WILDFIRE ECOLOGY OF BIG CYPRESS NATIONAL PRESERVE: PROCESS AND DISTURBANCE IN A WETLAND LANDSCAPE

By

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A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2012

To my uncle, Coach Fred Gill, the embodiment of strength and wisdom, whose advice I will always remember: “In life, we do whatever it is that we want to do;”
and to my friend and teacher, Roger, who taught me to see with the beginner’s mind

ACKNOWLEDGMENTS

No matter the amount of altruism in one's motivations, undertaking a doctoral degree involves a considerable degree of selfishness. For indulging my fixation on this goal I want to thank my great friends, especially Tim, Liz, and Adam, who have been so understanding of unreturned messages, and missed opportunities to renew our friendships: their encouragement and advice have been so important to me. I appreciate the patience of my family when I have prioritized a research trip over a visit, as well as the early example to appreciate the interesting and to do kind things.

I am grateful to all the teachers I have had, for their tireless work that I might read, add, understand, and know. This group has come to include my committee: brilliant and insightful Matt Cohen; Tim Martin, whose perspective and wisdom have inspired peace and confidence (and more than a little hard work); Todd Osborne, who has done so much to facilitate, encourage, and focus my work; my longtime mentor, Franklin Percival, who has contributed knowledge and advice—I mean, opinions—on unpredictable animals such as alligators and bureaucracies; and Jim Snyder, whose generosity in helping a new researcher in an unfamiliar place is matched only by his editorial skill. Leda Kobziar has performed remarkably in her role as committee chair, alternately (sometimes simultaneously) pulling strings, pulling reins, dreaming big, deflecting administrivia, tolerating larks, and providing many opportunities to set things on fire. Perhaps the highest compliment to her abilities as an advisor is this dissertation, if it turns out to be any good.

The work that produced this manuscript involved much sweat and insect repellent, and I would like to express my great appreciation to the people and groups who have provided assistance, advice, or labor: Nate Benson, Mike Camp, Mike Duever, Bill

Evans, Joshua McCafferty, Alex Kattan, Caroline Noble, John Nobles, Marissa Streiffel, and Justin Vogel. Funding for my research projects was provided by the Association for Fire Ecology, Joint Fire Science Program, National Park Service's Fire Ecology Program, and U.S. Geological Survey's Southeast Ecological Science Center. The Alumni of the University of Florida generously supported my education with their Alumni Fellowship during my four years, and I appreciate the help and support of the staff of the School of Natural Resources and Environment: Steve Humphrey, Cathy Ritchie, Karen Bray, and Meisha Wade.

Finally, Danielle Watts deserves the thanks that comes too infrequently for spouses of graduate students, in addition to my gratitude for her strongly interdisciplinary contributions: supportive spouse, insightful reviewer, programming tutor, and field assistant…not to mention wonderful friend and skilled collaborator.

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August 2012

Chair: Leda Kobziar
Major: Interdisciplinary Ecology

This dissertation presents a collection of studies that investigate fire's influence in a spatially patterned landscape, as well as the evidence of processes that derive from and contribute to spatial patterns of landform occurrence. In small (averaging less than five hectares) cypress swamps, wildfire was found to be a determinant of the stand structure which contributes to the swamps being commonly referred to as domes. Also, fire severity was found to be significantly lower in the centers of desiccated domes than at their edges, following a 2009 wildfire that occurred during historic drought conditions.

With landscape position and microclimate implicated as potential mechanisms behind observed differences of severity, a second study determined the existence of these edge effects on the microclimate of domes. Temperature was found to be significantly lower, and relative humidity significantly higher, in the centers of domes compared to their edges and in the sparsely-wooded upland plant communities adjacent to them. Edge effects were stronger with increasing distance, and models were developed to describe these changes in microclimate and compare the effects of inundation and wildfire. Edge effects were strongly present during the dry season, much

less discernable under inundated conditions, and remained present following a wildfire, contrary to expectations.

