.04	0.23	0.48	0.83	0.36	1.65	1.61	0.46
CHRICA	Chrysobalanus icaco										0.31	
CLAJAM	Cladium jamaicense	13.85	32.05	3.30	12.13	36.55	24.73	31.69	25.49	34.27	27.12	35.50
CRIAME	Crinum americanum		1.12		0.05	0.05	0.97		0.79	1.48	0.96	1.15
DICDIC	Dichanthelium dichotomum			0.30								
DICSPP	Dichanthelium sp.											
DIOVIR	Diodia virginiana			0.03					0.07			
ELECEL	Eleocharis cellulosa	0.56	2.07	4.05	2.90	0.63	9.55		6.11	3.74	4.69	3.42
ELEELO	Eleocharis elongata	8.60	0.88		2.15	1.68	1.02			1.84	0.65	1.21
ELEINT	Eleocharis interstincta									1.03		
ELESPP	Eleocharis sp.											
ERISPP	Eriocaulon sp.											
FUIBRE	Fuirena breviseta	0.03		0.13								
FUISCI	Fuirena scirpoidea	0.25										
HYDCOR	Hydrolea corymbosa		0.04									
HYMLAT	Hymenocallis latifolia											
HYMPAL	Hymenocallis palmeri		1.14	0.17	0.25		1.60		0.13	0.19	0.24	0.36
ILECAS	Ilex cassine	0.34										
IPOSAG	Ipomoea sagittata		0.19				0.35			0.13	0.02	0.06
JUSANG	Justicia angusta		0.32	0.01			0.17			0.29	0.22	0.16
LEEHEX	Leersia hexandra			0.36	0.40		0.45		1.08	0.21	0.21	0.06
LUDALA	Ludwigia alata			0.12					0.07			
LUDREP	Ludwigia repens											
LYGMIC	Lygodium microphyllum	0.61										
MIKSCA	Mikania scandens			0.03								
MORCER	Morella cerifera	1.32	0.05				0.12			0.03	0.51	0.19
NEPBIS	Nephrolepis biserrata	0.52									0.08	
NYMAQU	Nymphoides aquatica	2.45	1.69		2.77	0.28	3.07		0.55	0.05	0.04	0.16
NYMODO	Nymphaea odorata	14.25	15.67		25.99	8.62	5.98	0.26	14.78	0.00	0.02	0.02
OSMREG	Osmunda regalis	0.11	0.12		-0.77	0.02	0.06	0.20	1.1.70		0.04	0.05
OXYFIL	Oxypolis filiformis	0.11	0.05	0.18			0.02				0.02	0.00
PANHEM	Panicum hemitomon	3 33	0.86	1 10	0.62	0.03	2.14		1 67	0 94	0.19	0.51
PANTEN	Panicum tenerum	0.03	0.00	0.03	0.02	0.05	2.1 1		1.07	0.71	0.19	0.01
PASGEM	Paspalidium geminatum	0.05	0.42	0.05	0.31		1 10		0.42	0 38	0.17	0.02
PELVIR	Peltandra virginica	3 30	1.58	0.10	0.25	0.05	0.06		0.42	0.26	0.13	0.02
PERHYD	Persicaria hydronineroides	5.50	1.50	0.83	0.23	0.05	0.00			0.20	0.15	0.22
PERSET	Persicaria setaceum			0.05								
PLUBAC	Pluchea baccharis			0.26						0.01		
PONCOR	Pontederia cordata	1.69	0.63	1.23	0.54	0.11		0.02	0.68	0.27	0.20	

