

DETERMINING THE EFFECTS OF FIRE ON RIDGE SHAPE COMPLEXITY IN
THE CENTRAL EVERGLADES

by

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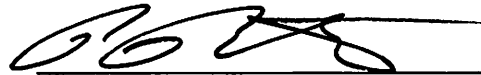
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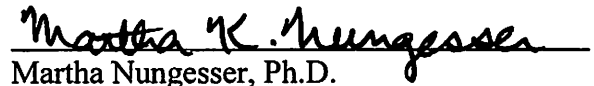
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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Brian Benscoter, Department of Biological Sciences, and has been approved by the members of his supervisory committee. It was submitted to the faculty of the Charles E. Schmidt College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

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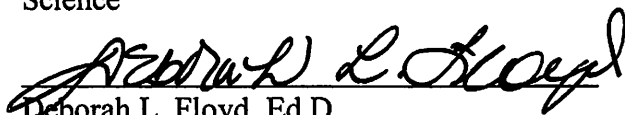
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ABSTRACT

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Self-organized spatial patterning of microtopographic features is a trademark characteristic of the Everglades landscape. Anthropogenic modifications to Everglades' hydrology have reduced and degraded pattern, where ridges occur at higher elevations and spread into open water sloughs under dryer conditions. Wildfire is an important ecological force in the central Everglades and may maintain ridge-slough patterning through reducing ridge size and complexity, and thus preserve habitat heterogeneity. To investigate fire as a patterning mechanism in the central Everglades I examined the shape complexity and area distribution of ridges along a chronosequence of time since fire. Shape complexity did not change following fire, but small and large ridges became more prominent and eventually spread as time since fire increased, suggesting fire may maintain ridge area distribution. Documentation of fires' effect on ridge size will inform ecosystem and conceptual models detailing the complex interactions that maintain the Everglades ridge-slough patterning.

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1. GENERAL INTRODUCTION

Natural landscapes often exist as complex spatial mosaics of discrete patches that occur within a larger matrix. Patches are homogenous units that are arranged in a heterogeneous spatial pattern and exhibit different biotic and abiotic characteristics such as vegetation communities, soil class and elevation, or landform type (Turner 1989). Spatial distributions of dominant vegetation communities are the most commonly observed patterns (Turner et al. 2001), and often occur as the simple patch-gap dynamics of forests or uniform arrangements of distinct geometries (Dale 2000, Rietkerk et al. 2004). Species interactions, environmental constraints, and disturbance create homogenous patches that vary over time and space in a heterogeneous pattern (Urban et al. 1987). Feedbacks created by species interactions reinforce or enhance environmental conditions, promoting the maintenance of the current patch. Patches can also inhibit the formation or maintenance of others through competitive interactions, which can give rise to spatial pattern even in the absence of environmental heterogeneity (Dale 2000, Rietkerk et al. 2004). Pattern is further shaped by disturbance, which disrupts community structure and alters the physical environment, providing the opportunity for local differentiation between patches (Levin and Paine 1974). Disturbances occur at multiple spatial and temporal scales as well as different levels of severity, creating a mosaic of different sized patches at various successional states.

Wildfire is a dominant driver of landscape pattern in multiple different ecosystems such as tallgrass prairies (Collins 1992), lodgepole pine forests (Schoennagel

et al. 2006), and boreal peatlands (Benscoter and Vitt 2008). Wildfire varies in its behavior and impact across the landscape, completely consuming some patches while leaving others intact or relatively undamaged. The resulting mosaic of undisturbed and disturbed locations produces emergent spatial patterns. Furthermore, vegetation communities among patches are left in various states of succession and regeneration (Schoennagel et al. 2006, Benscoter and Vitt 2008). Over time as communities regenerate, repeated fires continually reshape the landscape, creating a shifting mosaic of patches that maintains spatial heterogeneity.

Landscape patterning can have profound impacts on the structure and function of ecosystems (Turner 1989, Pickett and Cadenasso 1995). Processes such as primary productivity and nutrient cycling fluctuate across the different abiotic and biotic conditions created by pattern (Turner et al. 2001). For example, aboveground net primary productivity varies tremendously in the resulting spatial mosaic of stand densities created by large scale fires (Wu and Hobbs 2007). Grazing animal communities must adapt to the newly shaped landscape following large fires, further changing species abundance and diversity (Pickett and Cadenasso 1995). Disturbances themselves can also be affected by the pattern, where the connectivity of patches limits their spread and subsequent intensity (Turner et al. 2001).

Spatial configuration of patches and drivers of pattern influence the stability and resilience of an ecosystem at different scales. Perturbations to an ecosystem can cause a shift to an alternate state, often resulting in loss of or changes in ecosystem services. Landscape heterogeneity prevents shifts through providing increased ability to absorb disturbances, which often regulate the diversity and arrangement of organisms temporally

and spatially (Levin and Paine 1974, Turner et al. 1993), so that over larger and longer scales equilibrium can be observed. High ecosystem resilience is particularly evident in self-organized landscapes that arise from scale-dependent feedbacks, where local autogenic processes coupled with distal allogenic forces produce emergent regular patterns (Rietkerk and van de Koppel 2008). Microtopographic variation of organic soil is a common form of self-organization, occurring in many peatland ecosystems. Here, interactions between hydrology, plant communities, and wildfire produce a highly resilient patterned system (Eppinga et al. 2009, Cohen et al. 2011, Benschoter et al. 2015).

The Everglades Landscape

The Everglades is a subtropical peat forming wetland that once encompassed roughly 1.2 million ha of southern Florida (Davis and Ogden 1994). Much of the system is covered by self-organized patterning, which historically composed roughly 55% of the landscape's extent (McVoy et al. 2011). Deemed ridge-slough patterning, it is characterized by elevated peat ridges that are interspersed between depressed open water sloughs. Ridges are dominated by sawgrass (*Cladium jamaicense*) while open water sloughs contain floating vegetation such as water lilies (*Nymphaea odorata*; Davis and Ogden 1994). These communities are largely dependent upon different water depths as well as particular lengths of inundation that are provided by the slight differences in soil elevation (Givnish et al. 2008). Both ridges and sloughs are aligned parallel to the north-south flow throughout the landscape and have a characteristic width ranging from 50-150 m (Watts et al. 2010, Nungesser 2011). Historically, ridges and sloughs are speculated to have differed in elevation ranging from 30-60 cm (Larsen et al. 2011) or more (McVoy et al. 2011). Recent empirical studies, however, have shown the difference to be

considerably lower at 6-25 cm (Watts et al. 2010). Much of the ridge-slough landscape has become degraded as a result of extensive drainage and compartmentalization reducing water levels and hydroperiods, ultimately creating a more homogenous system (Watts et al. 2010, Nungesser 2011).

The freshwater marshes of the Everglades extend southward from the shores of Lake Okeechobee to the southern edges of the Florida peninsula. Historically, water is estimated to have moved through the system as a slow sheet flow of 4 cm/s over a gentle slope from near Lake Okeechobee toward the south/southwest coasts (Larsen et al. 2007). Although there are inputs from Lake Okeechobee during rare overflow events, the primary input of water into the system is precipitation, with most rainfall occurring during the wet season (Davis and Ogden 1994). The wet season lasts from May until October with water levels reaching their highest in October and steadily decreasing throughout the dry season to their lowest levels in April (Davis and Ogden 1994). Much of the system is inundated for large portions of the year with lower elevation areas often inundated year round (Givnish et al. 2008, Watts et al. 2010). Long periods of inundation as well as the slow flow of water through the system provide the opportunity for the deposition and accumulation of organic matter and nutrients.

History of Everglades management

Management of the Everglades has occurred throughout the past 130 years in an effort to transform the landscape, making it more suitable for human use. Reclamation of the drainage basin began in the late 1800's with canal networks already being established between the Kissimmee River, Caloosahatchee River, and Lake Okeechobee (Davis and Ogden 1994). Further canals dissecting the Everglades south of Lake Okeechobee were

constructed by 1917 (Allison 1948), and were expanded upon following extensive damage from hurricanes and flooding in the early 1900's (Davis and Ogden 1994). Over the remainder of the 20th century additional canals and levees were constructed to provide increased flood protection and allow for agricultural expansion, eventually completely compartmentalizing the Everglades landscape into the Water Conservation Areas and Everglades National Park.