Smoldering combustion was investigated in the soils of cypress domes, and soil moisture was found to be a major determinant of burning on these organic soils. However, hypothesized relationships between soil physical and chemical properties and depth of burn—a commonly-used metric for ground fires—were not observed. These soils were found to sustain smoldering above 200% soil moisture, however, and observed soil moisture values observe across the landscape indicate potential consumption of large amounts of soil organic carbon during drought fires.

Finally, the occurrence of cypress domes across large areas of the study region was observed to be nonrandom. Elevations of bedrock and soil were bimodal as well. This evidence is consistent with hypothesized coupled, reciprocal ecohydrological feedbacks to the formation of depressions in limestone bedrock. Further, differences in means separations for bedrock and soil elevations suggests primary operation of biotically-mediated dissolution operating on the bedrock itself, and opposition to the “smoothing” influence of hydrologic sediment transport at the surface.

CHAPTER 1
INTRODUCTION

Fire is among the primary abiotic processes of many upland ecosystems, particularly in areas where natural ignition sources such as lightning are common phenomena. (Anthropogenic ignition sources such as those from longstanding pastoralism or swidden agriculture also are increasingly recognized as contributors to contemporary landscapes in many areas.) Globally, natural and anthropogenic wildland fires in upland ecosystems are intensively studied. Conversely, the elimination of fire from ecosystems or communities where species assemblages or interactions are adapted to the regular occurrence of this disturbance has been shown to result in significant ecological changes such as the elimination of habitat for endangered species, dramatic shifts in vegetation communities. In these fire-dependent ecosystems, the return of fire following its suppression is an important step in restoration and poses significant challenges to managers.

Across landscapes where the upland component is adapted to natural fires, the effects and ecological importance of fire in associated wetland ecosystems are relatively poorly understood. Perhaps the geographic region where fire-wetland research is best studied is the US Southeastern coastal plain, which represents a confluence of modern fire ecology and management. This region also boats many low-relief landscapes where fire-dependent upland communities occur adjacent to varied and widely occurring wetlands which have been the subject of intensive study. Limited work has occurred on the physical and chemical aspects of combustion in wetland ecosystems with peat-based soils such as pocosin ecosystems in North Carolina, where soils smolder when desiccated; chemical changes to peat soils following severe fires also have been

observed in the Everglades region of Florida. In mosaic landscapes where small and isolated wetland patches occur among a mosaic of fire-prone uplands, research on fire effects has been primarily confined to the effects of adjacent fires on water chemistry following transport of mineralized nutrients via runoff.

Effects of fire on wetland vegetation in upland-wetland landscape mosaics generally have been described in terms of qualitative terms rather than in quantitative studies. Authors such as Casey and Ewel (2006), Hermann et al. (1991), Duever (1984, 2009), describe low-intensity fire (which is generally assumed able to occur more frequently than more-severe fires) as a maintainer of peat-based depressional wetlands dominated by shrubs such as wax-myrtle (Morella cerifera, formerly Myrica cerifera) or by cypress (Taxodium distichum), which is highly resistant to fire (Oosting 1939). Fires of moderate intensity are important to the maintenance of cypress-dominated depressional wetlands (called domes), as they kill less fire-resistant hardwood species that have the potential to outcompete and eventually replace cypress in scenarios where fire is absent. This “dome cleansing” hypothesis is well established in the literature (e.g., Ewel and Mitsch 1978; Duever et al. 1984; Hamilton 1984, Casey and Ewel 1996) and empirically supported by the high survival of cypress following fires (Hare 1965). Severe fire, generally defined in these systems as fire causing widespread and considerable consumption of peat, is thought to facilitate succession toward a community composed of species more tolerant of deeper water; this successional sere is proposed as an explanation for the observation of many cypress domes with central willowhead communities (Salix spp.). Repeated severe fires and the consequent erosion of soil elevation is thought to lead to the development of open-water marshes,

as water depths and/or hydroperiods increase beyond the tolerance and germination abilities of woody species.

