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Michael S. Ross
*Southeast Environmental Research Center & Department of Earth and Environment, Florida International University*

James B. Heffernan
*Nicholas School of the Environment, Duke University*

Jay P. Sah
*Southeast Environmental Research Center, Florida International University*

Pablo L. Ruiz
*Southeast Environmental Research Center, Florida International University*

Adam A. Spitzig
*Southeast Environmental Research Center, Florida International University*

***See next page for additional authors***

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**Authors**
Michael S. Ross, James B. Heffernan, Jay P. Sah, Pablo L. Ruiz, Adam A. Spitzig, and Ewan Isherwood

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# Year 2 Annual Report: Everglades Ridge, Slough, and Tree Island Mosaics

**Date of Submission:**

**By:**

**Michael S. Ross,** Southeast Environmental Research Center & Department of Earth and
Environment, Florida International University, 11200 SW 8th ST, Miami, FL 33199
Tel 305-348-1420; Fax 305-348-4096; Email: rossm@fiu.edu

**James B. Heffernan,** Nicholas School of the Environment, Duke University

**Jay P. Sah,** Southeast Environmental Research Center, Florida International University,
OE 148, 11200 SW 8th ST, Miami, FL 33199;
Tel 305-348-1658; Fax 305-348-4096; Email: sahj@fiu.edu

**Pablo L. Ruiz,** Southeast Environmental Research Center, Florida International University,
OE 148, 11200 SW 8th ST, Miami, FL 33199;
Tel 305-348-1658; Fax 305-348-4096; Email: ruizp@fiu.edu

**Adam A. Spitzig,** Southeast Environmental Research Center, Florida International University,
OE 148, 11200 SW 8th ST, Miami, FL 33199;
Tel 305-348-1658; Fax 305-348-4096; Email: aspitzig@fiu.edu

**Ewan Isherwood,** Florida International University, Department of Biological Sciences

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# INTRODUCTION

## *Status and history of the Ridge-Slough Mosaic*

The Florida Everglades is a large subtropical wetland with diverse hydrologic, edaphic, and vegetative characteristics. Historically, a significant portion of this system was a slow moving river originating from the Kissimmee River floodplain, flowing into the vast but shallow Lake Okeechobee, and draining south-southwest over extensive peatlands into Florida Bay (McVoy 2011). Human-induced alterations to the hydrologic regime, including reduction, stabilization, and impoundment of water flow through diversion and compartmentalization of water via canals and levees have degraded pre-drainage vegetation patterns and microtopographic structure (Davis and Ogden 1994, Ogden 2005, McVoy 2011).

The Everglades peatland emerged 5,000 years ago with the stabilization of sea level at approximately current elevations (Loveless 1959, Gleason and Stone 1994). This, combined with subtropical rainfalls, allowed a vast mass of water to slowly flow over a limestone bedrock platform 160 km long and 50 km wide at a near uniform descent totaling about 6 m, ultimately reaching Florida Bay (Stephens 1956, Gleason and Stone 1994, McVoy 2011). Vegetation quickly colonized the area, and peat, in the absence of adequate respiration, accumulated on the limestone bedrock to a depth of 3-3.7 m (Gleason and Stone 1994, McVoy et al. 2011). The "River of Grass" referenced by Douglas (1947) alludes to the dually intertwined processes of the historic riverine nature of the Everglades and the vast sawgrass (*Cladium jamaicense*) communities that have dominated the landscape for about the last 1,000 years (Bernhardt and Willard 2009).

McVoy et al. (2011) identify eight major historic landscapes that comprised the greater Everglades: Custard Apple Swamp, Sawgrass Plains, Ridge and Slough, Peat Transverse Glades, Rockland Marl Marsh, Marl Transverse Glades, Perrine Marl Marsh, and the Ochopee Marl Marsh. Of these, the Ridge and Slough (c. 6,000 km$^2$) encompassed slightly over 50% of the total extent (c.11,000 km$^2$). Prior to hydrologic modification, this landscape provided biotic communities with distinct elevational niches that were organized in a characteristic pattern parallel to flow (Figure 1). Ridges, comprised almost totally of dense stands of sawgrass, were located in areas of higher topographic relief (and therefore lower water depths), whereas sloughs containing white water lily (*Nymphaea odorata*), other macrophytes, and periphyton were at lower elevation and therefore deeper water (Loveless 1959, Ogden 2005, McVoy 2011). A third community, the wet prairie, was comprised of *Eleocharis cellulosa (*spikerush), *Panicum hemitomon* (maidencane), and *Rhynchospora tracyi* (beakrush), and usually occupied the physical zone between the boundary of ridges and sloughs, in areas of intermediate water depths (Loveless 1959, Ogden 2005). The Ridge and Slough landscape was interspersed with high elevation tree islands which support hardwood communities, and portion of which remain fully emergent throughout the year (Loveless 1959, Sklar and van der Valk 2002, van der Valk and Warner 2009).

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 Ridge and Slough landscape (Loveless 1959, Ogden 2005, McVoy 2011). In the current managed Everglades system, the pre-drainage, patterned mosaic of sawgrass ridges, sloughs and tree islands (Fig. 1) has been substantially altered or reduced largely as a result of human alterations to historic ecological and hydrological processes (Larsen et al. 2011).

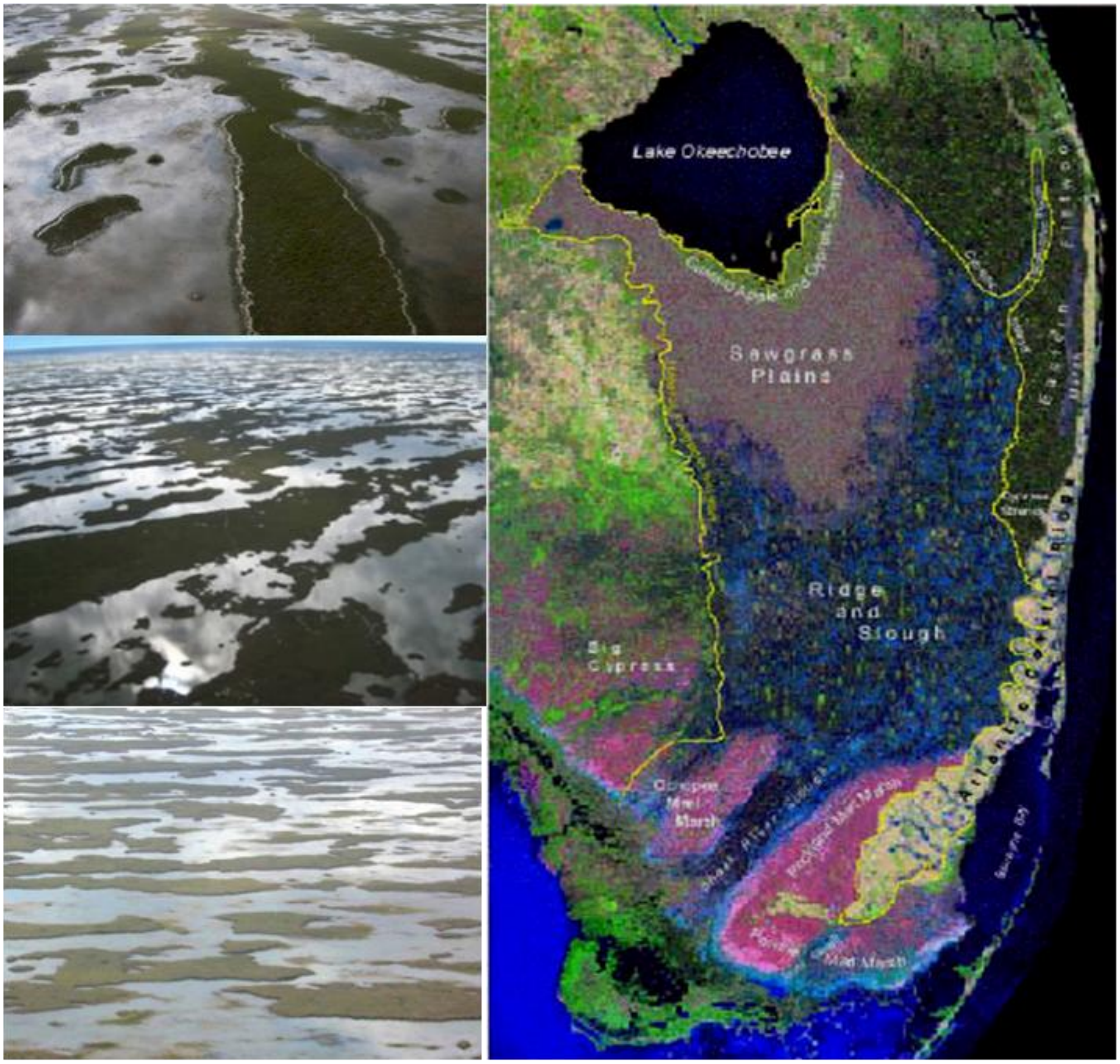


Fig. 1 – Aerial images and historic distribution of the ridge-slough landscape. (Left) Linear, flow-parallel orientation of ridges and sloughs under conserved conditions. (Right) Distribution of ridge and slough and other landscape types prior to major

The Ridge and Slough community has undergone dramatic structural, compositional and functional changes since anthropogenic modification of the hydrologic regime began in the early 20th century (Davis and Ogden 1994, Team 2003, Ogden 2005, Larsen et al. 2011, McVoy 2011). Average water levels across the Ridge and Slough landscape are estimated to be 30-45 cm lower between the pre-modification era and 1955, but have since rebounded slightly through concentrated restoration efforts (McVoy 2011). Nonetheless, sloughs in many areas of the Everglades frequently "dry-down" by the end of the dry season, but in the pre-modified landscape it is believed that sloughs dried very rarely, supported by an estimation of average depth at 90 cm (McVoy 2011). These changing hydrologic regimes result from some combination of altered water flows and loss of microtopographic structure.

Lower hydroperiods have severely restricted the range and abundance of many slough species, including the historically ubiquitous white water lily, and even more drastically restricted spatterdock (*Nuphar advena*), a species adapted to the deepest water (McVoy 2011). Similarly, hydrologic modification has led to an expansion among species better adapted to low water, such as sawgrass and southern cattail (Urban et al. 1993, Davis and Ogden 1994, Gunderson 2001, McVoy 2011). Woody vegetation may have been uncommon in the ridge community prior to hydrologic modification (Loveless 1959, McVoy 2011), but wax myrtle (*Myrica cerifcra*) and coastal plain willow (*Salix caroliniana*) now frequently inhabit ridges in drained areas (McVoy 2011). Ross et al. (2003) found that subtle but significant differences in hydroperiod define the boundaries between ridge, slough, and wet prairie communities in Shark Slough, ENP, but these boundaries are eroding with hydrologic modification. Similarly, working in a marl prairie environment in Taylor Slough, ENP, Armentano et al. (2006) found that changes in the hydrologic regime over periods as brief as three years had induced concurrent changes in vegetation composition and community patterning. Zweig and Kitchens (2008, 2009) found vegetation communities in southern Water Conservation Area 3A (WCA 3A) are influenced by both current and historic hydrologic conditions, and vegetation responses to hydrologic modification varied among species. Loss of historically distinct vegetation communities thus appears to be a characteristic of ridges and sloughs to hydrologic modification.

Hydrologic modification also has consequences for the landscape-scale structure of the ridge-slough mosaic (Fig. 2). Where hydroperiods have been reduced, ridges have invaded marsh areas (Team 2003, Ogden 2005), and much of the slough component of the landscape, particularly in the Everglades National Park, has been usurped by both wet prairie and ridge (Davis and Ogden 1994, Olmsted and Armentano 1997, Richards et al. 2011). Areas of reduced flow have lost the elongated ridge-slough topography, while areas with excessively long flooding duration 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, Larsen et al. 2007, Watts et al. 2010), and elevation differences between ridges and sloughs have become less distinct (Fig. 3; Watts et al. 2010, McVoy 2011). However, while many characteristics of degrading Everglades landscapes are known, to date no system-wide and systematic studies have addressed their spatial distribution, hydrologic constraints, and covariation.

### *Self-organization of the Ridge and Slough Landscape*

The characteristic ridge and slough mosaic has been theorized to be a self-organized landscape maintained by autogenic processes that balance ridge expansion and slough persistence.

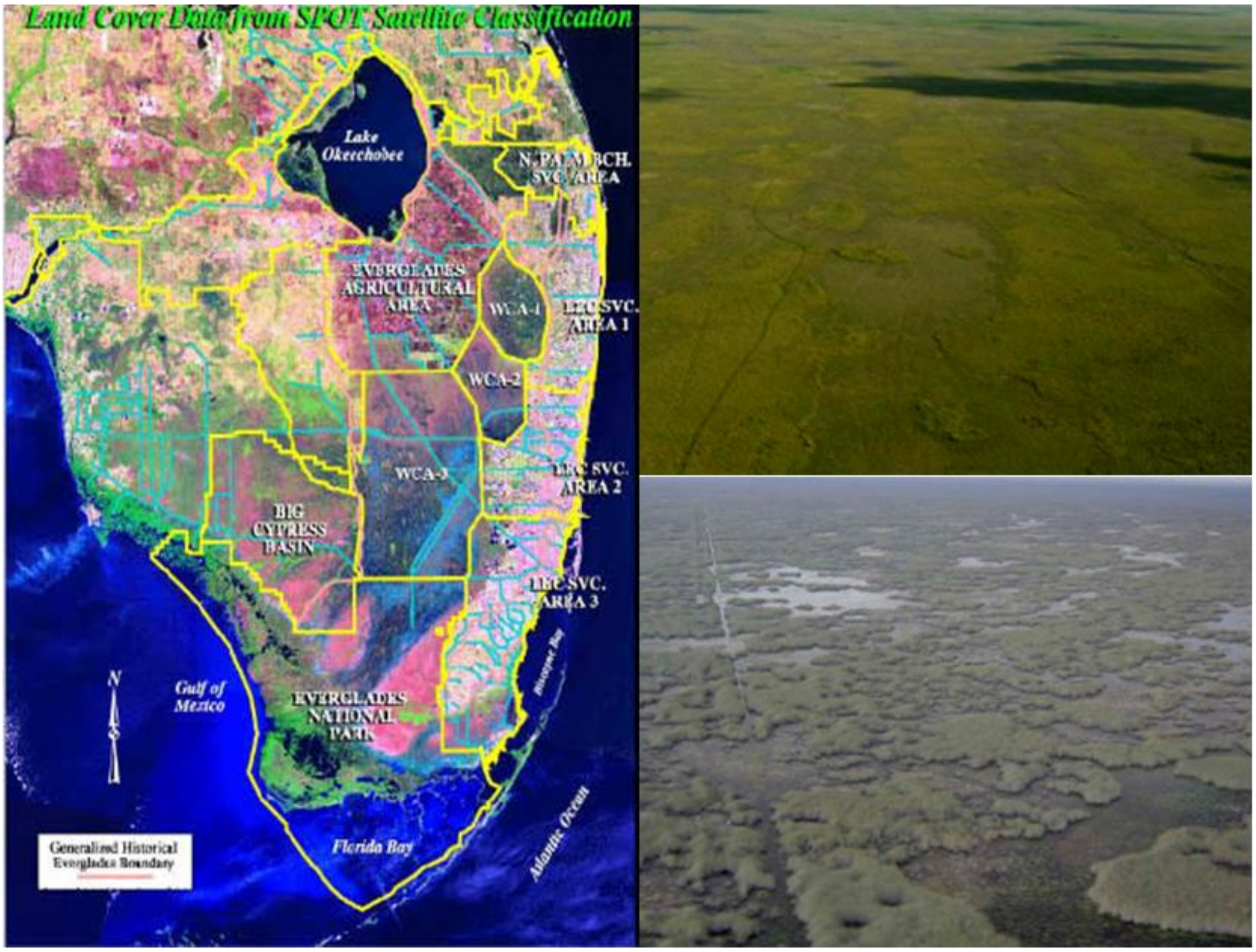


Fig. 2 – Present configuration of the greater Everglades, and associated changes in ridge-slough structure. (Left) The contemporary Everglades is subdivided into distinct management basins subject to varied uses and management objectives. These basins are bounded and separated by hydrologic engineering structures including canals and levees. (Right, top) Where hydrologic modification has reduced water levels and hydroperiod, historic ridge-slough landscapes have lost topographic structure and become dominated by sawgrass (Cladium jamicense). (Right bottom) Where impoundment has raised water levels and lengthened hydroperiods, ridges senesce and the landscape takes on a characteristic 'moth-eaten' pattern.

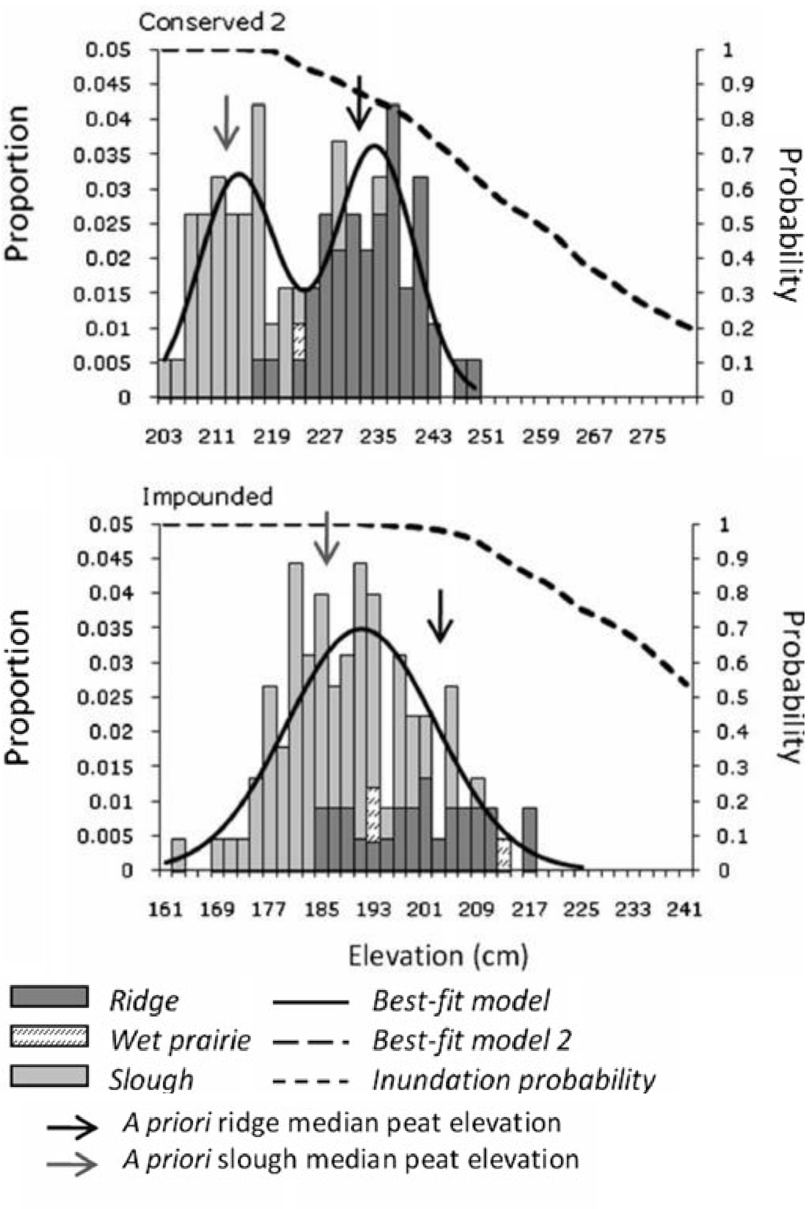


Figure 3 - Examples of conserved (top) and degraded (bottom) microtopographic structure. Conserved landscapes are characterized by high topographic heterogeneity and bi-modal elevation distributions. Degraded landscapes have lost these characteristics. From Watts et al. 2010. Shadings indicate vegetation 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.

(Larsen et al. 2007, Givnish et al. 2008, Larsen and Harvey 2010, Watts et al. 2010, Cohen et al. 2011). Decoupling of soil elevations from underlying bedrock topography in areas of relatively conserved landscape pattern suggests that historic microtopography and landscape structure have arisen largely from internal feedbacks between vegetation, hydrology, and soil elevations. Whether local geologic features have acted as nucleation sites for ridge initiation remains unresolved. In either case, pressure exerted by the hydrologic regime has been theorized to promote the stable existence of the ridge and slough communities (Givnish et al. 2008, Watts et al. 2010, Cohen et al. 2011). 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. Peat depth is maintained by decomposition of biomass, and the loss of peat 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. Community shifts in microtopographic range when the hydrologic regime changes may help maintain vegetation zonation, and thus potentially feed back on microtopographic structure (SCT 2003, Larsen and Harvey 2010, Cohen et al. 2011, D'Odorico et al. 2011).

Regular self-organized spatial patterning of ecological systems results from spatially-dependent feedbacks whose strength and sign vary with distance (Rietkerk and Van de Koppel 2008). While strong local feedbacks can generate discrete patches on the landscape (Silliman et al. 2005, D'Odorico et al. 2011), regular patterning of such mosaics is generated by distal negative feedbacks, by which the presence of organisms at one location inhibits their establishment or persistence at some distance (van de Koppel et al. 2005). In some cases, organisms concentrate a limiting resource such as water or soil nutrients (Rietkerk et al. 2002, Rietkerk et al. 2004b, Ludwig et al. 2005, Eppinga et al. 2009), facilitating local expansion while limiting suitability of locations outside of occupied patches. In others, plants or animals may locally mitigate a stressor such as temperature, salinity, or shear stress but exacerbate the stressor outside the area of biotic influence (Bader et al. 2007, Weerman et al. 2010). The diversity of potential distal feedbacks in any given ecosystem requires the development of distinctive predictions that discriminate among plausible mechanisms (Eppinga et al. 2010).

When distal negative feedbacks are coupled to strong local positive feedbacks, spatial patterning can exhibit global bi-stability (Fig. 4), meaning that alternative equilibria may exist at the scale of entire landscapes. In such cases, either regular patterning or unstructured, homogenous states may exist under the same set of environmental conditions. As a result, transitions between patterned and homogenous states may be sudden, and trajectories of recovery may exhibit hysteresis (meaning that transitions in one direction occur at a different threshold condition than transitions in the other direction (Rietkerk et al. 2004a). While some researchers have argued that regular spatial patterning always exhibits global bi-stability across some range of conditions (Rietkerk et al. 2004a), others have illustrated that regular patterning can arise via stochastic processes that do not produce such landscape-scale transitions (D'Odorico et al. 2007). Nonetheless, the potential for hysteretic responses of patterning to environmental drivers presents a challenge to their conservation and restoration (van de Koppel et al. 2002, Suding et al. 2004, Suding and Hobbs 2009), particularly since the loss of patterning can have important implications for ecosystem function (Rietkerk et al. 2004a, D'Odorico et al. 2006) and habitat value (Ogden 2005).

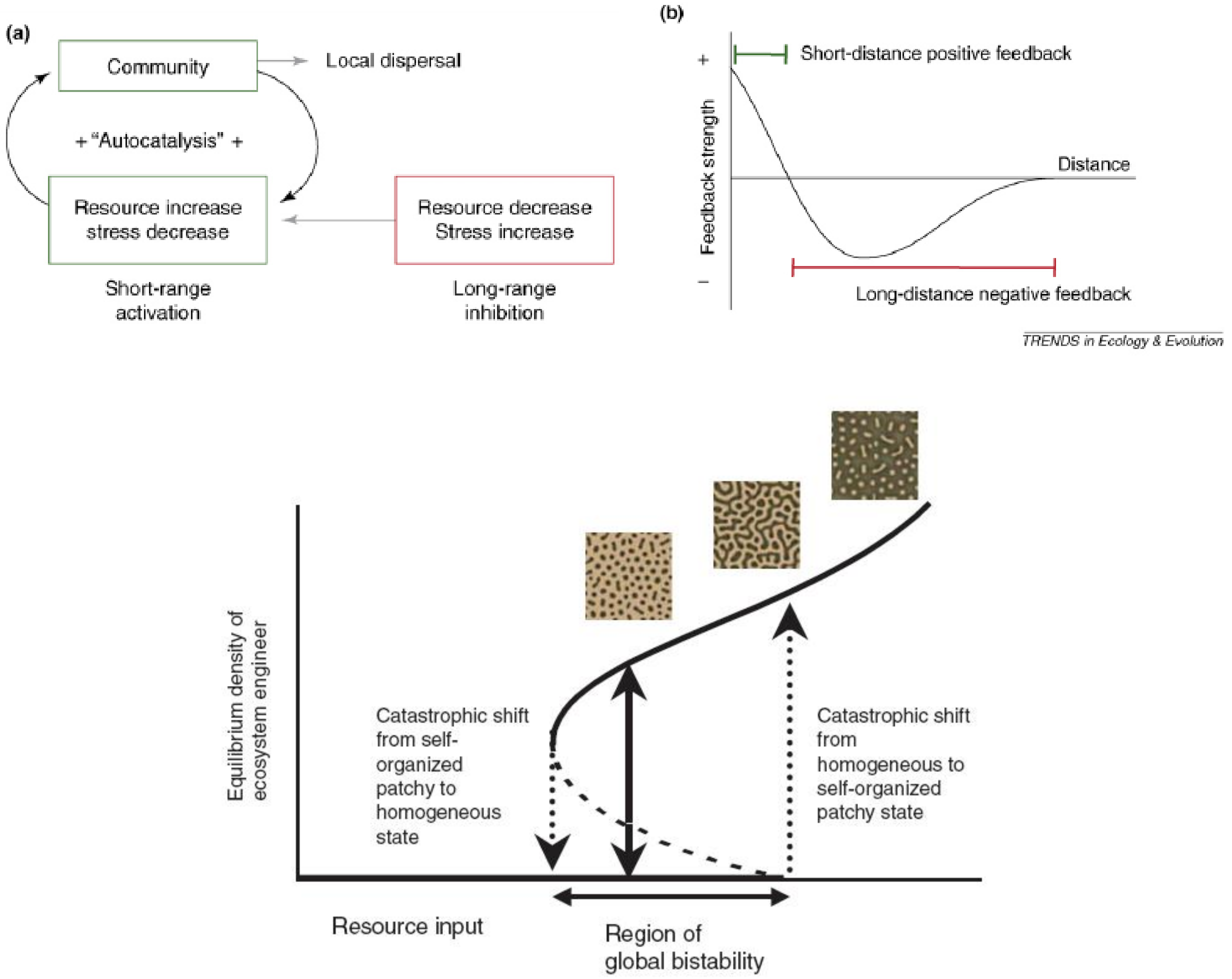


Figure 4. Feedback processes that generate regular pattern and landscape-scale alternative stable states, as is hypothesized to occur in the Everglades Ridge and Slough. (a and b) Biota can, in some cases, create positive local feedbacks via resource increases and stress decreases, but as a consequence reduce the suitability of habitat at greater distances. (c) In response to varied resource inputs (or stressors), patterned landscapes may undergo catastrophic transitions to a homogenous state. Across some range of conditions, both the patterned and homogenous states may be stable, in which case the degraded condition may resist restoration. (a) and (b) from Rietkerk and van de Koppel 2008; (c) From Rietkerk et al. 2004.

The emergence of flow-parallel patterning in the Everglades suggests that the spatial feedbacks that create pattern must act anisotropically (i.e., differently with direction), and that water flow is an important component of those feedbacks. 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. in revision). While the relative importance of and interactions between these mechanisms remains an active area of research, observations of pattern loss in response to hydrologic management, nutrient enrichment, and other disturbances points to the disruption of those feedbacks as a primary cause of landscape degradation (Sklar et al. 2004).

The coupling of microtopography, hydrology, vegetation composition and productivity, and their responses to hydrologic modification and other disturbance can create challenges in disentangling causal relationships and diagnosing trajectories of change. One objective of this monitoring study is 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 sometime after hydrologic modification (Ross et al. 2003, Givnish et al. 2008, Zweig and Kitchens 2008, Zweig and Kitchens 2009), vegetation changes may also influence microtopography (Cohen et al. 2011, Larsen et al. 2011). Watts et al. (2010) hypothesize that topographic changes are more rapid than those of vegetation structure. They argue that drainage and stabilization of the Everglades hydrologic regime leads to more rapid peat loss through aerobic bacterial respiration in higher elevation ridges compared to sloughs, flattening landscape scale topography. Simultaneously, but over much longer timeframes, drained and stabilized hydrologic regimes facilitate ridge expansion through the more drained sloughs, resulting in vegetation structure homogeneity (Larsen and Harvey 2010). Then, after some time period, both topography and vegetation structure equilibrate to a relatively homogenous landscape. Nonetheless, the relative timescales of changing vegetation and topographic structure are not well understood.

Simultaneous assessment of microtopographic structure and vegetation community composition provide one means to assess the relative time scales over which these characteristics respond to hydrologic modification (Fig. 5), i.e., whether landform or vegetation is more resistant to change in water regime. If vegetation change precedes topographic change, then we should observe a subset of sampled landscapes in which vegetation community composition is relatively conserved, but topographic structure is degraded. If topographic change precedes vegetation change, we will observe only the converse configuration.

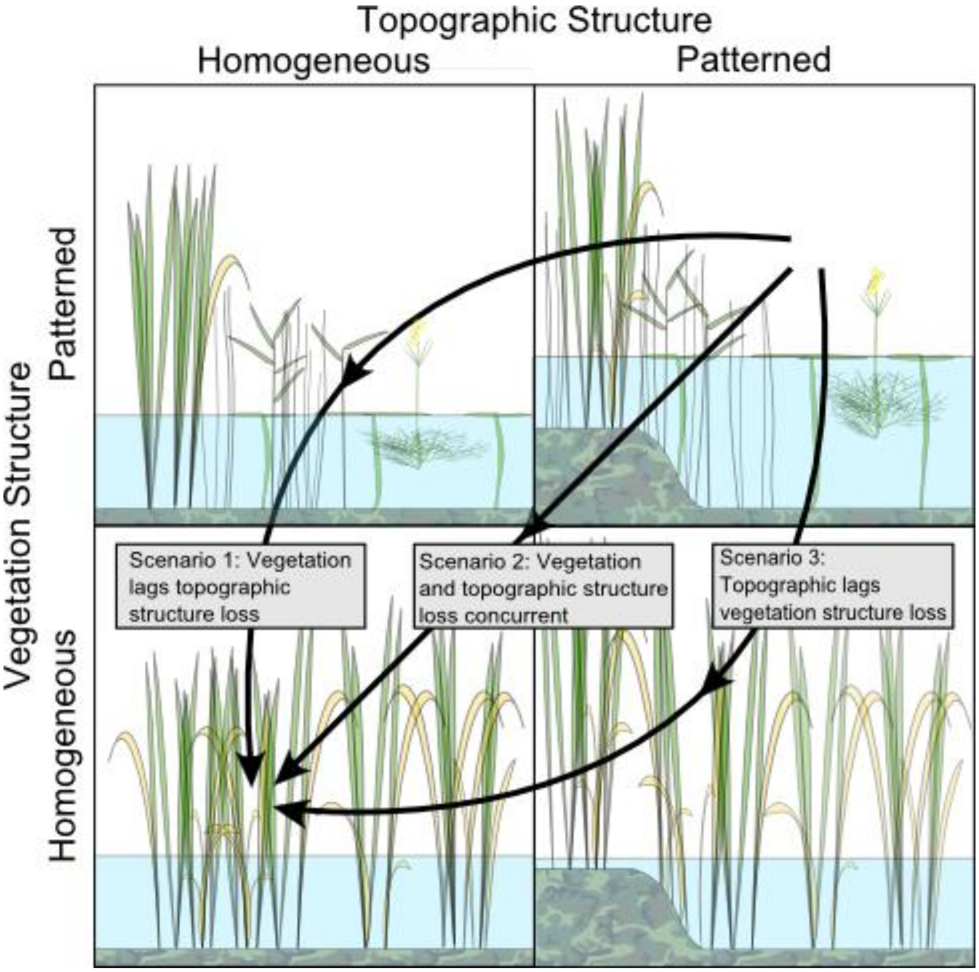


Figure 5. Possible pathways of microtopographic and vegetative degradation in the ridge-slough landscape. In one scenario (uppermost arrow) topographic structure is reduced after modification of the hydrologic regime, followed by a lagged response from the vegetation structure; alternatively (lowermost 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, but both lag behind modification of the hydrologic regime. Depending on which pattern accurately describes pathways of ridge-slough degradation, either vegetation or microtopography may serve as a leading indicator of change in the other characteristic. Pathways of degradation may differ depending on the nature of hydrologic alteration and other disturbances.

*Monitoring rationale and goals*

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 ecosystem. 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) 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. Investigators are encouraged to refer to this document for details on the methods and procedures outlined below. These documents can be accessed from the following web sites: http://www.evergladesplan.org/pm/recover/recover_map.aspx and http://www.evergladesplan.org/pm/recover/recover_map_part2.aspx.

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. These system-wide performance measures address the responses of the South Florida ecosystem that the CERP is explicitly designed to improve, correct, or otherwise directly affect. A separate document, the Development and Application of Comprehensive Everglades Restoration Plan System-wide Performance Measures (RECOVER 2007), has been prepared by RECOVER and provides the scientific, technical, and legal basis for the performance measures. This document and performance measure documentation sheets can be downloaded from: http://www.evergladesplan.org/pm/recover/eval_team_perf_measures.aspx.

The general goals of restoration are to stem, and possibly reverse, degradation of the ridge-slough-tree island landscape by redirecting flows now released unused 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 first system-wide landscape monitoring project. This monitoring effort supports the Greater Everglades Wetlands module of the MAP and is directly linked to the monitoring or research component identified in that module as number 3.1.3.6.

This monitoring project seeks to provide information necessary for the evaluation of the efficacy of the Comprehensive Everglades Restoration Program (CERP), as delineated in the Water Resources Development Act (WRDA) of 2000. The work described provides indices of system-wide applicability of performance measures related to the response of the ridge-slough mosaic, tree islands, and other landscape features of the central Everglades 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 (RECOVER 2004).

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 (including tree islands) within the historic distribution of the ridge and slough landscape and provides a baseline to detect changes/trends in the patterns and vegetation communities of these systems as a result of 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. Particular attention is paid to how these dynamics might: 1) be affected by restoration and 2) relate to CERP hypotheses from the MAP.

The specific objectives of this work are:

> 1) To determine extant reference conditions for each of the performance measures described below (including variability of those measures in time and space).
>
> 2) To establish the 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.
>
> 3) To detect unanticipated changes in ecosystem structure and processes that result from hydrologic management or manipulation, CERP restoration activities, or climatic variation
>
> 4) 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 monitoring work is designed to address the needs identified in the Greater Everglades wetlands performance measures: (1) Wetland Landscape Patterns – Ridge-Slough Community Sustainability; and (2) Wetland Landscape Patterns - Marl Prairie Cape Sable Sparrow Habitat. The program 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 along elevation gradients as water depths and thus hydroperiods change (RECOVER 2006).

### *Overview of approaches*

Monitoring efforts for 2010-12 consisted of three core components: (1) mapping vegetation features from aerial photographs, (2) aerial surveys for classification of tree island type, and (3) ground surveys of water depth and plant community structure (in both tree islands and surrounding marsh), which were used to quantify aspects of the hydrologic regime, determine relationships between vegetation structure and water depth, quantify the distribution and spatial structure of peat elevations, and ground-truth broader-scale maps based on remote sensing and aerial surveys. These activities were linked both logistically and analytically (Figure 6). For example, vegetation mapping from photographs were supported by aerial marsh reconnaissance that was supplemented by tree island characterization activities. Mapping accuracy can be determined from vegetation observations made during surface pattern sampling. Perhaps most importantly, analysis of pattern based on multiple variables (vegetation and soil micro-topography) at multiple scales (aerial photos, helicopter reconnaissance, ground surveys) will maximize the likelihood of change detection, allow inference about interrelationships among stressors and response variables, and present an integrated picture of the pre-restoration structure of the Greater Everglades Wetland Ecosystem. The ability to compare multiple measures of landscape condition may provide a more robust understanding of spatial patterns and temporal trajectories of landscape degradation,

This study takes advantage of a previously established framework for representative sampling of the entire Everglades landscape. This Generalized Random-Tessellation Stratified sampling network (GRTS; Phillipi 2007) divides the Everglades landscape into a grid of 2x5 km landscape blocks (primary sampling units [PSUs]), with the 5 km edge of each PSU aligned parallel to the historic water flow. A spatially-stratified random sample of 80 PSUs were selected for sampling over a 5 year period (n=16 per year), and each year a subset of these were drawn to achieve a spatially balanced sample of the modern Everglades compartments (Everglades National Park (ENP), Water Conservation Area 3A North (WCA 3A N), Water Conservation Area 3A South (WCA 3A S), Water Conservation Area 3B, Water Conservation Area 2, and the Loxahatchee National Wildlife Refuge (LNWR); Figure 7). Mechanistic analyses for this study focus on 27 PSUs (from sampling years 1 and 2) found within the historic distribution of the Ridge and Slough landscape (McVoy et al. 2011). These PSU's represent the full range of contemporary hydrologic regimes, and their vegetative and microtopographic structure range from well-conserved to severely degraded (Wu et al. 2006, Watts et al. 2010, Nungesser 2011).

This Year 2 Summary Report includes results of mapping, marsh landscape structure, and tree island structure through the first two full years of sampling. Marsh data collected in the first year of sampling are incorporated in a separate Year 1 Data Report.

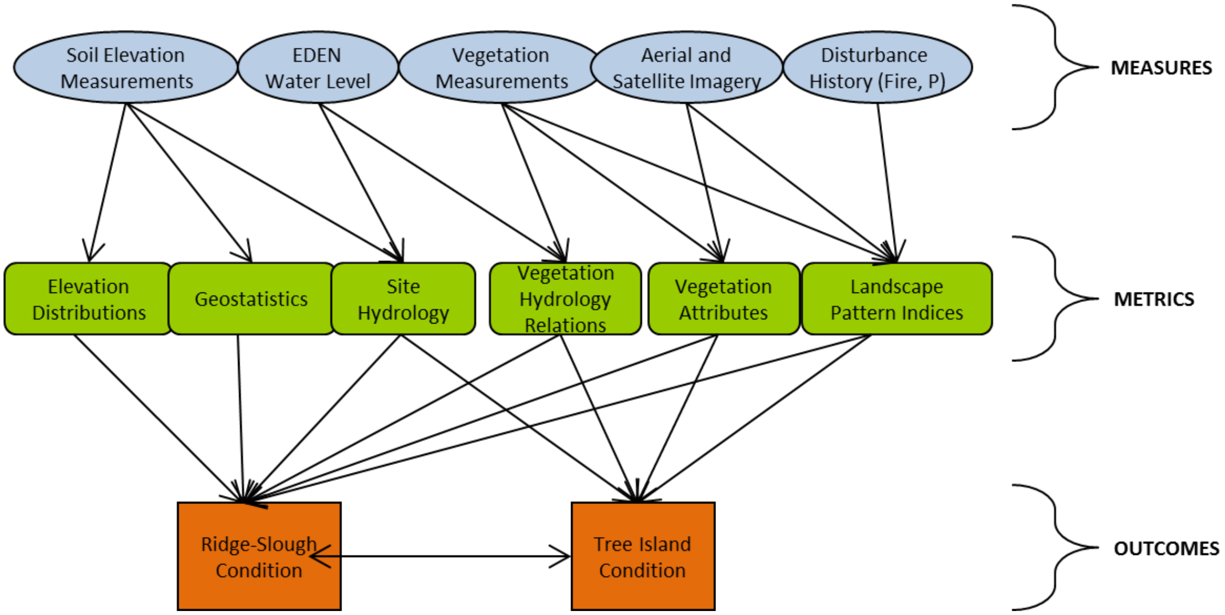


Fig. 6 - Relationships among direct measurements to be collected, metrics derived from those measurements, and assessment outcomes.

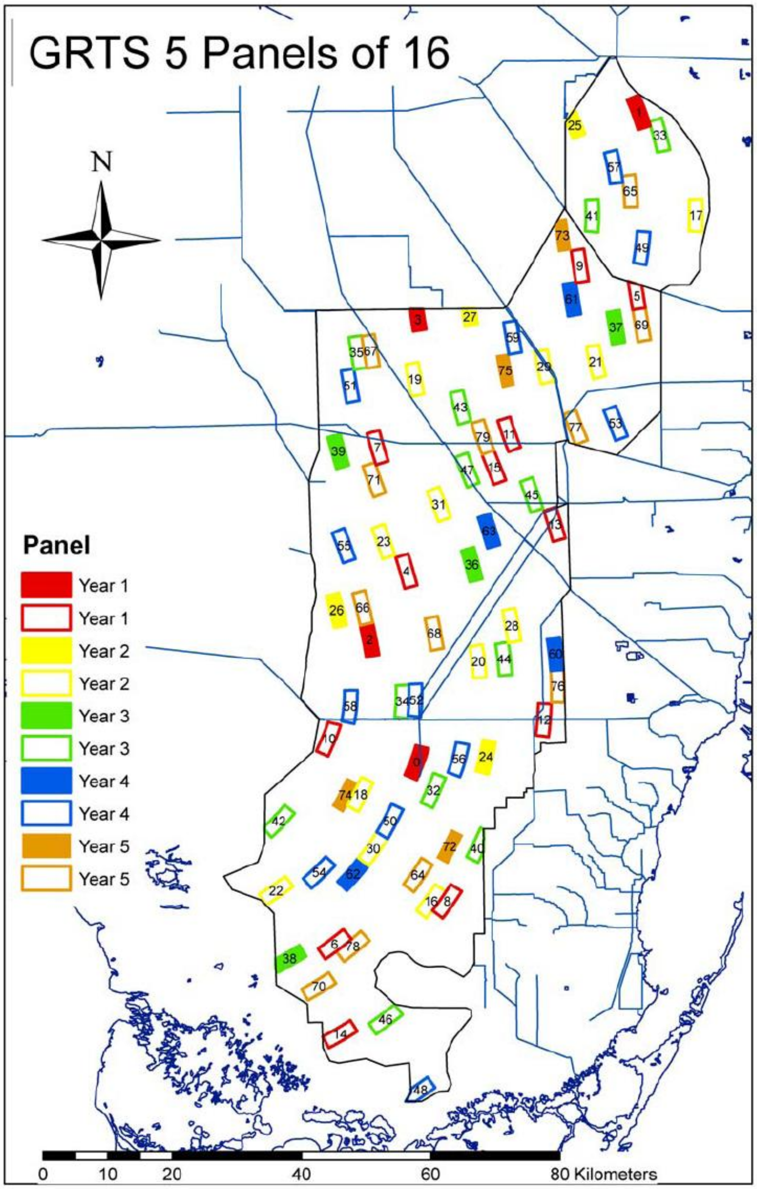


*Fig. 7. Map of all PSUs for landscape sampling (from Phillipi 2007). Colors indicate years for sampling of individual PSUs. A selection of tree islands were sampled in solid landscape blocks in Years 1 and 2.*

## MAPPING OF MARSH AND TREE ISLAND VEGETATION

Developing tools for remote detection of ecological condition is of obvious utility for large area surveillance of restoration progress. Some research has already been done to discern landscape pattern metrics that may be of use in long term monitoring efforts (Wu et al. 2006), and one objective of this component of monitoring is to evaluate these existing metrics. A second objective is to develop landscape metrics that are predicated more on the mechanisms of landscape pattern maintenance (i.e., flow and longitudinal slough connectivity). A third objective is to compare field metrics of ridge-slough landscape condition with those obtained from imagery to determine patterns of association and critical transition thresholds that may be useful for restoration assessment.

The narrow objective of the vegetation mapping component of this project is to map and characterize the vegetation in each PSU using the classification scheme developed for CERP vegetation mapping. However, the incorporation of a mapping component in the Ridge – Slough-tree island mosaic project facilitates achievement of a broader goal: the development of a better understanding of the relationships between hydrology and other drivers of vegetation pattern. It does so by allowing hypotheses about these relationships to be addressed at an intermediate scale – much coarser than the plot data collected in the land surface elevation component of this project, and considerably finer than the vegetation mapping component for the entire Everglades (MAP Section 3.1.3.4).

Vegetation maps of each PSU have been produced, with a minimum mapping unit of 200m$^2$ for non-woody vegetation and 36 m$^2$ for tree islands (See Appendix II). The mapping effort or area mapped within each PSU varied by year. PSU mapped during the first year were mapped to their full 2 km x 5 km extent while those mapped in the 2nd year were limited to a central 2 km x 2 km portion within each PSU (see Figure 9 for locations of PSU's sampled in Years 1 and 2). The base map of these vegetation maps consisted of either color infrared CERP aerial imagery from 2003 or 2009, for PSU 4 and 5 and PSU 0 and 14, respectively, or NAIP 2010 color infrared aerial imagery for the other 28 PSU. Features within each PSU were classified according to the classification system developed by a consortium of south Florida vegetation scientists (Rutchey et al. 2006). Most community types have been distinguished to Level 3 of this classification system

Each tree island within a given PSU has been mapped and characterized. Tree island >36 m$^2$ in size within each PSU were identified and digitized. Based on helicopter aerial surveys, each tree island was classified into one of the following seven types:

1. Hardwood hammocks (forests or woodlands with >50% relative cover of upland & transitional tree species)
2. Bayhead (closed crown forest with >50% relative cover of swamp and transitional tree species)
3. Bayhead Swamp (open woodland community with >50% relative cover of swamp and transitional tree species)

4. Willow head or strand
5. Cypress dome or strand
6. Exotic-dominated tree island

In subsequent analysis, maps of each PSU will be used to determine the 5 indices utilized by Wu et al (2006) to evaluate the integrity of ridge-slough patterning: Lacunarity index (LI), Average Length of Straight Flow (ALS), Average Width of Slough (ASW), Percentage of Ridge Area (PRA), and Average Length-Width Ratio (ALW). Responsiveness of map-derived indices of vegetation pattern degradation will be compared to statistical descriptors of peat surface patterning and multivariate descriptors of hydrologic regime (see below) in order to determine the circumstances under which each approach provides a more robust and sensitive indication of landscape integrity.

## SAMPLING AND ANALYSIS OF MARSH VEGETATION

### *Field measurement of soil elevation and vegetation composition*

The approach adopted in this monitoring component is strongly informed by recent studies of relationships between hydrologic regime and peat surface structure in eight landscape blocks (structurally similar to current PSUs) stretching from WCA 3AN to ENP and encompassing historic ridge and slough landscapes currently subject to drained, inundated, and stabilized hydrologic regimes (Watts et al. 2010). The central finding of these efforts is that the frequency distribution and spatial structure of peat surface elevations provides a directionally-sensitive indicator of ridge-slough landscape response to hydrologic regime, in that each of these metrics responds differently to inundation, drainage, and flow stabilization. Importantly, metrics based on peat surfaces appear to diverge in some cases from metrics of the landscape structure of vegetation in identifying conserved and degraded patterning. The present analysis adds measures of vegetation community distinctiveness and fidelity to elevation as core metrics. Geostatistical measures of plant community dissimilarity and microtopographic variation will provide additional measures of landscape structure, but are not included in this analysis.