SDCODE	Species -	Year-5										
SPCODE		65	66	67	68	69	71	73	79	BS1	BS2	BS3
POTILL	Potamogeton illinoensis				0.01				0.27	0.04	0.04	
PROPAL	Proserpinaca palustris			0.08						0.02		
RHYINU	Rhynchospora inundata	0.36	0.15	0.05			0.33			0.03		
RHYMIC	Rhynchospora microcarpa	0.32		0.42			0.06			0.01		
RHYTRA	Rhynchospora tracyi	0.05	0.04	2.17			0.97		0.09			
SAGLAN	Sagittaria lancifolia	0.05	0.31	8.97	0.10	0.32	0.48	0.68	2.32	0.02		0.05
SALCAR	Salix caroliniana					0.42			0.70	0.38		
SALSPP	Salvinia Sp.	0.47										
THEINT	Thelypteris interrupta	0.11										
TYPDOM	Typha domingensis	0.06	0.08	4.10	0.76	4.54	0.22	20.48	4.93	3.21	0.23	0.05
UTRFOL	Utricularia foliosa	3.35	1.03	0.08	0.12	6.02	0.08		1.96	0.97	0.13	0.05
UTRGIB	Utricularia gibba											
UTRPUR	Utricularia purpurea	5.77	6.12	0.02	7.49	5.00	4.50	0.04	4.27	14.15	11.80	12.78
XYRCAR	Xyris caroliniana	0.17										
XYRSPP	Xyris sp.	0.22										

Cycle-2 Year	PSU	PSU_ID	Region	Number of plots (1 m ²)	species Richness /m² (α)	Species Richness/ PSU (γ)	Evenness	Shannon`s diversity	Beta Diversity (γ/α)
1	0	P000	ENP_W	135	2.6	25	0.378	1.217	9.561
1	1	P001	WCA1	114	4.8	36	0.478	1.713	7.558
1	2	P002	WCA3AS	129	3.8	23	0.525	1.646	6.055
1	3	P003	WCA3AN	71	4.8	31	0.557	1.912	6.493
1	4	P004	WCA3AC	121	3.6	28	0.502	1.673	7.789
1	6	P006	ENP_S	129	2.7	15	0.397	1.076	5.625
1	7	P007	WCA3AN	135	4.1	25	0.554	1.782	6.170
1	9	P009	WCA2	120	2.4	7	0.630	1.226	2.887
1	11	P011	WCA3AC	135	3.2	20	0.527	1.579	6.164
1	15	P015	WCA3AC	135	2.7	10	0.626	1.442	3.689
1	108	P108	WCA3B	119	3.1	27	0.472	1.555	8.684
2	17	P017	WCA1	120	3.8	39	0.445	1.631	10.196
2	18	P018	ENP_W	42	2.7	12	0.499	1.239	4.383
2	19	P019	WCA3AN	89	2.9	21	0.575	1.750	7.358
2	20	P020	WCA3B	135	2.6	16	0.439	1.217	6.154
2	21	P021	WCA2	129	1.8	7	0.324	0.630	3.909
2	23	P023	WCA3AC	132	4.3	26	0.736	2.399	6.085
2	24	P024	ENP_N	130	2.4	20	0.497	1.488	8.414
2	26	P026	WCA3AC	129	4.6	29	0.713	2.400	6.287
2	28	P028	WCA3B	135	3.1	19	0.577	1.699	6.181
2	30	P030	ENP_S	135	2.9	26	0.488	1.591	9.093
2	31	P031	WCA3AC	135	3.5	24	0.517	1.643	6.923
3	32	P032	ENP_N	133	2.4	19	0.236	0.695	7.872
3	34	P034	WCA3AS	134	3.2	29	0.529	1.781	9.122
3	35	P035	WCA3AN	28	3.2	15	0.762	2.062	4.667
3	36	P036	WCA3AS	109	2.2	11	0.546	1.308	5.017
3	37	P037	WCA2	109	2.5	14	0.550	1.452	5.673
3	39	P039	WCA3AN	134	3.2	22	0.503	1.554	6.904
3	43	P043	WCA3AN	125	2.9	22	0.316	0.977	7.660
3	44	P044	WCA3B	131	2.6	20	0.331	0.992	7.616
3	45	P045	WCA3AS	87	1.7	10	0.693	1.595	5.800
3	47	P047	WCA3AC	91	2.4	18	0.560	1.618	7.412
3	513	P513	ENP_N	103	2.0	20	0.205	0.614	10.198
3	DPM	PDPM	WCA3B	213	2.0	21	0.285	0.868	10.330
4	50	P050	ENP_W	135	2.1	23	0.290	0.909	11.050
4	51	P051	WCA3AN	123	2.4	26	0.593	1.933	10.915
4	52	P052	WCA3AS	112	2.9	21	0.633	1.926	7.304

Appendix 4: Plant species richness, evenness, and diversity indices in 58 PSUs surveyed during Year 1-5 (2015-2020).