Fires in desiccated wetlands are well known for their effects on air quality, visibility on adjacent roadways, and resistance to suppression techniques. Like other wildland fires, burning peat and organic soils release particulate matter in a range of sizes, including significant quantities of fine particulates (known as PM 2.5, or particulate matter with diameter smaller than 2.5 μm) that irritate nasal passages and the respiratory systems of sensitive individuals. The combustion products of smoldering peat tend to be dispersed less effectively because they are not carried aloft by rising air from flaming combustion, causing impacts to ground-level air quality. The ground fires that produce these products are notoriously difficult to extinguish, often persisting for days and occasionally for months. The tendency for fog droplets to condense on airborne fine particulates compounds the hazard when smoke from ground fires accumulates along roadways, where resulting dense fog can severely limit visibility. For these reasons, fire managers understandably favor strategies that carefully avoid or aggressively suppress fires in wetlands that may ignite organic soils or peat. These strategies include choosing to burn uplands during periods when adjacent wetlands are inundated, or when soils are too wet to support combustion. Effectively, these strategies represent a policy of either fire suppression or seasonal shift in wetlands that may occasionally experience severe fires. Because of our limited understanding of fire's role in many such systems in the first place, the ecological implications of these actions are unknown.

This dissertation presents four studies that attempt to advance our understanding of fire ecology in wetlands from multiple perspectives. The first examines the effects of a 2009 wildfire on the structure of cypress wetland patches (called domes) over a two-year period, during which substantial delayed mortality due to fire was observed among trees in cypress domes. Findings from the study include measurement of the amplification of the characteristic dome-shaped profile of these landscape features. The second chapter is an examination of the change in microclimate within these shaded domes, both in comparison to the more open communities adjacent to them and with increasing distance toward their centers. Due to the seasonally fluctuating water levels in the region and the deciduous nature of pondcypress, I investigated whether hydrology or the acquisition or senescence of leaves would function as a “switch” to the attenuation of microclimate within domes. Also, locating half of the study sites within the area burned by the Deep Fire provided the opportunity to test for effects of a previous wildfire on temperature and humidity, which can drive future fire behavior and effects. One implicit question in the second study is whether fire history influences future fires.

Because wildfires enter cypress domes during dry periods and can smolder through their organic soils (referred to as muck or peat depending on the amount of fibrous content), I conducted a third study to investigate the influence of soil moisture on smoldering combustion in peat soils of pondcypress domes. While the original intention was to conduct an in situ study in which a cypress dome would be subjected to a prescribed fire during drought conditions, the occurrence of the 2011 Jarhead Fire forced this investigation to be conducted as a lab-based study using small-scale combustions and a scaling approach.

At the other end of the spatial scale, the fourth study investigates landscape pattern as evidence of biotic process operating directly on bedrock. Satellite and aerial views of Big Cypress National Preserve and adjacent regions reveal what appears to the untrained eye to be regular, non-random distribution of cypress domes. These domes, which form in depressional basins in the limestone underlying the region, are thought to be generated as a result of dissolution due to slightly acidic rainwater as well as leachates and respiration products from biotic activity of wetland communities. With assistance from several collaborators, I used imagery and measurements of soil and bedrock elevation to ask whether patterning could be due to feedback between biotic processes and geomorphology.

CHAPTER 2
FIRE REINFORCES STRUCTURE OF PONDCYPRESS (*TAXODIUM DISTICHUM* VAR. *IMBRICARIUM*) DOMES IN A WETLAND LANDSCAPE

Background

Isolated wetland communities often are situated in landscape mosaics among uplands that experience relatively frequent fire events. Such landscape mosaics of widely divergent fire frequencies occur worldwide in regions where lightning strikes provide ignition sources. Due to seasonal variations in hydrology or occasional droughts, fires occurring in the upland components of these landscapes can occasionally enter wetland ecosystems. While the fire ecology of the upland component of these landscapes (e.g., cerrado in Amazonian South America; prairies and pine savannas in North America) tends to be well studied, the effects of fire in their embedded wetlands tends to be less understood due to fire's infrequency and the difficulty of accessing and assessing fire effects in normally inundated areas.