Wherever possible, 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.

Prior to the sampling of each PSU, the 2 x 5 km area was subdivided in 80 equal area zones (250 m x 500 m) and a sampling cluster was located at a random location within each (Figure 8). At each cluster, samples were then collected at the center and at two randomly selected distances between 3 and 35 m in two cardinal directions, east and north. Sampling at each location commenced with setting a 1-$m^2$ quadrat on the ground, centered on the target point, to delineate the sampling boundary. Within each quadrat, water depth was measured using a meter stick with a 10-cm diameter hard plastic foot anchored to one end; the foot ensures that water depth is measured to the soil surface. Field training of sampling personnel ensured that a standardized amount of pressure was applied to the foot such 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 depth to bedrock at each node.

Vegetation characterization within each quadrat consisted of identifying all taxa present to species level, estimating cover of each using a Braun-Blanquet scale (1 – 1-5%, 2 – 5-25%, 3 – 25-50%, 4 – 50-75%, 5 – 75-95%, and 6 – 95-100%). Based on these vegetation measurements, the vegetation within a 25 m radius of each sampling location was assigned to a community category (ridge, slough, tree island, wet prairie, cattail). In some PSUs, species cover was estimated as percentage cover of the plot area at either 1%, 5% or at 10% intervals; values from Braun-Blanquet scales were converted to these values for data analysis. Where quadrats span a transition from one community type to another, we assigned points to mixed categories (e.g., ridge/wet prairie).

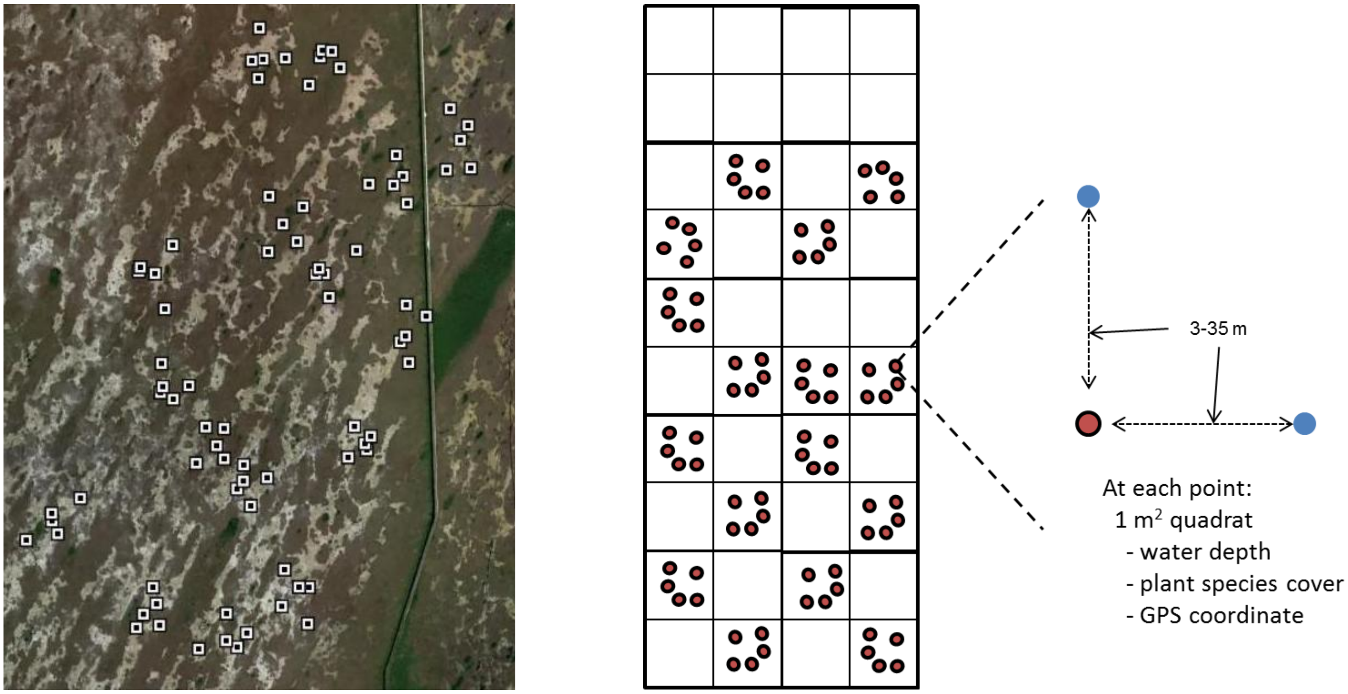


Fig. 8 – Locations of sampling clusters (red dots) within 2x5 km primary sampling units (PSUs); the location of clusters within each 500 x 500 m zone is assigned randomly. At each cluster, 3 sampling locations (green dots) are visited; sites are situated at the center of each cluster, and at a random distance between 3 and 35 m in the direction of the PSU azimuth and in the orthogonal direction. Measurements at each site include location, vegetation community composition and water depth.

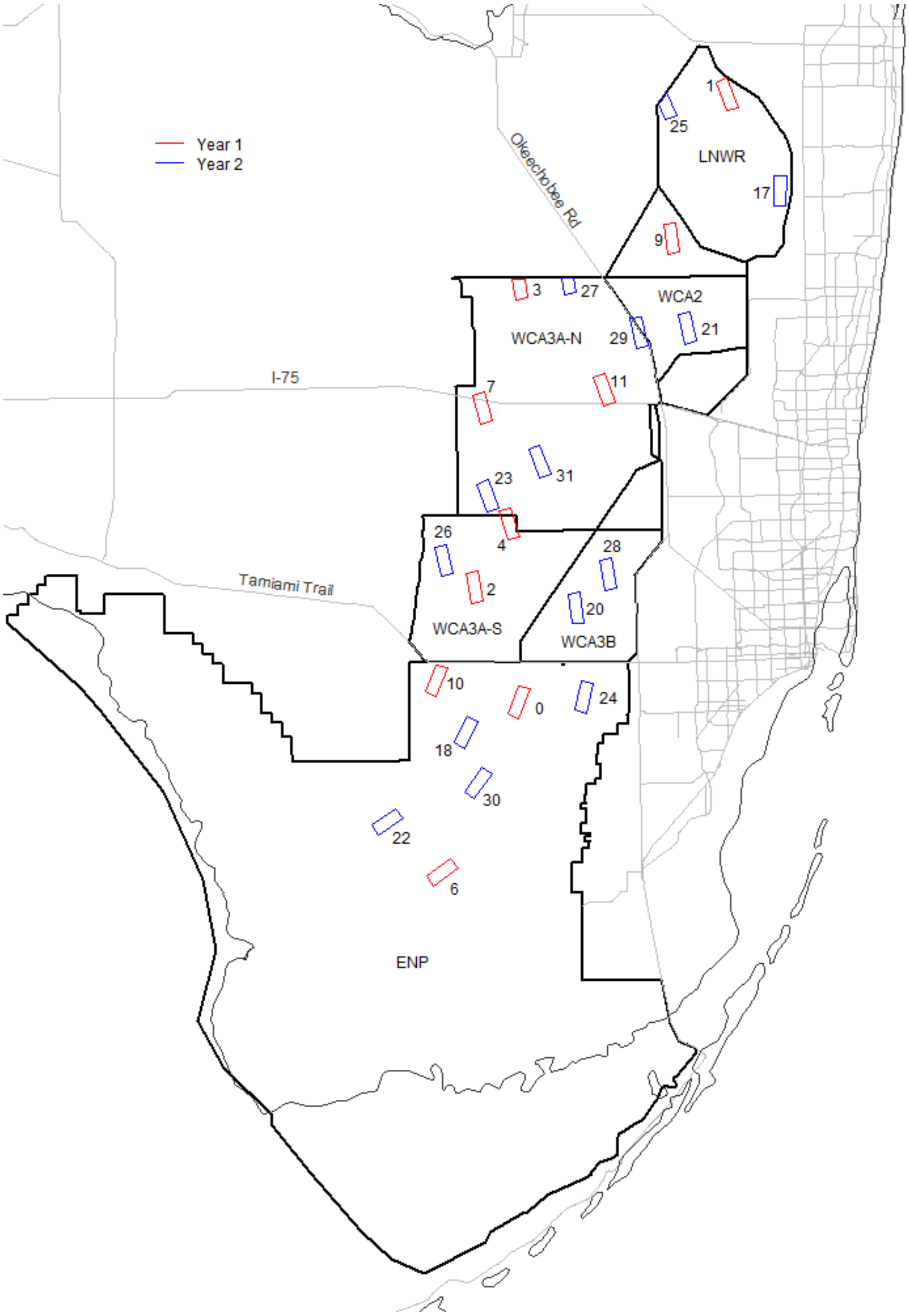


Figure 9. Map of the greater Everglades landscape showing the 27 study sites sampled within the historic ridge-slough landscape during years 1 and 2 of this project. Each site contains up to 240 sampling points in a spatially-stratified design. Year 1 PSU's are in red, Year 2 PSU's are in blue.

Table 1. Characteristics of PSUs sampled to date.

| | | | Classification | | Location | | | |
|---|---|---|---|---|---|---|---|---|
| **PSU** | **Cycle (Year)** | **Dates Sampled** | **Area[†]** | **Historic Ridge-Slough** | **Centroid Easting (UTM)** | **Centroid Northing (UTM)** | **Azimuth (Degrees)** | **UTM Zone** |
| 0 | 1 | 3/20, 3/22, 3/27/2012 | ENP | Y | 532345.51 | 2842696.30 | 19 | 17 |
| 1 | 1 | 9/18/2009 | WCA1 | Y | 566677.85 | 2942982.08 | 341 | 17 |
| 2 | 1 | 11/9, 11/23, 11/24/2009 | WCA3AS | Y | 525056.59 | 2861614.12 | 349 | 17 |
| 3 | 1 | 9/4/2009 | WCA3AN | Y | 532505.33 | 2910966.94 | 354 | 17 |
| 4 | 1 | 7/28,7/29/2009 | WCA3AS | Y | 530756.35 | 2872127.60 | 344 | 17 |
| 5 | 1 | NA* | WCA2 | Y | 566325.52 | 2914610.64 | 354 | 17 |
| 6 | 1 | 10/24,10/28/2009 | ENP | Y | 519649.37 | 2814585.30 | 39 | 17 |
| 7 | 1 | 12/8/2009 | WCA3AN | Y | 526262.38 | 2891226.13 | 345 | 17 |
| 8 | 1 | 11/30, 12/12, 12/16/2011 | ENP | N | 537019.49 | 2821237.51 | 30 | 17 |
| 9 | 1 | 8/17, 8/18/2009 | WCA2 | Y | 557549.62 | 2919280.24 | 352 | 17 |
| 10 | 1 | 4/19, 5/4, 5/5/2012 | ENP | N | 518729.07 | 2846327.59 | 339 | 17 |
| 11 | 1 | 8/5, 8/6, 8/11/2010 | WCA3AN | Y | 546603.34 | 2893273.01 | 342 | 17 |
| 81 | 1 | 12/13, 12/14, 12/16, 12/17/2010 | WCA3B | Y | 544130.08 | 2853456.03 | 360 | 17 |
| 13 | 1 | 8/24, 8/27, 9/3/2010 | WCA3AN | Y | 553652.16 | 2879348.07 | 344 | 17 |
| 14 | 1 | 9/9, 9/14, 10/7/2011 | ENP | N | 520452.78 | 2800699.28 | 348 | 17 |
| 15 | 1 | 6/17, 6/18, 7/30/2010 | WCA3AN | Y | 544263.57 | 2888174.08 | 340 | 17 |
| 16 | 2 | 12/19/2011, 1/4, 1/6/2012 | ENP | N | 534551.56 | 2821237.18 | 31 | 17 |
| 17 | 2 | 2/2/2010 | WCA1 | Y | 575467.53 | 2927079.79 | 350 | 17 |
| 18 | 2 | 5/18,5/25, 6/5, 6/7/2010 | ENP | Y | 523582.48 | 2837739.76 | 25 | 17 |
| 19 | 2 | 9/30, 10/8, 10/12/2010 | WCA3AN | Y | 532020.89 | 2901747.79 | 350 | 17 |
| 20 | 2 | 9/30, 10/3/2011 | WCA3B | Y | 541840.16 | 2858248.34 | 353 | 17 |
| 21 | 2 | 3/3/2010 | WCA2 | Y | 560020.33 | 2904486.44 | 348 | 17 |
| 22 | 2 | 11/4, 11/9/2011 | ENP | Y | 510586.67 | 2822844.43 | 346 | 17 |
| 23 | 2 | 9/23, 9/26, 9/28/2011 | WCA3AS | Y | 527209.63 | 2876687.70 | 342 | 17 |
| 24 | 2 | 2/28, 3/1, 3/6/2012 | ENP | Y | 543033.61 | 2843539.09 | 13 | 17 |
| 25 | 2 | 2/3/2010 | WCA1 | Y | 556804.01 | 2940955.57 | 342 | 17 |
| 26 | 2 | 9/10, 9/17, 9/23/2010 | WCA3AS | Y | 519957.43 | 2866106.03 | 346 | 17 |
| 27 | 2 | 10/12, 10/21/2011 | WCA3AN | Y | 540532.06 | 2911393.98 | 356 | 17 |
| 28 | 2 | 11/19, 12/2, 12/13/2010 | WCA3B | Y | 547035.43 | 2863766.37 | 350 | 17 |
| 29 | 2 | 9/16/2011 | WCA3AN | Y | 552008.07 | 2903701.35 | 349 | 17 |
| 30 | 2 | 9/6, 9/7, 11/16, 11/23, 11/28/2011 | ENP | Y | 525597.48 | 2882440.91 | 30 | 17 |
| 31 | 2 | 8/19, 8/22, 9/2/2011 | WCA3AS | Y | 535763.28 | 2882440.91 | 340 | 17 |

* Extremely high cattail density made all sampling points within PSU 5 inaccessible by airboat - no sampling of this area has been conducted

[†] 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

### *Site/Point Hydrology*

Synoptic water depths can be useful for evaluating the distribution of soil elevations over a particular PSU, but it does not allow comparison across PSUs (because observations are done under different hydrologic conditions) and it does not provide a full hydrologic context for each PSU. To establish site hydrologic conditions, we coupled our synoptic measurements of water depths to the US Geological Survey's Everglades Depth Estimation Network (EDEN) based on the geographic location of each point. EDEN collects water stage data daily from 253 stations, and interpolates water levels across the entire Everglades landscape at daily time steps at a grid size of ca. 400 $m^2$. For each sampling point, we established a hydrologic history spanning from the day of sampling back to 1991, the earliest current hindcast date, by benchmarking measured water depth and EDEN-estimated water elevation at the centerpoint of each PSU (Fig. 9). 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 centerpoint of that band.

To determine the particular conditions at a site requires first that soil elevation be determined from EDEN estimates of water elevation on the day of sampling and water depths (Fig. 10). From these hydrologic histories, we calculated mean water depth and inundation frequency at each point over the preceding 0.25, 0.5, 1, 2, 5, 10 and ca. 20 years (i.e. the complete hydrologic record). Because of strong correlation among these measures within PSUs, we use measures derived from the full hydrologic record as predictors of vegetative and microtopographic condition. Additional hydrologic metrics originally proposed include other attributes of point- and PSU- scale hydrologic regime: maximum annual water depth (point scale), water level variability (PSU scale); water level rates of change (PSU scales), and timing of water level maxima and minima (PSU scale). This full suite of hydrologic metrics for each PSU will ultimately be considered in point- and PSU scale analyses of hydrologic condition, but have not been incorporated into analyses presented here.

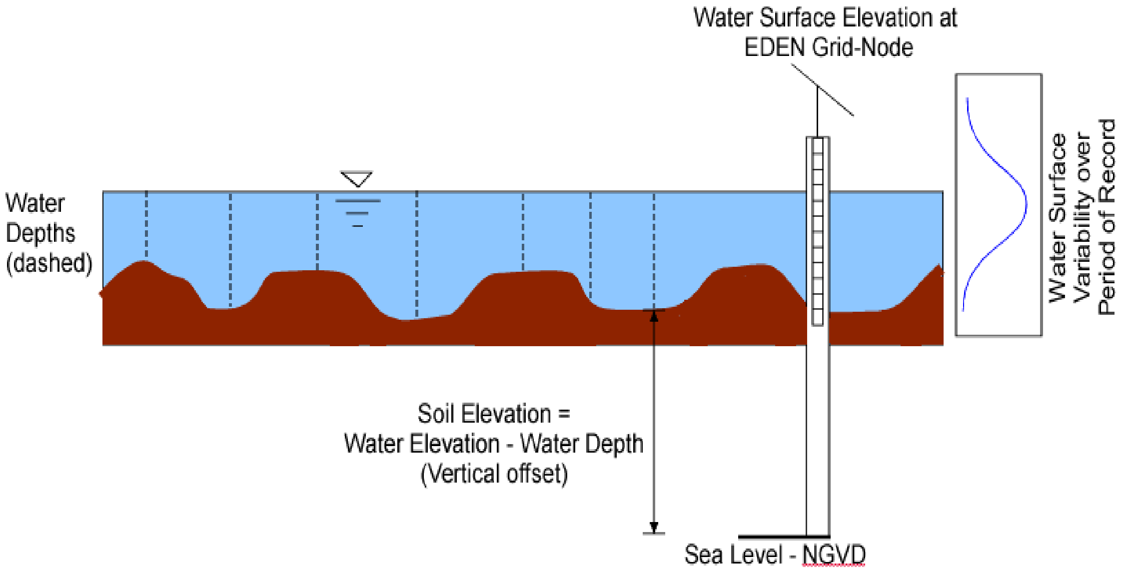


Fig. 10 – Determination of soil surface elevation from measurements of water depth (dashed lines) and water elevation (from EDEN) on the same day as water depths were measured. Hydrographs can be constructed from this soil elevation estimate and the time-series of water elevations (distribution at right). Time series of stage can be used to report hydroperiod, mean depth, water level variability, exposure frequency/duration/depth, etc.

*Data Analysis - Microtopography*

To assess microtopographic variation and hydrologic regime, we generated summary statistics of soil elevation and water level, including mean, standard deviation, skew and kurtosis (which describes the degree of shouldering in a distribution and can be used to diagnose bimodality). 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:

$$P_s = N(\mu_i, \sigma_i) \qquad (1)$$

$$P_m = q \cdot N(\mu_1, \sigma_1) + (1 - q) \cdot N(\mu_2, \sigma_2) \qquad (2)$$

where $q$ represents the probability of falling within the first normal distribution, and $N$ is a normal distribution with mean $\mu_i$ and standard deviation $\sigma_i$. We also determined whether models based on mixtures of larger number of normal distributions better fit the data; in the few cases where models with 3 or more modes had better goodness-of-fit, we report that finding but use the better of models 1 and 2 in subsequent data analysis. Model goodness of fit was compared using Bayes' information criterion (BIC). The best-fit model was considered to have the lowest BIC score. 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. To assess whether the persistence of microtopographic pattern might exhibit global bi-stability (Fig. 4), we generated histograms of PSU-scale elevation variance, and tested for bi-modality across PSUs in the same manner as tests of elevation bimodality within PSUs.

*Data Analysis - Vegetation structure*

In areas with relatively well maintained hydrologic regimes, vegetation communities are separated by clear topographic boundaries, and species preferentially inhabit distinct hydrologic niches. As the hydrologic regime degrades, this patterning is lost. If the topographic responses to changes in the hydrologic regime are the dominant environmental driver that maintains community distinctness, the similarity of communities within PSUs should be greater under either impounded or drained conditions than in relatively conserved landscapes.

To assess how the distinctiveness of vegetation communities changes in response to hydrologic and topographic change, we assessed the dissimilarity among vegetation community composition as the distance (in multivariate space) between artificially-imposed vegetation clusters. In this analysis, individual sampling points from all PSUs were ordinated using a Kruskal's non-metric multidimensional scaling (NMDS) ordination plot, in which more dissimilar sites align further apart in the NMDS plot with the objective of minimizing "stress" in the data. 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. Five dimensions (axes) for the global NMDS ordination plot were decided on before further analysis, based on a scree plot of stress scores against the number of dimensions, where the appropriate number of dimensions balances simplicity and ecological relevance (a satisfactory amount of total variation in the raw data explained). 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 centers

(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 distinctiveness. A higher BSS value (greater distance between the two clusters) means a more distinct vegetation community structure (Figure 11a). Conversely, more overlapping clusters (smaller BSS) indicates less distinctiveness between sites, and a more degraded landscape structure (Figure 11b). Because of the artificiality of segregating such data into two distinct clusters, rather than allowing for multiple clusters, we empirically assessed the extent to which this approach described the distinctiveness of ridge-slough communities, as described below.

We used three approaches to assess how well the clustering in the NMDS ordination plot described differentiation of ridge and slough communities. First, we analyzed the distribution of sawgrass (*C. jamaicense*) in the two clusters. We chose sawgrass because: a) it is overwhelmingly dominant in ridges, which are the most spatially extensive community type; b) it is found throughout the entire Ridge and Slough landscape; and c) it has a broad fundamental hydrologic niche, but finds optimal conditions within a narrower range. We calculated mean relative sawgrass abundance in points in each of the two clusters within each PSU, and examined how sorting of sawgrass varied among PSUs. Second, we analyzed the covariation among characteristic species of each community in NMDS space. We plotted the 22 most abundant species in two-dimensional ordination space, and categorized them based on the a priori vegetation community in which they were most abundant. If our ordination and clustering approach captures ridge-slough community structure, then species within each a priori community should be closely associated in NMDS space. Third, we assessed distribution of sample points along individual axes from the global NMDS for an illustrative subset of PSUs that included three well-conserved landscape blocks from central WCA3AS, and degraded landscapes characterized by different hydrologic alterations. If our ordination approach and measurement of community distinctness effectively differentiates ridges and sloughs, then conserved landscapes should exhibit distinct modes along one or more NMDS axes, and these modes should correspond to k-means clusters. Overall, variation in cluster distance corresponded to the degree of clustering: vegetation in conserved landscapes was well-described as two distinct clusters.

We used regression analysis between long-term mean water depth and community distinctiveness for each PSU to assess how hydrologic regime influenced vegetation community distinctiveness. To assess whether the vegetation community distinctiveness might exhibit global bi-stability (Fig. 4), we generated histograms of cluster distances, and tested for bi-modality across PSUs in the same manner as tests of elevation bi-modality within PSUs.

In addition to separate measures of microtopographic structure and vegetation community distinctiveness, we also evaluated landscape structure based on three measures of the co-variation between elevation and vegetation community composition. First, we used bivariate regression analysis to assess the strength of the relationship between sawgrass abundance and elevation within each PSU. Second, again for each PSU, we used a Mantel test to determine the relationship between matrices of between-site dissimilarities in elevation and in community composition. The resulting test statistic $r$ is a multivariate analog of Pearson's correlation coefficient. Finally, we evaluated the difference in elevation between points assigned to the two clusters in our k-means analysis. This suite of measures provides a more integrated view of vegetative and microtopographic structure of ridge-slough landscapes, and differ in the effort required for data collection and analysis. To assess whether elevation-vegetation relationships within PSUs supported the occurrence of global bi-stability (Fig. 4), we generated histograms of all three measures of elevation PSU-scale elevation variance, and tested for bi-modality across PSUs in the same manner as tests of elevation bi-modality within PSUs.

We assessed the geographic variation in community distinctiveness (as measured by cluster distance, microtopographic heterogeneity (as measured by standard deviation of elevation), and elevation-vegetation association (as measured by sawgrass-elevation correlation, Mantel r, and elevation differences between vegetation clusters) to determine whether these characteristics co-varied across the greater Everglades. Maps of sampled PSUs were used to depict the condition of each PSU based on these measures. Because these measures have different units and different structures of variability across each PSU, scaling of condition is not uniform across different metrics, and we were not able to explicitly assess the relative degree of degradation by comparison of different metrics. However, spatial covariation among these measures provided some information about the extent of agreement among them.

We used Pearson's correlation coefficient to assess covariation among measures of ridge-slough landscape condition in a non-spatial context. If microtopography and vegetation structure (and their association within PSUs) covary strongly, then measures of these characteristics provide little independent information. However, weaker correlations between these measures would indicate that microtopography and vegetation structure vary somewhat independently. In that case, independent measures of these characteristics are important for assessment of ridge-slough condition. Moreover, the covariation of vegetation structure and microtopography across PSUs may provide some insight into the trajectories of landscape degradation. To assess the relative timescales of vegetation and topographic change in response to modification of the hydrologic regime, we compared the changes in the distinctness of the vegetation communities and loss of peat elevation structure within each PSU. We sorted PSUs into four quadrants delineated by the distinct modes observed in the distribution of each variable. In this design, if vegetation changes first, co-occurrence of intact topography (bimodal elevations) and reduced community distinctness should be observed . However, if topography changes first, then the reverse pattern should occur (Figure 5). We tested this prediction by assigning for each PSU a single test statistic value for vegetation community distinctiveness (question 1, above) and another for microtopography distinctiveness, defined by the standard deviation of soil elevation. We then assigned each PSU to a quadrant, and compared these quadrants based on a variety of measures including hydrologic regime, vegetation community abundances, and vegetation-elevation correlations.

*Software*

All analyses and visualizations were performed in the open source statistical program R. The global NMDS plot was created using the metaMDS function in the vegan package (Oksanen et al. 2012). The default convergence criteria in monoMDS – the engine used by metaMDS which induces random starts – was too slack to find a convergent solution. The slack was tightened by using “sfgrmin = 1e-7”. The dissimilarity matrix for the NMDS was calculated using the vegdist function in vegan using the metric Jaccard index which was preferentially chosen over the popular semi-metric Bray-Curtis index. k-means clusters were created using the

R base package stats (R Core Team 2012). Maps were created using the base R plotting functions. All other figures were created using ggplot2 and combined by using lattice.

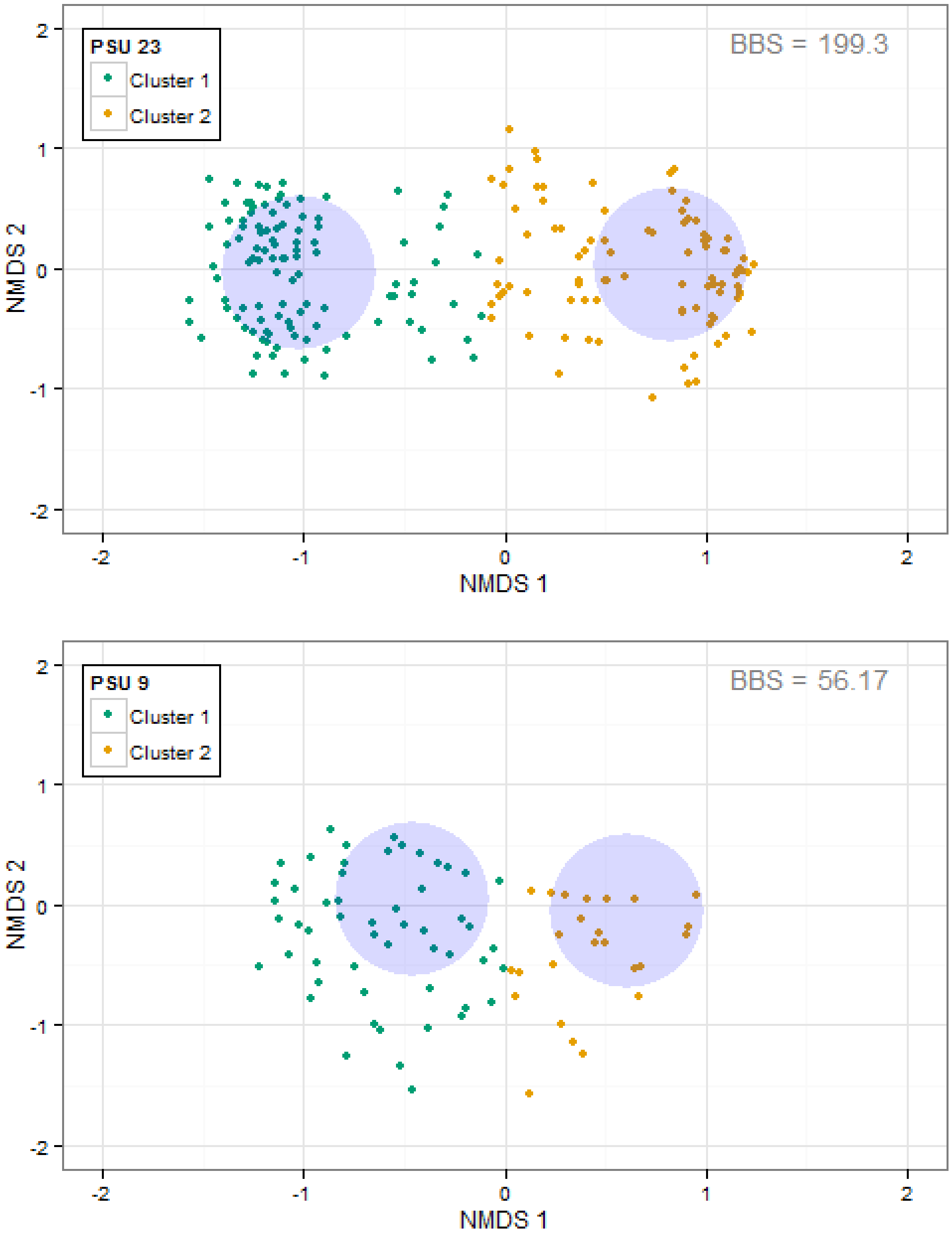


Figure 11. PSU 23 (a) and PSU 9 (b) species data ordinated by NMDS and clustered by k-means. In a), PSU 23 clusters are relatively far apart, indicating a significant separation of sites composed of species that occupy specific hydrologic niches; a relatively well preserved PSU. In b), PSU 9 clusters are closer, indicating a loss of distinctiveness in the vegetation community structure; a relatively degraded PSU.

### *Pending analyses*

To date, we have not assessed geostatistical measures of soil elevation, including semi-variance parameters (nugget and sill variance), anisotropy, or spatial auto correlation; derived metrics of landscape pattern from vegetation maps; or assessed marsh vegetation structure in a spatially-explicit manner. These analyses, based on data from Year 1-3 PSUs, will be included in the Year 3 Report.

## Results

### *Microtopographic and hydrologic patterns*

Microtopographic patterns varied substantially across our broad landscape sample (Table 2; Figures 12,13). Absolute mean elevations varied from 7 to 440 cm above sea level, and mean water level varied from 30 to 448 cm asl, both varying predominantly along the dominant north-south landscape slope from Lake Okeechobee to Florida Bay. Long-term mean water depths (spatially averaged over all points within each PSU) varied from -12 cm to 72 cm, with the lowest water depths found in units within the marl prairies of ENP. Temporal variability of water level also differed among PSUs, with the standard deviation of water elevation ranging from 15.3 to 34.4 cm. Within PSUs, water level and hydroperiod calculated over different temporal windows covaried strongly; as a result, shorter windows provide little additional information over long-term averages.

The magnitude and structure of microtopographic relief also varied considerably among PSUs (Table 2). Standard deviations of elevation ranged from 2.3 to 13.2 cm, with most values falling between 6 and 11 cm. The magnitude of topographic relief was generally highest in central portions of WCA3AS, but was also high in individual PSUs within WCA1, WCA2, WCA3N, and ENP (Figure 14). Landscape-scale variation in elevation was bi-modally distributed, with modes centered on 6-7 cm and ca. 12 cm (Figure 15). The skewness of elevations ranged from -0.92 to 1.47, with most values between -0.5 and 0.5. Kurtosis varied from -1.29 to 3.85, with most values slightly positive. Contrary to previous findings (Watts et al. 2010), kurtosis was not diagnostic of elevation bi-modality within PSUs.

Of the 27 PSUs sampled to date that fall within the historic distribution of the ridge and slough, 16 had elevation distributions that were better fit by a mixture of 2 normal distributions than by a single normal distribution (Table 2). These bimodal distributions were restricted to PSUs with long-term mean water depths of ca. 20-50 cm; differences in the elevation of these modes ranged from 9 to 20 cm, and increased with long-term mean water depth (Figure 16). Differences between elevation modes were slightly lower than those measured by Watts et al. (2010) at comparable long-term mean water depths. One anomalous PSU (PSU 3 in WC3AN) exhibited bimodal elevation distributions but with minimal separation between means. Two other PSUs with high cattail abundance (Table 3) also exhibited high elevation variance and bi-modal distributions. PSUs outside of the historic ridge slough landscape, predominantly those within the marl prairie habitat of ENP, generally had unimodal elevation distributions with minimal variance; confidence in these distributions is lower because data were collected during relatively dry periods when vehicle access permitted sampling, but when a large proportion of points were above the water surface.

Among PSUs with bi-modal elevation distributions, the difference in elevation between ridges and sloughs was closely correlated with the standard deviation of elevation; PSUs with unimodal elevation distributions generally occupied a lower and smaller range of elevation variance (Figure 17).

Table 2. Hydrologic and microtopographic characteristics of year 1 and 2 PSUs. Additional hydrologic descriptors at the point scale are included in data reports for each PSU.

| | **Water Elevation Statistics** | | | | | | **Elevation Cluster Analysis** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Water Elevation* | | *Peat Surface* | | | | *Mode 1* | | | *Mode 2* | | | |
| PSU | Mean (cm asl) | [§]St. Dev. (cm) | Mean Water Depth (cm) | [†]St. Dev. (cm) | Kurtosis | Skew | Depth (cm) | [†]St. Dev. (cm) | [††]Mode Weight (q) | Depth (cm asl) | [†]St. Dev. (cm) | [††]Mode Weight (q) | *Best Model |
| 0 | 180.0 | 24.8 | 30.80 | 7.31 | -0.32 | 0.80 | 25.45 | 2.35 | 0.52 | 39.38 | 6.28 | 0.48 | 2V |
| 1 | 448.4 | 15.3 | 8.18 | 5.98 | -0.25 | -0.16 | 8.18 | 5.97 | 1.00 | - | - | - | 1X |
| 2 | 254.4 | 24.5 | 50.11 | 10.65 | -0.27 | -0.48 | 36.12 | 7.42 | 0.23 | 54.23 | 7.42 | 0.77 | 2E |
| 3 | 305.0 | 25.9 | -4.61 | 3.63 | -1.07 | -0.19 | -6.28 | 2.88 | 0.71 | -0.50 | 0.95 | 0.29 | 2V |
| 4 | 261.9 | 26.3 | 40.77 | 11.89 | -1.03 | 0.16 | 32.64 | 6.63 | 0.59 | 52.66 | 6.63 | 0.41 | 2E |
| 5 | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND |
| 6 | 33.5 | 22.2 | 27.31 | 6.49 | 3.56 | 0.65 | 27.31 | 6.47 | 1.00 | - | - | - | 1X (7V) |
| 7 | 287.6 | 22.2 | 33.05 | 6.46 | 0.97 | 0.05 | 33.05 | 6.44 | 1.00 | - | - | - | 1X |
| 8 | 113.0 | 34.4 | -8.24 | 12.64 | 0.08 | 0.87 | -16.37 | 5.25 | 0.55 | 1.64 | 11.83 | 0.45 | 2V |
| 9 | 357.7 | 26.1 | 28.34 | 4.94 | 0.85 | 0.35 | 28.34 | 4.93 | 1.00 | - | - | - | 1X |
| 10 | 195.1 | 28.2 | 23.97 | 2.28 | 0.13 | 0.80 | 23.97 | 2.24 | 1.00 | - | - | - | 1X (3V) |
| 11 | 271.6 | 32.1 | 53.36 | 6.89 | 1.20 | -0.07 | 53.36 | 6.87 | 1.00 | - | - | - | 1X |
| 81 | 177.8 | 21.5 | 31.85 | 5.73 | 1.04 | -0.44 | 31.85 | 5.72 | 1.00 | - | - | - | 1X |
| 13 | 190.9 | 15.5 | 52.73 | 8.32 | 0.02 | -0.40 | 52.73 | 8.30 | 1.00 | - | - | - | 1X |
| 14 | 0.1 | 19.8 | -3.36 | 5.26 | 0.65 | 0.59 | -3.36 | 5.25 | 1.00 | - | - | - | 1X (5V) |
| 15 | 272.1 | 31.2 | 71.57 | 8.76 | 0.09 | 0.02 | 71.57 | 8.74 | 1.00 | - | - | - | 1X |
| 16 | 112.9 | 34.7 | -12.41 | 7.48 | 1.56 | 1.40 | -18.45 | 0.50 | 0.38 | -8.65 | 7.22 | 0.62 | 2V (3V) |
| 17 | 448.2 | 19.6 | 27.65 | 13.09 | 3.01 | 1.11 | 20.68 | 5.33 | 0.50 | 34.48 | 14.68 | 0.50 | 2V |
| 18 | 152.9 | 24.5 | 29.74 | 7.09 | -1.25 | -0.01 | 23.97 | 3.48 | 0.53 | 36.26 | 3.48 | 0.47 | 2E |
| 19 | 289.1 | 22.7 | 20.70 | 8.34 | -0.45 | 0.30 | 15.26 | 4.98 | 0.60 | 28.86 | 4.98 | 0.40 | 2E |
| 20 | 184.7 | 15.8 | 31.17 | 5.10 | -0.19 | -0.64 | 23.90 | 3.41 | 0.21 | 33.14 | 3.41 | 0.79 | 2E (9V) |
| 21 | 329.2 | 28.8 | 39.52 | 11.56 | -0.11 | 0.85 | 31.18 | 4.17 | 0.48 | 47.35 | 10.72 | 0.52 | 2V |
| 22 | 31.5 | 17.8 | 20.02 | 7.02 | -0.25 | 0.08 | 20.02 | 6.99 | 1.00 | - | - | - | 1X (13V) |
| 23 | 265.3 | 21.8 | 30.89 | 10.34 | -1.20 | 0.33 | 23.99 | 5.27 | 0.62 | 42.30 | 5.27 | 0.38 | 2E (3E) |
| 24 | 157.5 | 20.4 | 34.18 | 6.22 | -0.06 | -0.51 | 34.18 | 6.20 | 1.00 | - | - | - | 1X |
| 25 | 449.9 | 15.4 | 6.53 | 6.63 | 2.27 | 0.57 | 6.36 | 4.31 | 0.66 | 6.86 | 9.66 | 0.34 | 2V (8V) |
| 26 | 261.7 | 23.2 | 41.47 | 10.85 | -0.79 | 0.01 | 33.53 | 6.00 | 0.56 | 51.70 | 6.00 | 0.44 | 2E |
| 27 | 283.1 | 29.6 | 18.95 | 13.73 | -1.27 | 0.12 | 3.09 | 2.66 | 0.33 | 26.75 | 9.55 | 0.67 | 2V (4E) |
| 28 | 187.3 | 17.3 | 32.15 | 5.31 | 0.10 | -0.35 | 32.15 | 5.29 | 1.00 | - | - | - | 1X |
| 29 | 302.0 | 30.9 | -8.30 | 3.02 | 1.24 | -0.88 | -8.30 | 3.00 | 1.00 | - | - | - | 1X |
| 30 | 123.8 | 21.1 | 23.11 | 8.85 | -0.35 | 0.03 | 23.11 | 8.83 | 1.00 | - | - | - | 1X |
| 31 | 268.6 | 26.9 | 38.12 | 6.69 | -0.25 | 0.27 | 38.12 | 6.67 | 1.00 | - | - | - | 1X |

[§] Standard Deviation of water elevation describes the temporal variability of water level at the center 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.

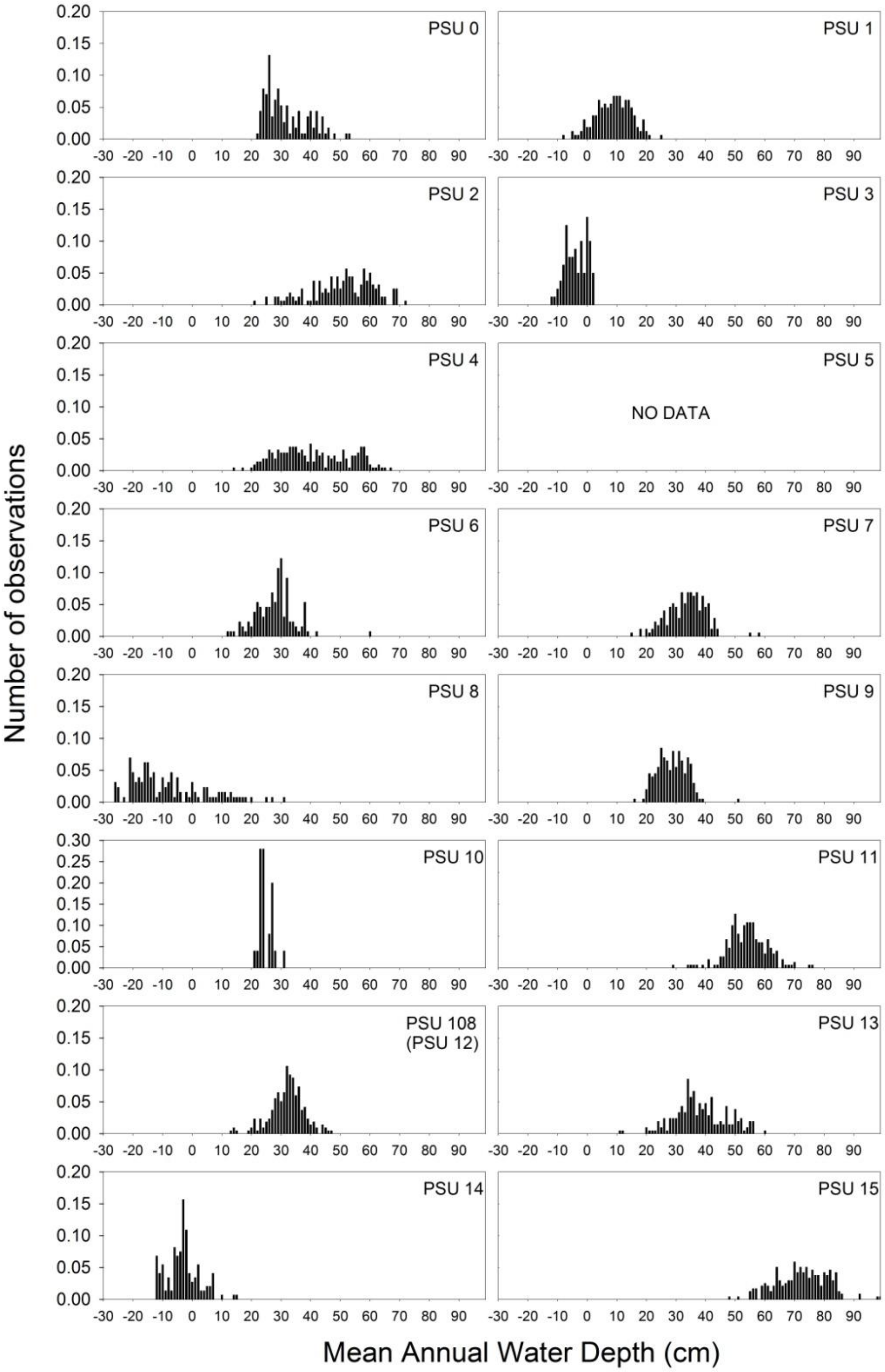


Figure 12. Elevation distributions of Year 1 PSUs. Bimodality and high variability in elevation (e.g. PSU 4) are characteristics of conserved conditions, while low variability and unimodality (e.g. PSU 11) are characteristic of degraded conditions. Mean annual water depth (our measure of relative elevation) is calculated from water depth on the day of sampling, and benchmarked to long-term average water level at the centerpoint of each PSU. Summary statistics and bimodality analysis for each PSU are presented in Table 2.

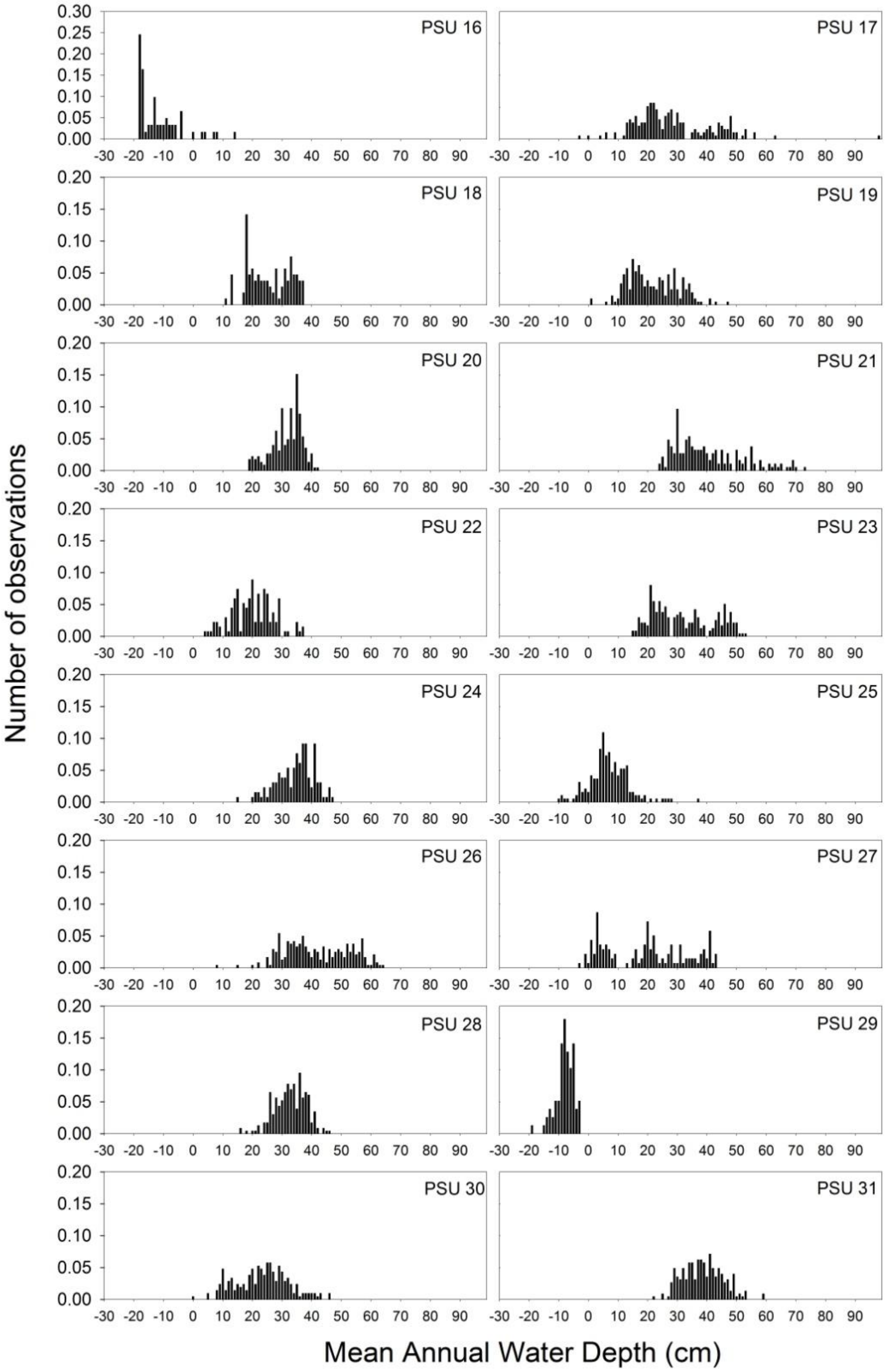


Figure 13. Elevation distributions of Year 2 PSUs. Bimodality and high variability in elevation (e.g. PSU 26) are characteristics of conserved conditions, while low variability and unimodality (e.g. PSU 28) are characteristic of degraded conditions. Mean annual water depth (our measure of relative elevation) is calculated from water depth on the day of sampling, and benchmarked to long-term average water level at the centerpoint of each PSU. Summary statistics and bimodality analysis for each PSU are presented in Table 2.