Extensive modifications to the ridge-slough landscape have resulted in alterations of the Everglades natural processes. Large amounts of discharge from canals have lowered water levels across the system and amplified natural fluctuations in hydroperiod (Leach et al. 1971), producing more frequent and severe droughts as well as overall drier conditions (Bernhardt et al. 2004). As a result, much of the peat soils have become more frequently desiccated leading to soil oxidation and severe peat fires, altering the landscapes microtopography (Smith et al. 2001). Compounding implications of drainage have not only reduced the extent of ridge-slough patterning but degraded the remaining portions as well. In areas where hydroperiod has been reduced or water levels are lower, sawgrass is capable of spreading into sloughs promoting the expansion of ridges (Bernhardt et al. 2004). As sawgrass ridges expand the system is becoming increasingly homogenous, further degrading both habitat diversity and hydrology.

Mechanisms of ridge-slough patterning

The formation and maintenance of ridge-slough patterning is influenced by the interactions of plant productivity, respiration, and hydrology (SCT 2003, Larsen et al. 2011). Raised local soil elevations support sawgrass communities with greater rates of production compared to slough communities. As soil elevation increases, the respiration

of organic matter increases as well, eventually reaching equilibrium with production (Givnish et al. 2008). Conversely lower elevation sloughs exhibit lower production, but also lower respiration as a result of persistent water saturated conditions.

The feedback between respiration and production supports the existence of two stable states, but does not explain the spatial configuration of ridges and sloughs (Watts et al. 2010). As both ridges and sloughs are oriented parallel to flow, it is likely that flow is a primary factor affecting their spatial configuration and shape (SCT 2003). Water flow could maintain and shape the ridge-slough landscape through differential flow velocity and sediment entrainment (Larsen et al. 2007). Water flow velocity across the landscape fluctuates as a result of various levels of resistance of the different vegetation communities (Harvey et al. 2009). Vegetation can also remove much of the suspended particles that are transported by water flow (Saiers et al. 2003). These particles originate from high enough flow velocities causing sediment particles to become entrained within sloughs (Larsen et al. 2011). Higher velocities increase the amount of particles that are entrained, which are then deposited in downstream ridges causing them to laterally expand. As ridges expand, water flow becomes more concentrated in neighboring sloughs increasing the flow velocity and particle entrainment within them. The feedbacks between sediment entrainment and redistribution coupled with different peat accretion could give rise to the observed geometry within the ridge-slough landscape (Larsen et al. 2007, Larsen et al. 2011).

An alternate mechanism for explaining how flow maintains and shapes the ridge-slough landscape is based upon specific discharge competence, or the ability of the landscape to shed water (Cohen et al. 2011, Heffernan et al. 2013). The amount of water

discharged influences the water level and hydroperiod locally, thus influencing whether ridges or sloughs are favored (Watts et al. 2010). Increased discharge locally would result in more water being lost, potentially decreasing the water level and hydroperiods allowing for ridge expansion. As ridges expand, more water would become concentrated in the adjacent slough, thus increasing water depth and hydroperiod to the point where ridges are no longer favored.

Feedbacks between differential peat accretion, sediment entrainment, and discharge competence remain plausible mechanisms for the formation, shaping and spatial configuration of ridge-slough patterning (Larsen et al. 2011, Heffernan et al. 2013). However, uncertainties remain of how these mechanisms could influence pattern generation. The exact extent of nutrient entrainment and redistribution across the landscape, as well as how efficiently ridges and sloughs intercept natural sediment are unresolved (Larsen et al. 2011). Furthermore, uncertainties exist regarding disturbance and the role it could also play a role in the shaping of ridges and sloughs. For example, sediment entrainment could require episodic events of flooding in order to provide the velocity needed for entrainment from sloughs (Larsen et al. 2007). Disturbances may play a key role in shaping ridge-slough patterning within the post-drainage landscape.

Fire in the Everglades

Within the Everglades, fire has shaped the landscape and the plant communities for millennia (Wade et al. 1980, Lockwood et al. 2003, Duever and Roberts 2013). Fire consumes the aboveground biomass of herbaceous vegetation such as sawgrass that is able to quickly re-sprout from below ground parts, accumulating enough post-burn

biomass that is ready to burn again within a few years (Wade et al. 1980). Combustion also causes the release of essential nutrients promoting the quick regrowth of sawgrass and allowing it to maintain its dominance (Forthman 1973). Sawgrass mortality is generally low as culms are located at the soil surface, acting as wicks and protecting plant meristems (Wade et al. 1980). Culm density can be greatly reduced however if post-fire flooding occurs (Herndon et al. 1991).

Water level is a key determinant of both fire size and severity. Open water areas act as natural fire breaks preventing large homogenous fires (Lockwood et al. 2003). The severity of fires is generally low, with most only consuming above ground biomass (Davis and Ogden 1994). Under very dry conditions, however, severe fires are possible, consuming peat and significantly altering the landscape by decreasing elevation and increasing water depth (Smith et al. 2001). More severe peat fires have become increasingly common due to increased soil desiccation in the post-drainage landscape (Davis and Ogden 1994, Smith et al. 2001).

Spatial and temporal patterns of fire in the Everglades are strongly tied to hydrologic conditions. The fire regime coincides with seasonal hydrology that is evident as an annual fluctuation in both size and frequency (Davis and Ogden 1994). At the end of the dry season the most frequent and largest fires occur, as water levels are at their lowest promoting relatively dry fuels readily ignited by frequent lightning strikes during the onset of the wet season. A longer 12-14 year cycle that coincides with climatic cycles is also evident, producing larger and more frequent fires during La Niña years due to reduced rainfall and water levels (Beckage et al. 2003). Fire size ranges from a few ha to roughly 75,000 ha, with varying mean sizes between Everglades National Park and the

WCAs; however small and moderate sized fires ranging from 500 ha to 2500 ha are the most common (Davis and Ogden 1994). Thus, it is likely that small to moderate sized fires occur at a seasonal and annual frequency, while very large fires only occur roughly every 10-14 years.

Fire effects on patterning

Similar to other fire prone landscapes, fire severity and frequency differ between alternating microtopographic states (Wade et al. 1980). Low elevation sloughs are generally damp or inundated year round and contain little to no standing dead biomass as fuel, so they do not often experience combustion (Lockwood et al. 2003). Sawgrass dominated ridges however experience very frequent low severity surface fires and occasionally large severe peat fires (Wade et al. 1980). This is largely due to the pyrogenic characteristics of sawgrass, such as large amounts of intertwined standing dead biomass that is readily ignitable. Surface fires are capable of removing all standing biomass within a sawgrass stand, though it quickly regrows following fire (Wade et al. 1980). Rises in water level immediately following fire however can submerge re-growing leaves, leading to high mortality rates and reduction of culm density by up to 90% (Herndon et al. 1991). The mechanism by which submergence kills plants is not clear, although it could be linked to leaf submergence or damage to the meristem (Herndon et al. 1991). Higher severity fires can also cause widespread sawgrass mortality, as these fires consume peat surface and thus remove vegetation (Davis and Ogden 1994). Otherwise, sawgrass culms often protect the plant meristem, allowing for rapid regrowth and continued dominance.

Through the differential combustion rates of sawgrass dominated ridges and open water sloughs, fire could act a mechanism in maintaining ridge-slough patterning. As a fire consumes the aboveground biomass of ridge sawgrass, plants along the ridge margin may experience higher mortality as they experience deeper inundation in the early part of the wet season. Reductions in the ridge margin would ultimately decrease both the ridge size and shape, preventing its expansion and maintaining habitat heterogeneity.