In wetlands, fuel loading and moisture-dependent availability can result in either of two general types of fires. Surface fires move through litter, grasses and short-stature shrubs, and may occur even when soil and large-fuel moisture contents are high. Ground fires, which consume not only the latter fuels but also organic-derived soils such as peat, can occur when organic soils are sufficiently dry to support combustion. Effects from fires in wetland ecosystems include nutrient mineralization from combustion (Smith et al. 2001), changes to soil properties as a result of heating (DeBano et al. 1998), and overstory tree mortality. Ground fires, which may smolder for weeks or months, also may consume large amounts of accumulated soil organic matter (e.g., Page et al. 1997). These events may cause local hydrologic changes, such as longer hydroperiods, due to combustion losses and decreases in soil elevation.

One regionally widespread example of wetlands embedded within a frequently burned upland community is found in the southeastern U.S. Coastal Plain, where fire-adapted longleaf pine (*Pinus palustris* [Mill.]) savannas or slash pine (*P. elliottii* [Engelm.]) forests occur in close proximity to forested wetlands dominated by pondcypress (*Taxodium distichum* var. *imbricarium* [Nutt.]), baldcypress (*T. distichum* [(L.) Rich.] var. *distichum*), or hardwood angiosperms. In addition to occasional lightning strikes, the relatively frequent presence of fire in neighboring upland communities [e.g., fire-return intervals of ca. 2-10 y in pine flatwoods (Abrahamson and Hartnett 1990) or pine rocklands (Snyder et al. 1990)], presents regular ignition sources to cypress wetlands. While these communities burn less frequently than their upland neighbors, fire may be second only to hydrology in its long-term influence on species composition and structure (Duever 1984). Yet despite their proximity to fire-prone communities and the generally recognized importance of periodic fire in cypress swamps, few studies have quantified the impacts of fire in these wetlands.

Periodically inundated cypress forests accumulate organic matter in a histic epipedon ranging in depth from only a few centimeters at their edges to meters near the centers of large, long-hydroperiod swamps. The latter communities are thought to experience fires every 100 years or more (Snyder 1991) because of consistently long hydroperiods. In contrast, smaller depressional cypress wetlands—called “domes” because taller trees toward the centers cause them to appear dome-shaped from a distance (Figure 2-1)—experience far greater seasonal and interannual variability in hydroperiod. This variability, and frequent sources of ignition from surrounding fire-adapted communities, cause cypress domes to experience natural fires more frequently

than larger cypress forests such as elongated strands or long-hydroperiod sloughs (Wade et al. 1980). Regular and prolonged inundation, and surface fires at approximately decadal intervals (with soil-consuming ground fires occurring perhaps once or twice per century), are proposed mechanisms for the nearly complete dominance of cypress over potential hardwood competitors in domes (e.g., Gunderson 1977, Ewel and Mitsch 1978, Duever et al. 1984, Hamilton 1984, Ewel 1995, Casey and Ewel 2006), due to the high resistance to and resilience following fire injury in cypress (Beaven and Oosting 1939, Hare 1965), and intolerance of many potential competitors to long hydroperiods.

Cypress domes may remain dry for up to 3-6 months per year (Ewel 1995), allowing sufficient desiccation of large fuels and organic soils to support smoldering combustion. Cypress trees may respond to fire differently depending on their size, as well as due to landscape factors such as dome size and edge effect that may influence local temperature or humidity (Leopold 1933, Forman and Godron 1986, Matlack 1993), with consequences for the structure and size of cypress domes. Beyond the persistence or intrinsic importance of these features, the consequences of fire may impact the quality of ecosystem services they provide (e.g., carbon storage in organic soils, hydrologic storage, and controlled water release to underlying shallow aquifers), and their value for wildlife species. Furthermore, improving our knowledge of the persistent effects of fires on cypress swamps is important in helping to determine whether management efforts to prevent ground fires because of the persistent and hazardous smoke they produce are ecologically justified (See et al. 2007).