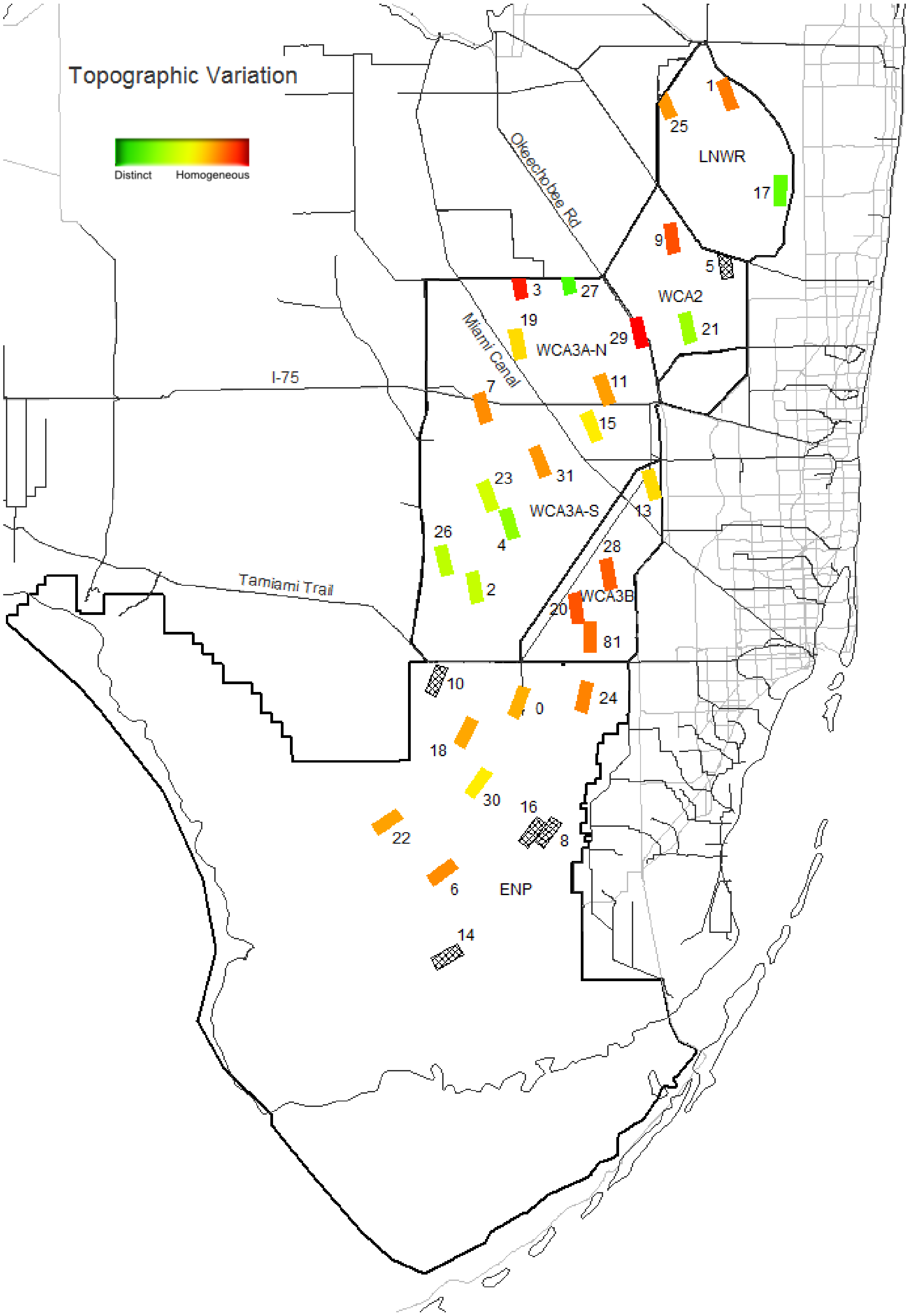


Figure 14. Spatial patterns of elevation variance across the historic ridge-slough landscape. Colors indicate the amount of microtopographic relief (measured as the standard devation of elevation within each PSU).

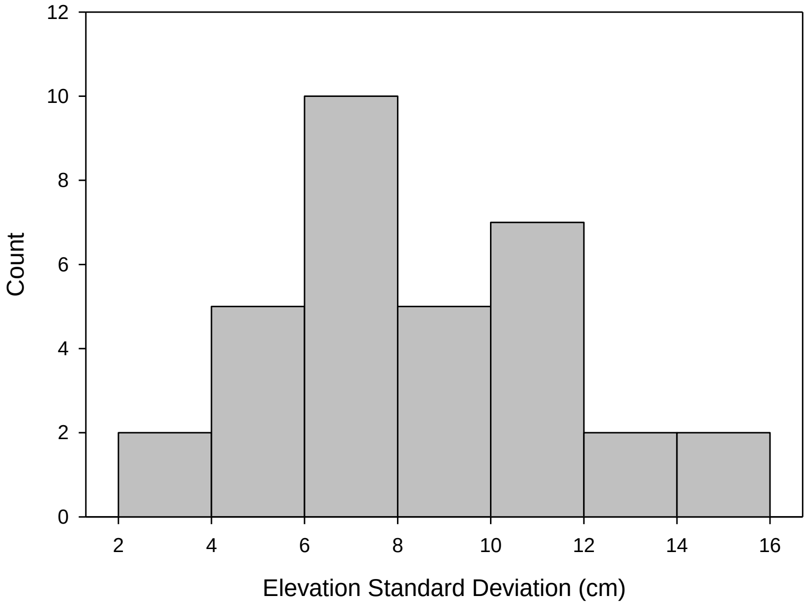


Figure 15. Frequency of elevation variation across PSUs. The bi-modal pattern observed in these data is consistent with current hypotheses about bistability of homogeneous and patterned configurations of the ridge-slough landscape. Data include PSUs sampled by Watts et al. (2010) but not any duplicate measurements of individual PSUs. Data from PSUs outside the historic ridge and slough are not included.

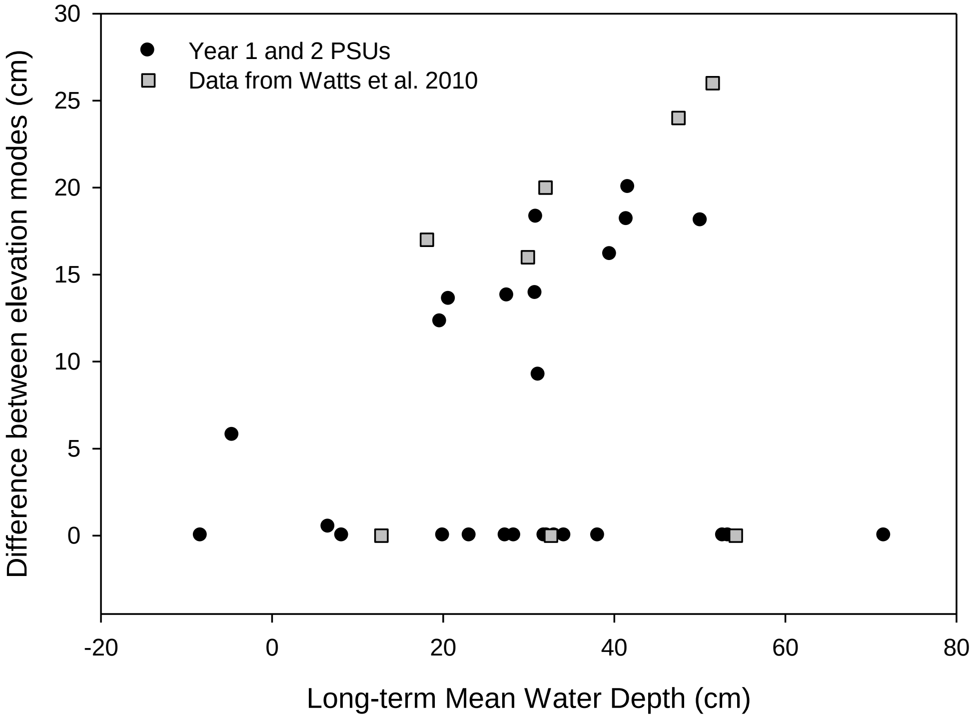


Figure 16. Relationship between hydrologic conditions and elevation mode separation across PSUs. Mean annual water depth is calculated as the difference between the temporal mean of water level since 1991 and the mean elevation of sampled points within each PSU. Elevation mode differences are based on cluster analysis results presented in Table 2. Points with zero difference between elevation modes are those whose elevation distributions were best fit by a single normal distribution. Data include PSUs sampled by Watts et al. (2010) but not any duplicate measurements of individual PSUs. Data from PSUs outside the historic ridge and slough are not included. The anomalous observation from PSU 27 was excluded based on severe recent fire history and incursion by cattail.

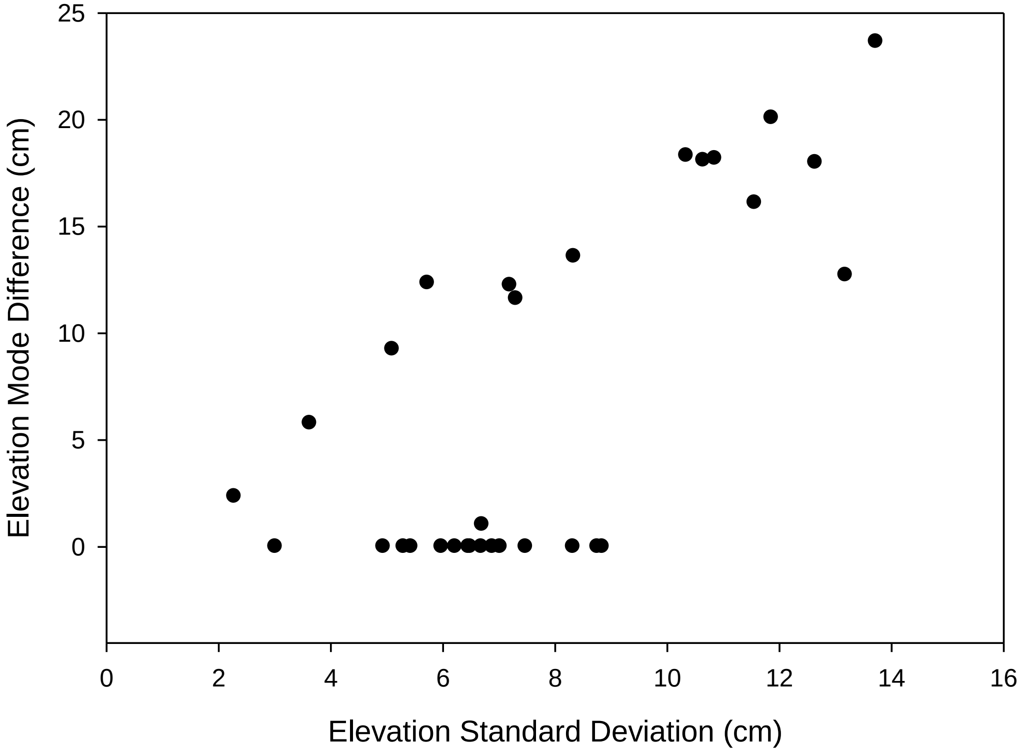


Figure 17. Covariation between two measures of landscape-scale microtopographic structure: the standard deviation of soil surface elevation within a PSU, and the difference between the means of elevation modes in the same PSU, as estimated from mixed distribution modeling. Points with zero difference between elevation modes represent PSUs whose elevation distributions were best described by a single normal distribution.

### *Vegetation community composition and structure*

The composition of vegetation communities varied considerably across sampled PSUs (Table 3). Overall, 4,859 points were sampled; the 2,570 ridge, 1,036 slough, and 593 wet prairie community samples were most abundant. Species were largely limited to their *a priori* defined communities (Table 4): sawgrass (*Cladium jamaicense*) was most abundant in ridges and then in the mixed ridge communities; *Eleocharis* spp. were most abundant in wet prairies and slough-wet prairie mix; *Utricularia* spp. and white waterlily were most abundant in sloughs and mixed slough communities; and *Typha domingensis* was almost entirely contained within the cattail community. Periphyton was more evenly distributed, occupying all community types in abundance except in the driest (tree island and mixed tree island) and likely most eutrophic (cattail) communities.

Across the Everglades landscape, field-assigned vegetation communities followed expected patterns, with tree islands, ridges, wet prairies, and sloughs occupying increasingly deep locations (Table 4). However, these patterns exhibited considerable variation among water management basins (Table 5). Across PSUs, the proportion of ridges, sloughs and wet prairies (based on field assigned categories) was weakly correlated with long-term mean water depth (Figure 18). Sloughs and wet prairies were most abundant in PSUs with long-term mean water depth between 25 and 60 cm, but both community types had low abundances in some PSUs within this range.

The contemporary hydrologic regime varied among all Everglades areas (Table 2). WCA 3A N had the highest 20 year mean water depth, but also the largest variance across all three major vegetation communities, indicating perhaps that it is hydrologically the most diverse area. LNWR had the lowest water depth over this period across all major vegetation communities. No wet prairie communities were observed at all in WCA 2, and only one in LNWR, and wet prairies were more common than sloughs in ENP. WCA 3A S and WCA 3A N had the most balanced community types in respect to the global system in Table 1. Within each Everglades area, the 20 year mean water depth decreased from sloughs to wet prairies (except in WCA 2 where they were absent), to ridges. However, the hydrologic conditions that characterized each community differed considerably among Everglades areas. For example, the 157 sloughs in LNWR were at a lower water depth than the 2,240 ridges in all other Everglades areas.

Non-metric multidimensional scaling ordinated species in a manner consistent with previous studies of vegetation communities in the Everglades (Fig. 19). Sawgrass and other species common on ridges and tree islands were clearly separated from slough species along axis 1, while wet prairie species were intermediate along this axis, and somewhat differentiated along axis 2. The abundance of individual indicator taxa, were correlated with PSU-scale long term mean water depth (Fig. 20). These relationships, though weak, aligned with expected patterns: *Cladium* abundance was negatively correlated with water depth, while *Utricularia* and *Nymphaea* increased. *Eleocharis* abundance peaked at intermediate water depth.

The global k-means clustering analysis strongly aligned with mean water depth over 20 years (Table 6). 81.3% of a priori defined ridge communities were located in cluster 1, with only 2.51% of sloughs. Wet prairie communities were predominantly located in cluster 2 (87.9%), suggesting greater similarity between sloughs and wet prairies than between either of these communities and ridges. Mixed communities were usually located between their constituent parts, for example, slough/wet prairie communities were situated between the slough and the wet prairie communities in terms of both water depth and how they aligned by cluster. However, this was not the case for the ridge/slough mixed community. The odds ratio for the three community types in each cluster (Table 7) reveals that a priori defined ridges were 169.1 times more likely to be in cluster 1 than sloughs based on the global k-means cluster analysis, and that wet prairies were more closely aligned to sloughs than ridges (5.37 versus 31.51).

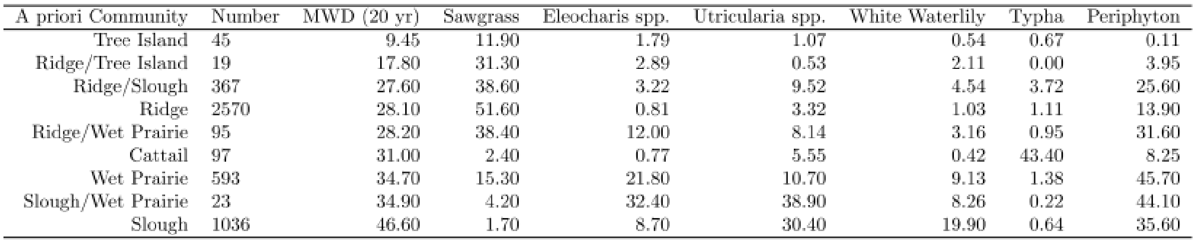
Within individual PSUs, sawgrass abundance was clearly differentiated between clusters (Figure 21). However, the effect was most apparent in the most conserved PSUs (i.e., those with relatively high community distinctiveness) with very low sawgrass abundance (<10%) in the lower cluster and moderately high abundances in the upper cluster (>55%) for all conserved PSUs. In degraded PSUs, the segregation of sawgrass was still noticeable, but the abundance of sawgrass within the clusters, and the differentiation between clusters in terms of sawgrass cover, was more varied.

Distributions of observations along NMDS axes from selected PSUs indicated that cluster distance was an effective proxy for the distinctness of ridge and slough communities distinctness (Fig. 22). In PSUs within central WCA3AS, local plant assemblages were strongly separated, with most observations occurring at the extremes of NMDS axis 1, in particular, which is the axis that most clearly differentiates ridge and slough communities. In PSUs with more extreme hydrologic regimes, observations tended toward intermediate values along the same axis, suggesting a blending of communities.

Table 3. Vegetation characteristics of PSUs sampled to date.

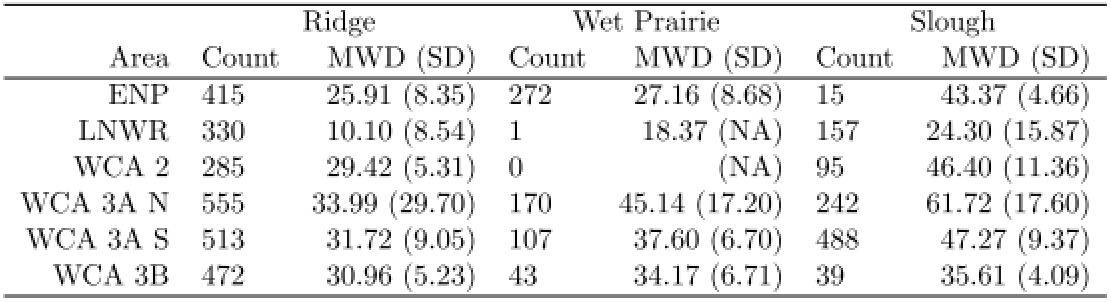
| | Field-Assigned Communities | | | | Species Mean Relative Cover (%) | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| PSU | Ridge (%) | Wet Prairie (%) | Slough (%) | Mixed/Edge (%) | *Typha spp.* | *Cladium jamaicense* | *Nymphaea odorata* | *Eleocharis spp.* | *Periphyton* | *Utricularia Spp.* |
| 0 | 57.9% | 18.4% | 7.9% | 2.6% | 0.0 | 53.2 | 0.0 | 14.0 | 20.8 | 4.4 |
| 1 | 48.1% | 0.6% | 39.5% | 1.2% | 0.3 | 38.1 | 7.2 | 26.2 | 0.0 | 13.5 |
| 2 | 34.6% | 0.0% | 57.2% | 4.4% | 0.8 | 27.1 | 10.7 | 0.4 | 30.3 | 22.7 |
| 3 | 100.0% | 0.0% | 0.0% | 0.0% | 0.0 | 37.2 | 0.0 | 1.5 | 1.9 | 1.3 |
| 4 | 44.4% | 7.0% | 47.7% | 0.0% | 0.4 | 37.3 | 28.4 | 4.4 | 1.7 | 15.5 |
| 5 | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND |
| 6 | 38.2% | 35.9% | 0.0% | 15.3% | 0.2 | 39.5 | 0.0 | 13.2 | 40.4 | 3.7 |
| 7 | 55.7% | 0.0% | 44.3% | 0.0% | 0.3 | 37.5 | 7.9 | 10.6 | 21.2 | 6.7 |
| 8 | 16.28% | 28.68% | 1.55% | | 0.0 | 33.9 | 0.0 | 1.4 | 47.0 | 1.4 |
| 9 | 92.0% | 0.0% | 8.0% | 0.0% | 0.5 | 52.5 | 1.4 | 0.3 | 0.0 | 0.1 |
| 10 | 85.93% | 8.89% | 0.00% | | 0.0 | 42.9 | 0.0 | 0.3 | 46.4 | 0.0 |
| 11 | 31.6% | 33.3% | 35.1% | 0.0% | 7.2 | 22.1 | 31.5 | 1.6 | 9.6 | 18.9 |
| 81 | 49.8% | 9.7% | 5.1% | 25.3% | 3.4 | 52.6 | 1.5 | 4.0 | 16.4 | 13.2 |
| 13 | 70.0% | 24.8% | 3.3% | 1.9% | 2.0 | 72.1 | 3.0 | 0.2 | 16.4 | 3.6 |
| 14 | 6.12% | 34.01% | 0.00% | | 0.0 | 30.1 | 0.0 | 0.5 | 64.8 | 0.1 |
| 15 | 38.7% | 3.4% | 56.3% | 1.3% | 2.5 | 17.1 | 11.5 | 0.0 | 39.5 | 29.1 |
| 16 | 11.11% | 45.19% | 0.00% | | 0.0 | 52.5 | 0.0 | 1.6 | 41.7 | 0.8 |
| 17 | 44.6% | 0.0% | 38.3% | 3.1% | 1.6 | 40.8 | 9.0 | 13.4 | 0.4 | 18.9 |
| 18 | 32.1% | 50.0% | 0.0% | 0.0% | 0.0 | 31.4 | 0.0 | 13.0 | 39.0 | 0.2 |
| 19 | 31.4% | 15.2% | 7.6% | 22.9% | 22.6 | 35.7 | 2.0 | 3.8 | 17.8 | 2.6 |
| 20 | 92.0% | 3.6% | 0.9% | 3.6% | 0.0 | 29.7 | 1.0 | 3.1 | 61.1 | 0.4 |
| 21 | 54.3% | 0.0% | 42.5% | 3.2% | 1.0 | 45.7 | 0.1 | 15.7 | 35.2 | 2.0 |
| 22 | 39.3% | 45.2% | 0.0% | 3.0% | 0.0 | 41.2 | 0.0 | 15.5 | 26.4 | 1.7 |
| 23 | 44.7% | 10.1% | 28.7% | 9.3% | 0.3 | 42.8 | 10.3 | 9.3 | 13.7 | 8.3 |
| 24 | 71.0% | 13.7% | 3.1% | 2.3% | 0.0 | 58.0 | 0.0 | 2.0 | 31.9 | 2.9 |
| 25 | 86.9% | 0.0% | 9.9% | 2.1% | 2.6 | 78.4 | 0.1 | 1.1 | 0.5 | 2.4 |
| 26 | 25.8% | 9.6% | 45.0% | 15.4% | 0.7 | 27.6 | 9.5 | 3.3 | 20.0 | 25.0 |
| 27 | 34.1% | 0.0% | 0.7% | 37.0% | 18.6 | 56.6 | 0.2 | 0.0 | 3.1 | 0.3 |
| 28 | 68.0% | 6.1% | 11.3% | 12.6% | 0.0 | 58.4 | 2.2 | 3.1 | 18.3 | 14.5 |
| 29 | 66.7% | 3.8% | 6.4% | 19.2% | 0.0 | 82.9 | 0.0 | 2.0 | 8.2 | 0.8 |
| 30 | 56.9% | 34.4% | 1.0% | 4.3% | 0.0 | 55.0 | 0.5 | 13.8 | 14.7 | 2.7 |
| 31 | 43.6% | 20.0% | 18.7% | 13.8% | 0.0 | 50.0 | 10.7 | 6.1 | 14.9 | 5.2 |

Table 4. Frequency and hydrologic condition of field-assigned vegetation community types, and the abundance of diagnostic taxa within each community type. Ambiguous sampling locations were in some cases assigned as mixed categories (i.e. slough/wet prairie). Species covers are given as mean relative abundance (in percent) within each category type. Correspondence between field assigned data and measured species composition indicates that these categories are reasonable proxies for vegetation community composition.



| A priori Community | Number | MWD (20 yr) | Sawgrass | Eleocharis spp. | Utricularia spp. | White Waterlily | Typha | Periphyton |
|---:|:--|--:|--:|--:|--:|--:|--:|--:|
| Tree Island | 45 | 9.45 | 11.90 | 1.79 | 1.07 | 0.54 | 0.67 | 0.11 |
| Ridge/Tree Island | 19 | 17.80 | 31.30 | 2.89 | 0.53 | 2.11 | 0.00 | 3.95 |
| Ridge/Slough | 367 | 27.60 | 38.60 | 3.22 | 9.52 | 4.54 | 3.72 | 25.60 |
| Ridge | 2570 | 28.10 | 51.60 | 0.81 | 3.32 | 1.03 | 1.11 | 13.90 |
| Ridge/Wet Prairie | 95 | 28.20 | 38.40 | 12.00 | 8.14 | 3.16 | 0.95 | 31.60 |
| Cattail | 97 | 31.00 | 2.40 | 0.77 | 5.55 | 0.42 | 43.40 | 8.25 |
| Wet Prairie | 593 | 34.70 | 15.30 | 21.80 | 10.70 | 9.13 | 1.38 | 45.70 |
| Slough/Wet Prairie | 23 | 34.90 | 4.20 | 32.40 | 38.90 | 8.26 | 0.22 | 44.10 |
| Slough | 1036 | 46.60 | 1.70 | 8.70 | 30.40 | 19.90 | 0.64 | 35.60 |

Table 5. Abundance and hydrologic characteristics of vegetation community types in different hydrologic management basins within the historic ridge and slough. Means and standard deviations are calculated across all points within each area. Vegetation communities are based on field assigned categories.



| | Ridge | | Wet Prairie | | Slough | |
|---:|:--|--:|:--|--:|:--|--:|
| Area | Count | MWD (SD) | Count | MWD (SD) | Count | MWD (SD) |
| ENP | 415 | 25.91 (8.35) | 272 | 27.16 (8.68) | 15 | 43.37 (4.66) |
| LNWR | 330 | 10.10 (8.54) | 1 | 18.37 (NA) | 157 | 24.30 (15.87) |
| WCA 2 | 285 | 29.42 (5.31) | 0 | (NA) | 95 | 46.40 (11.36) |
| WCA 3A N | 555 | 33.99 (29.70) | 170 | 45.14 (17.20) | 242 | 61.72 (17.60) |
| WCA 3A S | 513 | 31.72 (9.05) | 107 | 37.60 (6.70) | 488 | 47.27 (9.37) |
| WCA 3B | 472 | 30.96 (5.23) | 43 | 34.17 (6.71) | 39 | 35.61 (4.09) |

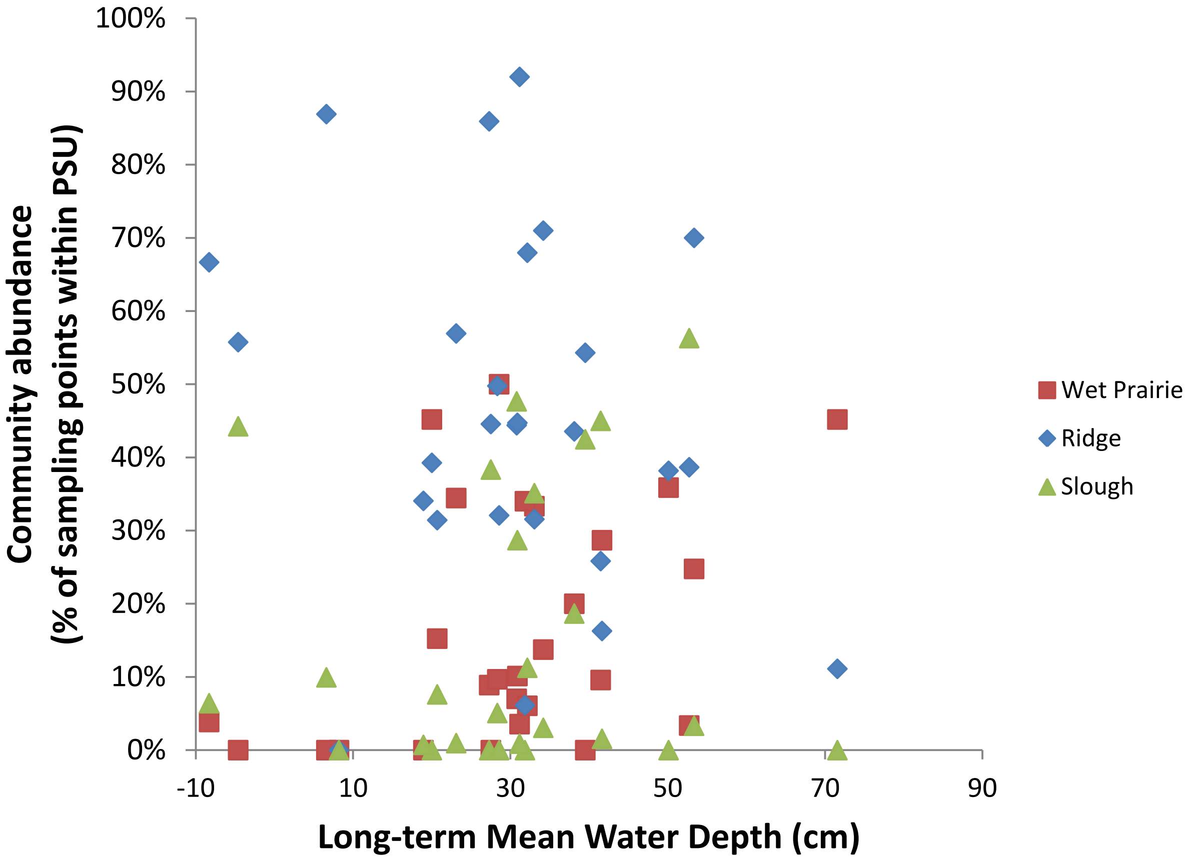
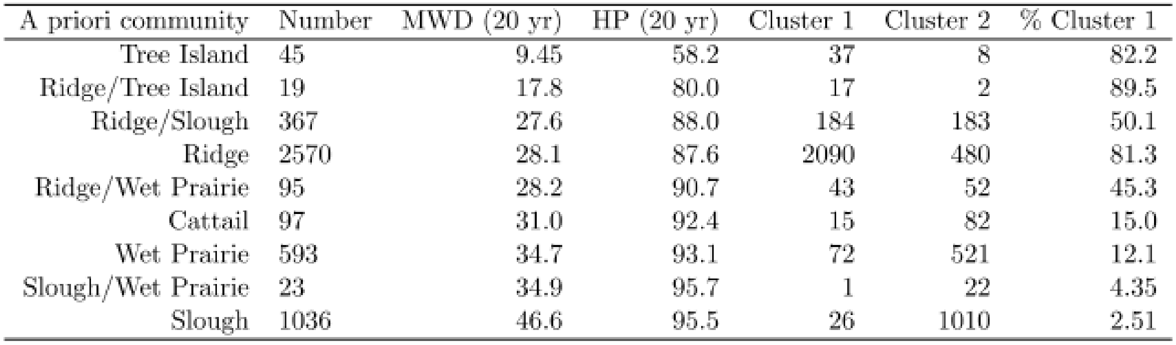


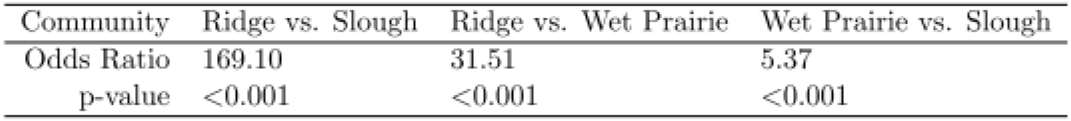
Figure 18. Relative abundance of vegetation communities (based on field-assigned categories) within PSUs as a function of PSU-scale long-term mean water depth.

Table 6. Hydrologic characteristics (mean water depth [MWD; cm] and hydroperiod [HP as inundation frequency]) of field assigned community communities data and correspondence between field assigned community categories and distribution between two clusters following NMDS ordination based on complete species composition data.



| A priori community | Number | MWD (20 yr) | HP (20 yr) | Cluster 1 | Cluster 2 | % Cluster 1 |
|---:|:---|---:|---:|---:|---:|---:|
| Tree Island | 45 | 9.45 | 58.2 | 37 | 8 | 82.2 |
| Ridge/Tree Island | 19 | 17.8 | 80.0 | 17 | 2 | 89.5 |
| Ridge/Slough | 367 | 27.6 | 88.0 | 184 | 183 | 50.1 |
| Ridge | 2570 | 28.1 | 87.6 | 2090 | 480 | 81.3 |
| Ridge/Wet Prairie | 95 | 28.2 | 90.7 | 43 | 52 | 45.3 |
| Cattail | 97 | 31.0 | 92.4 | 15 | 82 | 15.0 |
| Wet Prairie | 593 | 34.7 | 93.1 | 72 | 521 | 12.1 |
| Slough/Wet Prairie | 23 | 34.9 | 95.7 | 1 | 22 | 4.35 |
| Slough | 1036 | 46.6 | 95.5 | 26 | 1010 | 2.51 |

Table 7. Odds ratios for assignment of sampling locations to NMDS clusters based on field-assigned community types. Odds ratios list the relative likelihood of locations identified with each category in the field would be assigned to Cluster 1 (see Table 6 above).



| Community | Ridge vs. Slough | Ridge vs. Wet Prairie | Wet Prairie vs. Slough |
|---:|:---|:---|:---|
| Odds Ratio | 169.10 | 31.51 | 5.37 |
| p-value | <0.001 | <0.001 | <0.001 |

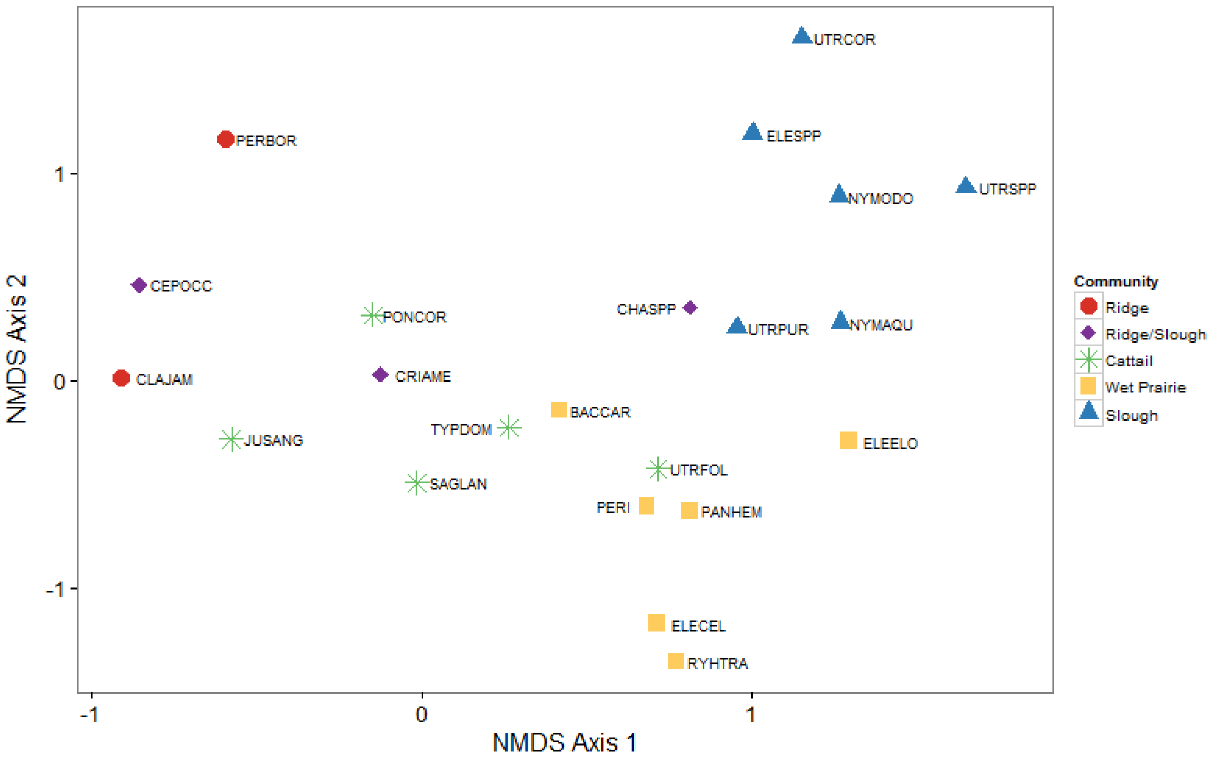


Figure 19. Distribution of the 22 most abundant ridge-slough plant species in ordination space. Note coherent clustering of species by community type.

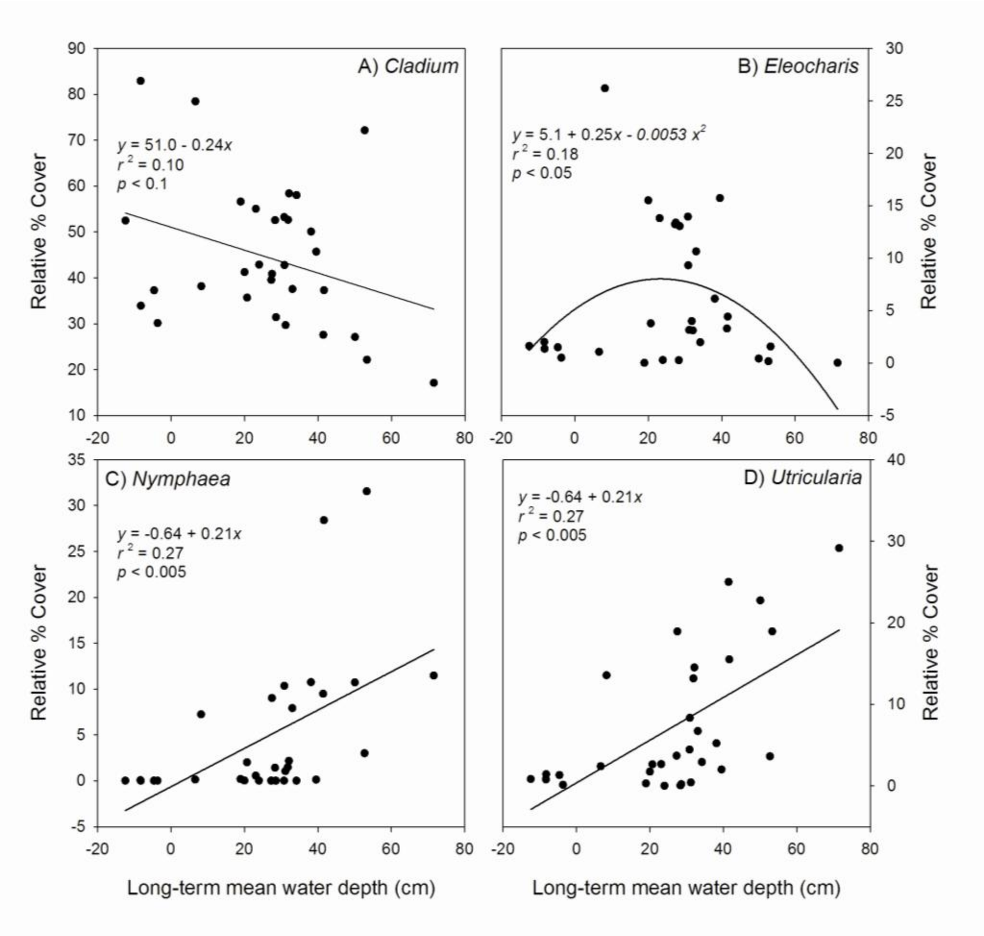


Figure 20. Mean abundance within PSUs of common ridge, slough, and wet prairie species as a function of long-term mean water depth at PSU scale. These data include PSUs outside the historic range of the ridge-slough landscape (i.e. marl prairie areas).

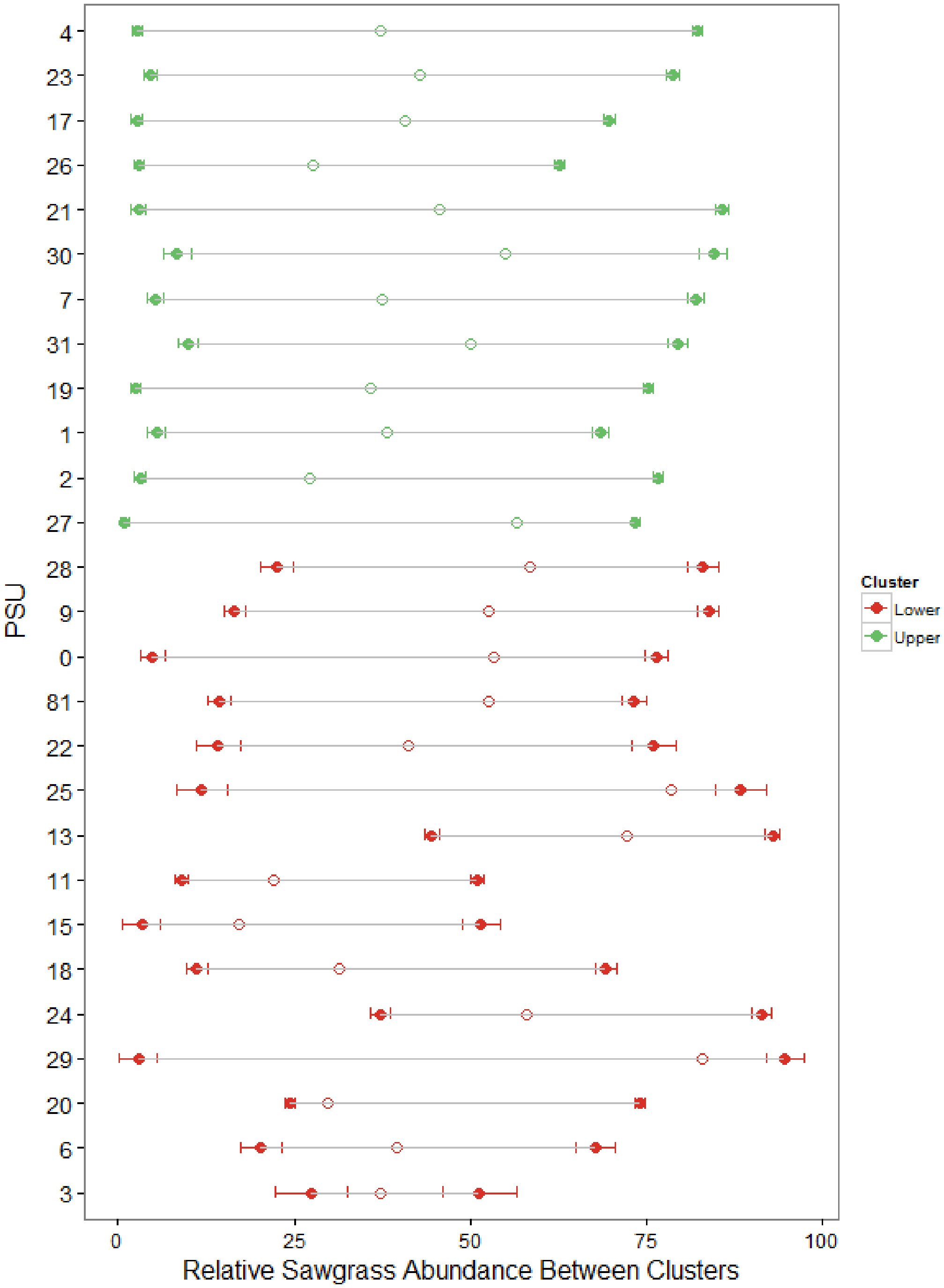


Figure 21. Differentiation of ordination clusters as measured by relative sawgrass abundance. Green symbols represent PSUs with distinct communities characteristic of conserved landscape conditions. Red symbols represent PSUs with relatively indistinct communities characteristic of degraded conditions. Closed symbols indicate sawgrass abundance in each of the two vegetation community clusters defined within each PSU. Open symmbols indicate mean sawgrass abundance across all points within each PSU.