In this thesis, I investigated the influence of fire on ridge-slough patterning within the central Everglades. To evaluate fire effects on pattern, I examined both the shape complexity and area distributions of ridges along a chronosequence of time since fire. The results of this study will provide a better understanding of the complex interactions that maintain ridge-slough patterning.

2. FIRE MAINTAINS SPATIAL COMPLEXITY OF THE CENTRAL EVERGLADES PATTERNED LANDSCAPE

Introduction

Natural landscapes often exist as spatial mosaics of vegetation communities that can occur as simple geometries in a regular pattern. These patterns arise through self-organization, where local positive feedbacks coupled with distal negative feedbacks concentrate resources or optimize feeding behaviors (Rietkerk et al. 2004). This concentration promotes high ecosystem complexity and stability, offering resilience to perturbations that would otherwise shift the system to an alternate state (Rietkerk et al. 2004, Rietkerk and van de Koppel 2008). Slight variations in organic soil elevations (i.e. microtopography) are a common form of self-organization, occurring in many subtropical and boreal peatlands (Eppinga et al. 2009, Cohen et al. 2011). Emergent differences in vegetation are produced by microtopography, which is then maintained by interactions between hydrology (Larsen et al. 2007, Eppinga et al. 2009, Cohen et al. 2011), vegetation (Givnish et al. 2008), and disturbance (Benscoter et al. 2015). Although these feedbacks maintain a highly resilient system they can be extensively altered following long term anthropogenic modifications, degrading both landscape pattern and the ecosystem services it provides.

The Everglades is a subtropical patterned peatland that once covered 12,000 km² of south Florida. A trademark characteristic of the Everglades is ridge-slough patterning, which consists of elongated, emergent ridges and open water sloughs (Davis and Ogden

1994). Current ridges and sloughs range in width from 50-150m, differing in elevation by only 6-25cm (Watts et al. 2010, Nungesser 2011). Historically, they were much higher, ranging from 33-70 cm or higher (McVoy et al. 2011). Interactions between hydrology and plant communities determine the soil elevation, maintaining the two stable states for 2700 years (Givnish et al. 2008, Bernhardt and Willard 2009, Larsen et al. 2011). Peat accretion equilibria are similar between ridges and sloughs, resulting from the differences in production and respiration rates (Watts et al. 2010). This however does not address their shape or prevalence. Both ridges and sloughs are aligned parallel to water flow, suggesting flow may exert primary control over their generation and maintenance (SCT 2003). Flow-based mechanisms likely regulate patch configuration and shape (Larsen et al. 2007, Heffernan et al. 2013); however uncertainty remains regarding the exact mechanism shaping ridges and how other allogenic forces may influence ridge-slough patterning.

Over the past century hydrology has been significantly altered to provide both flood protection and water supply to the expanding human populations adjacent to the Everglades (Davis and Ogden 1994). Extensive drainage and the construction of a system of canals and levees have effectively compartmentalized the remaining Everglades, disrupting the natural hydrology. Hydroperiods and water flow in particular have been reduced, allowing for the expansion of sawgrass (*Cladium jamaicense*) from ridge into slough (Bernhardt et al. 2004). As a result, the landscape has become increasingly homogenous as pattern is either lost or degraded into monotypic sawgrass plains of comparatively lower ecologic value (Watts et al. 2010, McVoy et al. 2011, Nungesser 2011).

While hydrology-vegetation feedbacks control the formation of microtopography, disturbances like fire may influence the distribution of features on the landscape. The Everglades fire regime is strongly linked to both hydrologic and climatic cycles, which determine the condition of fuels (Davis and Ogden 1994, Beckage et al. 2003). Fire occurs most frequently at the beginning of the wet season, where repeated lightning strikes often ignite the dry fuels following the end of the dry season. Size varies greatly depending on the connectivity of fuel, though 500-2500 ha fires are most common (Davis and Ogden 1994). The most common fuel is provided by sawgrass, the morphology of which encourages frequent low severity fires that consume its aboveground standing biomass (Wade et al. 1980, Lockwood et al. 2003). Fire induced sawgrass mortality is generally low as culms are situated at the soil surface, and act as wicks that protect the plant meristem (Wade et al. 1980). A rapid rise in water level however can submerge leaf regrowth, causing extensive mortality and reducing culm density (Herndon et al. 1991). Higher severity fires, however, are also possible during drought conditions, which consume organic soil and remove sawgrass. Peat loss is highest during summer droughts.

Fire may play a key role in preventing ridge expansion in the post-drainage Everglades landscape. Sawgrass located along the margin of a ridge may experience higher mortality following fire, as margins likely experience greater rises in water level post-fire than the core area. The resulting reduction in ridge margin would prevent the spread of ridges. In boreal peatlands, differential combustion of soil elevations acts as a key driver preventing the dominance of higher soil elevations (e.g. hummocks) across the landscape (Benscoter et al. 2015). In the Everglades fire may play a similar role through reducing both ridge size and shape complexity, thus preserving habitat heterogeneity. I

conducted a study to investigate fire as a mechanism preventing ridge expansion, utilizing a chronosequence of time since fire to investigate how fire influences ridge shape complexity and the distribution of ridge areas.

Methods

Study sites

This study was conducted in Water Conservation Area 3A (WCA-3A) within the Florida Everglades (Figure 2.1). The Everglades is a subtropical freshwater marsh that covers 7000 km² of south Florida. Precipitation is the primary input of water into the system that largely follows a seasonal pattern with most rainfall occurring during the wet season (Davis and Ogden 1994). Water flows through the system as a slow sheet flow over a north-south topographic gradient. Soils are primarily organic (85-92% organic content), increasing in mineral content to the south as peat thickness decreases (Richardson 2008). Ridge-slough patterning dominates the majority of the extent, where sawgrass ridges are interspersed between sloughs that primarily contain bladderwort (*Utricularia spp.*) and water lilies (*Nymphaea odorata*; Givnish et al. 2008). Tree islands also occur throughout the landscape, and are dominated by myrtle (*Myrica cerifera*) and dahoon holly (*Ilex cassine*). Site selection was constricted to WCA-3A as it contains the best conserved ridge-slough patterning and least modified hydrology (Watts et al. 2010).

Site selection consisted of identifying previously burned patterned areas through the use of historic fire records (courtesy of Florida Fish and Wildlife Conservation Commission). Three 1 km² study sites within the previously burned areas were selected along a chronosequence of years since fire (ysf), consisting of a 1, 5, and 10 ysf site. To avoid regional effects of hydrology and nutrient loading, sites were constrained to the

northern portion of WCA-3AS. The Everglades Depth Estimation Network (EDEN) was used to determine the average daily water depth of each site from 1992 to 2014 to evaluate any difference in hydrology between sites. The EDEN interpolates current and historical water surface and soil elevation for 400 m² cells based on a regional network of water gauges. The EDEN data indicate that hydroperiod was similar between selected sites (consistent annual inundation). A repeated measures ANOVA showed no difference in mean monthly water depth between sites ($F_{(22,726)} = .26, p=0.99$). Additionally, sites likely did not differ in nutrient loading as specific conductance only varied 60 S/ cm between sites. Sites did however vary in their pre-fire conditions within the available period of record (36 years), where the 1 ysf site burned 5 times, the 5 ysf site burned 3 times, and the 10 ysf site burned once.