Cycle-2 Year	PSU	PSU_ID	Region	Number of plots (1 m ²)	species Richness /m² (α)	Species Richness/ PSU (γ)	Evenness	Shannon`s diversity	Beta Diversity (γ/α)
4	53	P053	WCA2	126	2.7	15	0.539	1.461	5.478
4	54	P054	ENP_W	108	2.3	22	0.321	0.993	9.659
4	55	P055	WCA3AC	129	3.8	27	0.623	2.055	7.181
4	56	P056	ENP_N	126	2.1	23	0.278	0.871	11.146
4	58	P058	WCA3AS	117	3.1	26	0.590	1.922	8.403
4	59	P059	WCA3AN	134	2.1	18	0.153	0.443	8.493
4	61	P061	WCA2	129	2.0	9	0.469	1.030	4.448
4	62	P062	ENP_S	131	2.3	23	0.268	0.839	10.179
4	63	P063	WCA3AS	135	2.4	9	0.593	1.304	3.821
4	220	P220	WCA3B	125	1.8	17	0.169	0.479	9.487
5	65	P065	WCA1	110	5.7	39	0.682	2.498	6.799
5	66	P066	WCA3AC	132	4.3	27	0.564	1.859	6.275
5	67	P067	WCA3AN	120	3.8	38	0.660	2.402	10.022
5	68	P068	WCA3AS	135	3.5	19	0.578	1.702	5.481
5	69	P069	WCA2	108	3.0	16	0.533	1.477	5.417
5	71	P071	WCA3AC	126	4.9	27	0.654	2.155	5.514
5	73	P073	WCA2	133	1.3	6	0.428	0.766	4.560
5	79	P079	WCA3AC	114	3.8	21	0.677	2.060	5.466
5	BS1	PBS1	ENP_N	117	3.2	32	0.476	1.648	10.146
5	BS2	PBS2	ENP_N	127	3.1	28	0.433	1.444	9.118
5	BS3	PBS3	ENP_N	132	2.9	22	0.405	1.252	7.504

Appendix 5: Results of Generalized Linear Model for Species Richness and General Linear Model for Beta diversity (β) and Evenness showing the effects of long-term mean water depth (LTMWD), standard deviation of long-term water depth (LTWD_SD), fire frequency (FF Index), and time since last fire (TSLF).

Generalized Linear Model								
	Estimate	Std. Error	p-value					
<u>Plot-level Species Richness</u> (n = 4,178)								
(Intercept)	0.836	0.040	< 0.001					
LTMWD	0.006	0.001	< 0.001					
FF Index	0.218	0.030	< 0.001					
TSLF	0.003	0.002	0.084					
LTMWD:FF Index	-0.009	0.001	< 0.001					
<u>PSU-level Species Richness</u> (n = 58)								
(Intercept)	2.4150	0.3248	< 0.001					
LTMWD	0.0060	0.0092	0.514					
(LTMWD)^2	-0.0002	0.0001	0.019					
LTWD_SD	0.1722	0.0490	< 0.001					
(LTWD_SD)^2	-0.0067	0.0020	0.001					
FF Index	-0.0350	0.1182	0.767					
(FF Index) ²	0.0345	0.0173	0.046					
LTWD_SD:FF Index	-0.0223	0.0077	0.004					
Gener	ral Linear Model							
<u>Beta Diversity</u> (β) (n = 58)								
(Intercept)	8.650	1.223	< 0.001					
LTMWD	-0.066	0.020	0.002					
LTMWD_SD	0.136	0.111	0.223					
FF Index	-0.066	0.471	0.889					
LTMWD:FF Index	0.022	0.015	0.142					
LTWD_SD:FF Index	-0.089	0.057	0.129					
<u>PSU-level Species Evenness</u> (n = 58)								
(Intercept)	0.419	0.083	< 0.001					
LTMWD	0.003	0.001	0.056					
LTMWD_SD	0.000	0.007	0.982					
FF Index	0.036	0.032	0.260					
LTMWD:FF Index	-0.003	0.001	0.002					
LTWD_SD:FF Index	0.005	0.004	0.244					