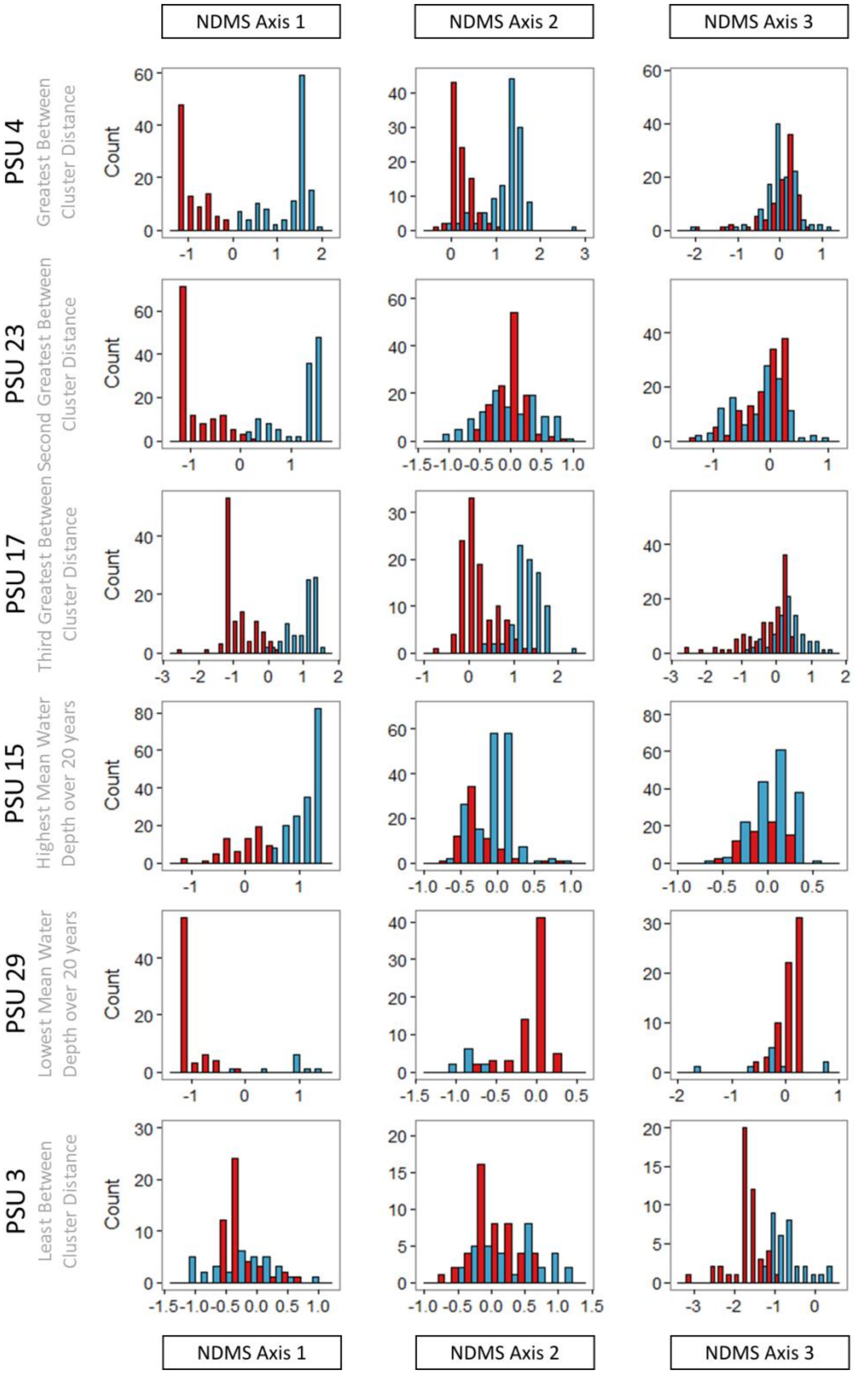


Figure 22. Examples of distribution of sample points in ordination space. In conserved PSUs (4,17,23), vegetation clusters (red and blue bars) are clearly differentiated, and most sample points occur at the extremes of ordination axes (particularly axis 1). In degraded landscapes, clusters are less clearly differentiated, less equally represented, and more commonly occur at intermediate values along ordination axes. These patterns support the inference that shifts in the mean value, rather than changes in variance, account for differences in community cluster separation, and that decreases in community cluster distance capture decreasing distinctiveness of vegetation communities.

Community distinctiveness followed similar geographic patterns to those observed for microtopographic variability (Fig. 23). Only a small fraction of the historic ridge-slough landscape – namely central WCA 3A S – is in a relatively conserved condition reminiscent of the pre-drainage conditions as measured by community distinctiveness. Large sections of ENP, WCA 3B, WCA 3A N, and to a lesser extent WCA 2 and LNWR, are in a more degraded state as defined by this community distinctiveness metric. We note that the scaling of these measures of landscape integrity do not yet allow for direct comparisons of condition as measured by elevation variance and community distinctiveness.

Distance between clusters representing distinctiveness of communities within a landscape was weakly positively correlated with long-term mean water depth (Figure 24). The slope of this relationship was strongly influenced by the three PSUs (PSU 11, PSU 13 and PSU 15) with low community distinctness at the highest 20 year mean water depths. PSUs in ENP, WCA 3A S and WCA 3B clustered relatively closely on both the community distinctiveness and the mean water depth axes; WCA 3A N PSUs were notably all indistinct but had very high 20 year mean water depth variability. Three PSUs that contained more than 5% cattail as a percentage of the total vegetation cover (PSU 11 at 6.29%; PSU 27 at 16.00%; and PSU 19 at 20.57%) had high cluster distances and therefore community distinctiveness (66.38, 126.2, and 153.1 respectively). Variation among PSUs in community distinctiveness followed a shallow bimodal shape (Figure 25) with a long tail represented by the three most conserved PSUs (PSU 17, PSU 23 and PSU 4).

Measures of local relationships between elevation and community composition corresponded to PSUs with strong community distinctiveness. PSUs with high distinctiveness also had higher separation of those communities in water depth; these PSUs also exhibited stronger correlations between point-scale water depth and sawgrass abundance and between local water depth and vegetation community composition (as measured by Mantel's *r*). The strongest vegetation-elevation relationships were observed at intermediate water depths, generally between 30 and 50 cm (Fig. 26). Spatial distribution of the vegetation-elevation association followed similar patterns to those observed for microtopographic variability and vegetation community distinctness (Figure 27-29).

Across PSUs, community distinctiveness increased with microtopographic variation (as measured by water depth standard deviation; Figure 30). Everglades areas generally clustered in discrete ranges of microtopographic variability and community distinctiveness. PSUs within WCA 3A S generally had both high topographic variability and distinct communities, whereas PSUs within ENP, LNWR, WCA 3B, and WCA 2 largely (but not exclusively) exhibited less topographic variability and reduced community distinctiveness.

The bimodality of both community distinctiveness (Figure 25) and topographic standard deviation (Fig 15) provide one way to partition PSUs into quadrants corresponding to positions along trajectories of degradation (Figs. 5, 30). Among PSUs sampled to date, the largest proportion had degraded conditions as measured by both elevation standard deviation and community distinctness. Seven PSUs, mostly in WCA3AS, had distinct communities and high elevation variance. Five PSUs exhibited distinct communities but low elevation variance, whereas no PSUs exhibited the opposite pattern.

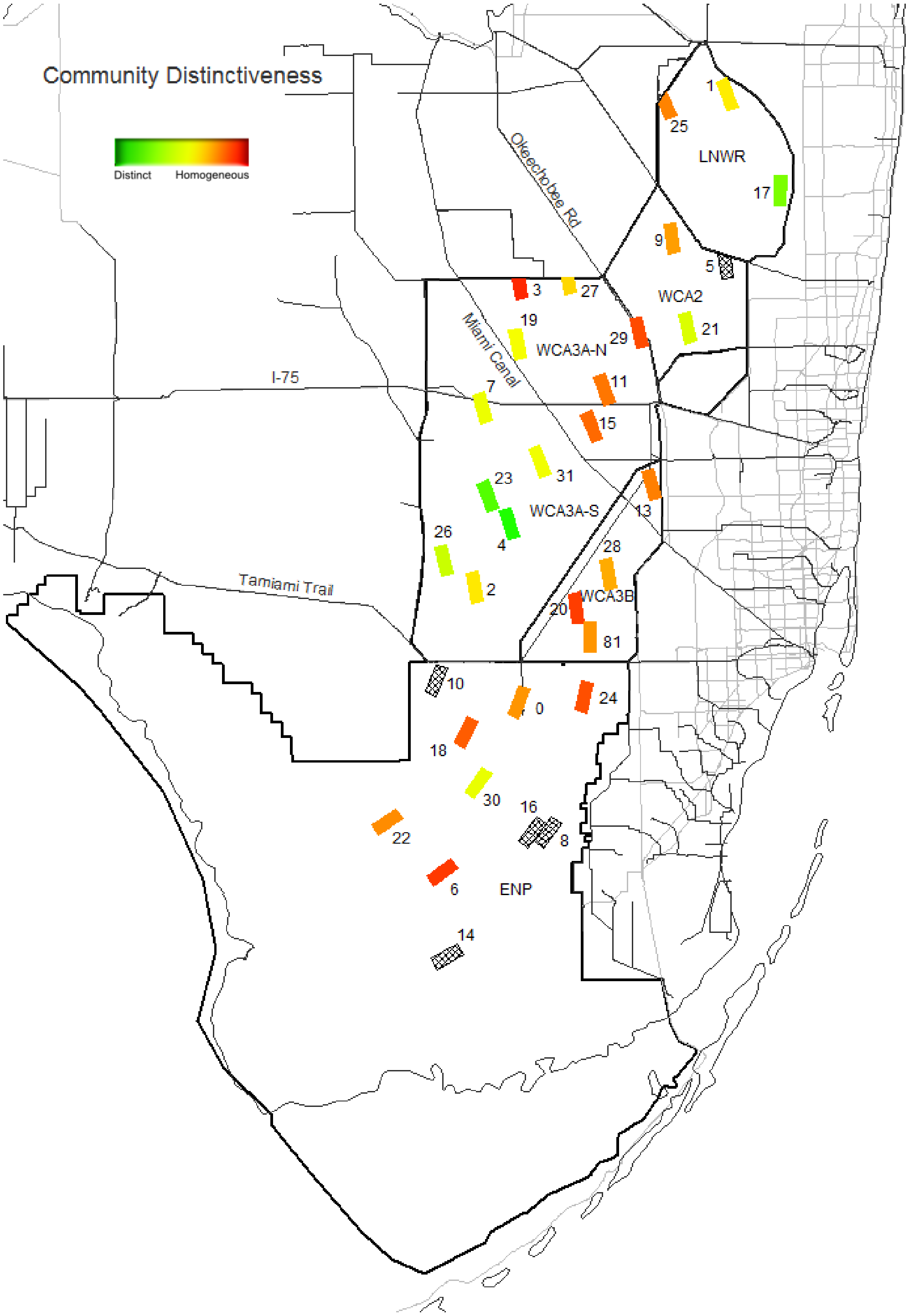


Figure 23. Spatial patterns of vegetation community distinctness across the historic ridge-slough landscape. Colors indicate the separation of vegetation communities (as measured by the distance between midpoints of clusters in NMDS ordination space).

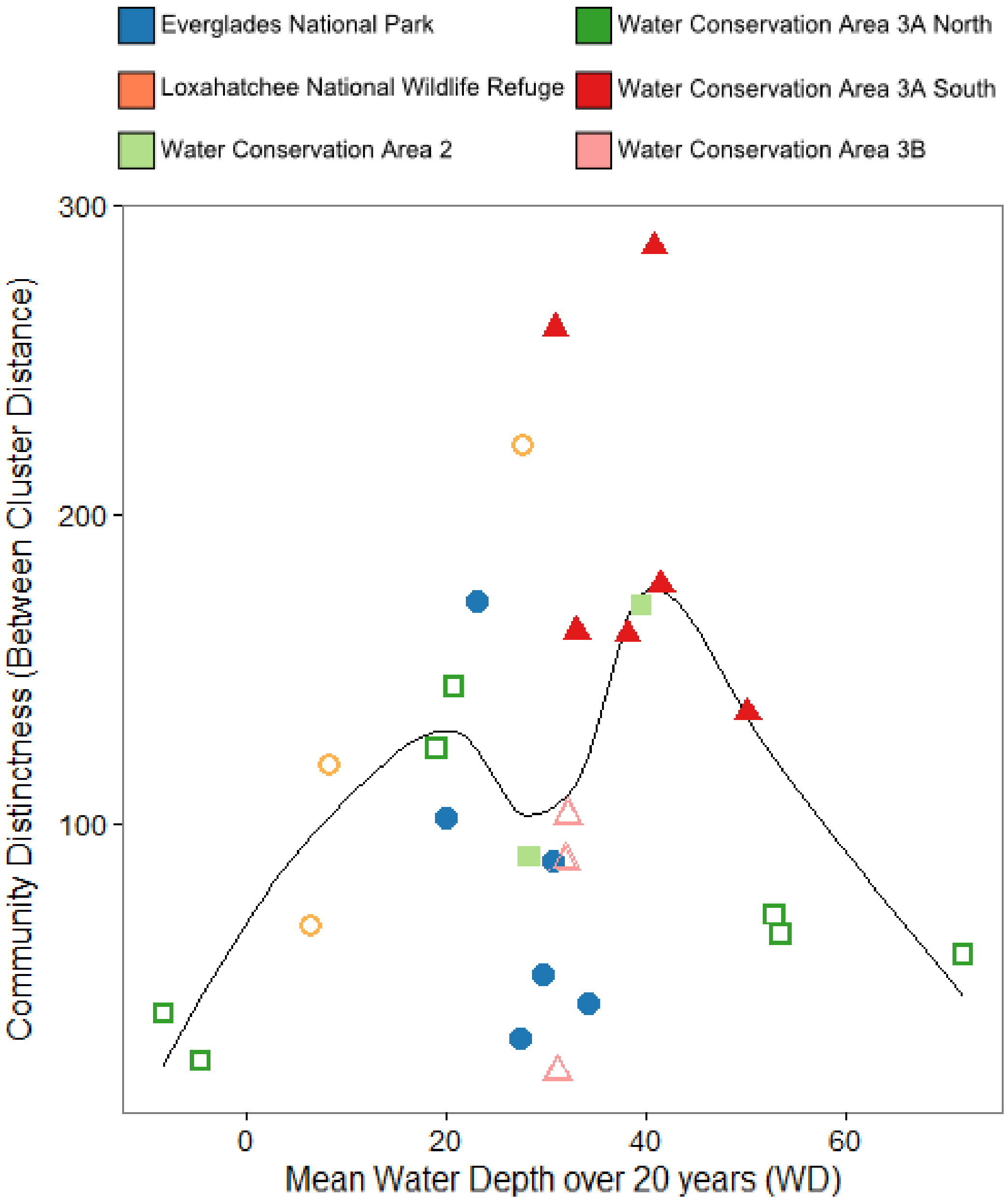


Figure 24. Relationship between hydrologic regime and vegetation community distinctiveness across PSUs within the historic ridge and slough. Symbols represent PSUs in different hydrologic management basins. Differences in community distinctness among PSUs with similar contemporary hydrologic regimes (e.g., ENP and WCA3B vs. WCA3S) may indicate that antecedent hydrologic regime and other past disturbances may continue to shape existing landscape structure. Line indicates best-fit regression on all data.

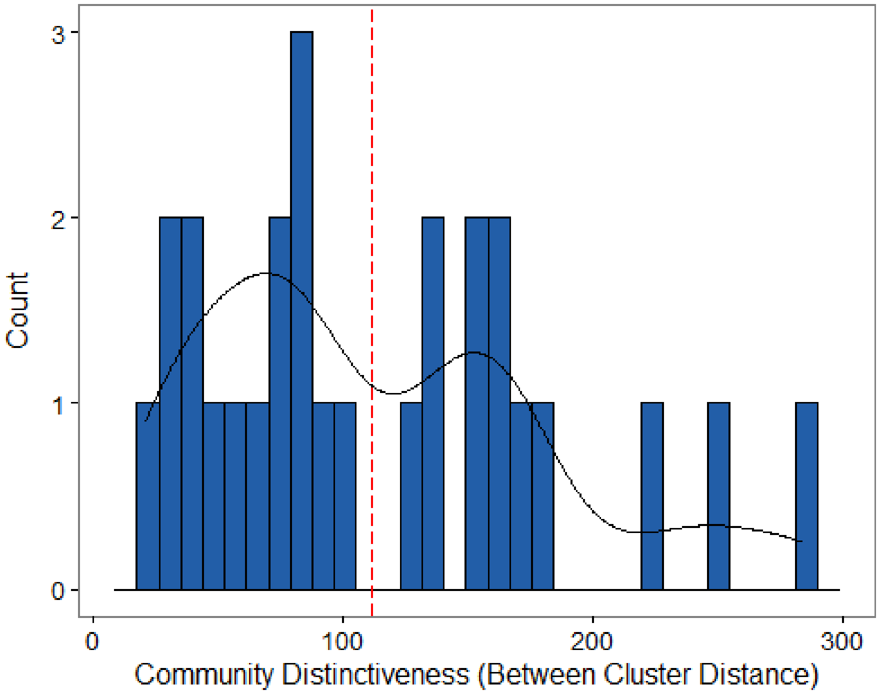


Figure 25. Frequency of community distinctiveness variation across PSUs. Black line indicates the best-fit model of frequency distribution. Red line is the boundary between distinctive communities characteristic of conserved landscapes and indistinct communities characteristic of degraded conditions, and is used to partition PSU condition in Figure 31. The bi-modal pattern observed in these data is consistent with current hypotheses about the self-organized character of the ridge-slough landscape.

Table 8. Measures of covaration among elevation, hydrologic regime, and vegetation community structure.

| | Community Elevation Distributions | | | | | | | | | | Community Distinctness | | Elevation-Composition Relationships | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Cluster 1 | | | | | Cluster 2 | | | | | | | | | |
| PSU | MWD | StDev | Kurtosis | Skew | % | MWD | StDev | Kurtosis | Skew | % | Cluster Distance | Cluster Distance (no peri) | k-means WD difference (cm) | Mantel's r | *r*2 Cladium-WD |
| 0 | 38.63 | 5.66 | -0.18 | 0.15 | 32.46 | 27.04 | 4.48 | 3.15 | 1.61 | 67.54 | 86.4 | 104.5 | 11.6 | 0.52 | 0.52 |
| 1 | 11.82 | 4.82 | 0.39 | -0.36 | 48.15 | 4.80 | 4.89 | -0.04 | -0.23 | 51.85 | 137.4 | 130.1 | 7.0 | 0.33 | 0.27 |
| 2 | 53.95 | 8.87 | 0.47 | -0.62 | 67.30 | 42.20 | 9.64 | -0.86 | -0.20 | 32.70 | 134.4 | 220.5 | 11.8 | 0.30 | 0.29 |
| 3 | -4.53 | 3.78 | -1.68 | -0.01 | 41.25 | -4.66 | 3.56 | -0.65 | -0.34 | 58.75 | 21.0 | 32.4 | 0.1 | 0.15 | 0.05 |
| 4 | 46.20 | 11.06 | -0.94 | -0.32 | 56.54 | 33.70 | 8.85 | 0.02 | 0.55 | 43.46 | 284.4 | 327.8 | 12.5 | 0.29 | 0.25 |
| 5 | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND | ND |
| 6 | 28.36 | 5.63 | -0.35 | -0.08 | 40.46 | 26.59 | 6.96 | 4.87 | 1.02 | 59.54 | 29.7 | 55.0 | 1.8 | 0.09 | 0.01 |
| 7 | 36.14 | 4.53 | 1.40 | 0.36 | 58.05 | 28.78 | 6.32 | 4.24 | 1.06 | 41.95 | 158.4 | 228.8 | 7.4 | 0.33 | 0.44 |
| 8* | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.24 | 0.01 |
| 9 | 28.82 | 5.17 | 1.64 | 0.49 | 53.50 | 27.77 | 4.63 | -1.05 | 0.04 | 46.50 | 91.7 | 96.5 | 1.0 | 0.01 | 0.00 |
| 10* | - | - | - | - | - | - | - | - | - | - | - | - | - | -0.09 | 0.02 |
| 11 | 53.93 | 5.98 | 1.96 | -0.51 | 68.89 | 52.09 | 8.48 | 0.40 | 0.50 | 31.11 | 66.4 | 85.1 | 1.8 | 0.08 | 0.05 |
| 81 | 32.68 | 6.83 | -0.39 | -0.06 | 35.02 | 31.40 | 5.01 | 2.22 | -1.16 | 64.98 | 86.3 | 126.1 | 1.3 | 0.22 | 0.03 |
| 13 | 54.00 | 7.46 | 0.44 | -0.26 | 57.14 | 51.04 | 9.12 | -0.62 | -0.33 | 42.86 | 72.1 | 60.5 | 3.0 | 0.01 | 0.00 |
| 14* | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.13 | 0.04 |
| 15 | 71.93 | 10.19 | -0.04 | 0.10 | 28.57 | 71.43 | 8.15 | -0.15 | -0.08 | 71.43 | 59.1 | 126.2 | 0.5 | 0.07 | 0.03 |
| 16* | - | - | - | - | - | - | - | - | - | - | - | - | - | 0.08 | 0.00 |
| 17 | 36.92 | 13.85 | 2.93 | 0.54 | 43.01 | 20.65 | 6.54 | 1.92 | -0.20 | 56.99 | 227.8 | 241.2 | 16.3 | 0.51 | 0.25 |
| 18 | 31.26 | 7.00 | -1.34 | -0.20 | 65.09 | 26.92 | 6.45 | -0.93 | 0.26 | 34.91 | 51.2 | 73.9 | 4.3 | 0.08 | 0.06 |
| 19 | 24.63 | 8.10 | -0.08 | -0.27 | 54.29 | 16.02 | 5.85 | 1.39 | 0.75 | 45.71 | 153.1 | 231.2 | 8.6 | 0.33 | 0.30 |
| 20 | 32.09 | 4.20 | -0.37 | -0.38 | 89.33 | 23.48 | 5.60 | -0.53 | 1.00 | 10.67 | 33.1 | 62.0 | 8.6 | 0.35 | 0.30 |
| 21 | 47.34 | 10.99 | -0.56 | 0.20 | 48.39 | 32.19 | 5.91 | 6.08 | 1.78 | 51.61 | 169.2 | 484.1 | 15.2 | 0.44 | 0.45 |
| 22 | 22.00 | 7.68 | -0.11 | -0.44 | 43.70 | 18.48 | 6.07 | 0.14 | 0.45 | 56.30 | 79.2 | 117.5 | 3.5 | 0.11 | 0.03 |
| 23 | 39.30 | 7.60 | -0.67 | -0.52 | 48.52 | 22.96 | 4.87 | 0.05 | 0.61 | 51.48 | 252.4 | 312.9 | 16.3 | 0.68 | 0.61 |
| 24 | 36.24 | 4.85 | -0.19 | -0.43 | 38.17 | 32.91 | 6.65 | -0.36 | -0.31 | 61.83 | 42.4 | 45.4 | 3.3 | 0.10 | 0.03 |
| 25 | 6.60 | 5.78 | 3.61 | 0.43 | 86.91 | 6.06 | 10.84 | -0.84 | 0.65 | 13.09 | 75.6 | 103.4 | 0.5 | 0.21 | 0.00 |
| 26 | 47.41 | 9.26 | 0.07 | -0.66 | 58.75 | 33.02 | 6.48 | 2.19 | -0.06 | 41.25 | 180.2 | 231.4 | 14.4 | 0.45 | 0.32 |
| 27 | 36.13 | 5.08 | 0.25 | -0.97 | 23.19 | 13.76 | 11.01 | -0.73 | 0.41 | 76.81 | 126.2 | 146.2 | 22.4 | 0.45 | 0.37 |
| 28 | 33.86 | 4.68 | -0.51 | -0.08 | 40.69 | 30.98 | 5.41 | 0.02 | -0.37 | 59.31 | 97.5 | 124.9 | 2.9 | 0.02 | 0.03 |
| 29 | -8.15 | 2.81 | -0.23 | -0.44 | 87.18 | -9.29 | 4.20 | 0.56 | -1.32 | 12.82 | 39.9 | 46.7 | 1.1 | -0.01 | 0.01 |
| 30 | 28.17 | 8.56 | -0.30 | -0.26 | 38.76 | 19.90 | 7.44 | -0.57 | -0.19 | 61.24 | 163.1 | 184.7 | 8.3 | 0.26 | 0.05 |
| 31 | 41.44 | 5.61 | 0.51 | 0.41 | 42.22 | 35.69 | 6.38 | -0.21 | 0.55 | 57.78 | 156.4 | 182.4 | 5.7 | 0.15 | 0.07 |

* Elevation mode analysis was not performed on PSUs outside the historic distribution of the ridge-slough landscape.

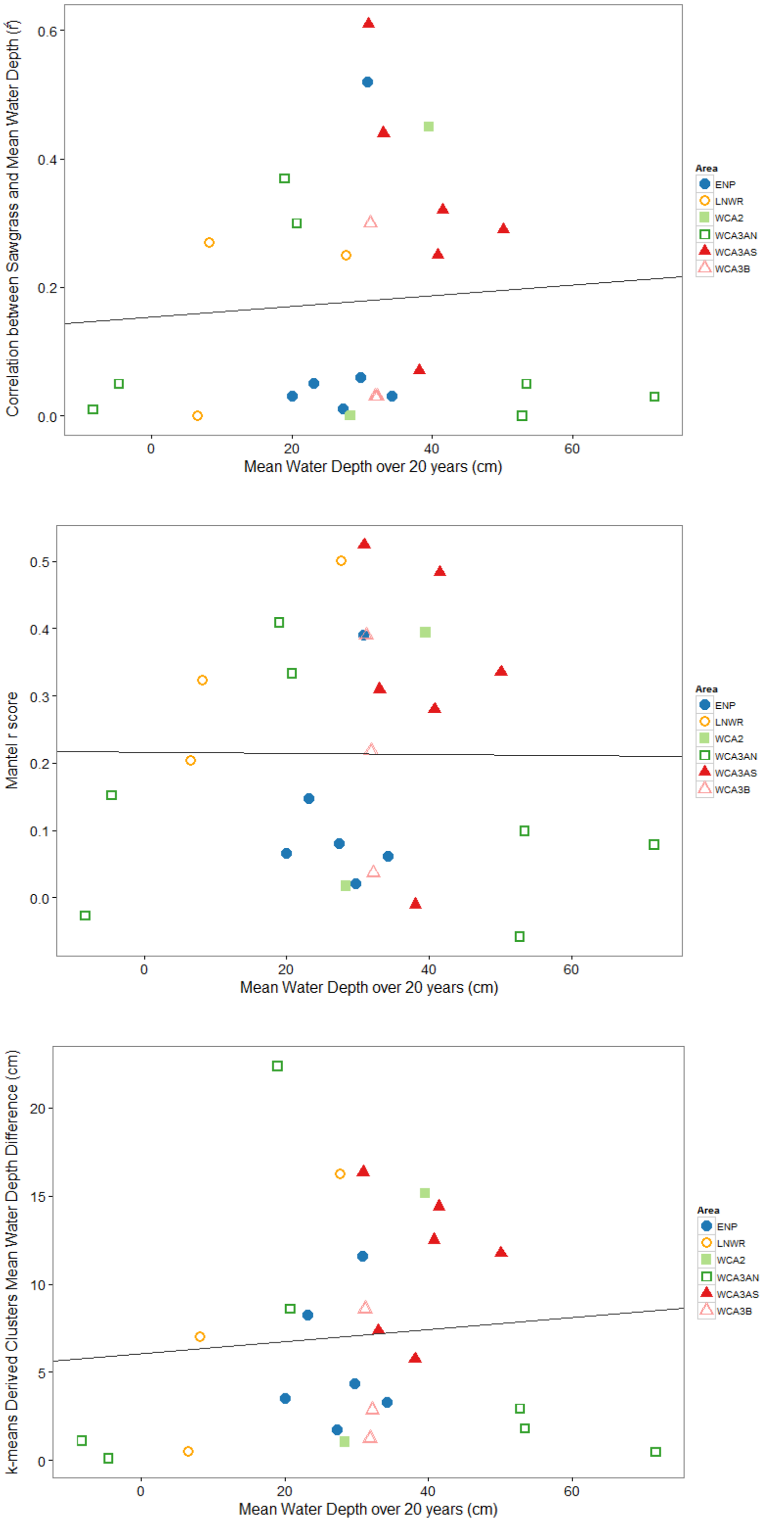


Figure 26. Relationships between long-term mean water depth (calculated at PSU scale) and 3 measures of the strength of elevation-vegetation associations (correlation between sawgrass abundance and elevation (top); Mantel's correlation coefficient [r], which is the multivariate equivalent of Pearson's correlation coefficient (middle); and the elevation difference between the two ordination clusters). Symbols represent PSUs in different hydrologic management basins.

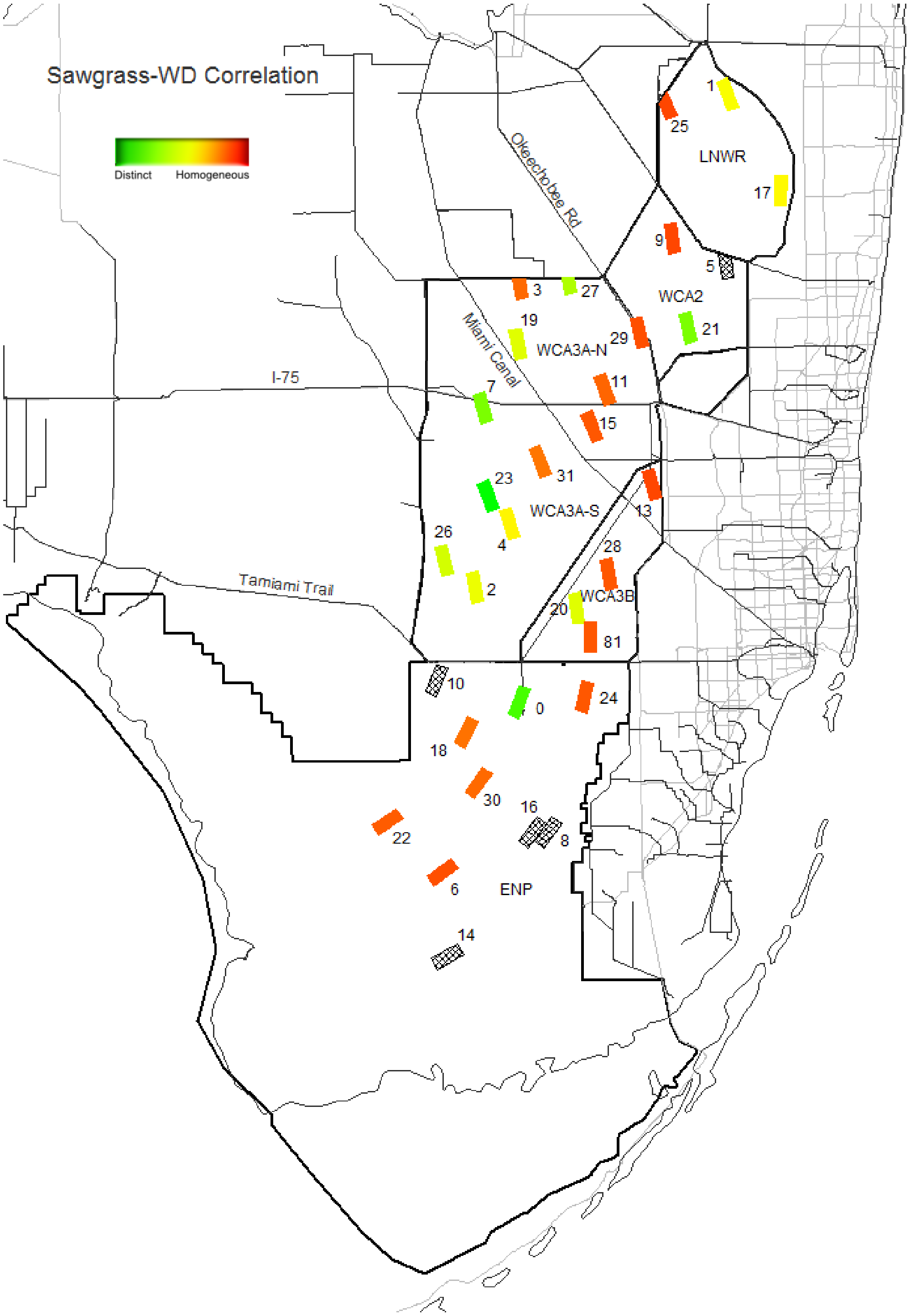


Figure 27. Spatial patterns of elevation-vegetation associations (as measured by the correlation between relative abundance of sawgrass and local elevation). Colors indicate the strength of association between elevation and vegetation community structure. Hatching indicates PSUs that were not sampled (PSU 5 in WCA 2) or that were excluded from the analysis because they lie outside the historic distribution of the ridge-slough landscape (PSUs 8, 10, 14,16 in ENP).

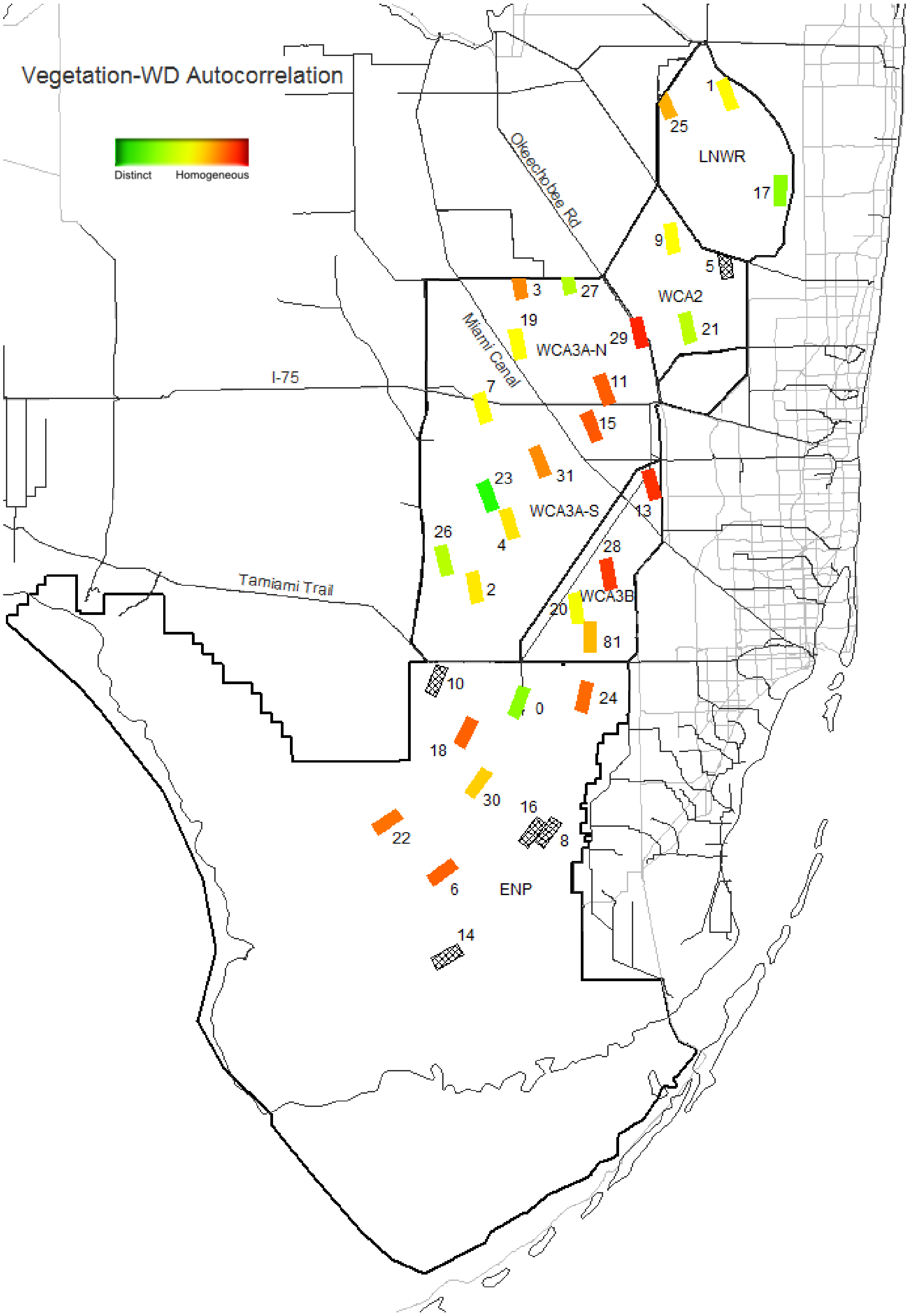


Figure 28. Spatial patterns of elevation-vegetation associations (as measured by Mantel's correlation coefficient [r], which is the multivariate equivalent of pearson's correlation coefficient). Colors indicate the strength of association between elevation and vegetation community structure. Hatching indicates PSUs that were not sampled (PSU 5 in WCA 2) or that were excluded from the analysis because they lie outside the historic distribution of the ridge-slough landscape (PSUs 8, 10, 14,16 in ENP).

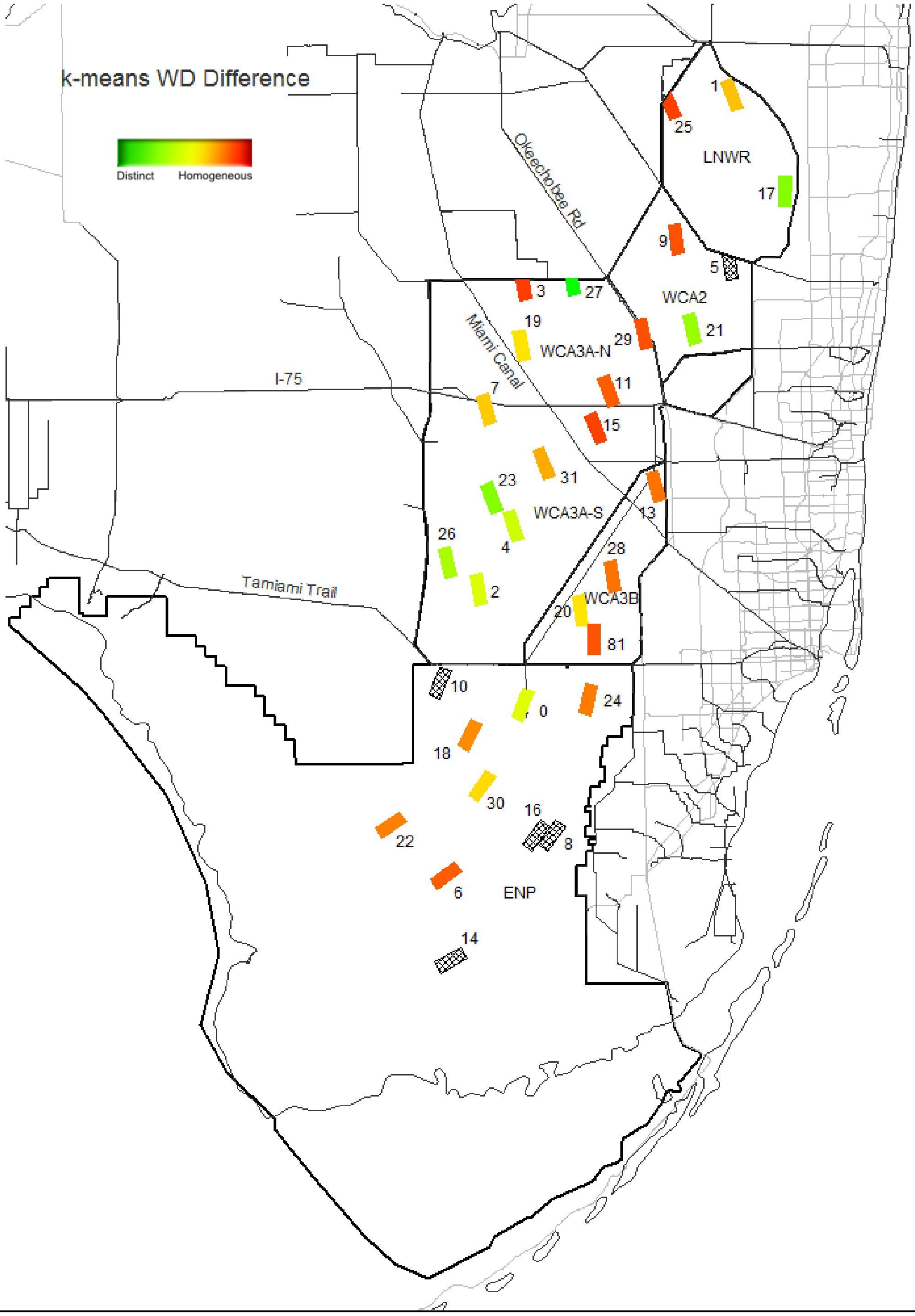


Figure 29. Spatial patterns of elevation-vegetation associations (as measured by the difference in elevation between points assigned to cluster 1 and cluster 2 in ordination space). Colors indicate the magnitude of elevation differences. Hatching indicates PSUs that were not sampled (PSU 5 in WCA 2) or that were excluded from the analysis because they lie outside the historic distribution of the ridge-slough landscape (PSUs 8, 10, 14,16 in ENP).

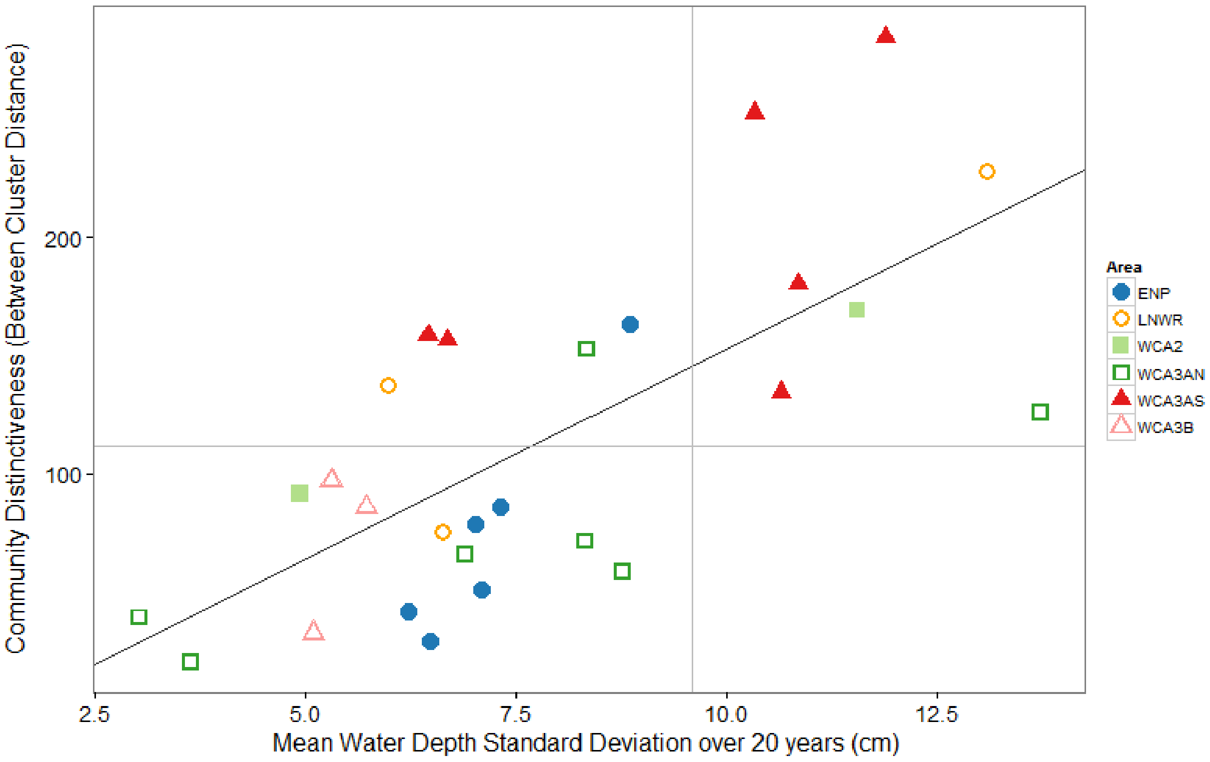


Figure 30. Relationship between microtopographic variability (as measured by standard devation of elevation within each PSU) and vegetation community distinctiveness (as measured by distance separating clusters in ordinations space). The vertical line separates PSUs in the upper and lower mode of elevation variance (Fig. 15), and the horizontal line separates PSUs in the upper and lower mode of community distinctiveness (Figure 25). Resulting quadrants correspond to hypothesized pathways of degradation (Fig. 5).

## Discussion

The results of this monitoring study support and expand on current understanding of landscape pattern in the ridge-slough-tree island mosaic, its responses to hydrologic regime, and the spatial distribution of its degradation and persistence. Microtopographic structure and vegetation structure exhibited broadly similar geographic patterns (Figs 14, 23); landscapes in southern and central WCA3AS had greater topographic variability, and bi-modally distributed soil elevations that maintained distinct ridge and slough communities. These features were less prevalent in areas that have or are currently experiencing hydrologic alteration. Bi-modal distributions of soil elevation variance (Fig. 15), community distinctiveness (Fig. 25), and the strength of elevation-vegetation associations provide tentative support for the hypothesis that the historic patterned structure and degraded landscape patterns represent alternative stable states (Scheffer and Carpenter 2003).

### *Topographic measures of ridge-slough landscape condition*

The microtopographic differentiation of ridges and sloughs is a fundamental feature of the historic ridge-slough landscape (SCT 2003, McVoy et al. 2011, USACE and SFWMD 2000). This differentiation is widely hypothesized to reflect local feedbacks among elevation, hydrologic regime plant community productivity and composition, and peat production and decomposition (Larsen et al. 2007, Cohen et al. 2011), although a variety of mechanisms have been proposed to account for the spatial patterning of these patch types. To date, our monitoring efforts have focused on two measures of microtopographic differentiation: elevation variance and the occurrence of distinct elevation modes. These measures are related in that the feedbacks hypothesized to create distinct elevation modes should also promote greater overall variation in elevation. The empirical relationship between the standard deviation of elevation and the difference between elevation modes (Fig. 17) supports this hypothesis, as the greatest elevation variance occurred only in PSUs with distinct elevation modes, and specifically among the PSUs with the greatest differences between elevation modes. However, it is also clear that the mere occurrence of bi-modality is insufficient to ensure strongly differentiated elevation modes, as some PSUs with bi-modal elevation distributions had relatively low overall elevation variance (Fig. 17).

The differences between elevation modes we observed in conserved areas are consistent with previous measurements in central and southern WCA3AS (Watts et al. 2010). In this study, elevation mode differences ranged from as low as 12 to as high as 24 cm, which is similar to the range observed by Watts et al (2010) in a smaller number of landscape blocks. Historical estimates of elevation differences between ridges and sloughs are generally higher, ranging from 30 to 60 cm, and in some cases as great as 90 cm (McVoy et al. 2011). A direct comparison of these historic and contemporary estimates suggests that considerable deflation of ridge-slough topography has occurred even in conserved areas. However, such a direct comparison may be inappropriate for several reasons. First, Kaplan et al. (2012) used a hydrodynamic model to assess the influence of spatial orientation of pattern features on hydroperiod, and found that maintaining presumed historic hydroperiods over ridges and sloughs separated by 50 cm would require twice the water volume thought to pass through the historic Everglades. This finding suggests that the upper range of estimated ridge-slough differences may be implausible on a physical basis. The second reason that direct comparison of historic ridge-slough elevation differences and our estimates of elevation mode differences is that these measure subtly different things. Historic ridge-slough measurements such as those reported in McVoy et al. (2011) measure elevation differences between the highest point in a ridge and the lowest point in an adjacent slough. Such isolated observations may be biased toward the greatest elevation differences, and certainly do not represent a random sampling of locations. In contrast, the elevation mode differences reported here are based on spatially-integrated means of ridges and sloughs over entire landscapes, and would not be biased toward higher or lower elevations within ridges and sloughs, respectively, or toward locations with particularly distinct elevations. As such, comparison of historic measurements of elevation differences may somewhat overestimate the incongruity of these measurements. However, the relationship between elevation mode difference and long-term mean water depth across PSUs (Figure 16) supports the underlying hypothesis of McVoy and co-authors that ridge-slough elevation differences are sensitive to hydrologic regime, and that elevation differences may have decreased even in relatively conserved areas in response to recent anthropogenic hydrologic alteration.