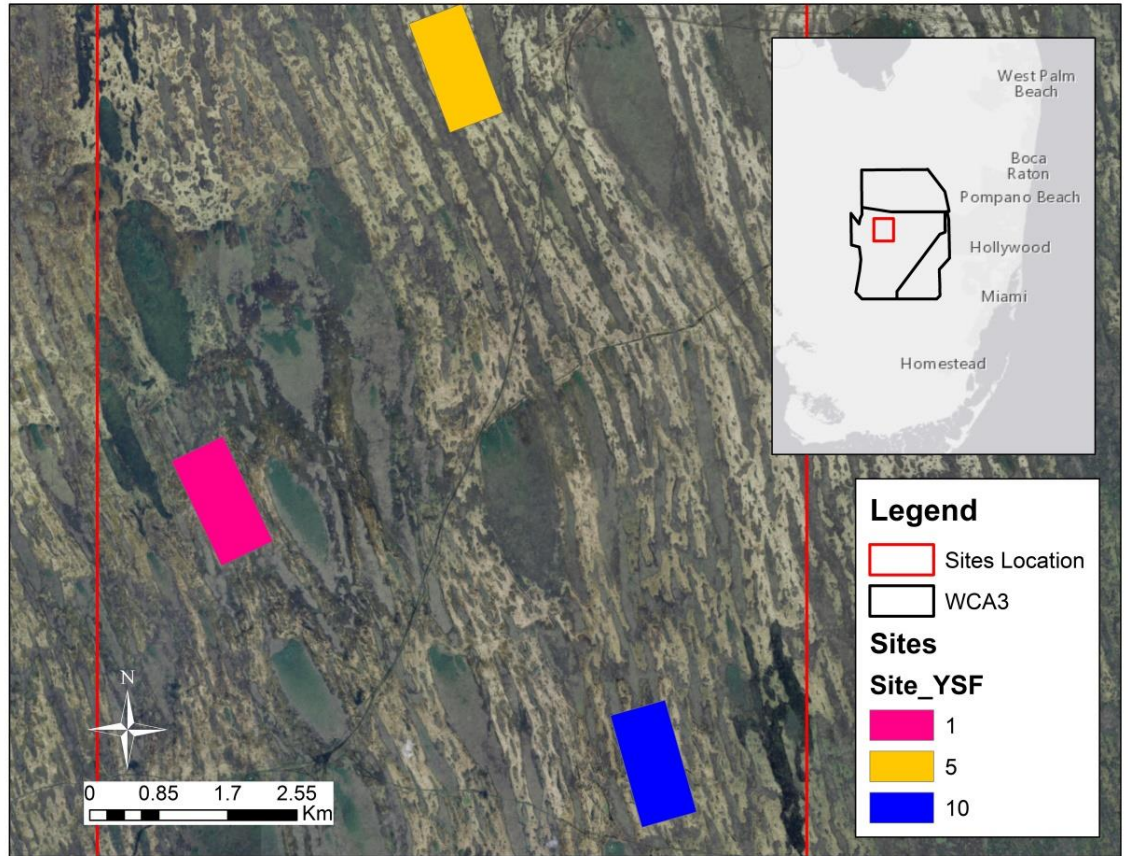


Figure 2.1: Map of study sites located within Water Conservation Area 3A south. The red box indicates the general area within WCA-3AS where study sites are located. 1 km² study sites are indicated by the pink, yellow and blue polygons (1, 5, and 10 ysf respectively).

Mapping surveys

Field surveys were conducted to determine the perimeter and area of individual ridge landforms between November 2015 and April 2016. Within each site ridges were mapped by logging their perimeter using Trimble high-accuracy GPS receivers which achieved approximately 50 cm accuracy in the field (Trimble Navigation Limited). Trimble Pathfinder Office and Trimble Positions were used to further post-process collected data, often increasing accuracy to 10-25cm. Each ridge within a site was mapped, though some ridges extended beyond the site boundaries. Boundary ridges were mapped entirely if more than half their area was within the site, otherwise only the portion within was mapped. Mapped perimeters were used to create polygons in ArcGIS that were assessed with complexity, size distribution, and landscape metrics.

Mapping criteria were established to delineate the ridge perimeter in areas where the edge was not clear. Sawgrass is the characteristic plant of ridges and acts as an indicator of ridge spread (Watts et al. 2010), thus the density and distance between sawgrass culms were used as criteria. Both criteria were determined through field measurements in WCA-3A. The density of live culms was measured in 1m² quadrats at 3m intervals along a transect spanning the lateral axis of a ridge (n= 9). Distance between culms indicated sawgrass rhizome length, which can vary from <5 to 50 cm (Brewer 1996). To confirm rhizome length, lateral expansions of sawgrass culms that followed a clearly linear pattern were measured at each ridge. Additionally, the nearest neighbor distances of culms were calculated from density measurements assuming a uniform distribution of culms/m². Using the mean culm density (10.59±1.22 culms/m²) and mean distance (42.66±2.49 cm), I established conservative criteria of 12 culms/m² and 50 cm

between culms for a plant to be included within a ridge as opposed to being treated as part of a separate ridge.

Shape Complexity

Ridge shape complexity was quantified at each site using both landscape metrics and frequency distributions. Patch level metrics used included the perimeter to area ratio, Mean Shape Index (MSI), Area-Weighted Mean Shape Index (AWMSI), Mean Patch Fractal Dimension (MPFD), and the Area-Weighted Mean Patch Fractal Dimension (AWMPFD). Patch level metrics were calculated using the following equations:

Equation 1: Mean Shape index

$$\mathbf{MSI} = \frac{\sum_{i=1}^n \left(\frac{p_i}{2\sqrt{\pi} * a_i} \right)}{N}$$

Equation 2: Area-Weighted Mean Shape Index

$$\mathbf{AWMSI} = \sum_i^n \left[\left(\frac{p_i}{2\sqrt{\pi} * a_i} \right) \left(\frac{a_i}{A} \right) \right]$$

Equation 3: Mean Patch Fractal Dimension

$$\mathbf{MPFD} = \frac{\sum_{i=1}^n \frac{2(\ln(p_i))}{\ln(a_i)}}{n_i}$$

Equation 4: Area-Weighted Mean Patch Fractal Dimension

$$\mathbf{AWMPFD} = \sum_i^n \left[\left(\frac{\sum_{i=1}^n \frac{2(\ln(p_i))}{\ln(a_i)}}{n_i} \right) \left(\frac{a_i}{A} \right) \right]$$

N is the total number of patches in the landscape

E' is the total length of perimeter (p_i) in the landscape

A is the total landscape area (m^2)

p_i is the perimeter of patch i (m)

a_i is the area of patch i (m^2)

n_i is the number of patches of patch type i

The MSI calculates patch shapes compared to a circle standard, measuring ridge complexity as departures from circular geometry. The MPFD instead measures complexity as perimeters become more plane filling, with values approaching 2 indicating highly complex and convoluted ridges. Both the MSI and MPFD were also area-weighted giving larger ridges more weight when comparing shape complexities. The landscape as a whole was assessed with the Landscape Shape Index (LSI) and Double-Log Fractal Dimension (DLFD), which are calculated as:

Equation 5: Landscape Shape Index

$$LSI = \frac{E'}{2\sqrt{\pi * A}}$$

Equation 6: Double Log Fractal Dimension

$$DLFD = \frac{2}{\left(\frac{N \sum_i^n (\ln(p_i) * \ln(a_i)) - [(\sum_i^n \ln(p_i))(\sum_i^n \ln(a_i))]}{(N \sum_i^n \ln(p_i^2)) - (\sum_i^n \ln(p_i))^2} \right)}$$

These metrics use similar techniques as their patch level counterparts, but instead compare total area to perimeter ratios. The DLFD is an alternate measure of fractal dimension that determines the complexity of the landscape as a whole by regressing the

natural log of the landscape perimeter on the natural log of the landscape area (McGarigal et al. 2002). Additionally, the shape index of individual ridges was plotted as proportional frequency distributions and compared between sites using Kolomogorov-Smirnov goodness-of-fit tests.

These common shape indices rely on a circular standard, though many ridges are actually more elliptical in shape. Thus, the Elliptical Shape Index (ESI), Area-Weighted Elliptical Shape Index (AWESI), and Elliptical Landscape Shape Index (ELSI) were created that instead use an elliptical geometric standard, and were calculated as:

Equation 7: Elliptical Shape Index

$$\mathbf{ESI} = \frac{\sum_{i=1}^n \left(\frac{p_i}{\pi(x_i + y_i)} \right)}{N}$$

Equation 8: Area-Weighted Elliptical Shape Index

$$\mathbf{AWESI} = \sum_i^n \left[\left(\frac{p_i}{\pi(x_i + y_i)} \right) \left(\frac{a_i}{A} \right) \right]$$

Equation 9: Elliptical Landscape Shape Index

$$\mathbf{ELSI} = \frac{\mathbf{E}'}{\pi(\mathbf{X} + \mathbf{Y})}$$

x_i is the primary axis of patch i (m)

y_i is the secondary axis of patch i (m)

X is the primary axis of the landscape (m)

Y is the secondary axis of the landscape (m)

Patterns in shape complexity were compared between the circular and elliptical based indices to determine if landscape geometry influenced their sensitivity. The ESI and MSI were also examined with Pearson correlation.