Following a 2009 drought-season wildfire that affected a characteristic landscape mosaic of cypress swamps among pine uplands, I assessed the effects of landscape, ecological, and edaphic factors on cypress tree survival and the resulting changes to forest structure. My objectives were to explore the effects of cypress dome characteristics on fire severity and their consequences for cypress mortality; to create a predictive model for future post-fire mortality estimation; and to explore potential feedbacks among fire, hydrology, and cypress dome structure. Because cypress domes occur as patches on the landscape, I predicted patch-size effects on severity; i.e., that measures of severity (fuel consumed, trees charred or killed) would be lower in the centers of domes than at the edges, that severities would be lower for larger domes, and that the magnitude of difference in severity would be greater for larger domes than for smaller domes. I also predicted an edge effect on mortality within domes: decreasing mortality with increasing distance from edges toward dome centers. I hypothesized that modeling of mortality would reveal the mechanisms of this predicted differential mortality to be related to increasing tree size and soil depth, and decreasing soil elevation, found at dome centers compared to their edges.

Methods

Study Area

Big Cypress National Preserve occupies 300,000 ha of pine uplands, mesic hardwood forests (called hammocks), prairies, and open or pondcypress-dominated forested wetlands in southern Florida (Figure 2-2). The latter occur as elongated and irregularly shaped forests called sloughs or strands with long hydroperiods, or as circular or teardrop-shaped patches (called domes) in shallow depressions in the underlying limestone. Regular spacing among adjacent domes (Figure 2-3) allows

surrounding upland communities, frequently pinelands, to become potential sources of ignition under conditions when fuels in these frequently inundated areas are available.

Ignited by lightning on 22 April and contained on 11 May 2009, the Deep Fire burned over 12,000 ha in the northwestern area of the Preserve under severe drought conditions. The area of the burn is characterized by low elevation and low topographic relief typical of southern Florida karstic geomorphology. Major vegetation communities comprise a mosaic of uplands and wetlands: south Florida slash pine (Pinus elliottii var. densa [Little and Dorman]) forests, prairies dominated by muhly grass (Muhlenbergia capillaris [Lam.]) or sawgrass (Cladium jamaicense [Crantz]), and infrequently flooded hammocks of dense hardwoods and palm (Sabal palmetto [Walter]) alternate with open-water marshes, cypress domes, and strands. Extreme drought conditions at the time of the fire allowed the fire to burn through nearly all wetlands in the region, and in many areas the organic soil was sufficiently desiccated to ignite. Although a lack of pre-fire soil data prevented an examination of the amount of soil combustion that occurred during the resulting ground fires, evidence of combustion extending 10-20 cm below the presumed level of pre-fire soil surfaces was observed in many locations.

Weather data collected by a local Remote Automated Weather Station (RAWS) located approximately 15 km from the study location indicated that during the five days when the study region burned (24–28 April), maximum daily temperatures ranged from 29.4 to 35.6˚C. Winds from the east or east-northeast reached maximum speeds of 32–38 km/h, and average relative humidity values during daylight hours ranged from 40–61%. Onsite observations by firefighting crews indicated relative humidity readings at or below 40% during afternoon hours of each day and relatively light winds (mean daytime

speeds of 8 km/h), conditions favorable for the development of smoldering combustion in desiccated organic soils.

Data Collection

From approximately 90 roughly circular cypress domes identified in the Deep Fire perimeter from satellite imagery, I selected a random sample of 25 domes in which to measure fire severity and cypress response to fire. Remote measurements of dome diameter along north-south and east-west axes of each circular dome, using 2.5 m resolution images from SPOT (Satellite Pour l'Observation de la Terre), were used to estimate area of each dome, and subsequently verified by perimeter circumnavigation of a subset of the domes using Wide Area Augmentation System (WAAS) enabled GPS. Sizes of these domes estimated from satellite imagery ranged from 0.2 ha to 3.4 ha, with a mean of 1.2 ha. During June 2009 I tagged each tree ≥ 2 m in height or with diameter at breast height (dbh) ≥ 2 cm within a randomly oriented strip plot 2 m wide running from the edge to the center of each dome. For each tree (n = 423) I recorded distance from dome edge in 5-m increments; height, using a laser hypsometer; diameter (at breast height, or above buttress swelling or flutes if present); presence of epicormic or basal sprouting; maximum height of charring on tree boles; and the number, height, and cumulative circumference of scorched areas on cypress boles due to epiphytic bromeliads consumed in the fire. For each tree I also recorded status, i.e., living or apparently killed by fire. Cypress trees observed within the fire perimeter that had obviously died prior to 2009 but remained standing experienced far greater consumption than those which remained alive; it was on the basis of these observations that I made determinations of fire-caused mortality.