### *Vegetation structure as a measure of ridge-slough condition*

The historic ridge-slough mosaic was characterized by the distinct zonation of plant species whose distributions were shaped by abrupt differences in elevation between ridges and sloughs (Ogden 2005, McVoy 2011). The distinct sawgrass-dominated ridges and *Nymphea*- and *Utricularia*-dominated sloughs observed in conserved landscapes of WCA3AS are consistent with these previous findings. While a number of studies have documented shifts in community composition in response to changing hydrologic regimes at relatively broad scales (Givnish et al. 2008, Zweig and Kitchens 2008, Zweig and Kitchens 2009, Todd et al. 2010, Foti et al. 2012, Todd et al. 2012), this study is the first to systematically document those differences at the scale of the entire Greater Everglades ecosystem, and to do so based on field observations. We found that high mean long-term water levels were associated with relatively low abundance of sawgrass, and more strongly with high abundances of *Nymphea* and *Utricularia* (Fig. 20). *Eleocharis cellulosa*, a characteristic wet prairie species, was most abundant in PSUs with intermediate long-term water depths. These patterns support the conclusions of a number of studies that hydrologic regime shapes plant species composition at broad spatial scales across the Greater Everglades ecosystem. However, considerable variation within and among PSUs in the abundance of individual taxa suggest that the simple prevalence of indicator species, at least as measured in this study, may be a relatively poor measure of landscape condition.

In addition to these compositional shifts, we observed declines in the distinctness of local plant communities. Previous studies have indicated that hydrologic alteration promotes the blending of ridge and slough communities, as well as increased prevalence of species characteristic of intermediate elevations (e.g., *Eleocharis spp.*). Our landscape-scale assessment confirms that in conserved landscape such as those found in central and southern WCA3AS, local vegetation communities are highly distinct (Fig. 25, 26). In areas subject to increased or decreased water levels by hydrologic alteration, this distinctness is reduced.

Our approach to measuring community distinctness is a newly developed measure based on measurements of distances between two artificially imposed clusters of plant communities in ordination space. To ensure that this measure is a reasonable proxy for the distinctness of ridge and slough communities, we assessed the prevalence of sawgrass in each of the two clusters within each PSU, and found that in conserved PSUs (those with large distances between communities in ordination space), one cluster was always characterized by very high sawgrass abundance, and the other characterized by very low sawgrass abundance; in degraded landscapes, abundance of sawgrass between the two clusters was more varied (Fig. 21). More sophisticated descriptions of plant communities similarly supported use of cluster distance as a measure of community distinctness within PSUs (Fig. 22). In conserved landscapes, most sampled plant communities occupied one or the other extreme of NMDS axis 1, whereas in degraded landscapes many local plant assemblages had intermediate values. These patterns are consistent with the positions of sawgrass and characteristic deepwater slough species at opposite ends of NMDS axis 1 in our ordination.

### *Vegetation-elevation relationships as a measure of ridge-slough condition*

Conceptual models and empirical observations of the ridge-slough landscape suggest that strong relationships between microtopography and vegetation community structure were characteristic of the historic and conserved ridge-slough landscape (Larsen et al. 2011, McVoy 2011). We used three approaches to characterize how the strength of this association varied across the historic ridge-slough landscape (Table 8). The first and simplest of these measures is the correlation coefficient between elevation and sawgrass abundance within a PSU. The second of these uses Mantel's *r* to measure the association between elevation and overall community composition. The third of these measures the difference in mean elevation between points assigned to each of the vegetation community clusters that we used to measure community distinctness. As for isolated measures of microtopographic and vegetation community structure, vegetation-elevation relationships were strongest in areas of conserved condition, principally in central and southern WCA3AS (Figure 29). Individual PSUs within other Everglades basins also exhibited strong associations between elevation and community composition.

### *Geostatistical and geospatial measures of ridge-slough landscape structure*

The historic ridge-slough landscape and current conserved portions are characterized not simply by topographic heterogeneity and distinct vegetation communities, but by a characteristic flow-parallel patterning of ridges and sloughs. A variety of metrics have been proposed to measure that spatial structure from aerial photographs and other remotely sensed measurements (Wu et al. 2006, Foti et al. 2012, Larsen et al. 2012). These include measurements of ridge geometry, slough connectivity, and the relative abundance of these patch types. The maps generated as part of this study could provide a more spatially and taxonomically resolved data set on which to base such measurements, but current approaches largely assume 2-3 patch types in their assessments of spatial pattern (Wu et al. 1997, Wu et al. 2006, Nungesser 2011). A strength of these approaches is that historic aerial imagery is available for some portions of the Everglades, allowing for more robust analysis of long-term trends (Nungesser 2011). However, because they use vegetation structure to assess overall landscape condition, these geospatial measures cannot evaluate changes to microtopographic structure that may in some cases precede degradation of vegetation structure.

Watts et al (2010) present several geostatistical measures of microtopographic structure based on field measurements of soil elevation similar to those reported for this study. One such measure is the spatial autocorrelation of elevation, which in patterned landscapes is predicted not simply to decrease with distance but to become negative at some distance. Such patterns are thought to reflect the operation of negative feedbacks at distance, which are necessary for the formation of regular spatial pattern (Rietkerk and Van de Koppel 2008). A second measure is the degree of spatial structure of elevation based on sill and nugget variance measured by semi-variance analysis. This measure describes the extent to which heterogeneity is structured in space, as opposed to randomly distributed. Conserved ridge-slough landscapes would be expected to exhibit strong spatial structure (Watts et al. 2010). A third measure, anisotropy, measures the directionality of elevation based on the semi-variance observed for points oriented perpendicular or parallel to some axis (in this case, the orientation of historic flow). Conserved ridge-slough landscapes would be expected to exhibit strong anisotropy. The results of these spatial analyses are not yet available for sampled PSUs, but will be included in future reports.

One potential avenue for development of additional measures of ridge slough structure would be application of the microtopographic measures developed by Watts et al. (2010) to vegetation community composition data. Such analyses could be based on the abundance of single species, such as sawgrass, or based on dissimilarity scores derived from ordination of whole plant community data. Such geostatistical analyses could, in principle, integrate microtopographic data with plant community composition, for example by analysis of cross correlation between these variables.

### *Hydrologic conditions supporting persistence of conserved conditions*

The current distribution of conserved microtopographic and vegetative conditions provides some information about the hydrologic regimes that support the persistence of relatively intact ridge-slough landscapes, and the conditions that promote degradation of landscape structure. Conserved microtopographic structure, as inferred from bi-modal elevation distributions, was observed in PSUs with long-term mean water depths between 25 and 51 cm. The difference between elevation modes was relatively small in most PSUs with long term mean water depths less than 35 cm, and a number of PSUs with long-term mean water depths less than 40 cm did not exhibit bi-modal distributions. At long-term mean water depths less than 25 and greater than 51 cm, we did not observe PSUs with distinct elevation modes (with a single exception in PSU 3, where the difference between elevation modes was <5 cm, and given the extremely dry conditions, probably represents a statistical artefact rather than a truly bi-modal distribution). In a previous study, Watts et al (2010) found bi-modal elevation distributions in PSUs with long-term mean water depths that ranged from 18 to 53 cm. In all, our data suggest that the preservation of microtopographic differentiation of ridges and sloughs is best maintained by long-term mean water depths between 40 and 50 cm, but that microtopographic structure sometimes resists degradation at water levels as low as 25 cm.

Using vegetation community distinctness yields similar estimates of hydrologic regimes that support relatively conserved landscape structure. Communities with distinct clusters in ordination space occurred in PSUs with long-term mean water depths ranging from ca. 15 cm to ca. 51 cm. The dry extreme of this range represents a single PSU within Loxahatchee National Wildlife Refuge, whose vegetation communities are not necessarily comparable to those of other areas. Within the other water conservation areas, we observed conserved vegetation structure at long-term mean water levels greater than 20 cm. As was observed for microtopographic structure, the drier end of this range (between 20 and 35 cm) also included PSUs with indistinct communities indicative of degraded conditions. All PSUs with long-term mean water depths between 35 and 50 cm had well-differentiated ridge and slough communities.

Previous studies have demonstrated that Everglades plant species respond to diverse characteristics of hydrologic regime that are not captured by the relative coarse metric of long-term mean water depth (Givnish et al. 2008, Zweig and Kitchens 2009). For example, the relative abundance of slough and wet prairie species can shift in response to seasonal and interannual variation in water level. However, given the topographic variation within PSUs, measures of local hydrologic regime cannot easily be scaled to broader landscapes. Moreover, the frequency of hydrologic extremes, especially drying, are likely to covary strongly with long-term mean water level. Finally, long-term mean water depth provides a relatively simple measure of hydrologic regime that may serve as a tractable management target. While future analyses will assess whether other measures of hydrologic regime help explain variation in landscape condition, we contend that long-term mean water depth provides the most useful measure of hydrologic conditions. Based on the general agreement between microtopographic and vegetation community structure as measures of ridge-slough landscape condition, **we recommend a range of long-term mean water depths between 35 and 50 cm as supportive of relatively intact ridge-slough landscapes.** Inclusion of the full complement of 80 PSUs will provide additional information that may further support or refine these estimates.

### *Spatial distribution of conserved and degraded ridge-slough landscape conditions*

The results of this study support previous conclusions (Wu et al. 2006, Nungesser 2011, McVoy et al. 2011) that historic ridge-slough landscape conditions are best conserved in central WCA3AS. PSUs in that area (specifically, PSUs 2, 4, 23, 26) are characterized by distinct ridge and slough communities that are well sorted along widely separated elevation modes. Microtopographic and vegetation structure and their covariation also indicated moderately conserved conditions in isolated portions of other water management basins, including southeastern WCA1 (17) and southern WCA2 (21). One PSU (27) in northern WCA3AN superficially exhibit conserved microtopographic structure and community distinctiveness; however, these characteristics appear to reflect a severe recent fire regime and significant invasion (and perhaps creation) of deep water areas by dense stands of *Typha*, rather than the persistence of historic ridge slough structure.

Microtopographic and vegetation structure and their covariation were also generally in agreement in their identification of highly degraded landscapes. PSUs throughout WCA 3B exhibited degraded conditions by most measures, as did PSUs in northern portions of WCA1, WCA2, and most peripheral areas of WCA3AN, WCA3AS and ENP. Because of relatively small sample size at the PSU scale, the complete complement of 80 PSUs will be essential for refining estimates of the spatial extent of conserved and degraded conditions in these regions.

Microtopographic and vegetative measures of landscape condition were generally in agreement, with the largest number of PSUs exhibiting degradation of both characteristics, and a smaller group exhibiting conservation of both characteristics. However, in 5 PSUs, measures of topographic and vegetation structure diverged in their assessment of conserved and degraded conditions. Two such PSUs (31 and 7) are in northern WCA3AS, one in WCA1, one in central WCA3AN, and one PSU in eastern Shark River Slough within ENP. In all five cases, we observed relative distinct vegetation communities occupying landscapes with reduced elevation variance; no PSUs sampled to date have indistinct vegetation communities but high microtopographic relief. One important conclusion to be drawn from this pattern is that concurrent monitoring of both vegetation and microtopographic structure is essential for a comprehensive assessment of ridge-slough condition. Remote assessment of changes in patch structure and landscape pattern provides important information about landscape change, but our data support and strengthen the inference of Watts et al. (2010) that **microtopographic changes are leading indicators of change in vegetation composition and structure**. On that basis, we conclude that PSUs with degraded topography but intact vegetation are likely to be undergoing transitions to fully degraded states.

### *Trajectories of and mechanisms of degradation*

The spatial feedbacks that create regularly patterned landscapes are also thought to produce global bi-stability, meaning that both homogenous and heterogeneous states can occur and persist under the same external or environmental conditions. In the ridge slough landscape, a variety of local positive and distal negative feedbacks have been proposed as explanations for the regularity of ridge-slough patterns (Larsen and Harvey 2007, 2010; Ross et al. 2006, Cheng et al. 2011, Cohen et al. 2011, Heffernan et al. *in revision*). Models of both the sediment re-distribution hypothesis (Larsen and Harvey 2010) and the discharge competence hypothesis (Heffernan et al. *in revision*) suggest the potential for global bi-stability of ridge-slough pattern, but in response to different hydrologic variables. The sediment redistribution hypothesis proposes that bistability of conserved and degraded (sawgrass-dominated) conditions should occur in response to variation in velocities during periods of high flow, which are controlled by landscape slope and by the density of sawgrass ridges. In contrast, the discharge competence hypothesis (Cohen et al. 2011) predicts global bi-stability of conserved and degraded (spatially homogenous elevations) conditions in response to variation in water level (Heffernan et al. in revision). Both models suggest that restoration of conserved conditions will be difficult to reverse once landscape degradation has occurred, but point to dramatically different management approaches (maintenance of hydroperiods vs. re-restablishment of peak flows) to preserve extant conserved landscapes and to restore degraded ones. Despite this integrated theoretical and applied rationale, no empirical studies have directly assessed the potential for global bi-stability in general nor rigorously discriminated between alternative patterning mechanisms.

We propose that the inter-relationships among hydrologic regime, microtopographic structure, and vegetation composition and structure presented as part of this study means to directly assess the potential for global bi-stability in the Everglades landscape, and to at least indirectly evaluate alternative patterning mechanisms. The bi-modal distribution of soil elevation variance and of vegetation community distinctness is consistent with the existence of two landscape equilibria: a patterned landscape characterized by well-differentiated ridges and sloughs, and a homogenous landscape with reduced topographic variation and poorly-differentiated vegetation communities. That conserved conditions were observed only within a restricted range of hydrologic conditions provides additional support for the general global bi-stability hypothesis. Finally, the occurrence of degraded landscape structure under hydrologic conditions that also support relatively conserved conditions is consistent with the existence of multiple landscape equilibria. Degraded landscapes whose contemporary hydrologic regime supports bi-modal soil elevations and distinct ridge and slough communities, but where those features are not actually observed, are concentrated in Everglades National Park and Water Conservation Area 3B; one PSU in northern WCA2 also fits this description. Current hydrologic regimes in these areas are much wetter than relatively recent historic conditions, owing to changes in hydrologic management during the last decade of the 20th century (McVoy 2011). The drier conditions that predominated during most of the 20th century may have caused degradation of landscape structure in these areas, and the absence of recovery of microtopographic structure and distinct vegetation communities may reflect the existence of an alternative landscape equilibrium. However, this failure to re-establish historic pattern could also reflect other aspects of the disturbance regime that could be inhibiting re-establishment of historic landscape, or more simply the slow rate of peat formation and spatial feedbacks. Overall, however, our results tentatively support the hypothesis that patterned and homogenous landscapes represent alternative equilibria.

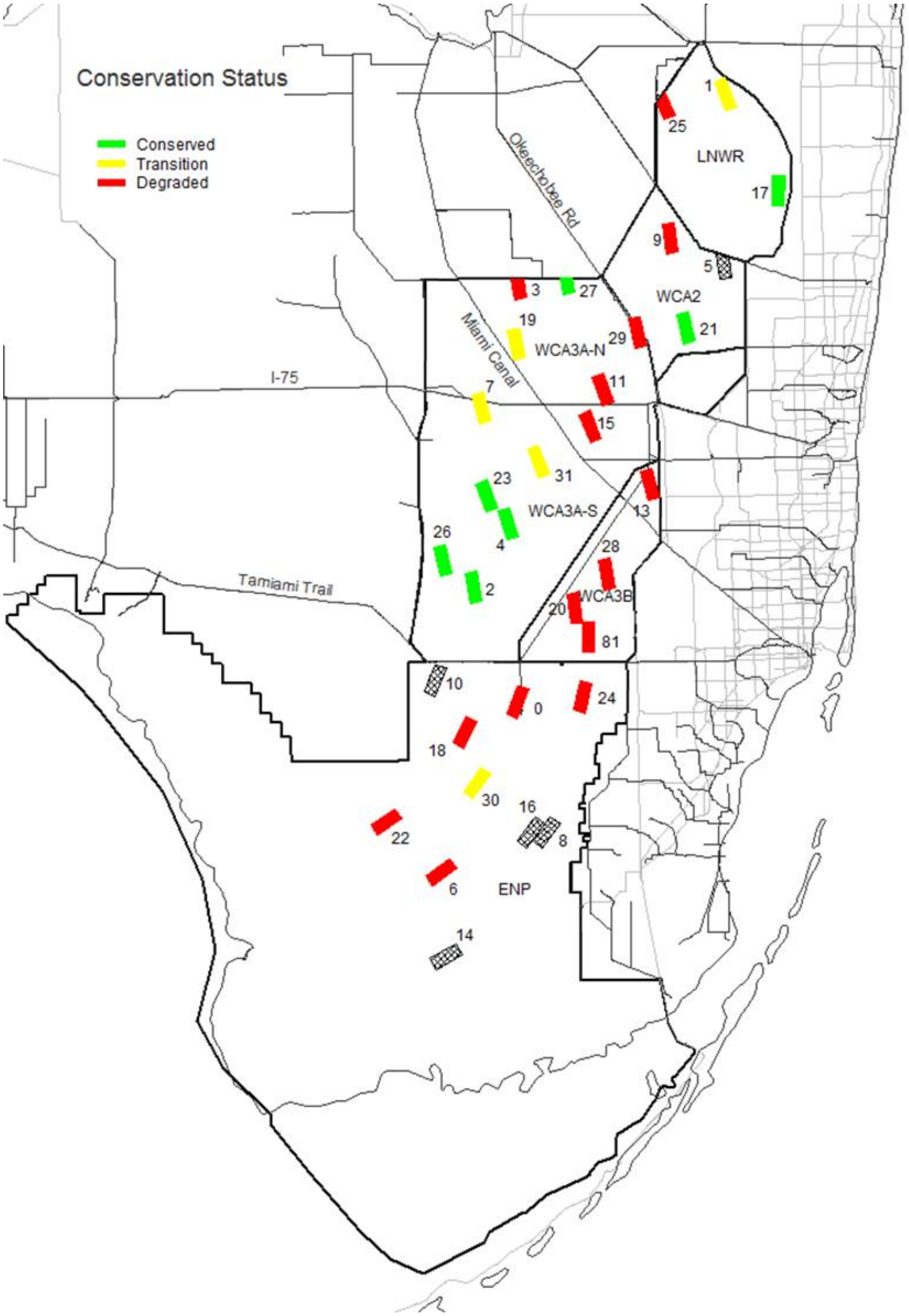


Figure 31. Spatial patterns of ridge-slough landscape condition. Green indicates PSUs with high elevation variance and distinct vegetation communities. Yellow areas are PSUs with distinct vegetation communities but reduced elevation variance. Red areas have indistinct vegetation communities and reduced elevation variance. Hatching indicates PSUs that were not sampled (PSU 5 in WCA 2) or that were excluded from the analysis because they lie outside the historic distribution of the ridge-slough landscape (PSUs 8, 10, 14,16 in ENP).

The divergence of microtopographic and vegetative measures of landscape heterogeneity suggest that peat degradation, rather than vegetation change, is the initial phase of landscape degradation. In addition to its implications for monitoring of these landscape characteristics, this observation provides some indirect support for the discharge competence hypothesis. Equilibrium solutions of a model of the discharge competence hypothesis lead to several predictions that can be assessed using data from this monitoring study (Heffernan et al. *in revision*). First, the model predicts that elevation differences between ridges and sloughs should increase with increasing landscape-scale water levels, as we have observed in this study. Second, the model predicts that under increasingly dry conditions, ridge-slough elevation differences should decline smoothly, but that under increasingly wet conditions, elevation differences should collapse catastrophically when water depths exceed a threshold. In this study, we observed a number of PSUs that exhibited relatively conserved vegetation structure, but dramatically reduced topographic variability; however, we did not observe any PSUs with intact microtopography and degraded vegetation (Fig. 29). This observation is consistent with the differential trajectories of change in response to drainage and inundation that are predicted by the model of Heffernan et al.; relatively gradual deflation of topography allows vegetation patterning to persist, while the rapid collapse of microtopography in response to impoundment disrupts vegetation-elevation relationships. In further support of this interpretation, we note that the small number of PSUs with reduced microtopography but distinct vegetation communities experience drier conditions than PSUs with degraded microtopographic and vegetative structure. Degraded landscapes occur under both extremes of hydrologic conditions, but the transient configuration of intact vegetation patterning and deflated microtopographic structure occurs only under relatively dry conditions. While more direct assessments of alternative patterning mechanisms are clearly needed, the results of this study appear to be consistent with several predictions of the discharge competence hypothesis.

## Summary of Recommendations for management and restoration

The systematic sampling enabled by the GRTS design provides a rigorous grounding for a comprehensive assessment of landscape condition using a suite of established and newly developed measures. This study confirms previous findings that substantial portions of the ridge-slough landscape are severely degraded. Moreover, because historic microtopographic structure appears to be even more geographically restricted than vegetation pattern, our results suggest that the extent of degraded or degrading conditions may be greater, and the extent of historic conditions lesser, than indicated by previous studies. Continued monitoring and data analysis will enable better spatial resolution of these patterns, and the incorporation of additional metrics of landscape structure into assessment.

Our data suggest that a relatively restricted range of hydrologic conditions are best suited to the persistence of existing areas of conserved pattern. Specifically, we observed conserved microtopographic and vegetation structure under long-term mean water depths of 35-50 cm. This range of spatially-averaged hydrologic regimes would be equivalent to maintaining mean slough water depths between 50 and 65 cm, if ridge-slough elevation differences are ca. 30 cm. This empirically-derived range of hydrologic conditions is comparable to those suggested by the RASCAL model (Larsen et al. 2010). Maintaining this relatively narrow range of hydrologic conditions across extensive portions of the Water Conservation Areas and Everglades National Park will be challenging under current hydrologic management, but restoration of sheet flow would enable relatively even distribution of water depths across larger areas. Whether other hydrologic conditions (e.g., magnitude of hydrologic variability, etc.) are also necessary for the persistence of conserved conditions remains unclear.

The results of this study suggest that restoration of degraded landscapes within the historic ridge and slough region may require active intervention. Large areas within Everglades National Park, and Water Conservation Areas 3A and 3B exhibit degraded conditions, but currently experience long-term mean water depths that support relatively conserved landscape structure in central WCA3AS and elsewhere. While this observation has several possible explanations, it is consistent with, and provides tentative support for, the hypothesis that degraded landscapes represent an alternative equilibrium that will resist restoration that relies strictly on re-establishment of historic hydrologic regimes.

# SAMPLING AND ANALYSIS OF TREE ISLAND VEGETATION

## 1. Background

Tree islands, an integral component of ridge and slough landscape in the Everglades, are sensitive to large-scale restoration activities associated with the Comprehensive Everglades Restoration Plan (CERP) authorized by the Water Resources Development Act (WRDA). More specifically, changes in hydrologic regimes at both local and landscape scale are expected to affect plant community structure and function on the tree islands and the surrounding marshes, in turn affecting the boundaries between islands and marshes. To strengthen our ability to predict the response of tree island plant communities to hydrologic alteration, including shifts in boundaries among community types, an improved understanding of existing conditions of vegetation composition and environment are needed. In this regard, a study of vegetation structure and composition in relation to underlying environmental drivers on a subset of tree islands present in selected Primary Sampling Units (PSU) was conducted with funding from the US Army Corps of Engineers (USACOE). This section describes the results of the FY-2011 study conducted on six tree islands in four intensively studied PSUs. Results from several other tree islands were previously reported (Heffernan 2009).

## 2. Sampling sites

Tree islands are of different types, such as hardwood hammock, bayhead, bayhead swamp, willow head, cypress dome, and exotics-dominated island (Armentano et al. 2002). The number of tree islands belonging to different types varies among PSUs, and not all PSUs have all types of islands. With the objective of studying vegetation along environmental gradients within tree islands, extending into the adjacent marsh, one island (>400 $m^2$) was randomly selected within each of the three most common island types in each intensive PSU. The cohort of PSUs sampled in Year 2 included four units --- PSU's 20, 21, 22 and 23 --- that met the sampling criteria. During the wet season of 2011, we sampled six islands that included representatives of three major types – hardwood hammock, bayhead, and willow head (**Figure 1**).

## 3. Field Sampling

### *3.1 Vegetation sampling*

Once the islands were selected for sampling, the azimuth of the longest axis and the orientation of transect that would be laid out in the field were determined from aerial photos. On each island a transect was established perpendicular to the island's longest axis and from the apparent highest point to approximately 8-10 m beyond the edge of the visible forest-marsh interface. The GPS coordinates of both terminal ends of the transects were recorded (**Table 1**). In the six islands studied this year, transect length ranged from 32 to 100 meters. The hardwood hammock in PSU-21 had the longest (100 m) transect, while in the willowhead within PSU-23, transect length was only 32 m. In these six islands, tree island vegetation was sampled within nested belt-transects, varying in width from 1 to 5 m of the central line (**Figure 2**). Trees of 5-10 cm dbh class were sampled within 1 m of the line, trees of 10-25 cm dbh within 2 m of the line, and trees >25 cm dbh within 5 m of the line. For each tree, we recorded species, position along the transect line, and diameter in 5-cm dbh classes. For trees with multiple trunks, we also recorded the number of trunks in measured 5-cm dbh classes.

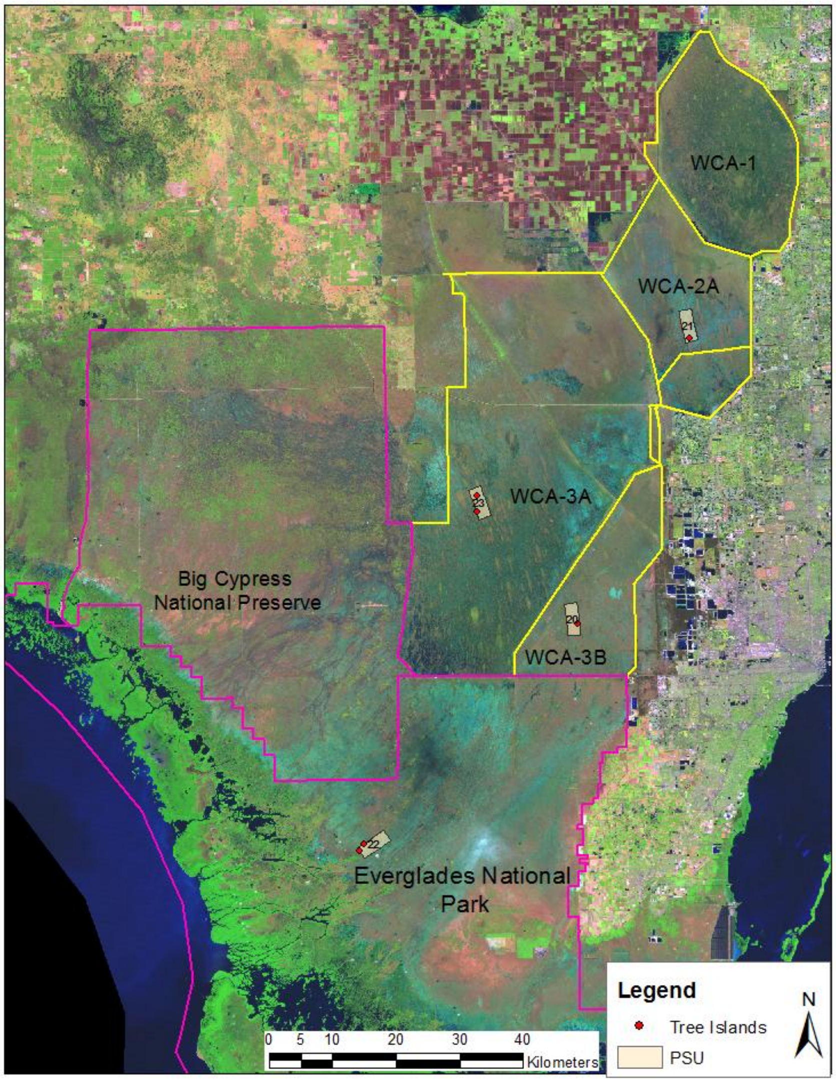


**Figure 1:** Location map of tree islands sampled.

**Table 1:** Tree Island transects established on six islands in four PSUs. HH = Hardwood hammock, BH = Bayhead, and WH = Willowhead.

| Sampling Date | PSU | Tree Island Type | Tree Island ID | Taped Transect Length (m) | GPS Transect Azimuth | GPS Coordinates (NAD 1983 UTM Zone 17) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | | | T_S_ Easting | T_S_ Northing | T_E_ Easting | T_E_ Northing |
| 8/12/2011 | PSU021 | HH | PSU021_HH_01 | 100 | 101 | 560265 | 2902576 | 560360 | 2902595 |
| 8/23/2011 | PSU022 | HH | PSU022_HH_01 | 54 | 289 | 509081 | 2822915 | 509132 | 2822897 |
| 10/28/2011 | PSU022 | BH | PSU022_BH_02 | 66 | 325 | 508373 | 2821797 | 508336 | 2821849 |
| 9/28/2011 | PSU023 | WH | PSU023_WH_02 | 32 | 259 | 526893 | 2875212 | 526862 | 2875206 |
| 9/1/2011 | PSU023 | BH | PSU023_BH_01 | 45 | 276 | 526893 | 2877761 | 526848 | 2877766 |
| 10/7/2011 | PSU020 | BH | PSU_020_BH_01 | 54 | 262 | 542556 | 2857628 | 542504 | 2857621 |

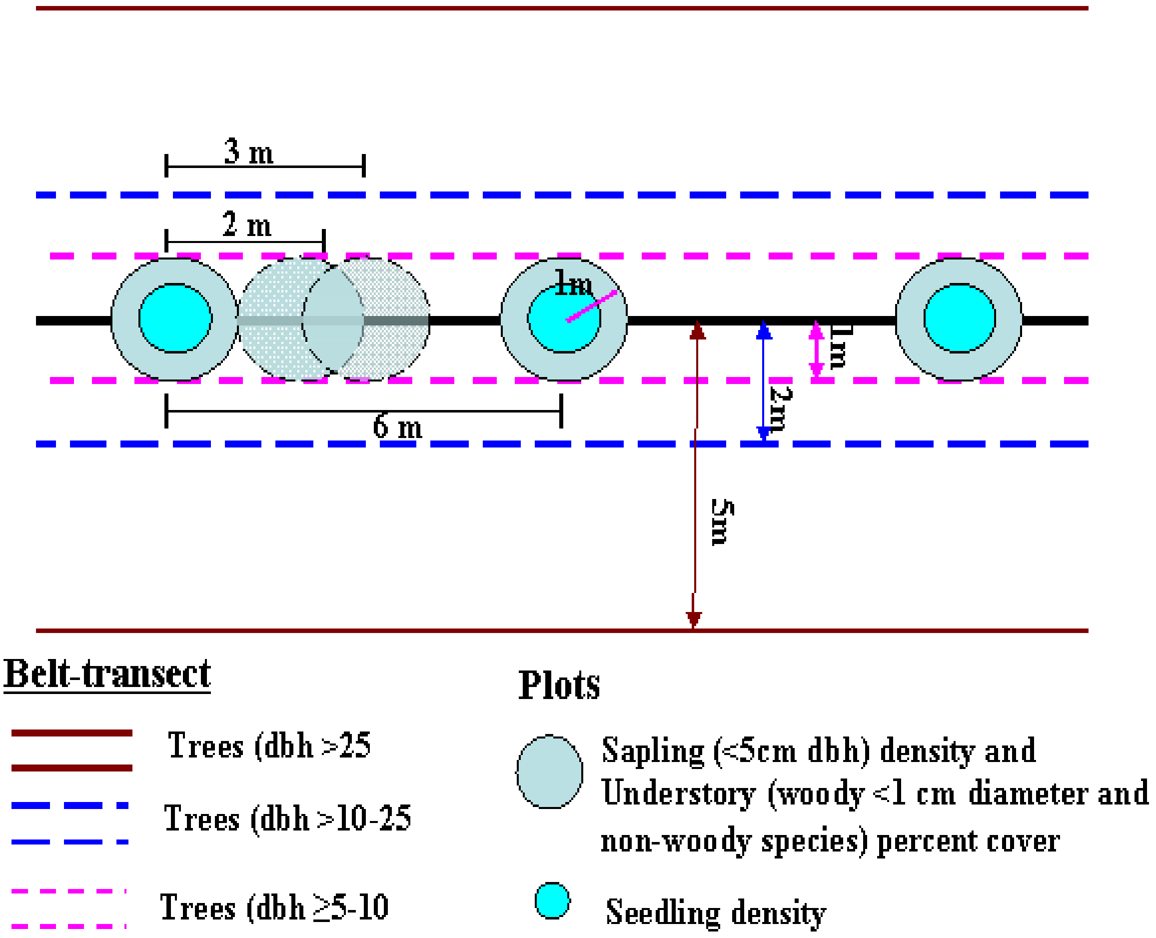


**Figure 2:** Schematic representation of sampling design used for vegetation sampling on six tree islands within four PSUs

Tree saplings (tree species ≥ 1 and < 5 cm DBH) and understory vegetation, including shrubs (woody species > 1 m in height but < 1 cm DBH) and ground layer species (woody and non-woody vegetation <1m in height), were sampled in a series of 1-m radius circular plots along the belt transect. However, depending on the length of transect, the number of plots and distance between adjacent plots varied among islands. In the hardwood hammocks and bayheads, the plots were arrayed at 3 m and 6 m intervals for transects 30 to 60 m, and >60 m, respectively. Along the 32 m transect on the willowhead, the plots were arrayed at every 2 m. In each plot, we recorded the number of stems of each species in the sapling and shrub layers, and estimated the cover class of each species of ground layer vegetation. Cover classes used for the ground layer vegetation were: 1 (<1%), 2 (1-4%), 3 (4-16%), 4 (16-33%), 5 (33-66%), and 6 (≥66%) (Ross and Jones 2004; Sah 2004). In addition, we recorded density of seedlings (≤1 m tall) of each tree species in 3 height categories: <30 cm, 30-60 cm, and 60-100 cm, in 0.57 m radius plot centered on the midpoint of the understory vegetation plots.

Canopy openness was measured using a densiometer (Englund et al. 2000) at the understory plot centers. In each plot, two measurements, one each in two cardinal directions, north and south, were taken.

### *3.2 Soil depth, ground elevation and hydrology*

In each understory vegetation plot, we measured soil depth at 1-3 random locations, and recorded relative ground elevation in relation to existing water table. In plots where water level was above the ground surface, we measured water depths at three random points. However, in the plots where water table was at or below the ground level, relative elevations were surveyed using an auto level, from the most interior plot (the first plot on the transect) to the first plot with standing water. We then calculated the ground elevation of each plot based on the relative elevation and the water surface elevation. Since nearest stage recorder was located at >1 mile distance from the tree islands, we used the EDEN (Everglades Depth Estimation Network) estimate of stage elevation (http://sofia.usgs.gov/eden/) as a measure of water surface elevation at the end of the belt transect on the date of sampling. We then calculated the ground elevation. Using ground elevation and EDEN time series data for water surface elevation, we calculated mean annual water depth and hydroperiod for seven water years prior to the vegetation sampling.

## 4. Analytical methods

Species abundance data were summarized separately for ground layer vegetation and the tree and sapling layer. For ground layer vegetation, percent cover of each species present in a plot was computed using the mid-point of cover class. For species in tree and sapling layer, the species abundance was importance value (IV), calculated as: (relative density + relative basal area)/2. Since the trees were sampled in belt transects on each island, density and basal area of each tree species were calculated using the 2-, 3- or 6-m segments of the belt, depending on the length of the transect, and the interval between understory vegetation plots in each island. Finally, the plot*species matrices were prepared for multivariate analysis.

### *4.1 Split moving-Window Boundary Analysis*

Species data gathered in the islands were analyzed using split moving-window (SMW) boundary analysis, a method widely used to identify boundaries between communities along gradients (Cornelius et al. 1991a, 1991b; Boughton et al. 2005; Munoz-Reinoso 2009; Sah et al. 2012). We used this method to delineate the vegetation units along a gradient outward from the center of a tree island or head of tear-dropped tree island to the adjacent marsh. In the SMW analysis, we first introduced a window of even number of plots at the beginning of the transect. The window was then divided into two half-windows, and the cover value of each species was averaged over the plots within each of them. Bray-Curtis (B-C) dissimilarity was calculated between each pair of adjacent half-windows. The window was then moved further along the transect, one plot at a time, and the steps were repeated until the end of the transect was reached. Finally, B-C dissimilarities were plotted against the location of window mid-point along the transect. The peaks in the dissimilarity profile plot were identified as the boundaries between vegetation units.

The SMW boundary analysis is sensitive to scale, and thus we explored different window sizes (2, 4, 6, and 8 plots). In our analysis, we used the window size of 4, as the use of windows smaller than the size of 4-plots resulted in many peaks representing small-scale variation within otherwise homogenous vegetation unit. In contrast, use of the larger windows resulted in fewer peaks overshadowing the ecological meaningful variation in species composition. Moreover, dissimilarity profile diagrams using larger windows also had 'blind zone', i.e. omission of a small number of plots equal to or fewer than a half-window size that differs evidently in vegetation composition from the neighboring half-window (Int Panis and Verheyen 1995). The blind zone was usually present at one or both ends of the transect. Furthermore, the identification of boundaries delineating vegetation units along gradients within the transects was primarily based on ground layer vegetation. In four of six tree islands sampled this year, the number of tree and sapling individuals was sparse, and were not enough to use split moving-window approach. On those islands, the boundary analysis was based on only ground layer vegetation.

### *4.2 Landscape level vegetation-environment relationship*

Vegetation units identified along the gradients were grouped using the broader tree island vegetation categories: hardwood hammocks, bayheads, bayhead swamps, willow heads, and marsh. We examined relationship among hydrologic regimes, soil characteristics, community structure (canopy cover), and ground layer vegetation composition across all tree islands at the landscape level, using nonmetric multi-dimensional scaling (NMDS) ordination with environment vector fitting method (Kantvilas and Minchin 1989; Minchin 1998). We performed NMDS on B-C dissimilarities among vegetation units, with species cover data first standardized by species' maximum (Faith et al. 1987). In the vector fitting method, the vector defines the direction of the measured environmental attribute in the ordination space that produces the maximum correlation between the attribute and the ordination scores of the sampling units (Faith and Norris 1989). The statistical significance of the correlations was tested using Monte-Carlo permutation test with 10,000 permutations, with values of environmental variables randomly shifted among vegetation units. The NMDS ordination and vector fitting procedure were performed using the computer program DECODA (Minchin 1998).

## 5. Results

In all six tree islands, vegetation in both tree and understory strata were arranged along an environmental gradient. Ground layer species-based B-C dissimilarity profiles revealed one to three distinct boundaries resulting in two to three vegetation units (**Figures 3-8**). In the Bayhead Island in PSU-20, only two communities, bayhead and marsh, were distinguished (**Figure 3**), while distinct peaks separated three identifiable vegetation units in each of other five islands. In general, the boundary between woody plant-dominated community (bayhead, bayhead swamp or willowhead swamp) and marsh vegetation was well distinguished by a peak represented by the maximum B-C dissimilarity between the segments of two half-windows. However, in two of six islands, where distinct boundaries were identified in ground layer and tree/sapling layer vegetation, the location of boundary separating the woody and marsh vegetation units did not overlap.

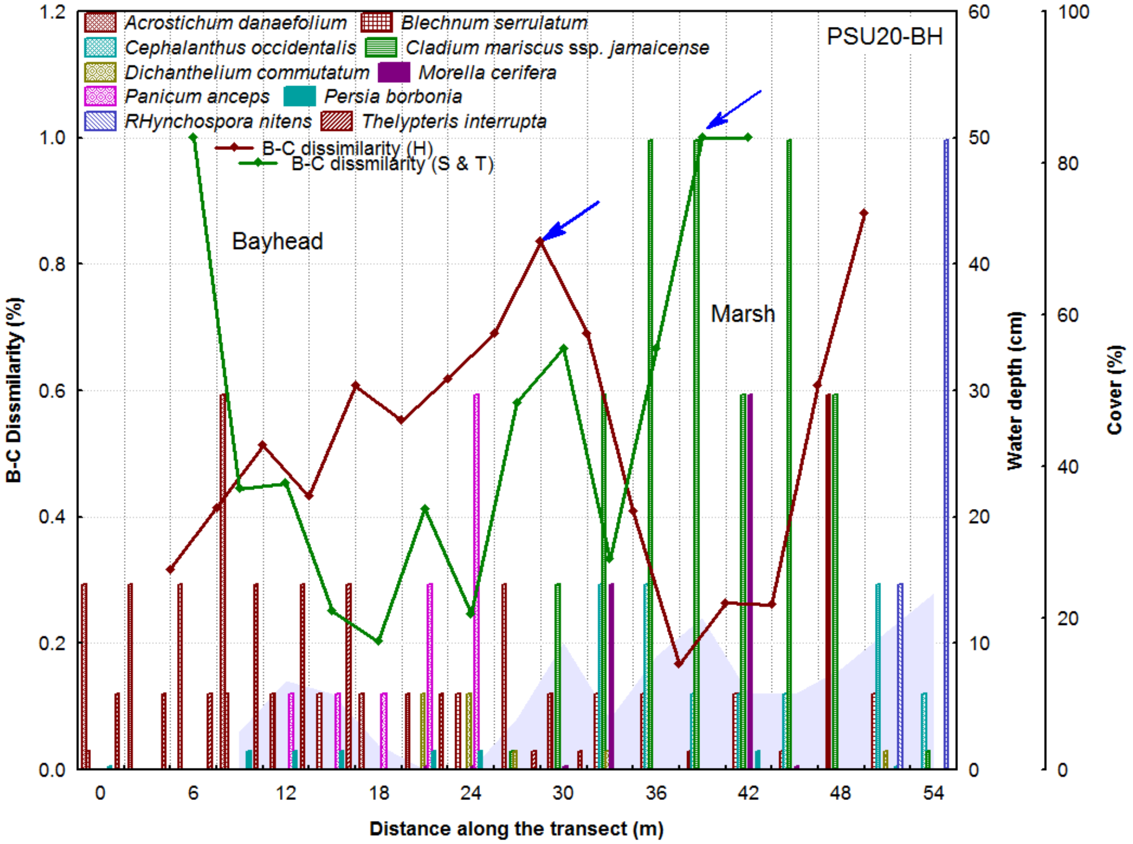


**Figure 3:** Vegetation units identified using split moving window (SMW) boundary analysis (window size 4 plots) of understory vegetation in the Bayhead Island in PSU-20

In tree and sapling layer species-based dissimilarity profiles, the boundaries between vegetation communities were not always distinct. However, in all six islands 100% B-C dissimilarity (100%) for contiguous pairs of half-windows toward the outer end of the transect represented a rapid turnover of species near the edge of the islands (*Results not shown*). Among the vegetation units that were identified based on understory species-based dissimilarity profiles, the vegetation at the high elevation ground, where mean annual water table was more than 20 cm below ground, was dominated by hammock species: gumbo limbo (*Bursera simaruba*), white stopper (*Eugenia axillaris*), live oak (*Quercus virginiana*), paradise tree (*Simaruba glauca*), and myrsine (*Myrsine floridana*) (**Table 2**). In the middle ground, strangler fig (*Ficus aurea*), wax myrtle (*Morella cerifera*) and red bay (*Persia borbonia*) were present. Interestingly, in one hardwood hammock (in PSU 21), cypress (*Taxodium disticum*), which is commonly associated with wet areas in the Everglades, was present on the highest ground where mean annual water table was >50 cm below ground. In the same island, however, tree and sapling layer vegetation in the rest of the transect, was dominated by coastal plain willow (*Salix caroliniana*). The topography in the bayhead islands was undulating, and vegetation on those islands was dominated by flood tolerant species: pond apple (*Annona glabra*), red bay (*P. borbonia*), sweet bay (*Magnolia virginiana*), dahoon holly (*Ilex cassine*), and willow. (*S. caroliniana*). In two of three bayhead islands, there were distinct zones of bayhead and bayhead swamps, the later dominated by mostly sapling layer vegetation. In both willowhead and willowhead swamp on the Willowhead Island, tree and sapling layer vegetation were solely dominated by *S. caroliniana*.

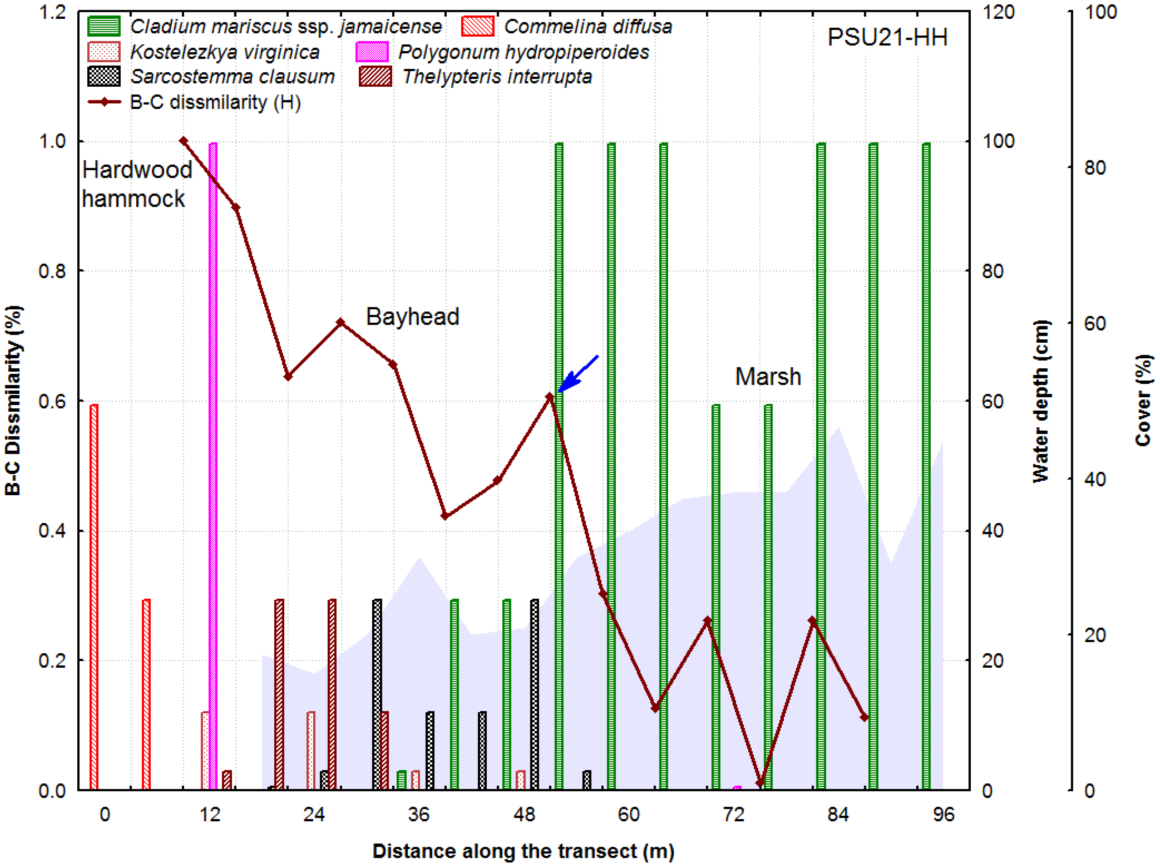


**Figure 4:** Vegetation units identified using split moving window (SMW) boundary analysis (window size 4 plots) of understory vegetation in the Hardwood Hammock Island in PSU-21.