Area distribution

Ridge area was assessed at each site with landscape metrics and frequency distributions. Metrics used include patch frequency, mean patch area, mean patch perimeter and the total proportion of the landscape that was occupied by ridge area. Individual ridge areas were plotted as proportional frequency distributions and compared between sites using Kolomogorov-Smirnov goodness-of-fit tests. Only ridges that were mapped entirely were used in analysis, though boundary ridge fragments were included in the total ridge proportion of the landscape. Both ridge area and perimeter were \log_{10} transformed before statistical analysis. All statistical analyses were performed using SAS (version 9.3; SAS institute, Cary, NC, U.S.A.).

Results

Shape complexity varied little between sites with inconsistent patterns and minimal relative differences between metrics (Table 2.1). At the patch level, the distribution of ridge shapes only differed significantly between the 1 and 5 ysf sites ($D = 0.45$, $p < 0.0001$; Figure 2.3), where complexity was highest within the 1 ysf site ($MSI = 2.197$) and lowest at the 5 ysf site ($MSI = 1.705$). When area-weighted each site has a higher complexity than the un-weighted values, with the 5 ysf site the most complex ($AWMSI = 4.994$). At the landscape level, shape complexity did not appear to differ between sites. The LSI was slightly higher with the 5 ysf site, although the DLFD was similar between sites. Similar trends between sites were observed between sites with the

elliptical standard indices (Table 1), and the ESI and MSI were strongly correlated ($r=0.906$, $n = 156$, $p < .0001$).

Ridge area distribution varied significantly between the 1 ysf and 5 ysf sites ($D = 0.44$, $p < 0.0001$), and between the 1 ysf and the 10 ysf sites ($D = 0.42$, $p = 0.0007$; Figure 2.4). There was no significant difference in area distribution between the 5 and 10 ysf sites ($D = 0.14$, $p = 0.69$; Figure 2.4). Total ridge proportion of the landscape was highest within the 5 ysf site (46.11%) and contained the highest frequency of ridges ($n = 66$), although the mean ridge area was the smallest (Table 2.1). Conversely, the 10 ysf site contained the largest mean ridge area, but the least ridge proportion (34.93%).

Table 2.1: Landscape metrics (\pm SE) including Mean Shape Index (MSI), Area-Weighted Mean Shape Index (AWMSI), Mean Patch Fractal Dimension (MPFD), Area-Weighted Mean Patch Fractal Dimension (AWMPFD), Landscape Shape index (LSI), and Double Log Fractal Dimension (DLFD). Also included are the created indices using an elliptical standard: the Elliptical Shape Index (ESI), Area-Weighted Shape Index (AWESI), and Elliptical Landscape Shape Index (ELSI).

	1ysf	5ysf	10ysf
Patch			
Area (m²)	4992 \pm 2544	4778 \pm 3672	5384 \pm 2064
Perimeter (m)	412 \pm 113	305 \pm 156	417 \pm 115
P:A RATIO	0.34 \pm 0.05	0.58 \pm 0.07	0.63 \pm 0.09
MSI	2.20 \pm 0.10	1.71 \pm 0.08	2.00 \pm 0.11
AWMSI	3.29	4.99	3.30
MPFD	1.62 \pm 0.03	1.76 \pm 0.04	1.80 \pm 0.06
AWMPFD	1.48	1.49	1.48
Landscape			
LSI	5.23	5.69	5.30
DLFD	1.22	1.19	1.21
Proportion	42.98%	46.11%	34.93%
Elliptical			
ESI	1.75 \pm 0.06	1.43 \pm 0.03	1.50 \pm 0.05
AWESI	2.11	2.60	1.95
ELSI	5.39	5.86	5.46

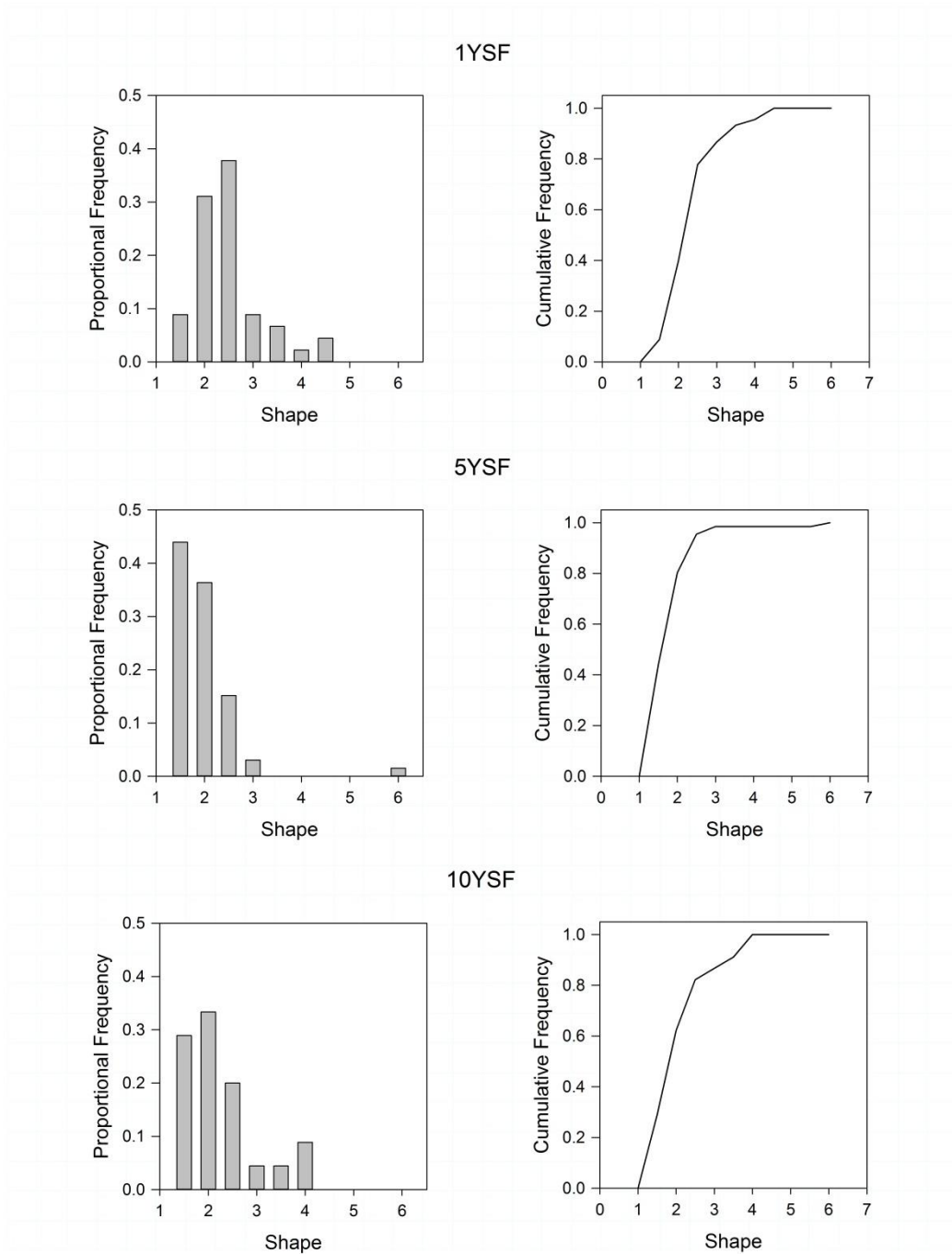


Figure 2.2: Proportional frequency (left) and cumulative frequency (right) distributions of the patch level shape index for individual ridges in the 1 ysf (top), 5 ysf (center), and 10 ysf (bottom) sites.