To estimate fire severity within each cypress dome I assessed changes in five strata of fuels (surface fuels; vegetation <1 m in height; shrubs and trees 1–5 m in height; subcanopy trees; and canopy trees) and calculated index scores of 0 (unburned) to 3.0 (high severity; all fuels completely consumed) based on estimates of canopy scorch, amount and height of char on stems, and change in fuel loads for various fuel classes (i.e., soils, 1-hr fuels, 10-hr fuels, 100-hr fuels, etc.). The ability to estimate consumption of soils was limited by rainfall and landscape inundation that occurred subsequent to the fire. This ground-based index assessment for fire severity closely follows ground-truthing methods for large-scale fire severity assessment in the widely used Composite Burn Index (CBI, Key and Benson 2006) method (e.g., Picotte and Robertson 2011). Advantages of this method include the integration of fire effects among soil, groundcover, and mid- and upper-story vegetation; use of CBI methods also allow findings to be meaningful in the context of future assessments of wildfire severity using remote methods. One departure of my methods was to use 10 m x 10 m plots, smaller than the 30 m x 30 m plots normally used in the CBI method to correspond to LANDSAT imagery pixels. This difference was necessary to avoid plot overlap in the smallest domes, and to allow me to make comparisons of fire severity at the edges and centers of domes of varying sizes. These plots were located at either end of the mortality-assessment strip plots (i.e., one at the center of each of the 25 cypress domes and one near the edge), to allow us to relate severity assessments with mortality, edaphic, and hydrologic measurements.

In May-June 2010, I revisited the domes to assess delayed mortality among cypress, indicated by a lack of new growth to replace leaves lost by this deciduous

species during the intervening winter dry season. During this survey I collected information on soil depth to bedrock at three locations around the base of each tree using a steel probe; high water levels at the time of sampling also enabled the estimate of mean local soil elevation using water depth measurements adjacent to each tree benchmarked to elevation and hydrographic data from a nearby Everglades Depth Estimation Network (EDEN, Telis 2006) monitoring station.

Data Analyses

I compared severity measurements at dome-edge and dome-center locations using Wilcoxon's signed-rank test for equality of means (Dalgaard 2008), and among domes of different sizes using Wilcoxon's test and ANOVA, to determine whether dome size or location within dome with respect to edge (i.e., distance from edge) affected the severity of this drought fire in cypress domes and the degree to which severity affected tree survival. These comparisons were performed separately for overall severity values, as well as for understory strata scores (i.e., the average of scores for substrates and vegetation less than 1m in height) and overstory strata scores (i.e., average of those for tall shrubs and intermediate and canopy trees). Regression analyses were performed to determine whether dome radius, tree height or diameter, or tree density predicted either severity values for dome centers or the difference between severity values at dome edges compared to centers; models were compared using Aikake's corrected information criterion (AIC-c). The influence of environmental (fire severity scores, dome size, distance from edge, soil depth, soil elevation, tree density within plots) and tree (height, diameter at breast height) characteristics, on probability of survival were analyzed using logistic regression, which is commonly employed to assess tree mortality drivers (Kobziar et al. 2006). Logistic regression equations take the form

$$P_m = (1 + e^{[-(\beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n)]})^{-1} \quad 2\text{-}1$$