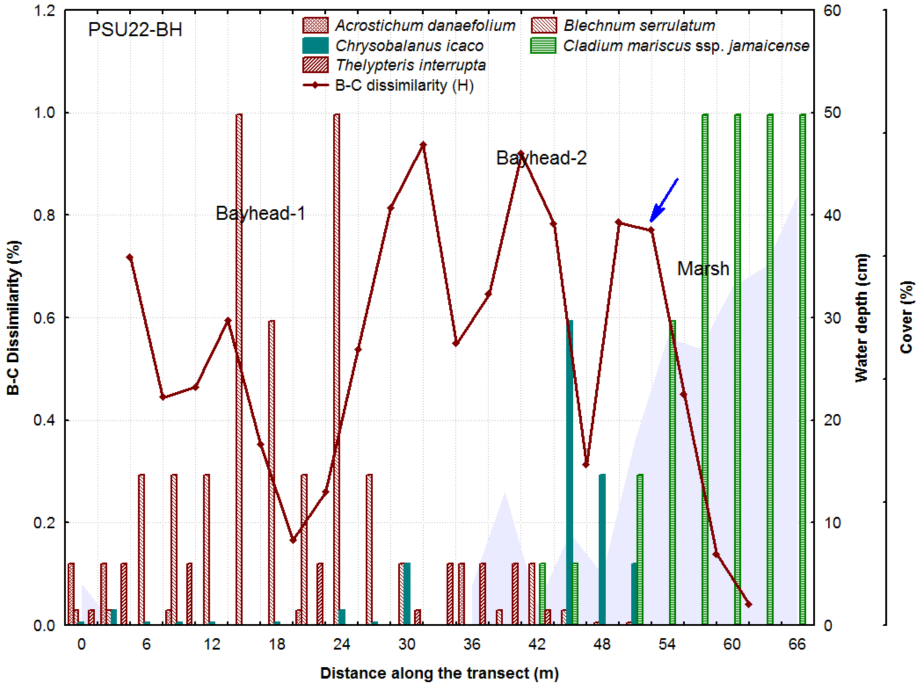


**Figure 5:** Vegetation units identified using split moving window (SMW) boundary analysis (window size 4 plots) of understory vegetation in the Bayhead Island in PSU-22. Bray-Curtis dissimilarities are scaled between 0 and 1.

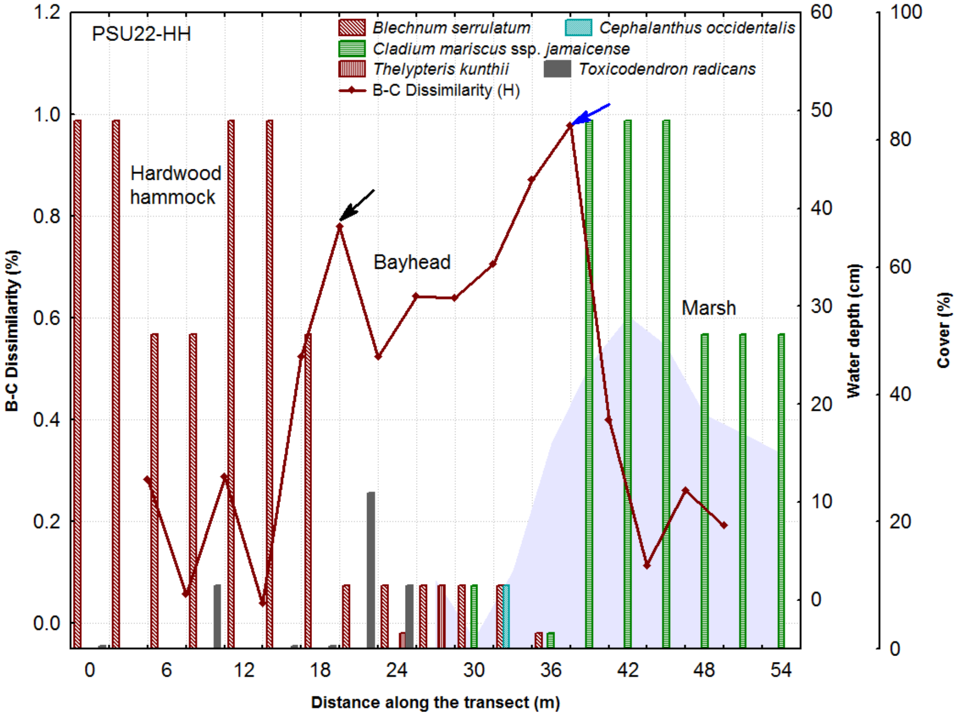


**Figure 6:** Vegetation units identified using split moving window (SMW) boundary analysis (window size 4 plots) of understory vegetation in the Hardwood Hammock Island in PSU-22.

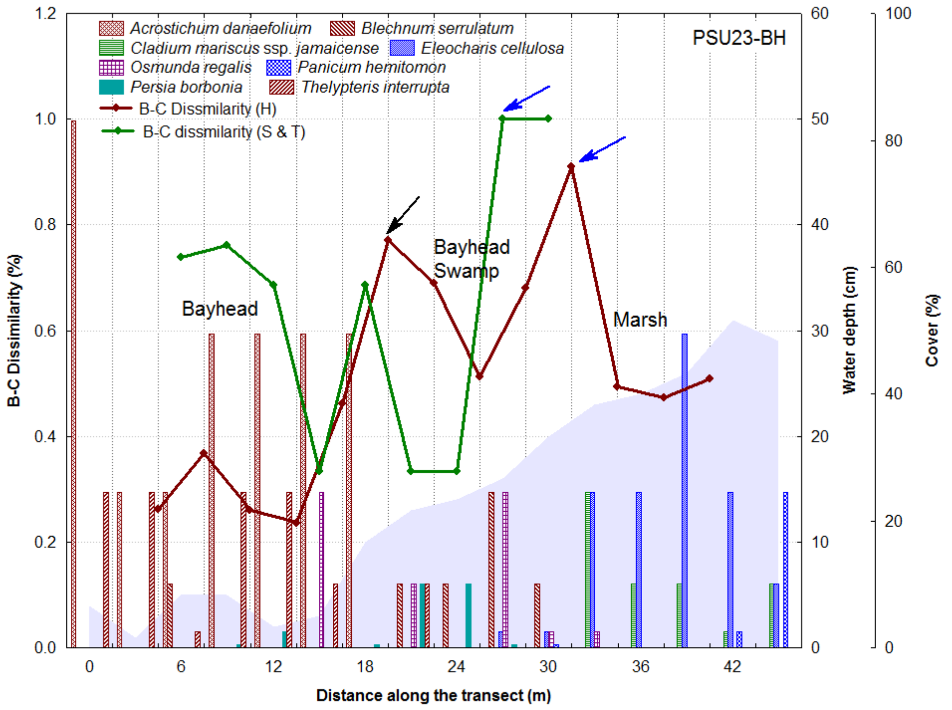


**Figure 7:** Vegetation units identified using split moving window (SMW) boundary analysis (window size 4 plots) of understory vegetation in the Bayhead Island in PSU-23.

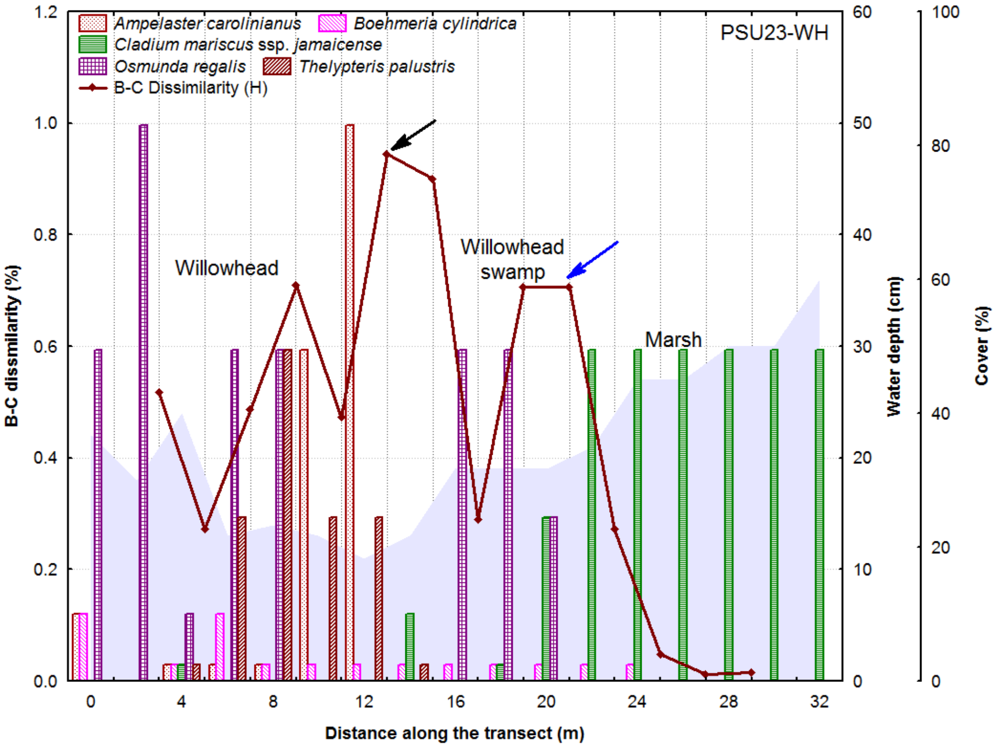


**Figure 8:** Vegetation units identified using split moving window (SMW) boundary analysis (window size 4 plots) of understory vegetation in the Willow head Island in PSU-23

**Table 2:** Mean importance value (IV) in tree and sapling layer of woody vegetation types identified along transects on six tree islands sampled in four PSUs. HH = Hardwood hammock, BH = Bayhead, BHS = Bayhead swamp, WH = Willowhead, and WS = Willowhead swamp.

| **Species name** | **Species Code** | **Vegetation assemblages** | | | | |
|---|---|---|---|---|---|---|
| | | **HH** | **BH** | **BHS** | **WH** | **WS** |
| *Annona glabra* | ANNGLA | | 10.3 | | | |
| *Bursera simaruba* | BURSIM | 23.9 | | | | |
| *Celtis laevigata* | CELLAE | | 2.6 | | | |
| *Chrysobalanus icaco* | CHRICA | | 1.3 | 1.9 | | |
| *Eugenia axillaris* | EUGAXI | 11.1 | | | | |
| *Ficus aurea* | FICAUR | | 2.0 | | | |
| *Ilex cassine* | ILECAS | | 9.3 | 6.8 | | |
| *Magnolia virginiana* | MAGVIR | | 0.7 | 20.4 | | |
| *Morella cerifera* | MYRCER | | 7.4 | 3.1 | | |
| *Myrsine floridana* | MYRFLO | 11.1 | 1.0 | | | |
| *Persea borbonia* | PERBOR | 5.6 | 22.7 | 19.8 | | |
| *Pisonia aculeata* | PISACU | | 2.6 | | | |
| *Quercus virginiana* | QUEVIR | 11.1 | | | | |
| *Sabal palmetto* | SABPAL | | 1.2 | | | |
| *Salix caroliniana* | SALCAR | | 13.4 | 35.4 | 42.9 | 80.0 |
| *Simarouba glauca* | SIMGLA | 3.8 | | | | |

Understory vegetation assemblages identified through the SMW analysis showed some level of clustering in the NMDS ordination (stress = 0.15), and they were more or less arranged along hydrological gradient (**Figure 9**). Vector fitting of environmental and community characteristic variables in ordination space revealed that hydroperiod, mean annual water depth, and canopy cover were significantly correlated with sample scores (**Table 3**), indicating that these environmental drivers had a strong influence on the species composition across vegetation assemblages. The correlation between soil depth and sample score was marginally significant.

**Table 3:** Mean (± SD) of environmental and community characteristic variables used for vector fitting in the non-metric multidimensional scaling (NMDS) ordination. $R_{max}$ is the maximum correlation between fitted vector and sample coordinates in the ordination for herb layer species cover data for 20 vegetation units identified along transects on six tree islands.

| **Variable** | **Mean (**±S.D.) | $R_{max}$ | **p-value** |
|---|---|---|---|
| Hydroperiod (days) | 236 (± 99) | 0.91 | **<0.001** |
| Mean Water depth (cm) | 9.9 (± 21.5) | 0.95 | **<0.001** |
| Soil depth (cm) | 109 (± 89) | 0.55 | **0.046** |
| Canopy cover (%) | 50.1 (± 42.6) | 0.68 | **0.003** |

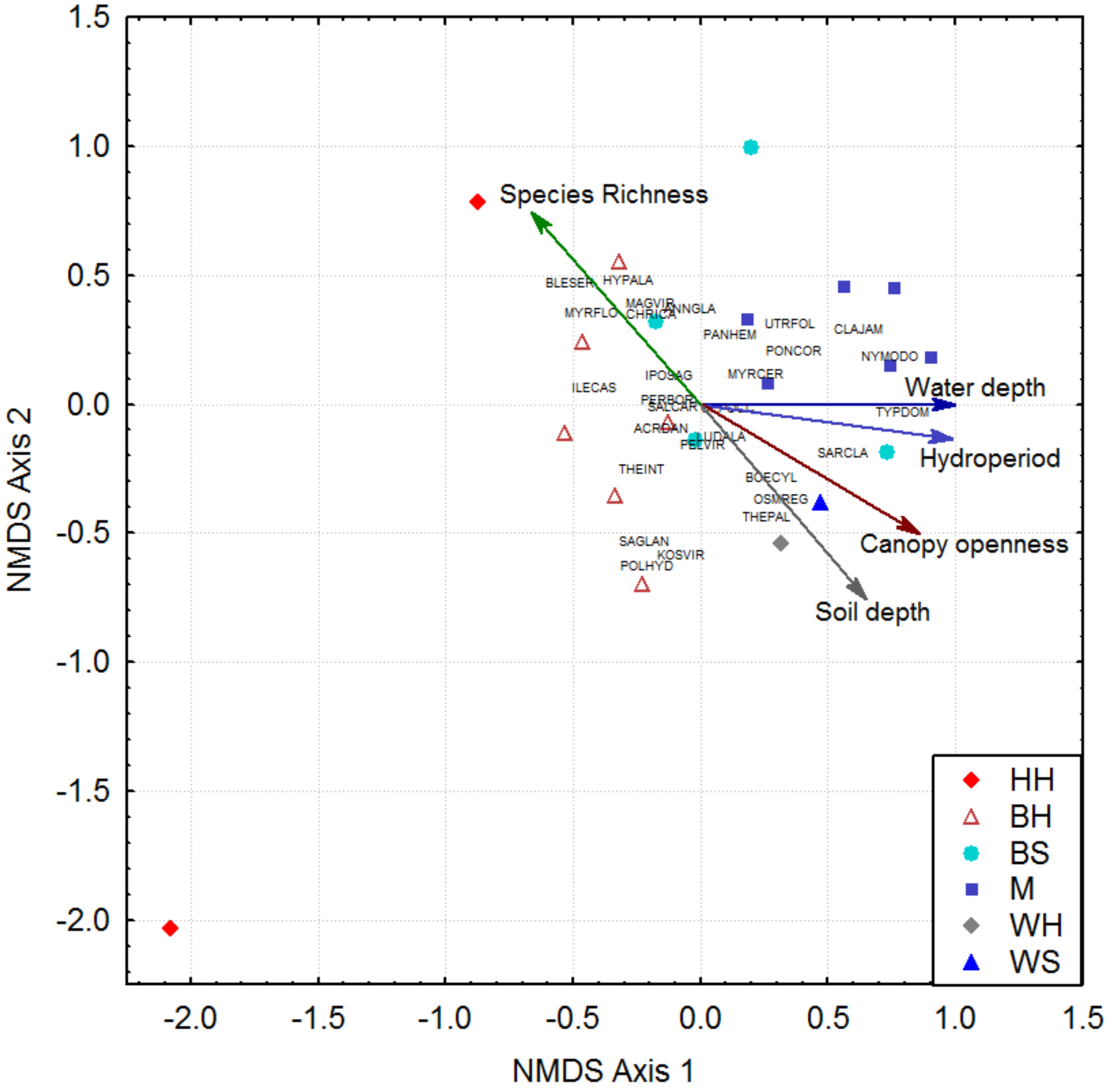


**Figure 9:** Bi-plots of site and species scores and fitted environmental and community characteristic vectors in a non-metric multidimensional scaling (NMDS) ordination ordination of 20 understory (herb-layer) vegetation assemblages identified on six islands using split moving-window (SMW) boundary analysis.

In general, vegetation units were arranged along hydrology gradient represented by Axis 1. However, hardwood hammock, bayhead and bayhead swamp showed a great variation on Axis 2, possibly representing regional differences in species composition within these types. Moreover, willowhead, willowhead swamp and marsh vegetation units exhibited much overlap in hydrologic regime.

In the hardwood hammock islands, understory vegetation on the high ground where water table remains below ground during most of years was very sparse, and the understory vegetation mostly dominated by tree seedlings (**Figure 9**). In contrast, in the bayheads of both hammock and bayhead islands, the understory vegetation was species rich, and was dominated by ferns (*Acrostichum danaeifolium*, *Blechnum serrulatum*, and *Thelypteris* ssp.) and seedlings of water tolerant tree species (*P. borbonia, M. virginiana, I. cassine*). *Osmunda regalis* was common in bayhead and willowhead islands in PSU-23 within WCA-3A. Marsh vegetation near most of study islands was dominated by sawgrass, whereas that near the bayhead in PSU-23 within WCA-3A was dominated by spikerush (*Eleocharis cellulosa*) and maidencane (*Panicum hemitomon*). On three islands, understory/herb layer vegetation composition present along the hydrologic gradient was also strongly influenced by canopy openness, as was evidenced by the highly significant (p-value <0.01) canopy cover vector in ordination space.

## 6. Discussion and Conclusions

Plant communities on Everglades tree islands are arranged along environmental (hydrology and edaphic) gradients. Sampling along transects extending from the interior of the islands to the surrounding marsh, and use of the SMW boundary analysis method in this study allowed us to identify the boundary between vegetation units arranged along the hydrologic gradient in the surveyed tree islands. However, the sharpness of the boundary, between vegetation units was not the same in all the transects, and in the analysis of both vegetation layers; tree and sapling and ground vegetation data. In general, the ground vegetation-based boundary between woody plants-dominated community and herbaceous marsh vegetation was well distinguished by the peak represented by high B-C dissimilarity between two groups of plots. A similar pattern in the tree and sapling layer species-based boundary analysis was not observed in all transects, probably due to low tree density and local scale variation in the distribution of tree species on the islands. However, in the islands in which the boundary between woody and herbaceous marsh vegetation units was identifiable in both tree and ground layer species-based analysis, the location of boundaries did not always overlap (**Figures 3 and 7**). While vegetation layers within forests may respond to similar or different environmental gradients, the response of vegetation layers to similar gradients may also differ spatially, affecting the correspondence between them (Rogers 1981; Sagers and Lyon 1997). In this study, discrepancy between two layers in the location of boundary may be due to differences between them in resource use pattern. For instance, trees usually use rain water during the wet season and the ground water in the dry season (Saha et al. 2010). Whether shrubs and herbaceous plant in tree islands exhibit similar pattern in water use, has not yet been fully explored. However, in other ecosystems, researchers have shown that understory herbs and shrubs are more dependent on rainwater regardless of their topographic position (Sagers and Lyon 1997). Similar differences between vegetation layers exist in using light resources. Overstory vegetation uses broader range of light, but herb and shrub layer vegetation in the understory experiences a relatively narrow range of light (Sagers and Lyon 1997). Also, species in the understory layer may differentiate themselves along the light gradient irrespective of the overstory species composition.

Variation in vegetation composition along gradients can be gradual or abrupt corresponding to the underlying environmental drivers. In the Bayhead Island in PSU-22 and Willowhead Island in PSU-23, the boundary between woody-dominated communities and herbaceous vegetation in the surrounding marsh was not sharp, but extends over several plots, representing a relatively wide transition zone (Hennenber et al. 2005). In this study, we have used SMW method for exploratory purpose. A more vigorous analysis that can quantify the width of transition zone, and relate them to variation in underlying environmental drivers is possible when data from repeated samplings are available.

Besides the local scale variation in vegetation composition on individual islands, a broad scale pattern in vegetation composition in the tree islands and their surrounding marshes reflects landscape variation in hydrologic conditions and disturbance regimes. For instance, in our analysis of vector fitting in the ordination space, the vegetation units were primarily arranged along the hydrologic vector (**Figure 9**). Understory vegetation in the bayheads on Hardwood Hammock islands were similar to the vegetation in the Bayhead islands. Similarly, the vegetation in the bayhead swamps present in the exterior portion of the Hardwood Hammock and Bayhead islands were similar in species composition. Despite a similarity in species composition on the bayhead and bayhead swamps across the islands in different water management regions, islands similar to the Hardwood Hammock present in PSU-22 within the Everglades National Park were not found in any of three intensively studied PSUs in WCA-2A, WCA-3A and WCA-3B. The water regimes in these areas are managed differently, resulting in hydrologic conditions considerably different from what are present in ENP. In the Water Conservation Areas, management-induced hydrologic changes have caused an extensive loss of tree islands (Patterson and Finck 1999) and significant alterations in vegetation composition on existing islands (Wetzel et al. 2008). In addition, continuing human use of the islands in these areas in recent years might have affected vegetation composition on the tree islands. In this study, in the Hardwood Hammock in PSU-21 within WCA-2A, the interior part of the island was cleared with only very few trees left. Open canopies and frequent disturbances might have also influenced the understory vegetation causing small scale variation in species composition (Ruiz et al. 2011), as reflected in high dissimilarity in species composition at high ground towards the interior end of the transect (**Figure 4**). In this island, woody vegetation on the rest of the transect resembles that of a willowhead suggesting a kind of degradation in island elevation. Marsh vegetation surrounding a majority of tree islands surveyed in this study was similar in species composition, primarily dominated by sawgrass, which is not only most abundant macrophyte in the Everglades but also has the widest amplitude of hydrologic tolerance (Todd et al. 2010).

Several scale dependent ecological processes, including hydrologic variation, nutrient dynamics, disturbance, and biological processes are important in determining vegetation pattern within individual tree islands as well as at the landscape level (Wetzel et al. 2005; Ross et al. 2006; Givnish et al. 2008). Therefore, only a comprehensive synthesis of results from multiple years of study of vegetation structure and composition and ecological processes by several researchers from different disciplines would help to explain the detail of community pattern and process in the Ridge, Slough and Tree islands of the Everglades. However, a well understood pattern of community transition along known gradients from within the islands to the marsh will allow managers to adjust water management operations to achieve desired vegetation pattern within the tree islands and surrounding marshes. While the present study of six islands has reiterated the use of SMW analysis method in identifying the boundaries between tree islands and surrounding marsh, our results indicate that the effective use of this method to monitor changes in tree island morphology throughout the system would require a large number of samples, and more importantly intensive sampling along multiple transects within individual islands. Researchers have used air-borne imagery to examine the changes in tree island acreage within Water Conservation Areas and Everglades National Park (Patterson and Finck 1999; Sklar et al. 2013.

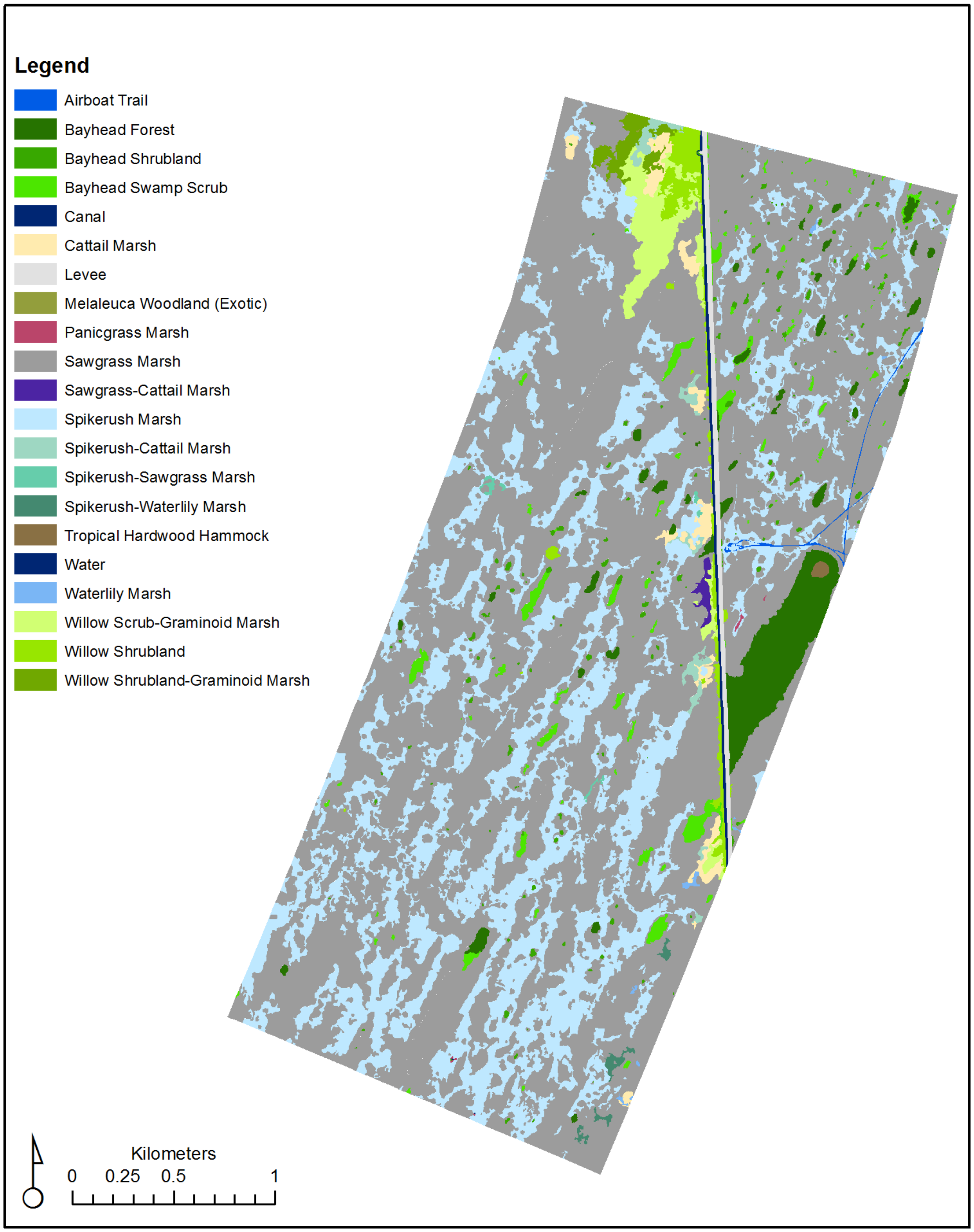
Ruiz et al. (2013) also have devised an automated method to map marl prairie tree islands using air-borne imagery from different time periods that can effectively be used to examine the temporal changes in tree island boundaries within the specific landscape. However, the major challenge is to use similar method to map diverse communities localized within and around islands at the broader scale using more frequently and readily available space-borne imagery. Currently, a USACE-funded research project (Cooperative Agreement # W912HZ-09-2-0019) to characterize the vegetation composition along the gradients in tree islands in different water management areas using both field data and multispectral space-borne Landsat 5 (TM) and WorldView-2 Imagery is underway. In that project, a model to characterize the vegetation structure and spectral reflectance is being developed using several spectral indices (Crippen 1990; Motohka et al. 2010) that, after verification at reference sites, can be used to characterize and examine vegetation structure in islands over time at the landscape level. Therefore, limited ground sampling can be supplemented with a cost-effective means of system-wide monitoring, such as use of high resolution air-borne and/or multispectral space-borne imagery to effectively monitor temporal changes in tree island boundary as well as community pattern in the islands and surrounding marshes.

## Appendix I – Marsh and tree island vegetation monitoring field data

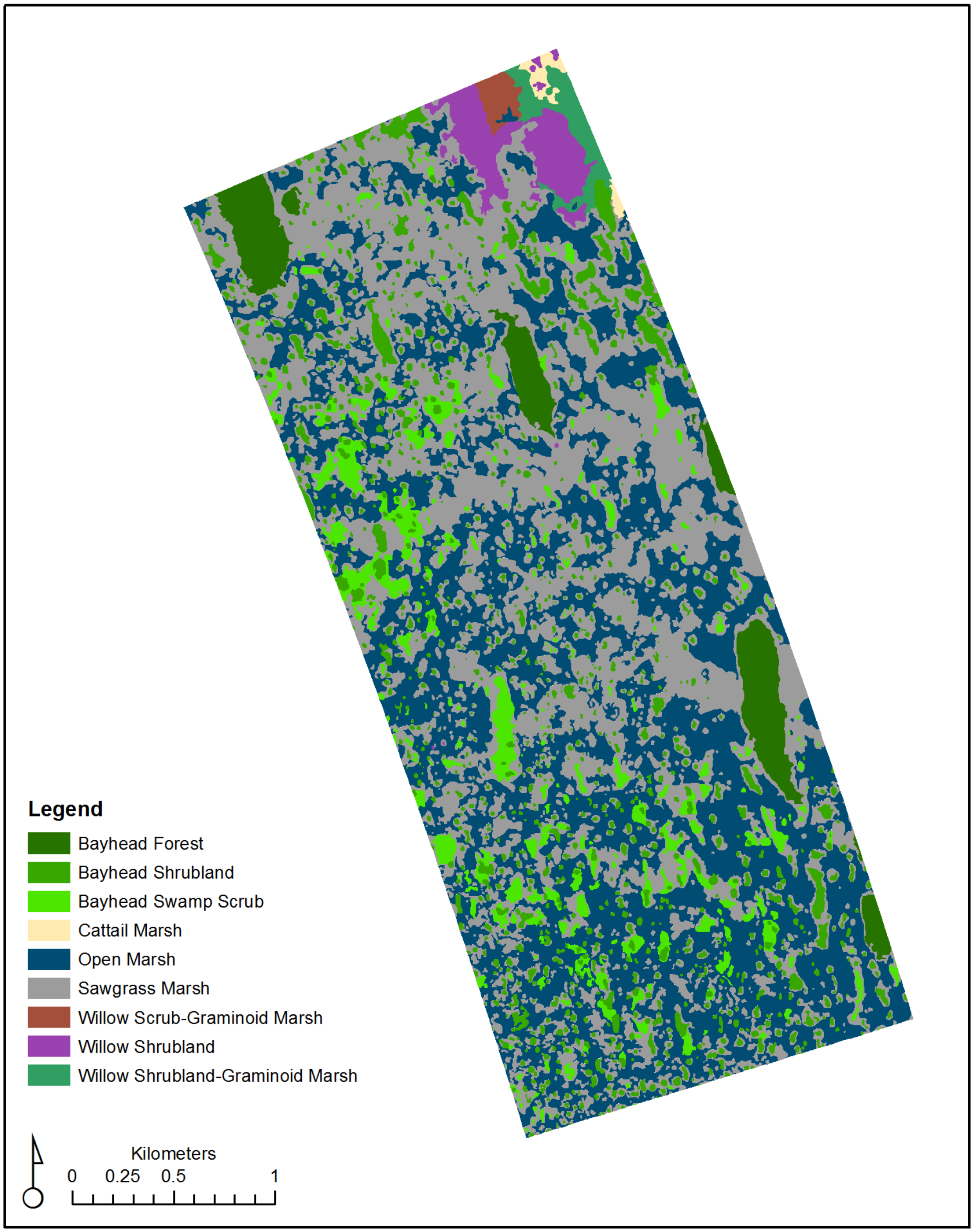
[INSERT DATA] or [ATTACH DATA, and modify any references to Appendix I above accordingly]

## Appendix II – Maps of marsh and tree island vegetation

# 2009 Vegetation Map of PSU 0

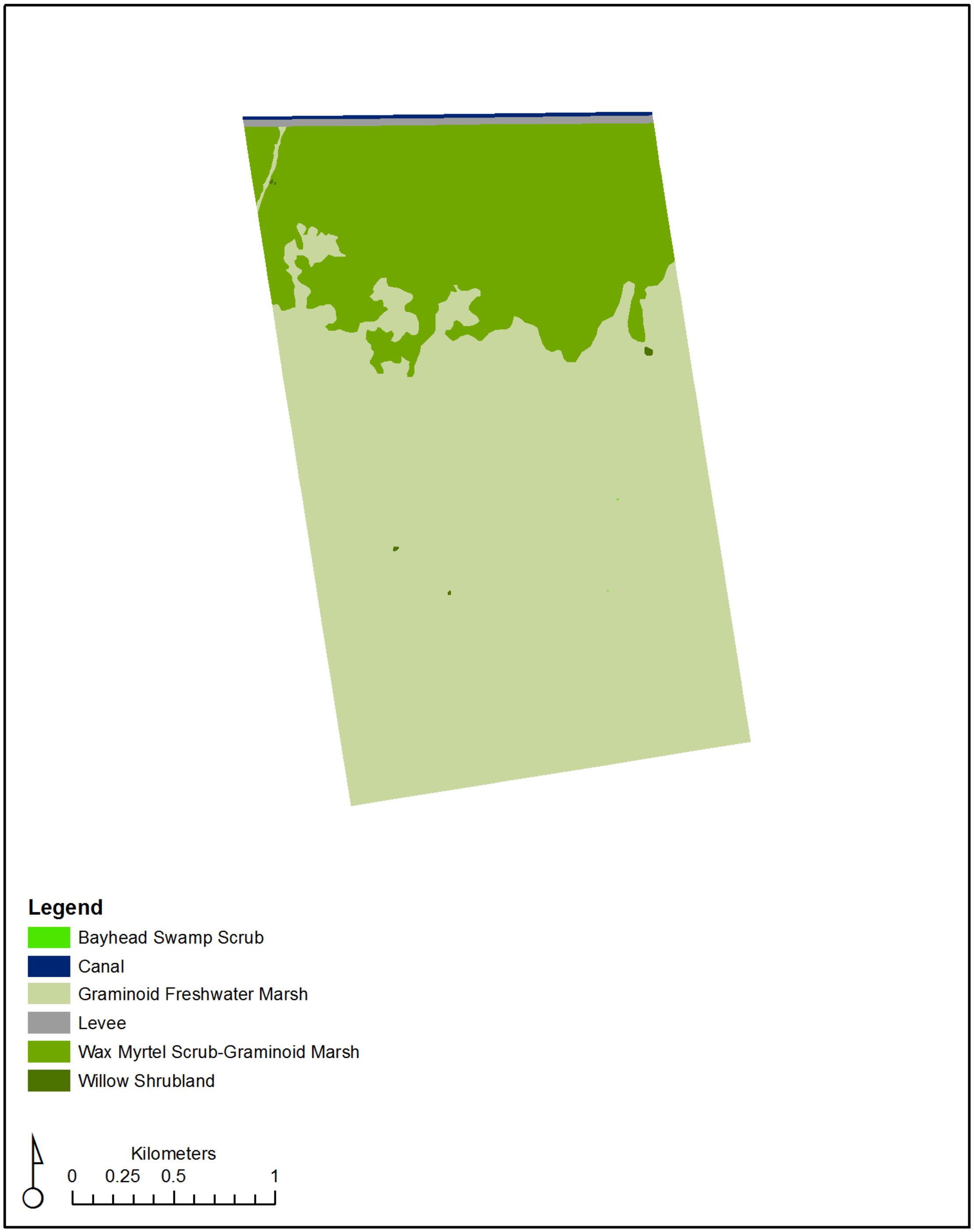


# 2010 Vegetation Map of PSU 1

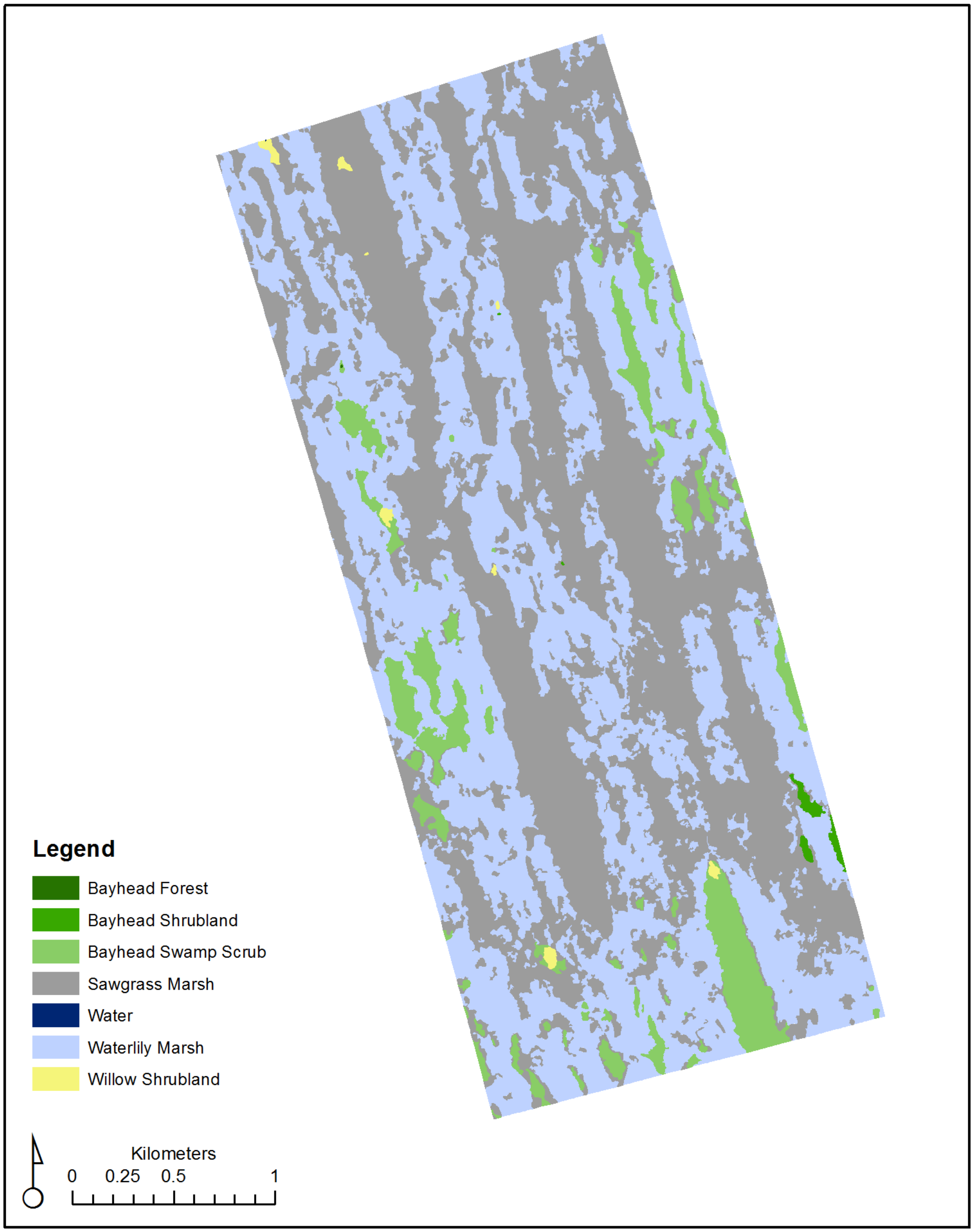


# 2010 Vegetation Map of PSU 2

# 2010 Vegetation Map of PSU 3



# 2003 Vegetation Map of PSU 4



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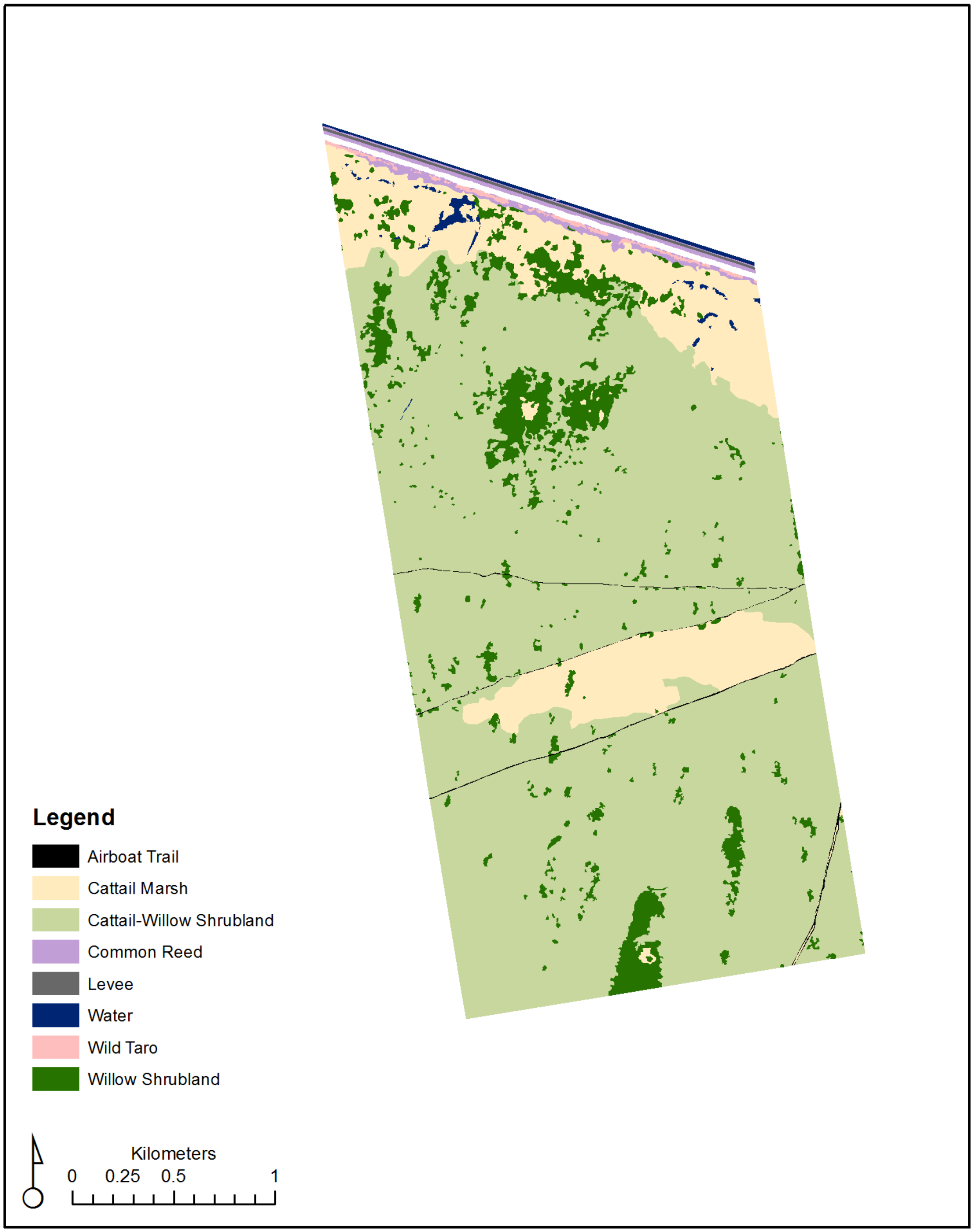

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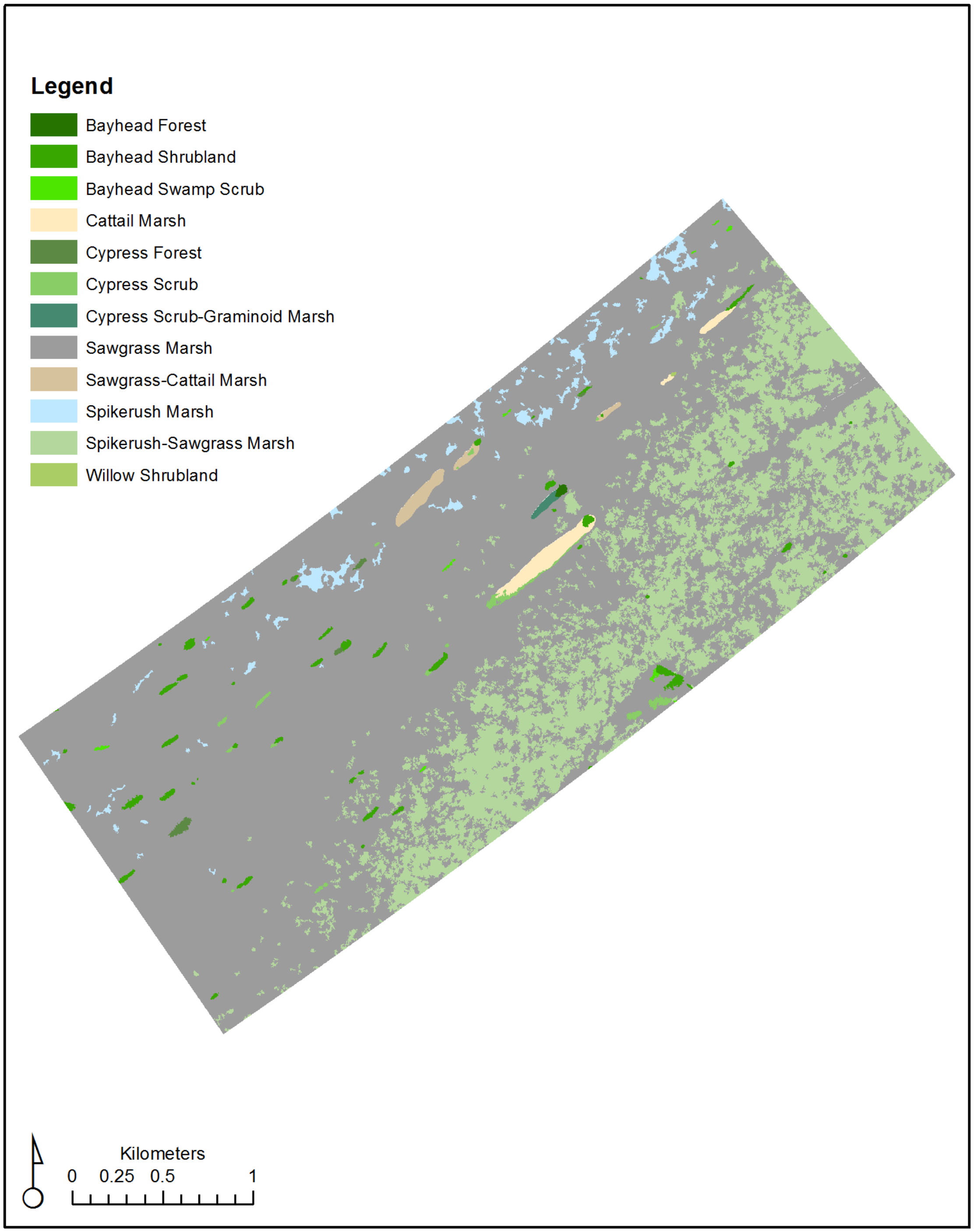