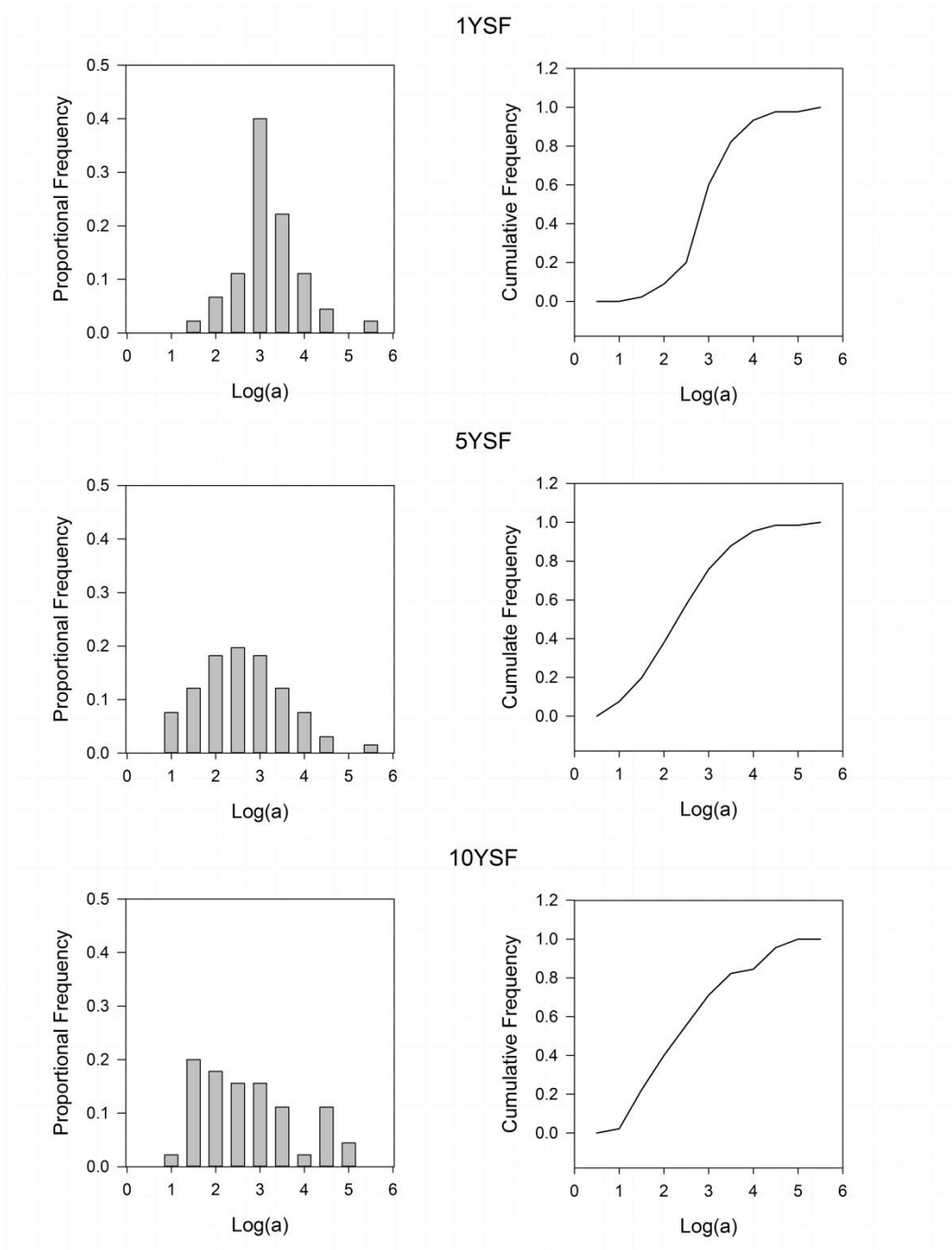


Figure 2.3: Proportional frequency (left) and cumulative frequency (right) distributions of \log_{10} transformed individual ridge area (m^2) for the 1 ysf (top), 5 ysf (center), and 10 ysf (bottom) sites.

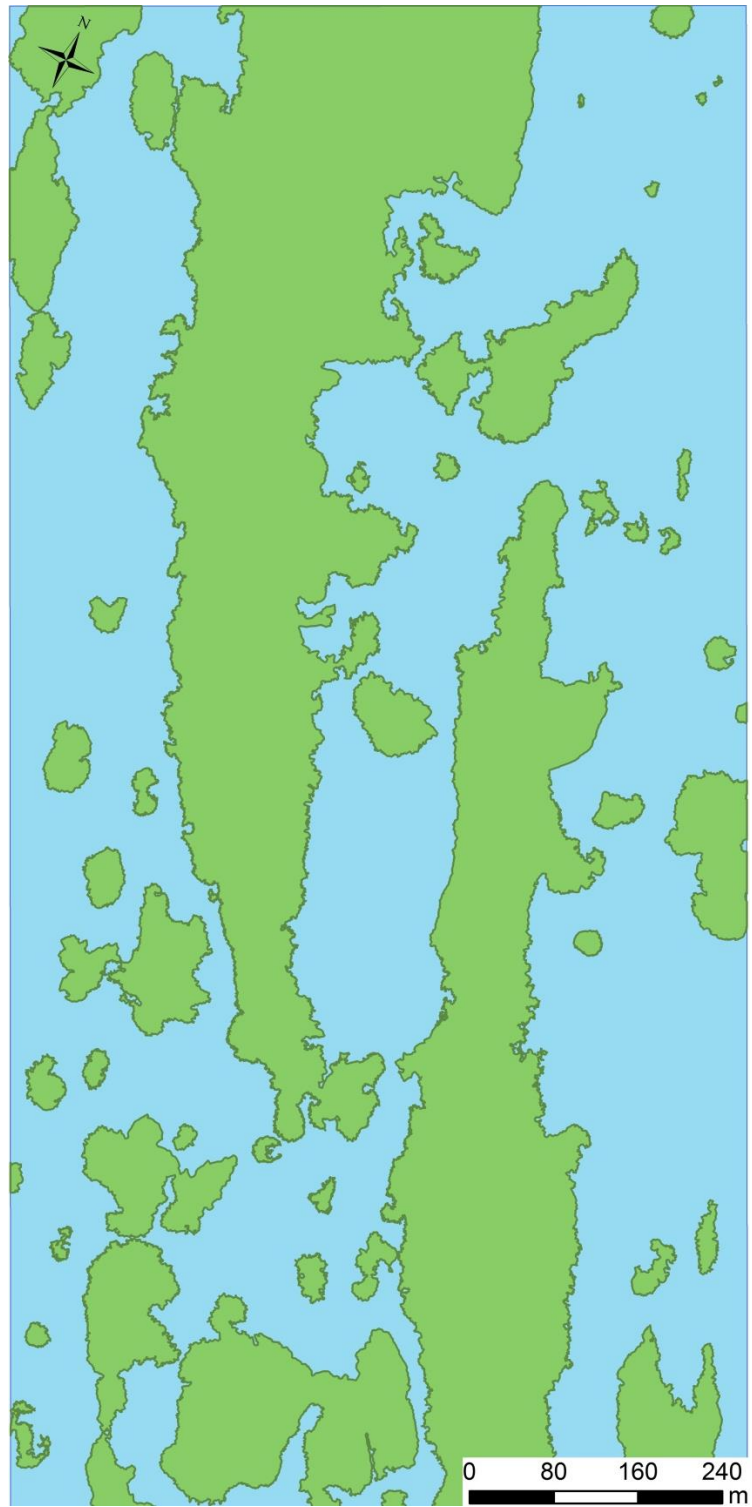


Figure 2.4: Map of completed ridge perimeters within the 1ysf site. Ridges are indicated by green and unmapped area is blue, generally indicating slough.

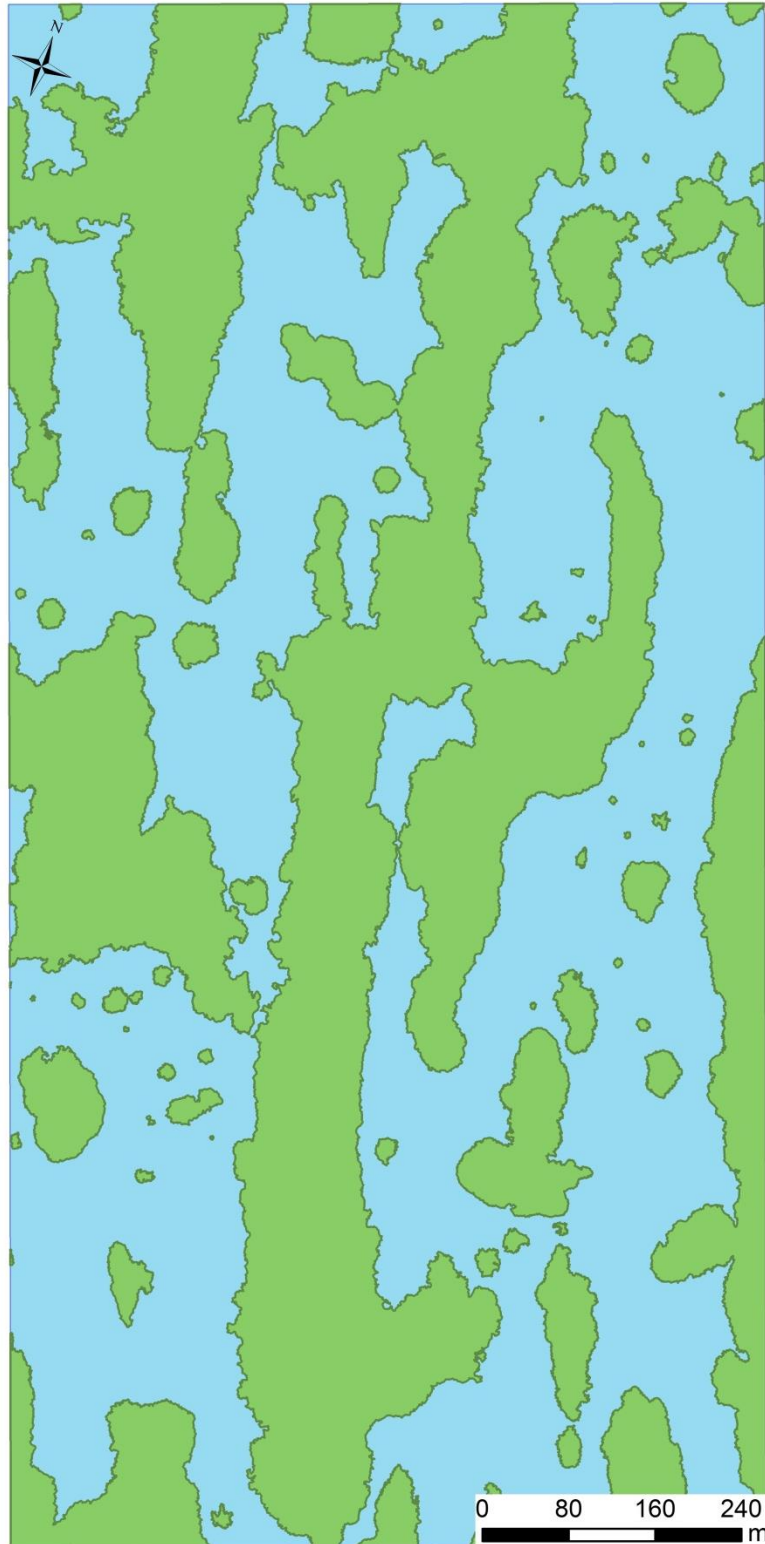


Figure 2.5: Map of completed ridge perimeters within the 5ysf site. Ridges are indicated by green and unmapped area is blue, generally indicating slough.

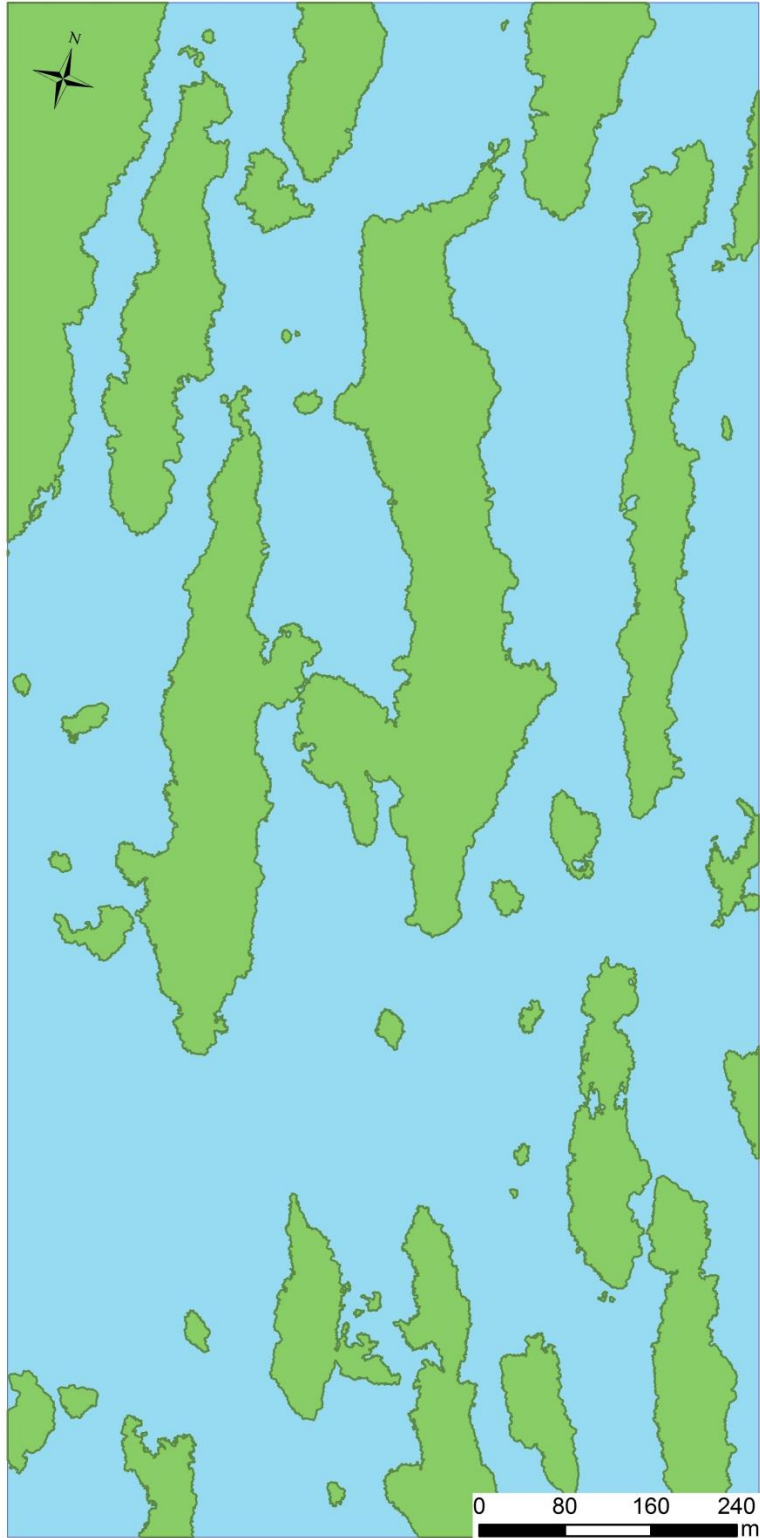


Figure 2.6: Map of completed ridge perimeters within the 10ysf site. Ridges are indicated by green and unmapped area is blue, generally indicating slough.