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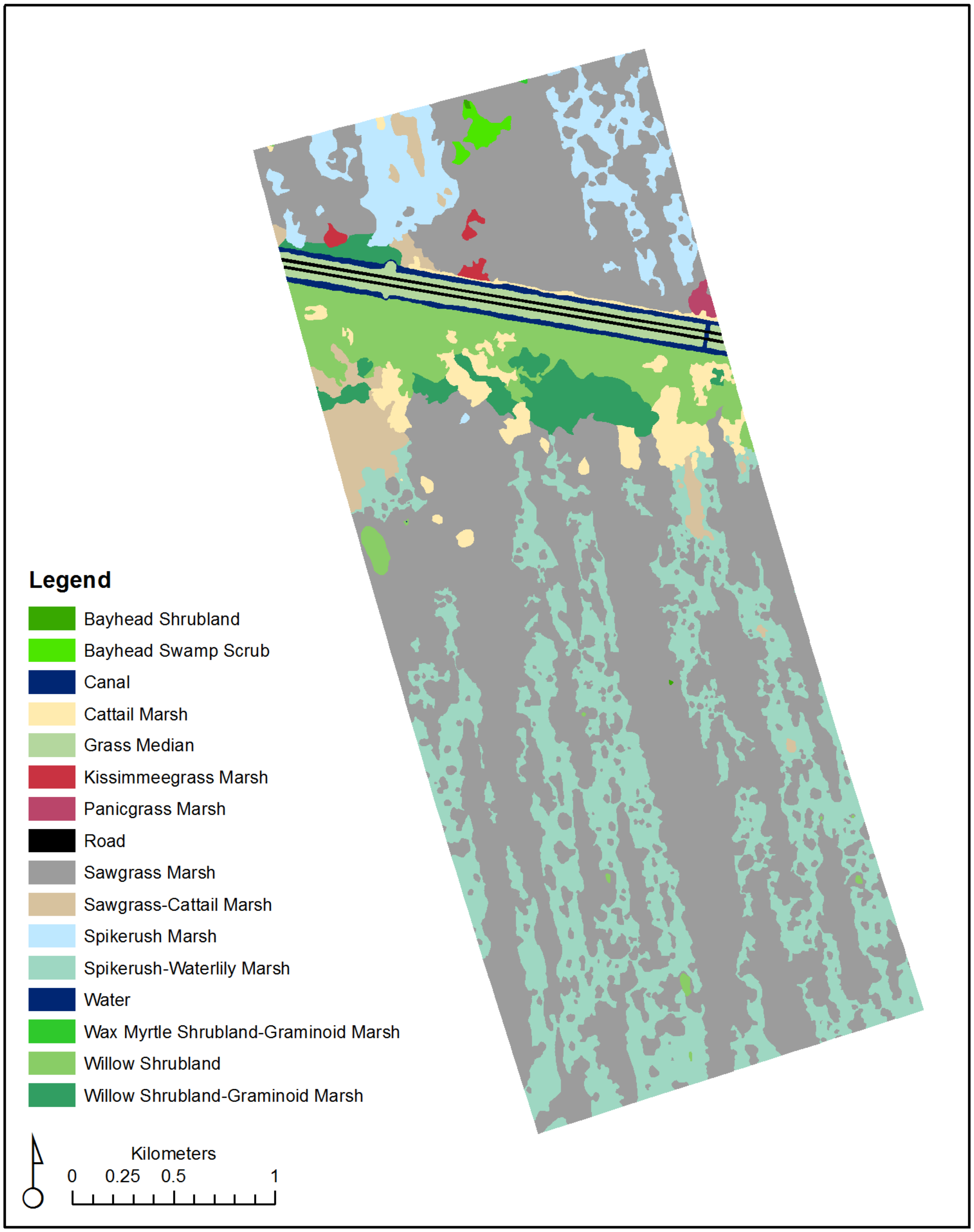

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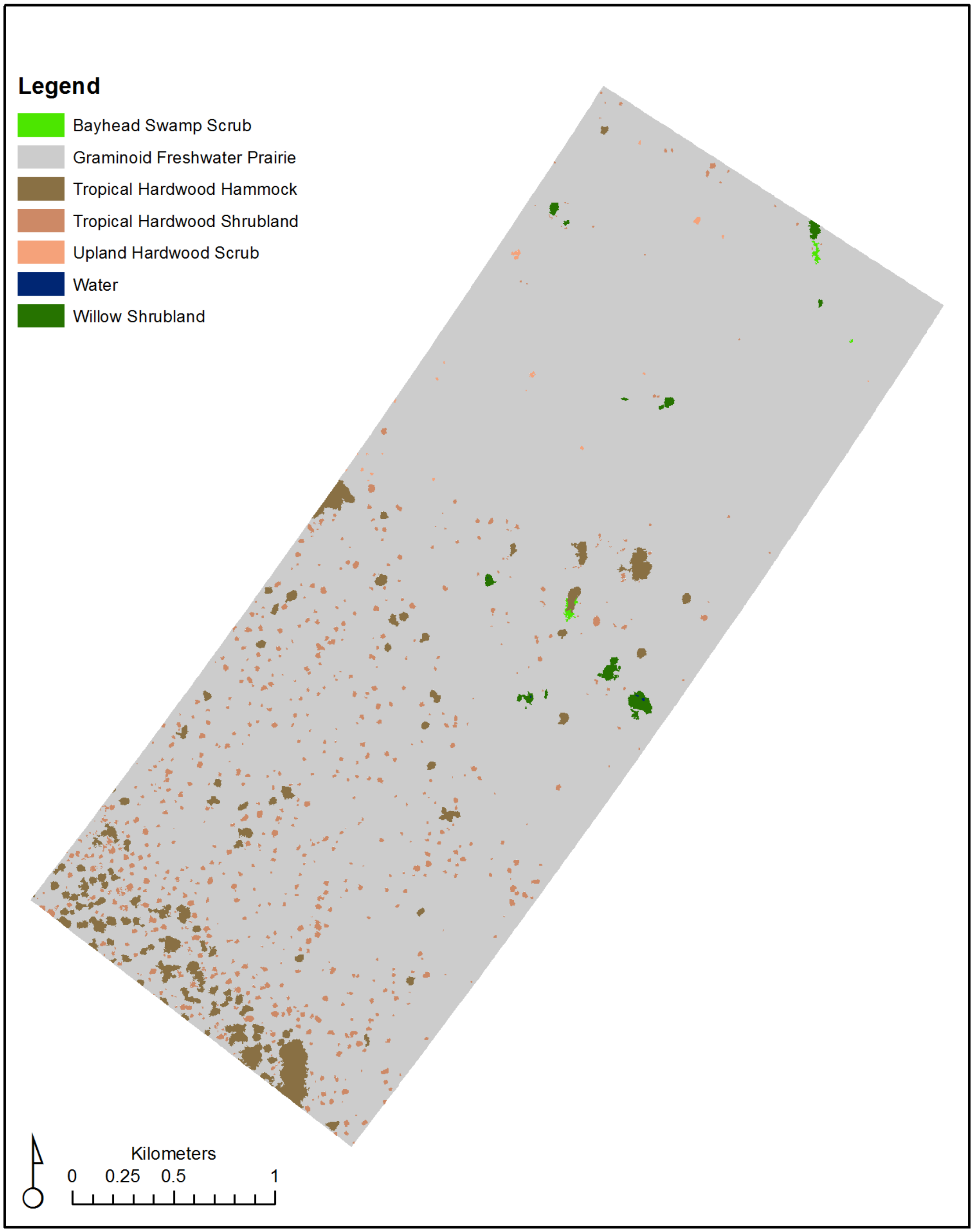

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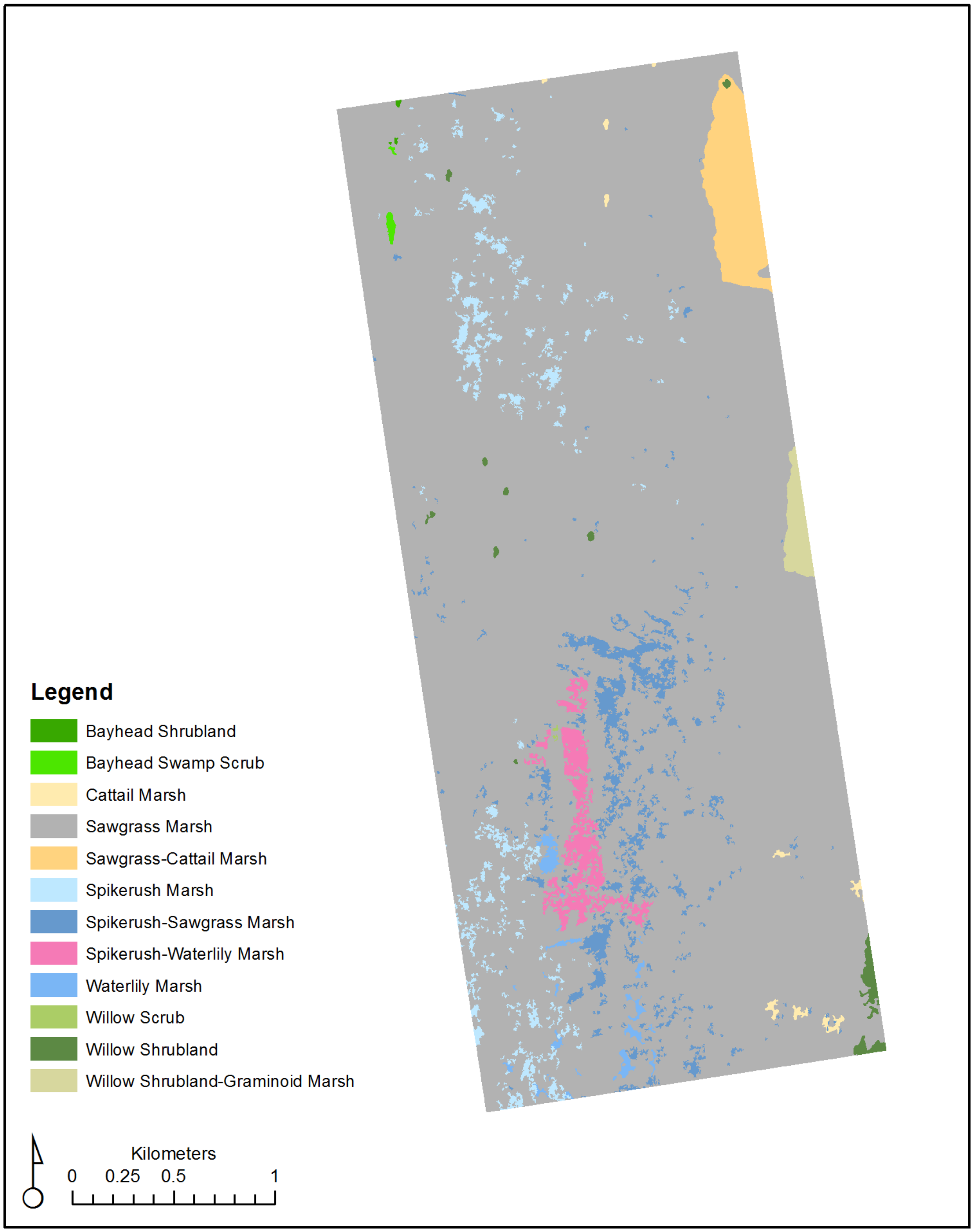

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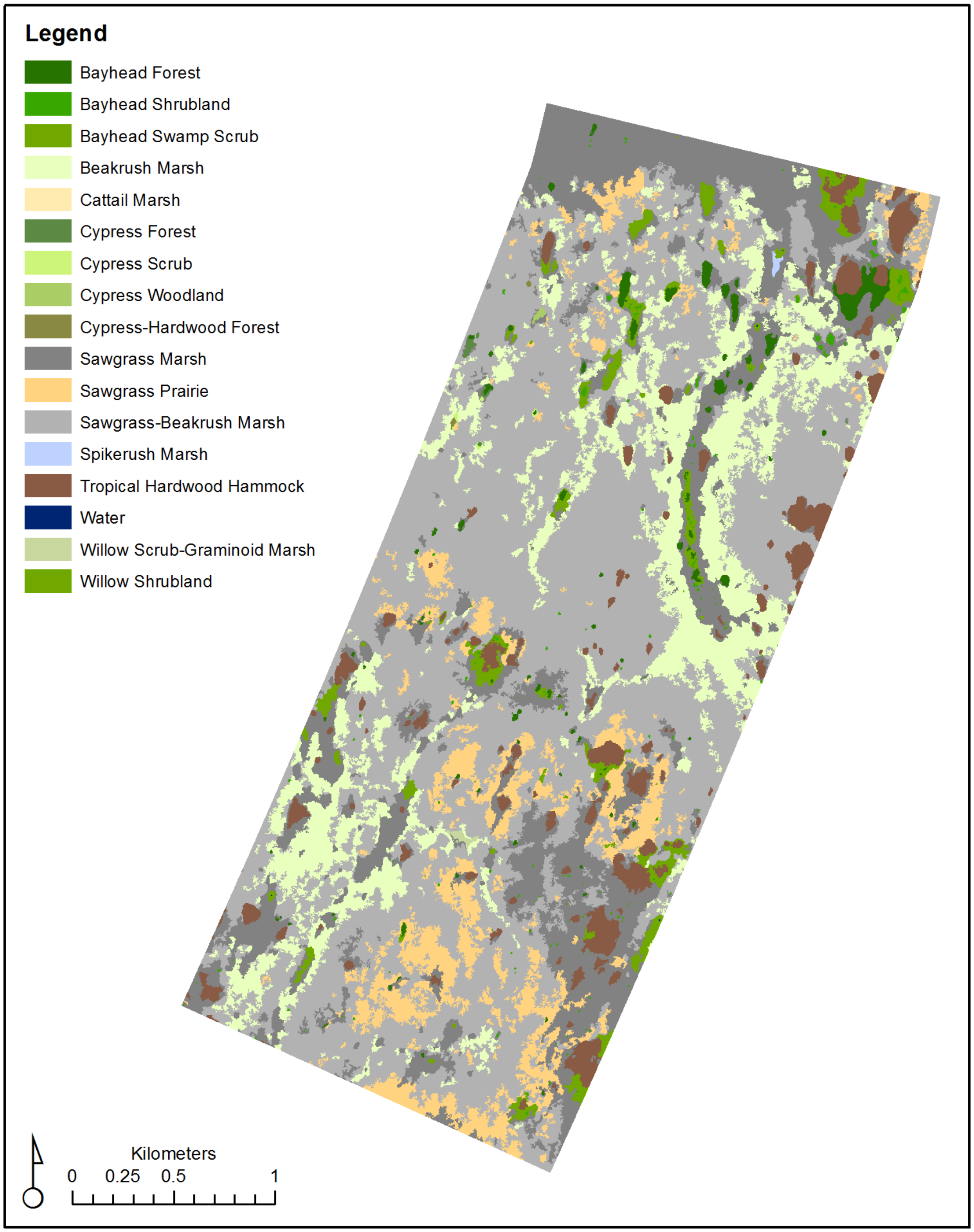

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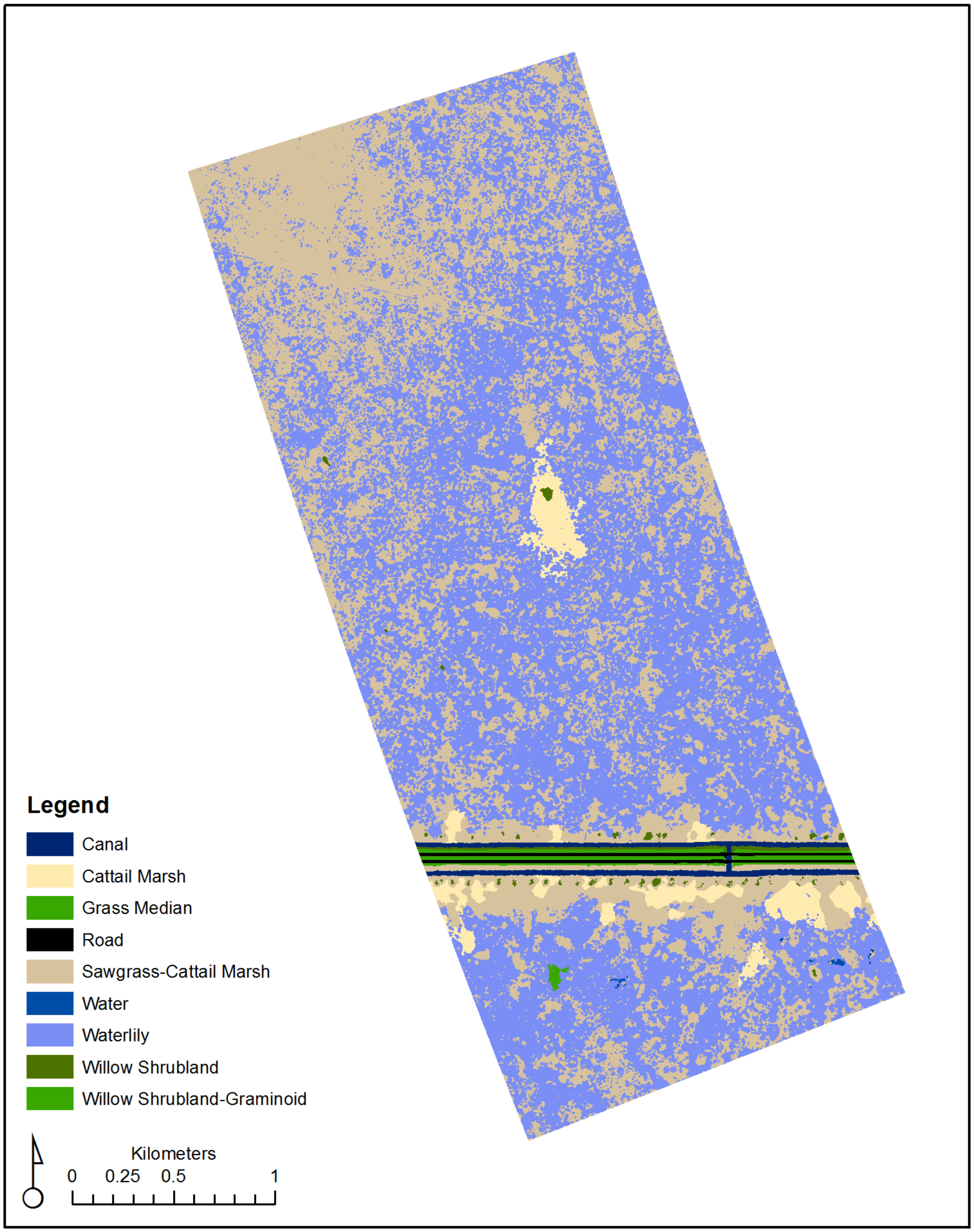

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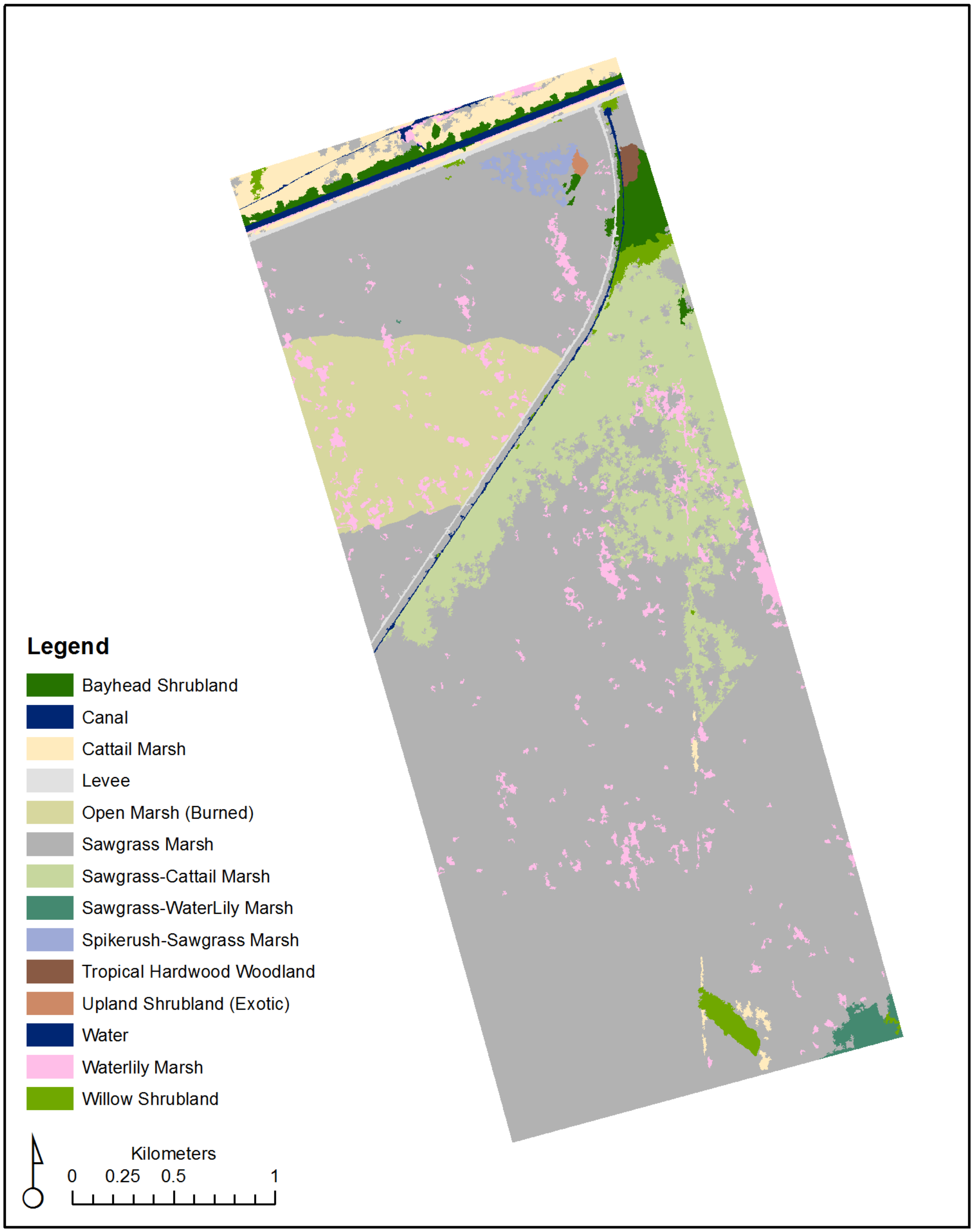

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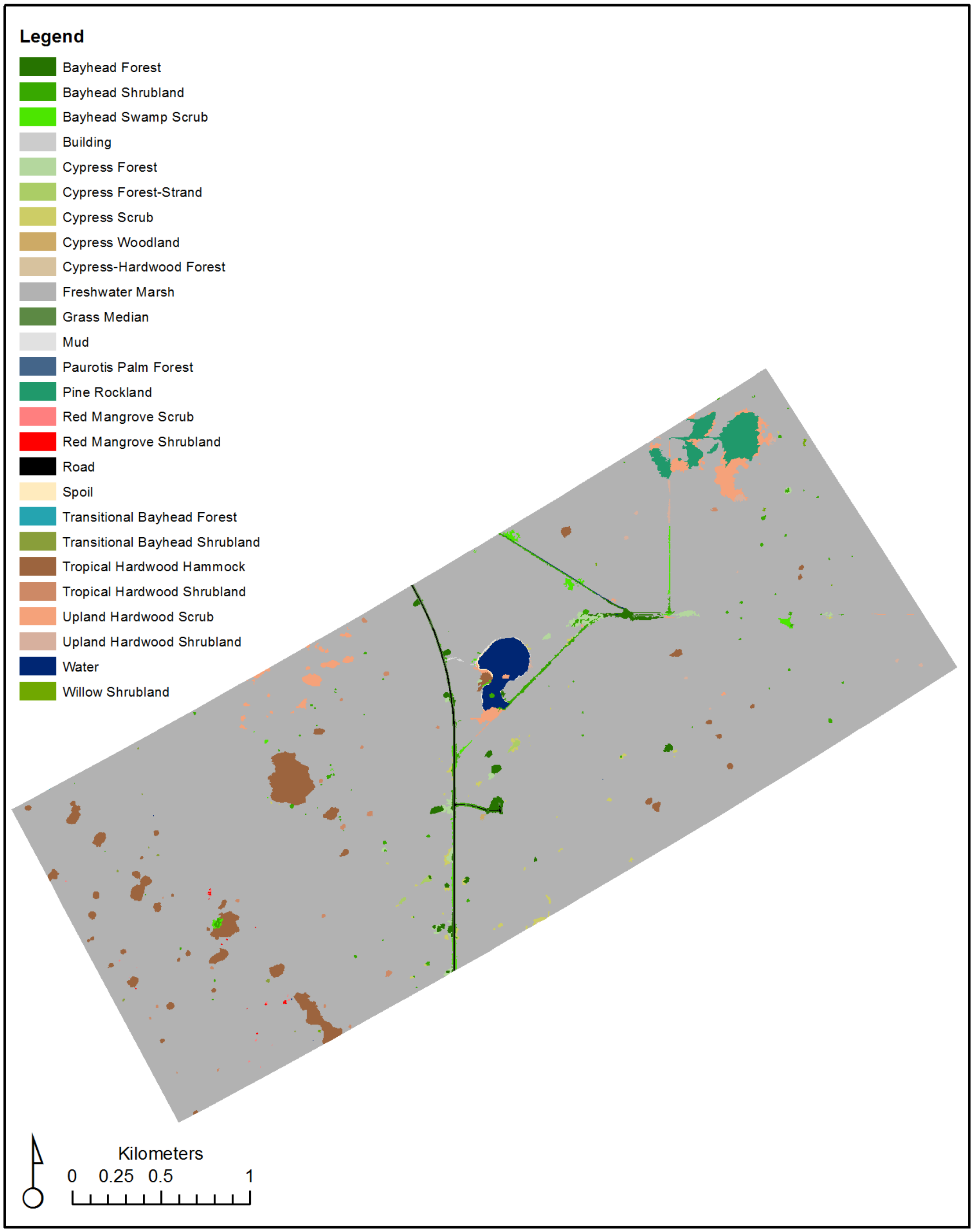

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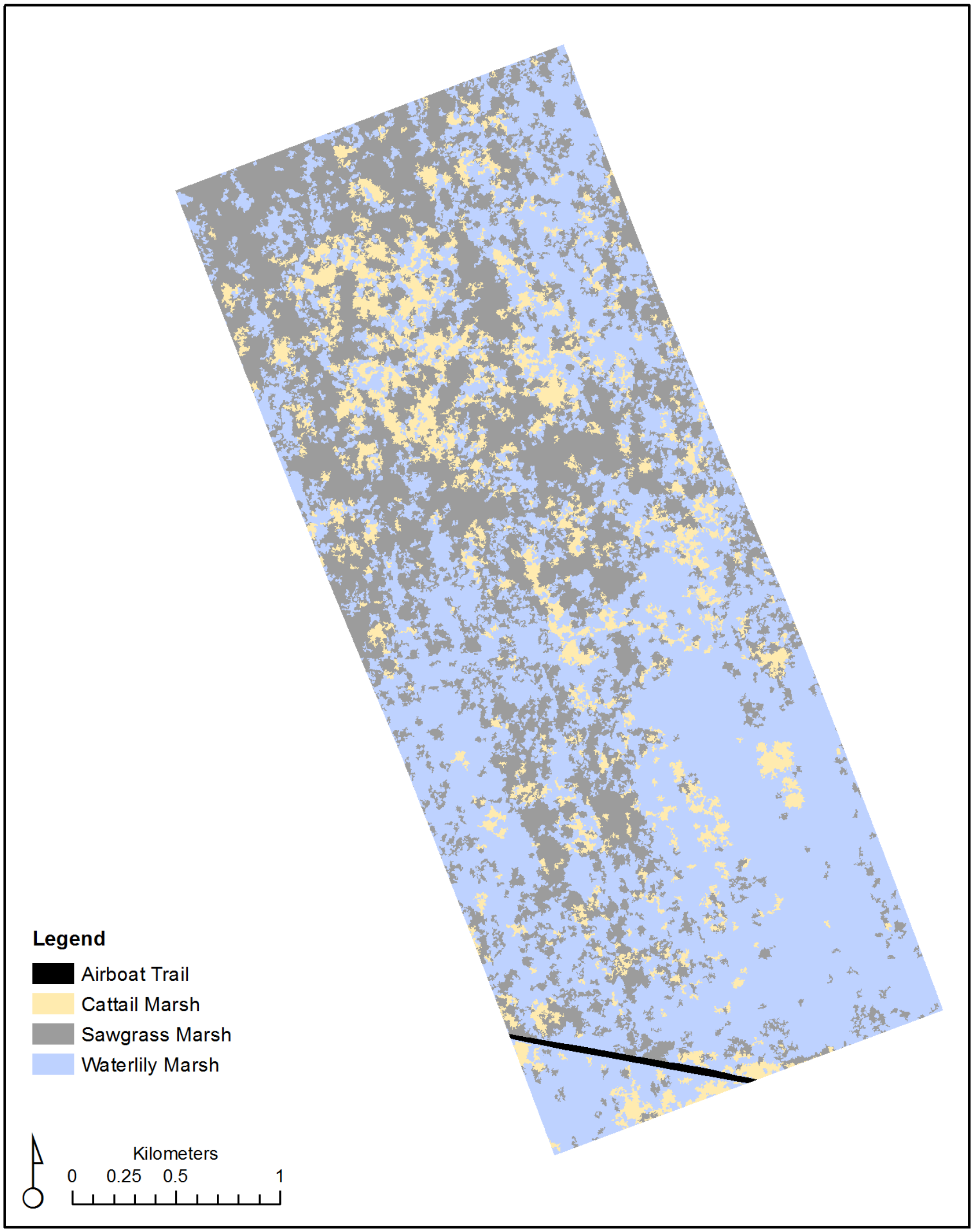

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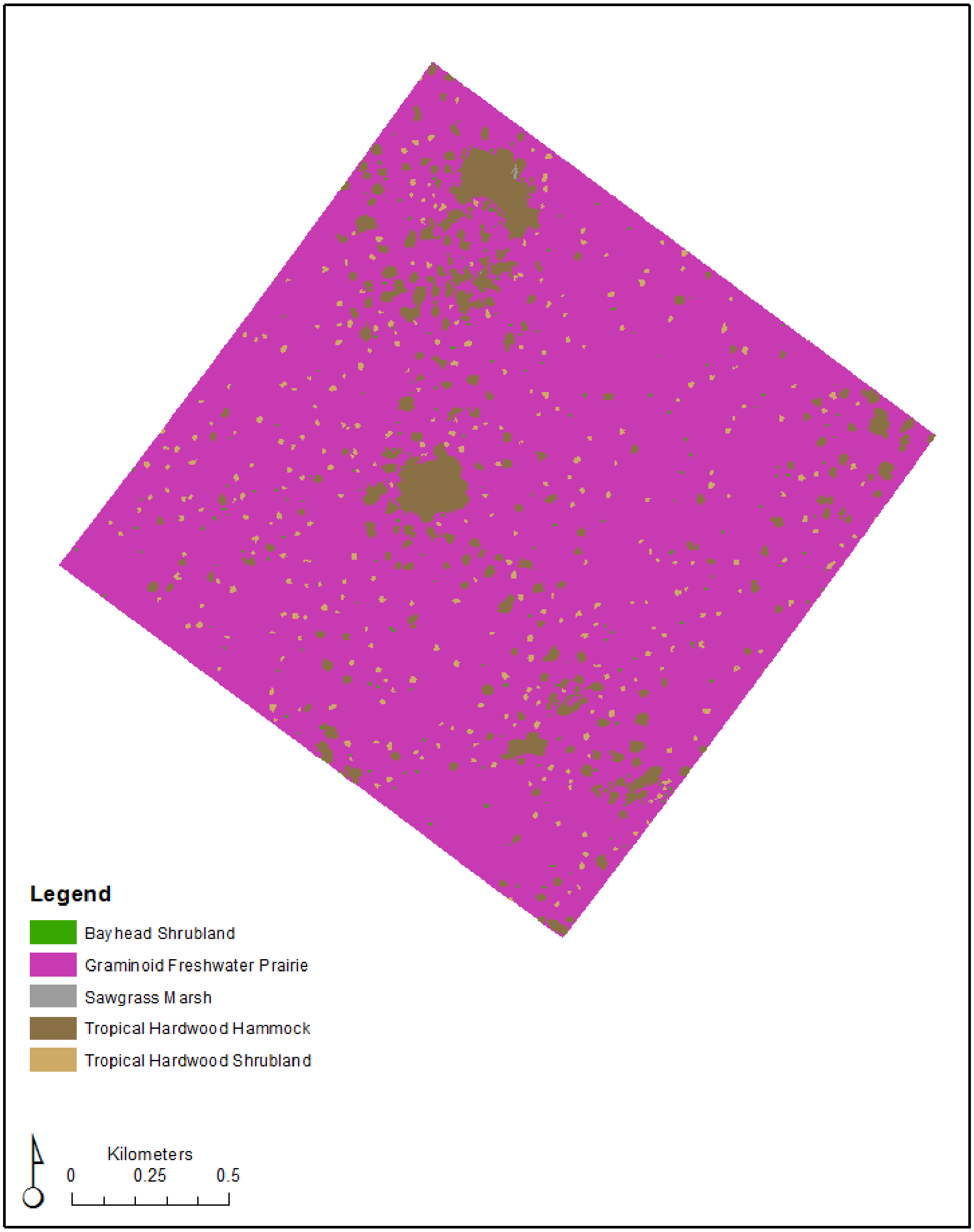

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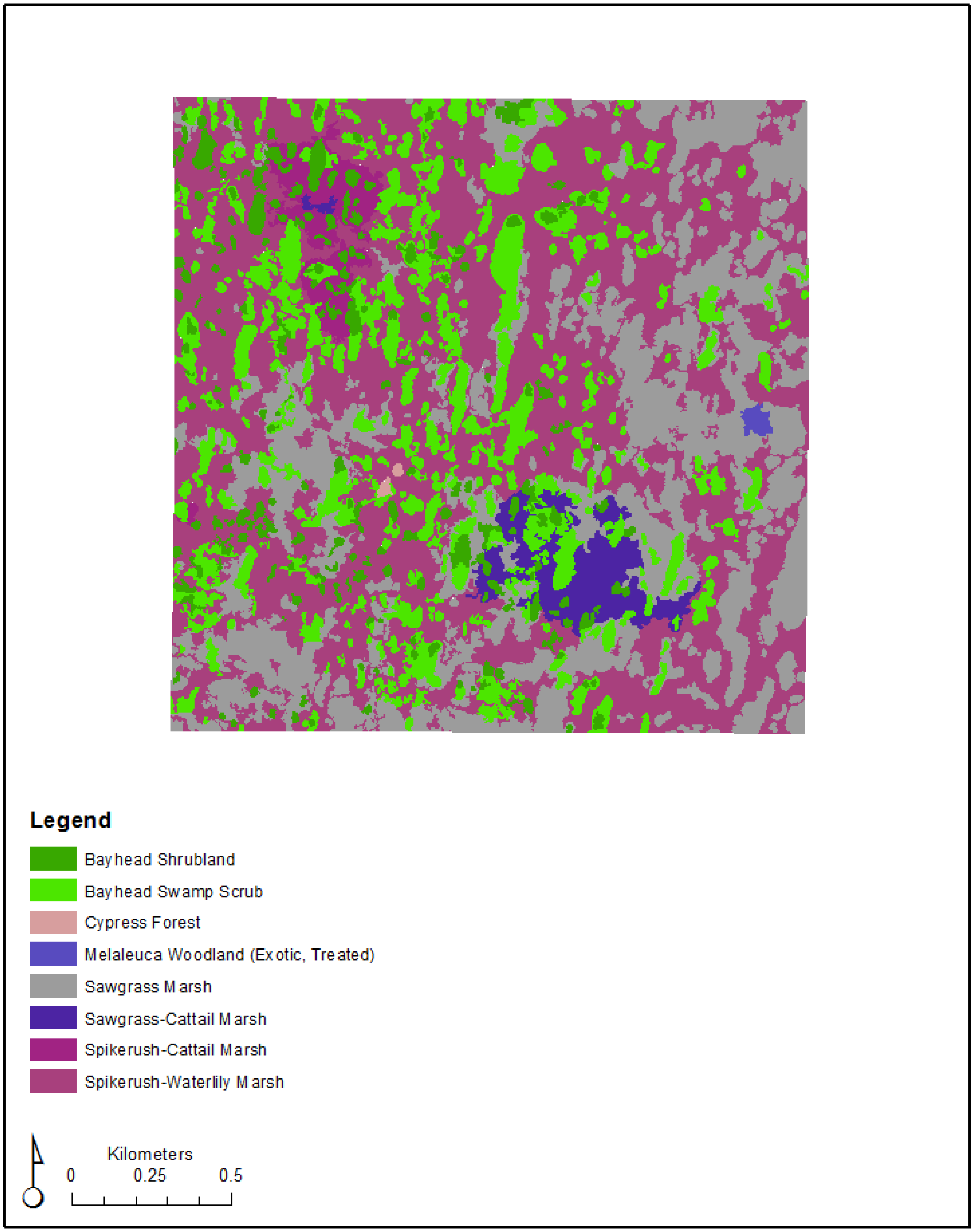

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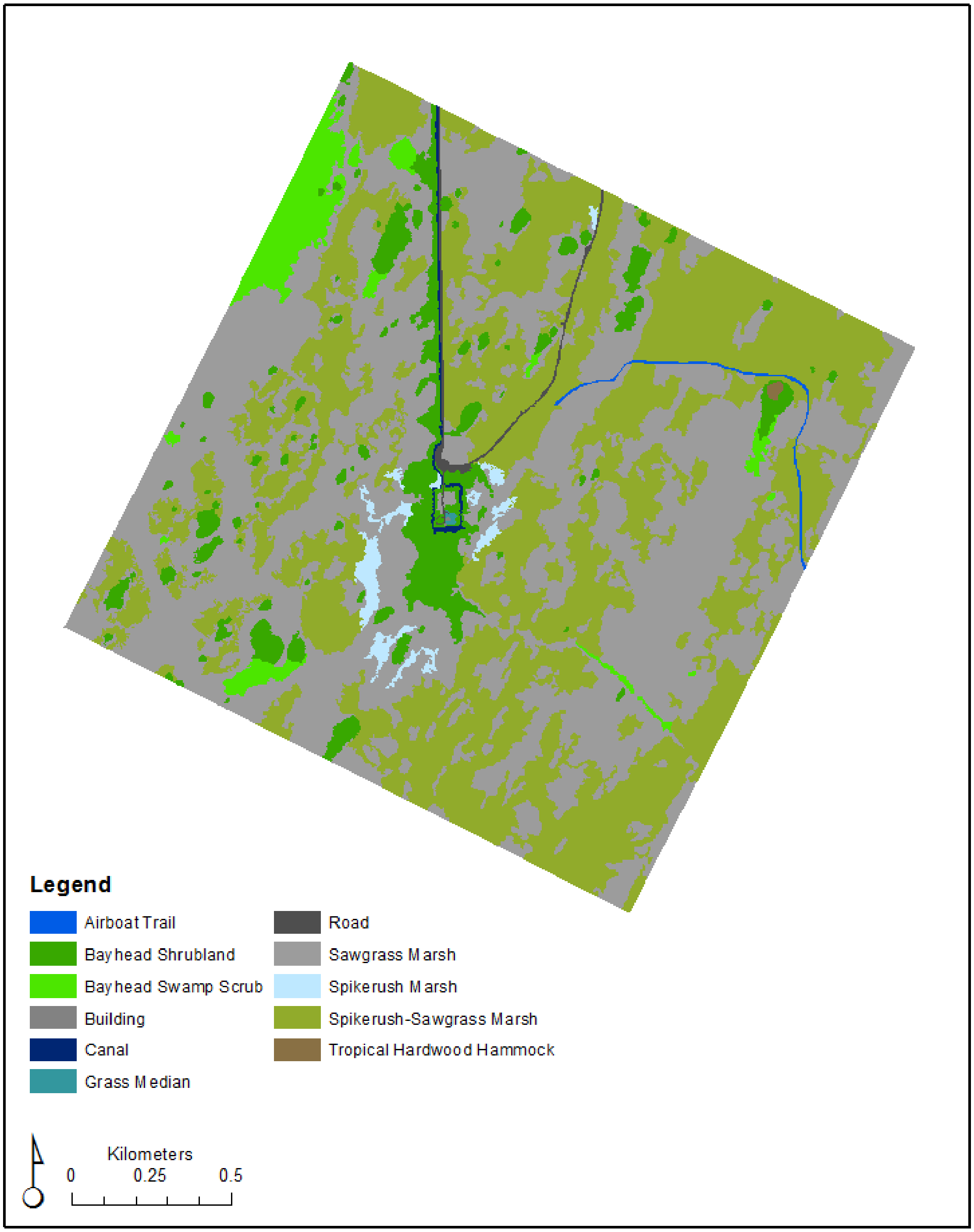

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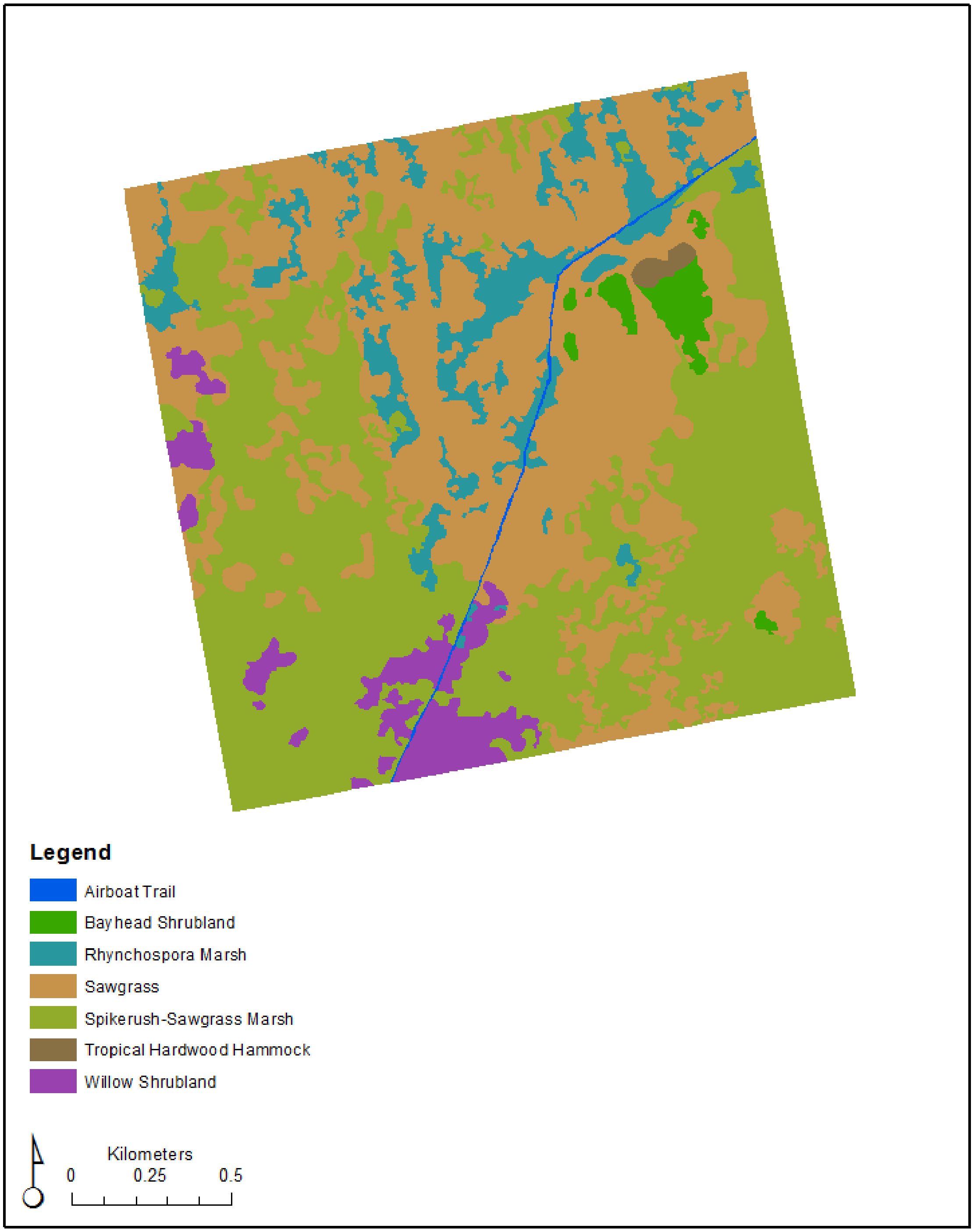

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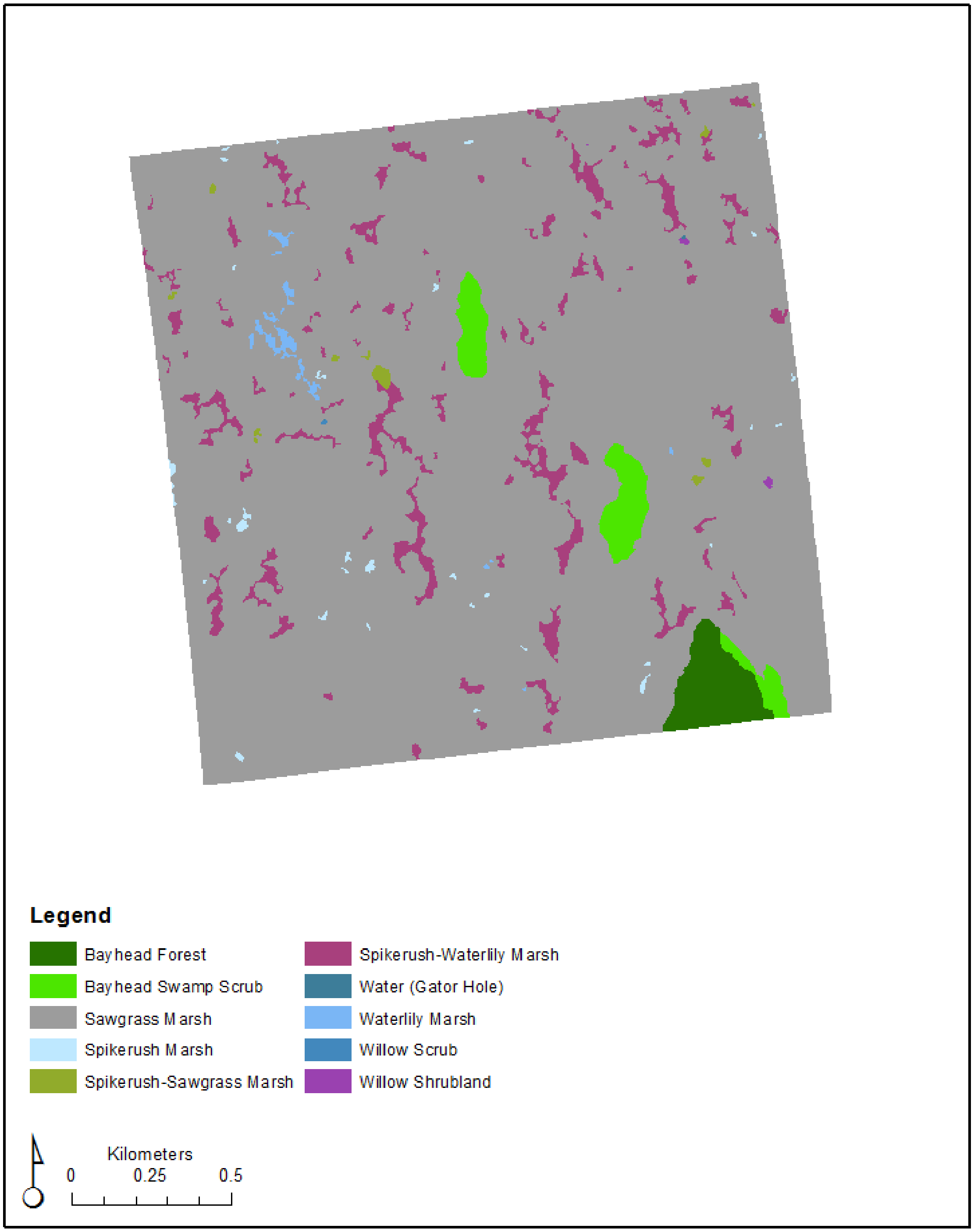

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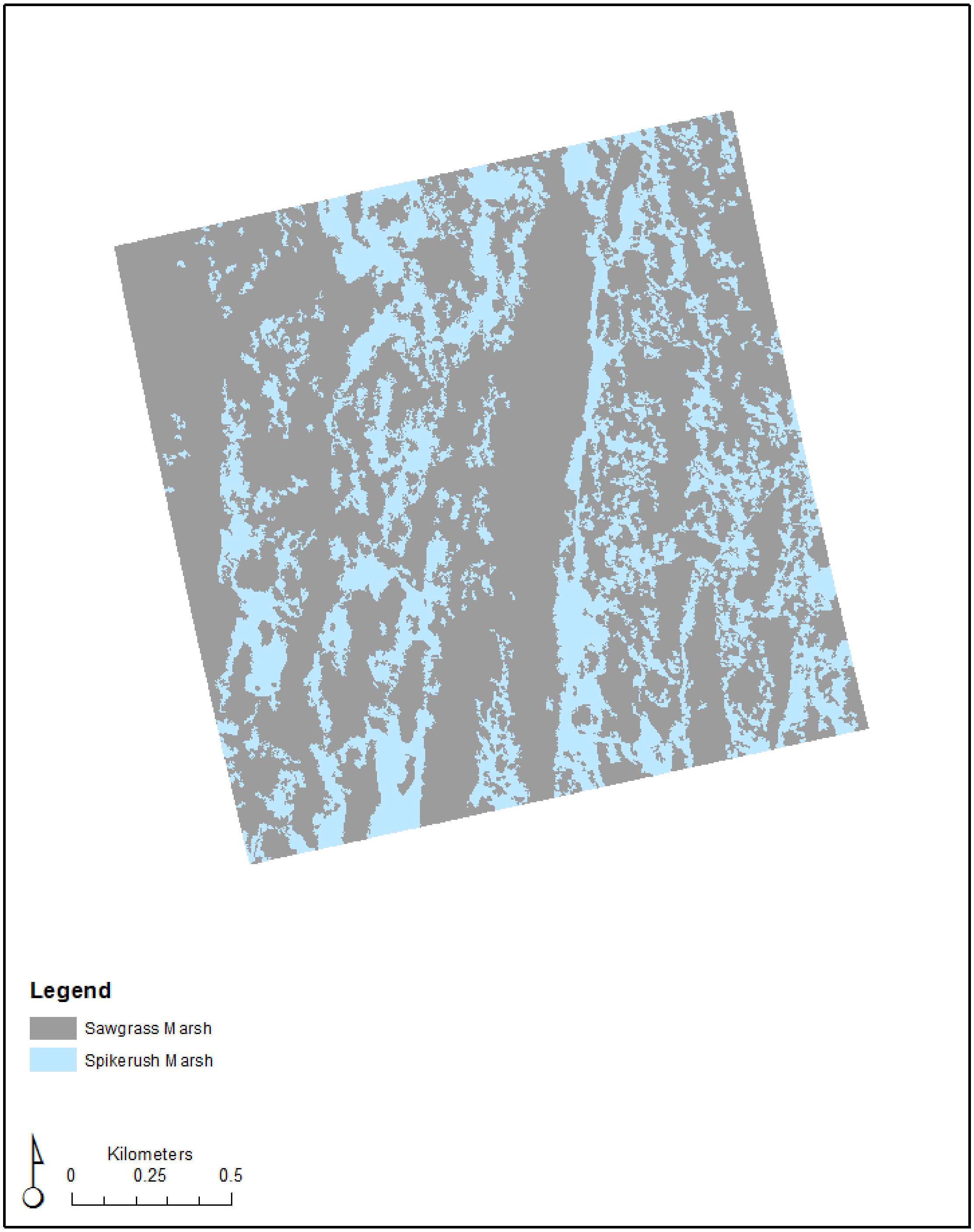

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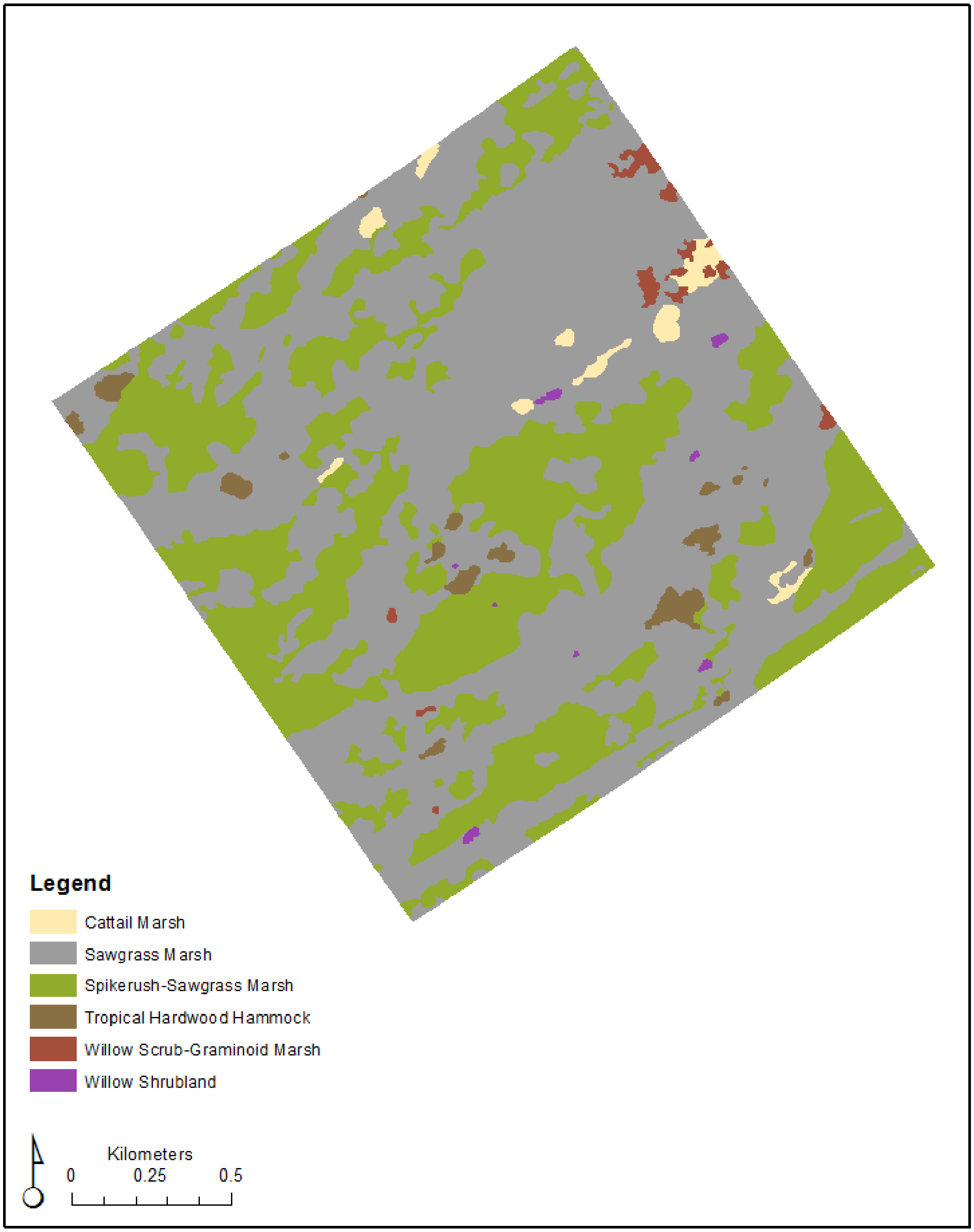

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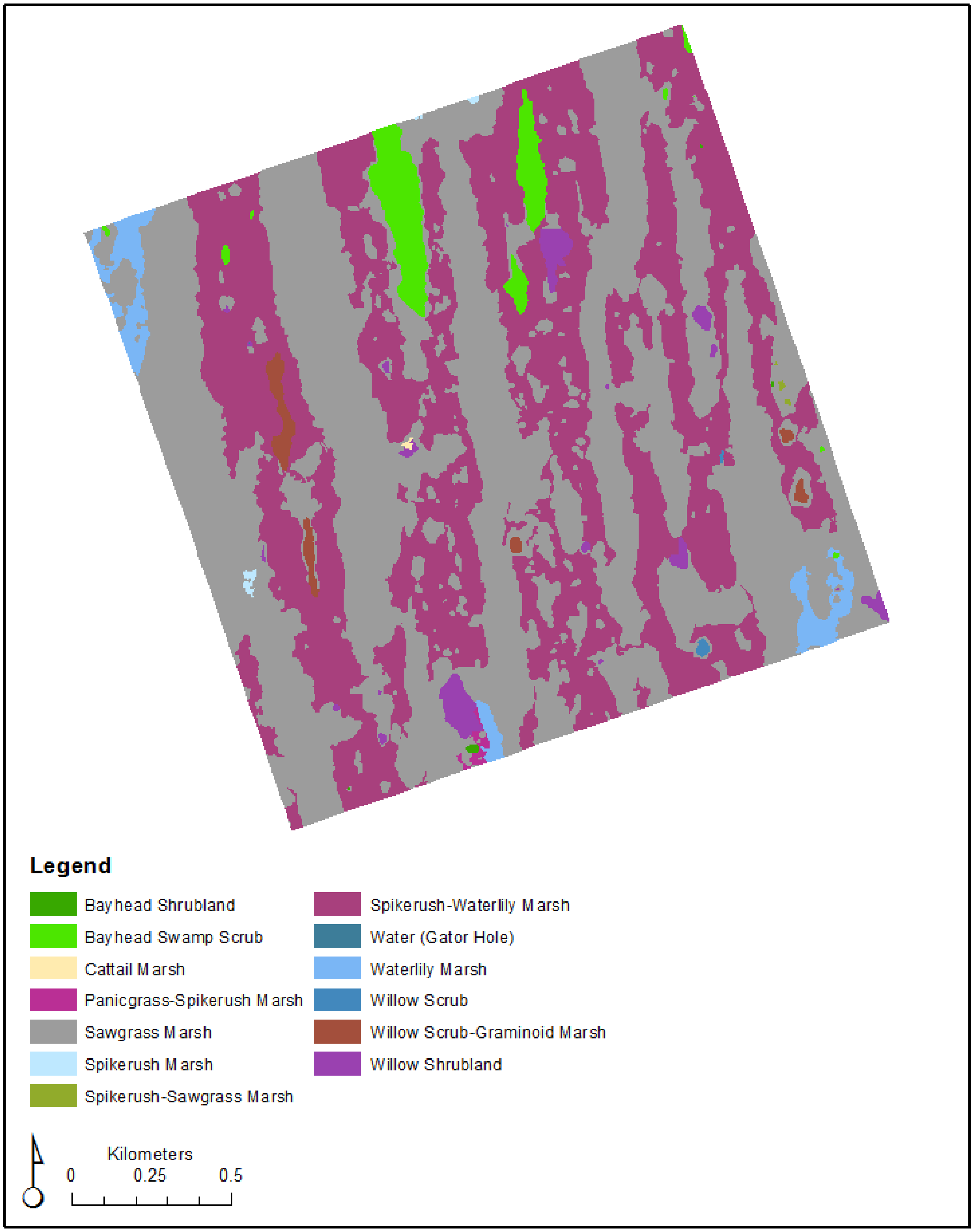

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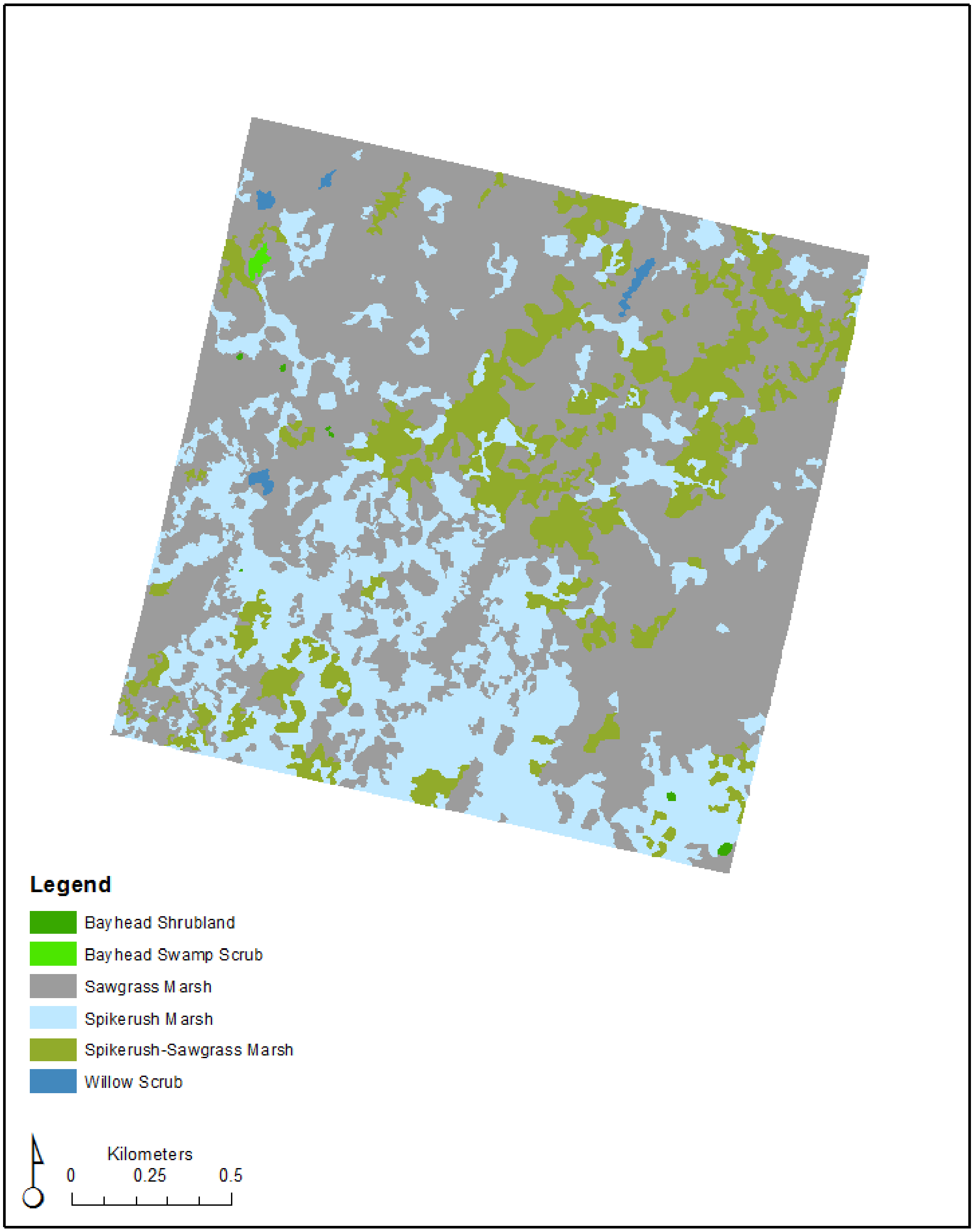

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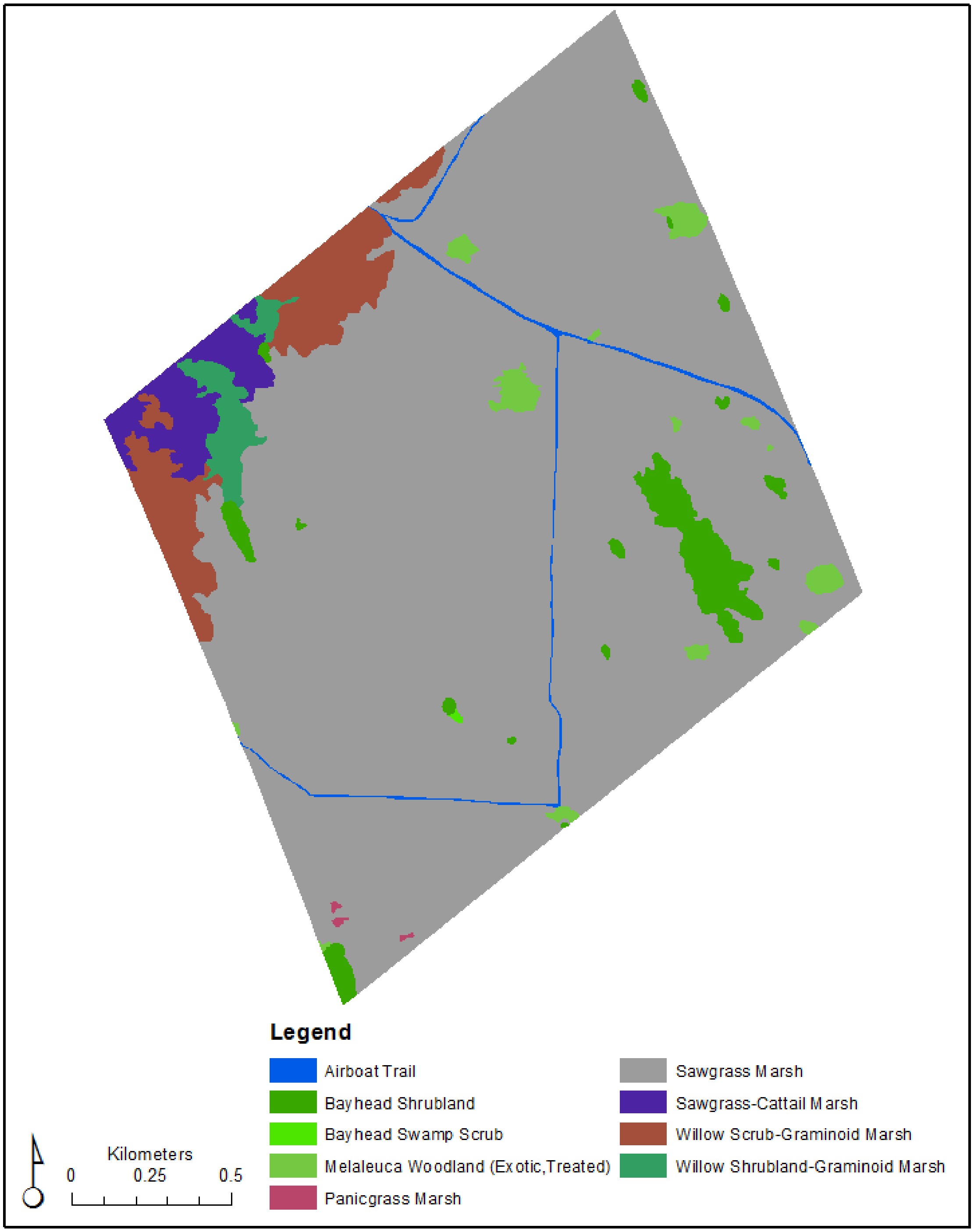

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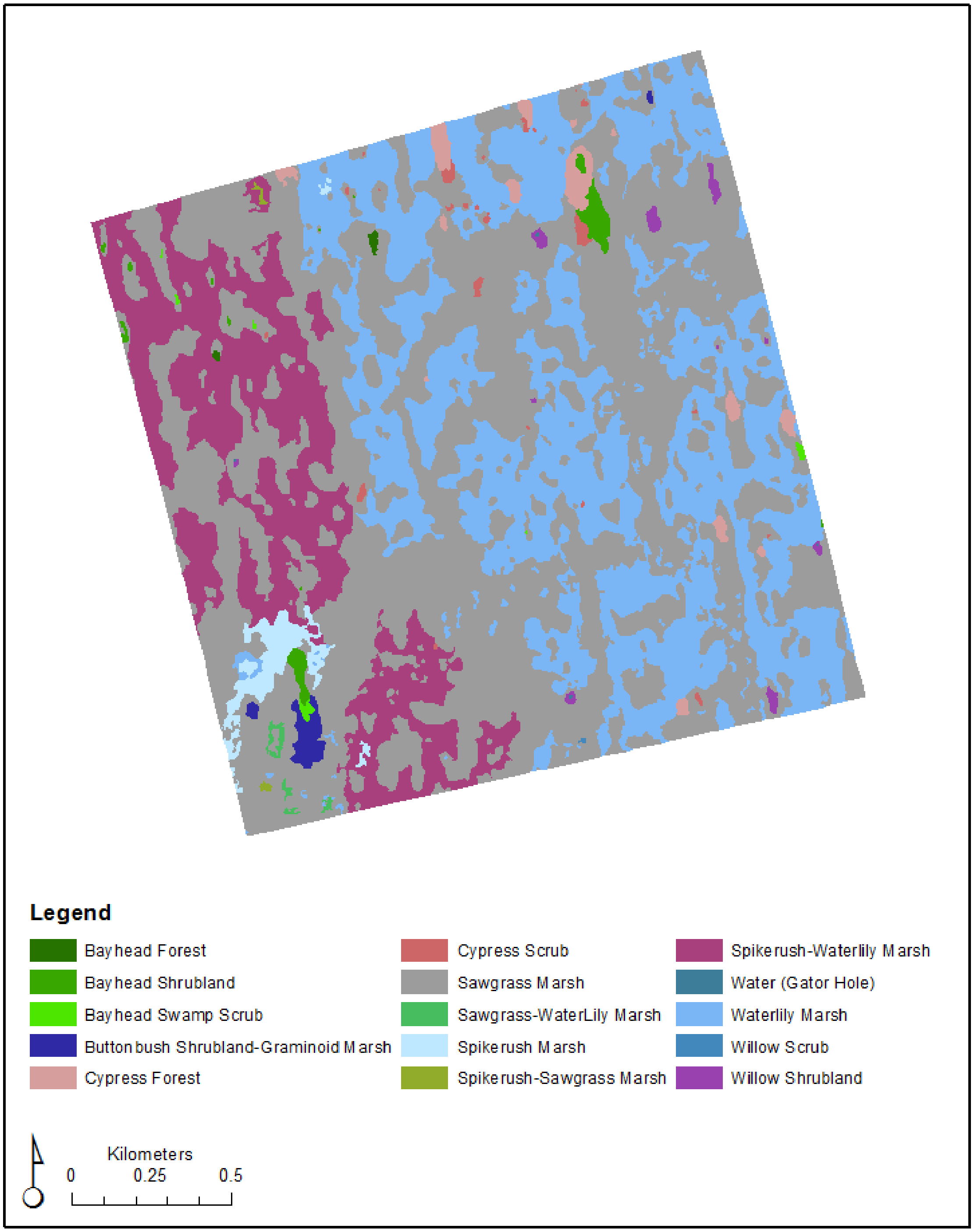

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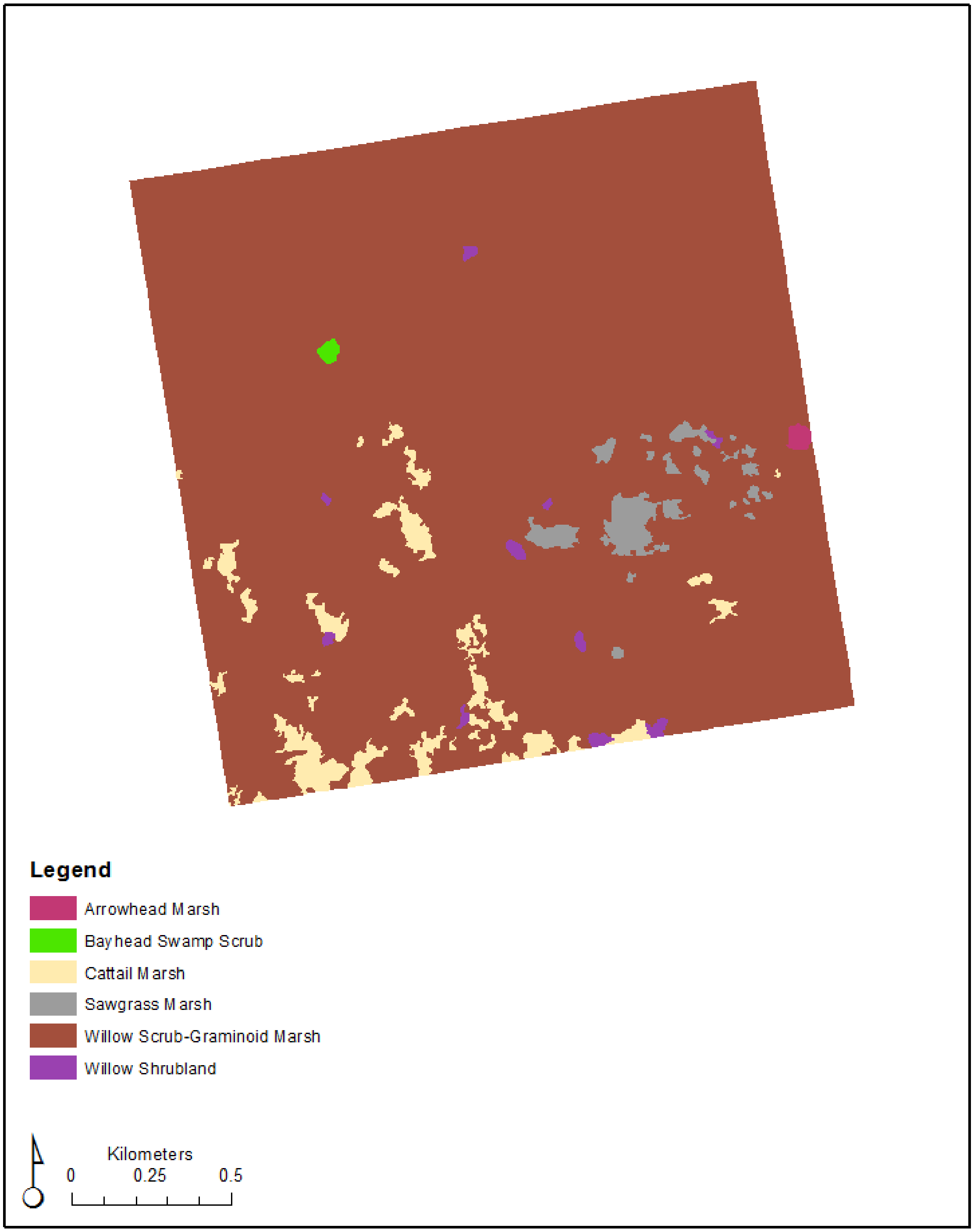

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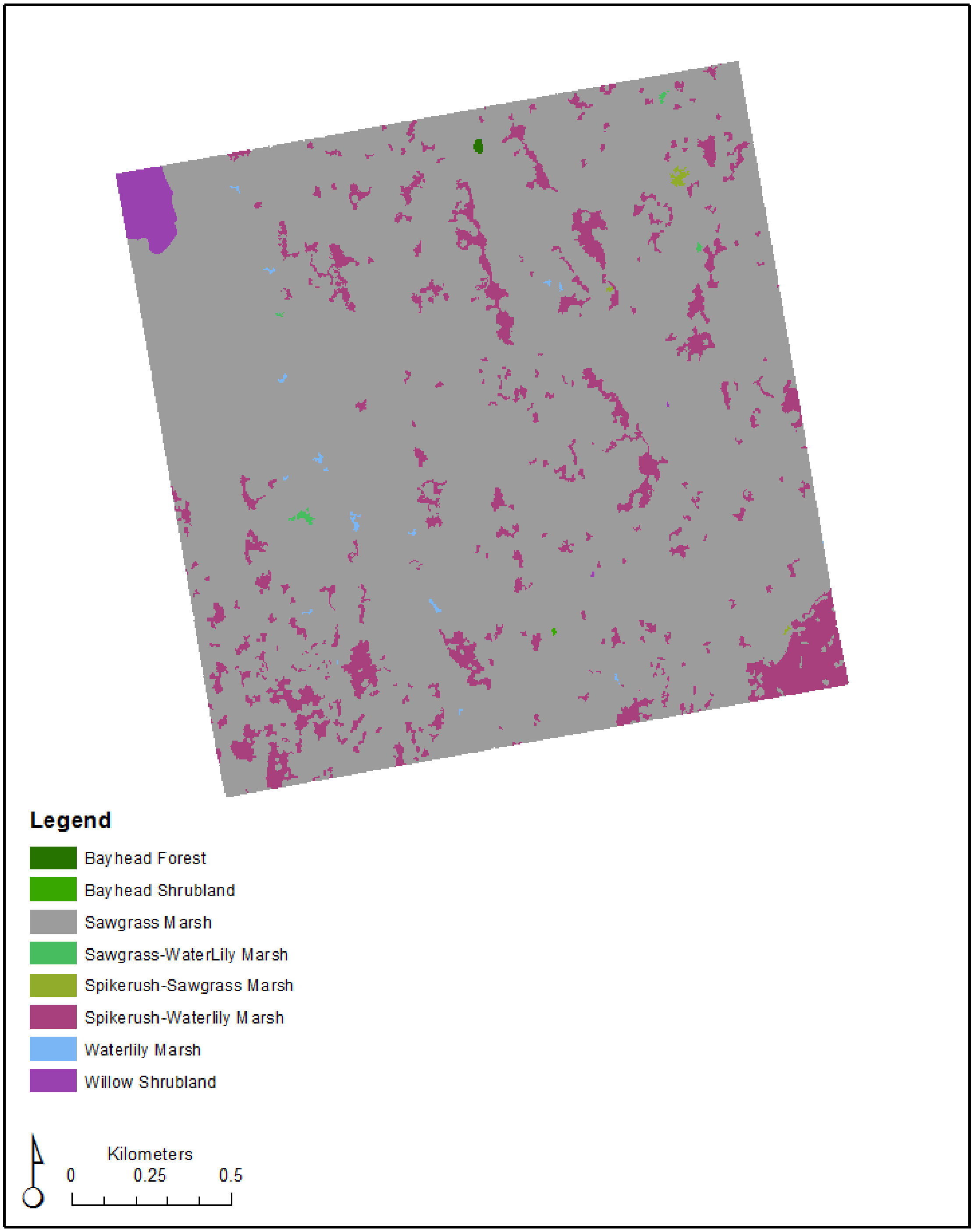

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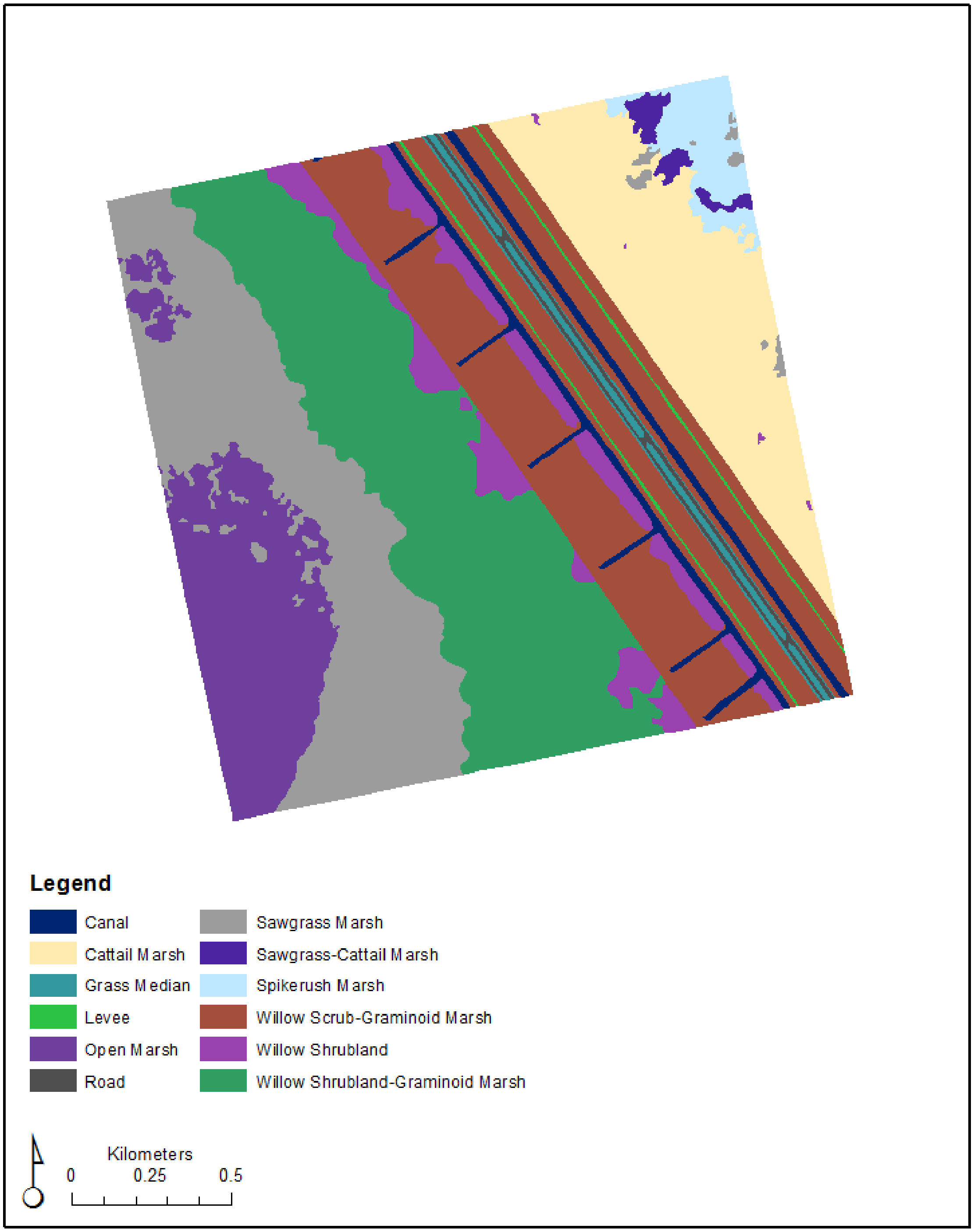

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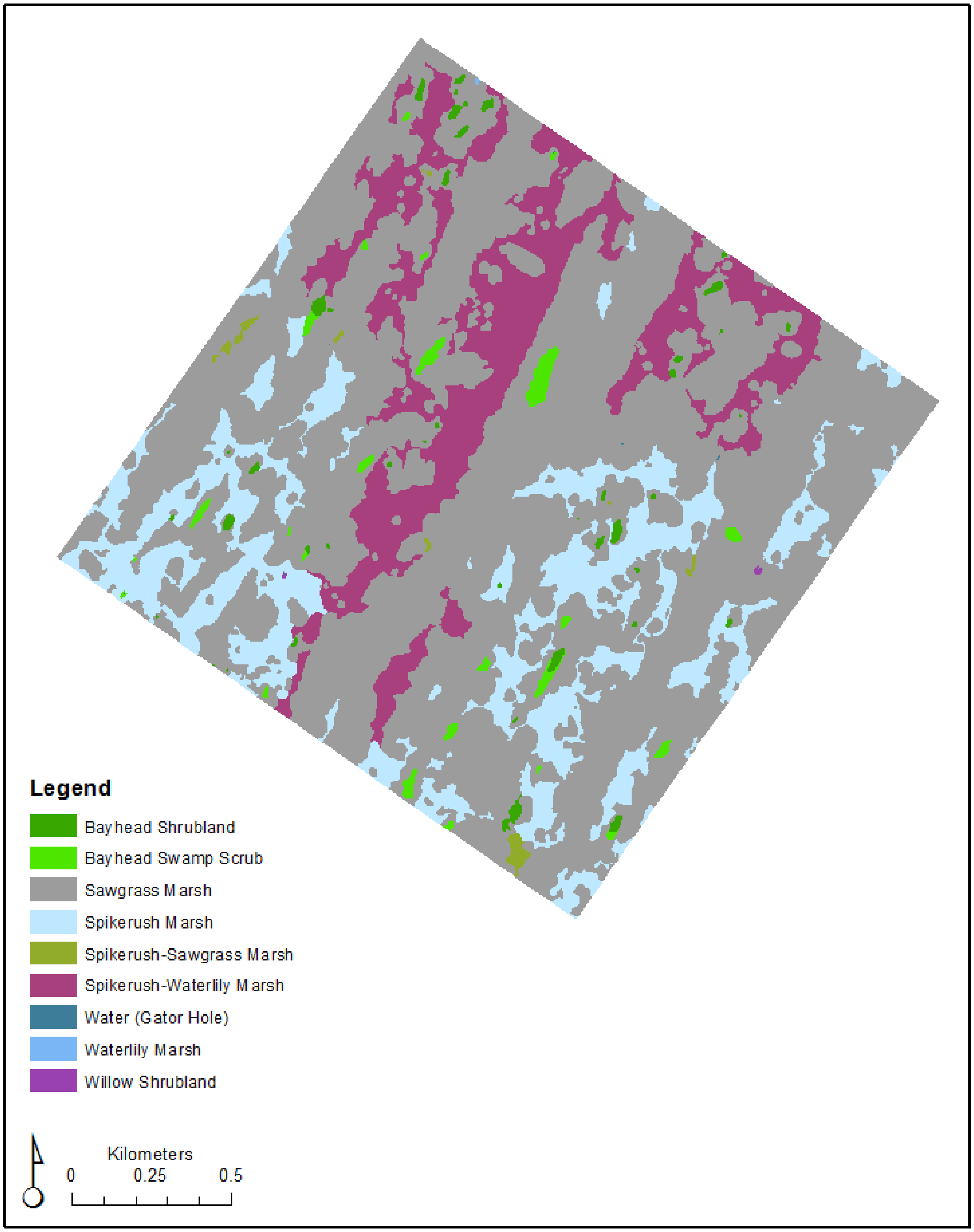

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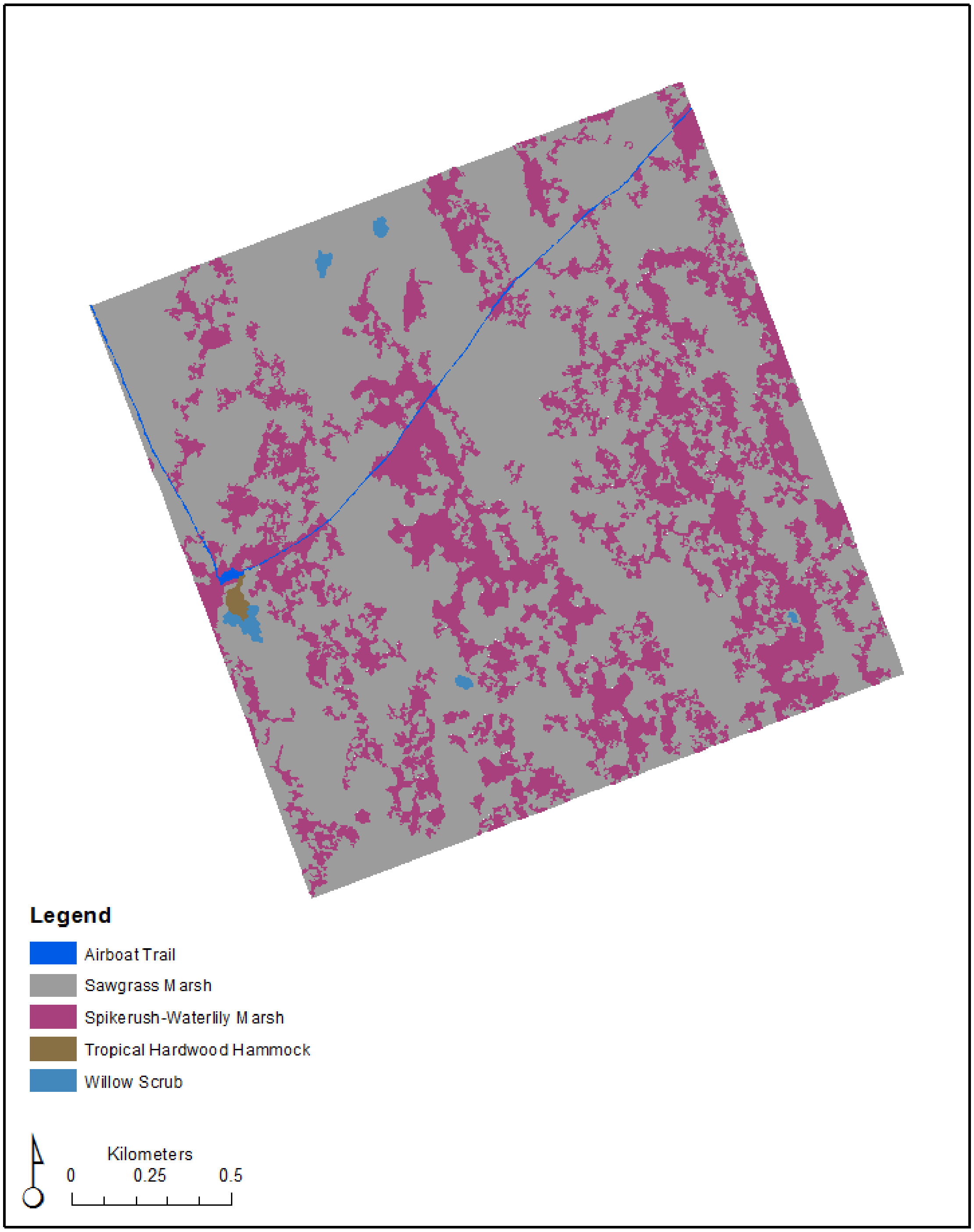

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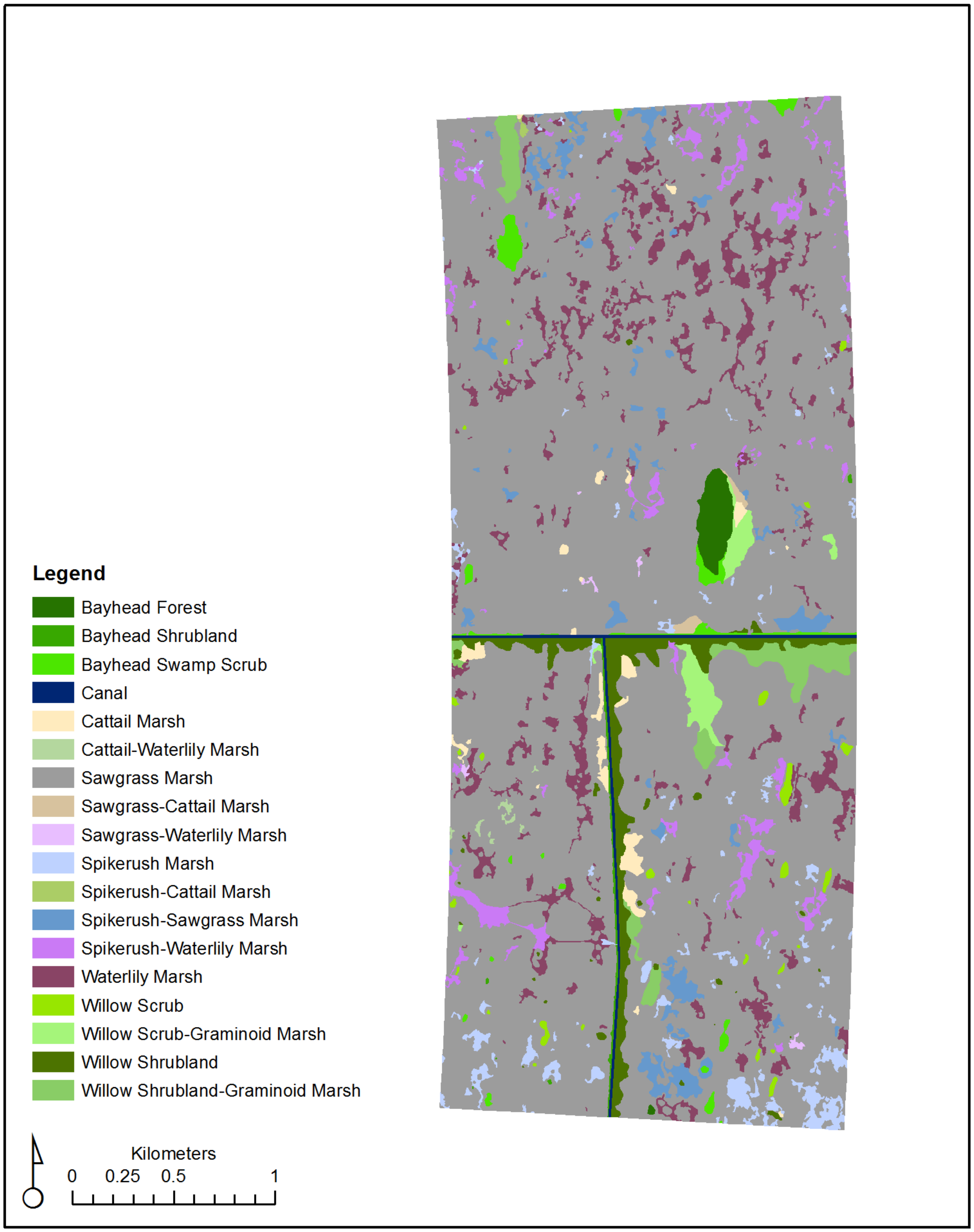

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