Discussion

While there was minimal effect of fire on ridge shape complexity, fire may play a dominant role in maintaining ridge size distribution across the ridge-slough landscape. Small ridges ($< 250 \text{ m}^2$) are mostly absent following fire, shifting the size distribution to favor both medium ($\sim 1000 \text{ m}^2$) and large ridges ($> 10,000 \text{ m}^2$). Over time as sawgrass regenerates and spreads, smaller ridges are reinitiated while medium ones increase in size, producing a more even size distribution on the landscape while reducing the coverage of sloughs. This shift occurs 5 years following fire and roughly coincides with the 3-5 year natural fire return interval of moderate sized fires in the central Everglades (Davis and Ogden 1994).

Ridges may be removed from the landscape and reduced in size through burning and reduced growth at the margins. Although sawgrass meristems are generally protected from heat exposure, an increase in water level post-fire can cause wide-spread culm mortality (Alexander 1971, Herndon et al. 1991). The most frequent and largest fires occur during the transition to the wet season, where water level can rise rapidly up to 6 cm/ day, outpacing sawgrass leaf elongation and submerging leaf regrowth (Herndon et al. 1991, Davis and Ogden 1994). Sawgrass culms along a ridge's margin would more likely be exposed to such an increase, as lateral extensions from the ridge core area are at lower soil elevations and thus deeper water depths. These marginal plants are likely younger as well, making them more vulnerable to edge effects. Similarly, smaller incipient ridges could experience flooding induced mortality as they have not persisted long enough to accumulate substantial peat elevation, and thus are more prone to rises in water level. The most recent fires in the 1 and 5 ysf sites occurred during the dry season

at either low or consistent water levels. Water conditions within these sites and the season of burning may have limited flood related mortality, although the low water level within the 1ysf site potentially promoted mortality by heat exposure. The most recent fire in the 10 ysf site, however, occurred prior to a rise in water level during the seasonal transition, so flood related mortality would be very likely. Post-fire flooding across the Everglades may remove significant amounts of marginal and incipient sawgrass culms, preventing ridge expansion.

Contrary to my initial predictions, there does not appear to be any effect of time since fire on ridge shape complexity. A lack of effect was consistent at both the patch and landscape scale, which could be explained by sawgrass' ability to rapidly regenerate following fire. Within two weeks well-established plants are able to resprout and grow 20-40 cm, potentially outpacing a rise in water level (Forthman 1973). Rapid regrowth promotes re-accumulation of biomass, reaching pre-fire levels within 1-3 years and allows sawgrass to quickly establish dominance (Loveless 1959, Steward and Ornes 1975). Furthermore, sawgrass rapidly expands horizontally through a complex network of belowground rhizomes. These vegetative propagations are sawgrass' primary form of reproduction (Alexander 1971), expanding outwardly from parent plants in all directions approximately $39 \pm 5 \text{ cm y}^{-1}$ (Benscoter unpublished data). Therefore, plants may regenerate quickly enough following fire that a discernible effect on shape complexity is not evident even within a 1 year period.

Larger ridges may diminish the sensitivity of the complexity metrics to identify distinguishable differences on the landscape. Area-weighted metrics indicate more irregular shapes than un-weighted metrics, suggesting that larger ridges are more

irregular than their smaller circular counterparts. This could be due to the circular standard of the common shape indices utilized in this study when comparing departures from common geometry for patch and landscape complexities. The greater complexity of larger ridges may be a result of their elliptical shape, which could outweigh differences detected by complexity metrics when compared to smaller, more circular ridges. Similar patterns of shape complexity between sites were observed with the elliptical standard indices and both indices were strongly correlated, suggesting that regardless of differences in geometry fire did not affect shape complexity. Metrics based on fractal dimensions, which are not dependent upon particular geometric standards, further support no difference in complexity. Thus, it is likely ridge complexity does not differ as a function of time since fire, regardless of size or geometry.

While site differences in hydrology in this study were minimal and likely had little influence on the patterns observed, hydrologic conditions vary across the Everglades both temporally and spatially. For example, drained northern portions may contain only 10 cm of standing water, while impounded southern areas can reach 60 cm or greater (Watts et al. 2010). Both hydrology and nutrient loading strongly influence vegetation and thus fire behavior through altered growth patterns or favoring invasion of fire resistant species (Davis and Ogden 1994, Givnish et al. 2008). This could potentially produce alternative results under different chronic or immediate conditions. Vast monotypic stands of sawgrass are common in shallow depths, where resources are dedicated to biomass production (Toth 1987). Larger differences and temporal variations in environmental characteristics are common and cause sawgrass to form tussocks in deep water (Toth 1987), or facilitate the invasion of fire resistant species (e.g. Cattail

Typha domingensis; Willow *Salix caroliniana*) where phosphorus levels are elevated (Davis and Ogden 1994, Newman et al. 1996). Variations these large however are generally constrained to the northern and southern extents of the Everglades where they have extensively degraded pattern.

The results obtained from this study provide a better understanding of the effects of fire on ridge-slough patterning in the central Everglades. Knowledge of mechanisms that maintain ridge size and shape are particularly crucial in understanding the post-drainage landscape. Currently, fire may not be adequately represented in conceptual and ecosystem models as there is uncertainty regarding the extent to which it can influence ridges and how the fire regime might change in a warming climate. Future studies documenting ridge expansion at a larger scale and long term monitoring of individual locations following fire will help to resolve uncertainties surrounding fire effects on ridge slough patterning. This study provides findings that ridges may be reduced in size or removed following fire, suggesting fire may play a key role in preventing ridge expansion and preserving Everglades landscape heterogeneity.

3. IMPLICATIONS FOR RIDGE-SLOUGH MANAGEMENT

Management of the Everglades ridge-slough landscape will likely be adapted to changes in a warming climate. Projections of climate scenarios vary, although most the realistic scenarios predict an overall reduction in water level (Obeysekera et al. 2015). Drier conditions will have severe ecological implications ranging from loss of pattern to peat loss and alterations to the fire regime (Nungesser et al. 2015). Land managers will need to modify fire management practices as natural fires become less frequent but more severe (Beckage et al. 2003). Further management adaptations could benefit the maintenance of ridge-slough patterning through reducing ridge extent and preventing the establishment of fire resistant species. During fire free intervals ≥ 5 years, ridges increase in extent and are invaded by fire resistant and woody species (Cattail *Typha domingensis*; Willow *Salix caroliniana*). Altering practices to maintain a fire return interval of < 5 years within currently patterned areas may reduce or prevent the expansion of ridges and the establishment of fire resistant species. A higher frequency interval would also prevent hazardous fuel loading, reducing the probability of severe peat fire events. It has been speculated that severe fires can convert ridge to slough (Craighead 1971, Larsen et al. 2011), although the subsequent nutrient release during peat fires can stimulate the spread of cattail (Wu et al. 2012). Furthermore, the release of fine particulate matter during peat fires poses a risk to human health. Current fire records indicate that prescribed burns in many areas throughout WCA-3A are conducted at intervals > 5 years. Given the adverse

effects of higher severity fires, higher frequency prescribed surface fires may be required in the ridge-slough landscape.

Future water management practices may further impact the current fire regime within the ridge-slough landscape. Restoration goals primarily focus on restoring the continuous flow and natural variations in hydroperiod (SFWMD 2012), which would help to alleviate hydrologic effects in areas that are drained or impounded. The greatest degradations of ridge-slough pattern can be observed in these areas, where changes to plant communities, fire frequencies, and the feedbacks between them are evident. Impoundments have largely been excluded from natural and prescribed fires, partially resulting in the establishment of fire resistant cattail. Here, ridge slough patterning still persists albeit in a degraded form (Watts et al. 2010). The application of a more frequent fire return interval (<5 years) may help contain ridge expansion and remove the establishment of fire resistant species. This may be especially beneficial under future water management regimes as impoundments are returned to a more natural depth. Drier regions however now lack microtopography and are dominated by sawgrass monocultures that perpetuate large homogenous wildfires. Maintenance of high fire frequency will help to reduce dangerous fuel loading, though restoration of these plains to a patterned state will likely require more than improved water and fire management practices.

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