with P_m the probability of mortality; X_1, X_2, ... X_n independent predictor variables; and β_1, β_2, ... β_n are coefficients estimated from mortality data. This equation is used to generate maximum-likelihood estimators for logit-transformed mortality data (Sokol and Rolfe 1995). Analyses were performed using the software package R (R Development Core Team 2005); models were compared using Aikake's information criterion (AIC; Crawley 2007) and Receiver Operating Characteristic (ROC) values (Hanley and McNeil 1982). While AIC is widely accepted as an indicator of the goodness of model fit, ROC curve analysis assesses the ability of a model to correctly predict the outcome as opposed to generating false positive (Type I error) and is frequently used in evaluating fire-mortality models (Saveland and Neuenschwander 1990, Kobziar et al. 2006, Sah et al. 2010). ROC values of 0.5 indicate that a model's predictions are no better than a chance-occurrence prediction, while perfect predictive ability of a model results in a value of 1.0. Hosmer and Lemeshow (2000) argue that values 0.70 or higher indicate good model discrimination. In addition to regression analyses to detect the influence of ecological or edaphic factors on tree mortality, I also examined influence of dome size and edge effect on tree survival and community structure using Wilcoxon's signed-rank test. For the former, I performed linear regressions on changes in average size of living (or surviving) trees against dome size; I also performed Wilcoxon's signed-rank tests on tree sizes and post-fire size changes for three size stratifications (<0.5 ha, 0.6–1.0 ha, >1.1 ha) of cypress domes. To assess post-fire changes to pondcypress community structure in domes, I compared the sizes (heights and diameters) of cypress trees presumed to be alive prior to the fire with trees surviving one year beyond the fire.

Results

Fire Severity and Initial Effects on Pondcypress

The 423 pondcypress trees tagged were 2.0 to 19.0 m in height (mean 8.9 m); diameters ranged from 1.5 cm dbh to 81.0 cm dbh (mean 16.9 cm). All trees had at least one additional charred area on the bole resulting from burned bromeliads. Two of the trees surveyed during the initial 2 mo following the fire did not display new growth, indicating a 0.5% initial post-fire mortality rate.

Mean values for severity assessments among the 50 plots in which we conducted severity assessments ranged from 0 (nearly unaffected) to 3.0 (high severity; i.e., substantial consumption of fuels, considerable loss of branches, and charring of tree trunks to heights of several meters). Most plots displayed moderate or moderate-high fire severity among understory strata (>40% consumption of light and medium fuels, >50% mortality among understory herbaceous and woody plants) and low-moderate to moderate severity among overstory fuel strata (i.e., cypress trees; <50% incidence of torching, <50% canopy mortality; char heights <4 m on canopy trees). Severity values measured at dome edges were significantly higher than those in dome centers, for both the understory strata ($P < 0.05$) and all strata combined (i.e., overall severity score; $P < 0.01$; Figure 2-4).

There was no significant correlation between dome size and the severity scores we recorded at dome edges or centers, neither in overall measures nor among individual fuel classes. Also, the edge-to-center difference between severity values was not correlated with dome size. Comparisons using AIC-c scores of models incorporating combinations of dome size, tree height, tree diameter, and tree density indicated that

addition of these additional variables did not improve upon the simple linear regression model using dome size alone.

Delayed Mortality

Follow-up census in 2010 revealed that an additional 98 of 417 trees censused (23.5%, excluding three trees which could not be re-identified due to missing tags) had died. Among the 25 domes, this delayed mortality ranged from 0 to 66.7%. There were no correlations or predictive relationships between dome size, tree density, or overall severity scores for domes and the percent tree mortality in a given dome one year following the Deep Fire. However, a difference was noted in the mean severity scores for overstory strata in dome centers between surviving trees and those that died in 2009-2010 (1.3 vs 1.5, $P < 0.05$). Logistic regression analyses indicated that tree size and soil surface elevation at the location of a particular tree were the strongest predictors of mortality. Including tree diameter in regression models, rather than tree height, achieved better model performance measured by both AIC scores and ROC values (Table 2-1, Figure 2-5).

Structural Changes

Compared with trees that resprouted immediately following the Deep Fire, those which succumbed during 2009–2010 were shorter (mean height 7.7 vs 9.3 m, $P < 0.01$) and smaller in diameter (mean DBH 12.1 vs 18.6 cm, $P < 0.001$). Additionally, some 10% of surviving trees experienced topkill, i.e., regrowth only occurred via epicormic or basal sprouting. Topkill was negatively correlated with tree size, occurring predominantly in trees shorter than 3 m and rarely in trees exceeding 4 m. As a result of the effective decrease in height due to topkill, mean height of surviving trees were significantly shorter ($P < 0.001$) than mean heights of trees prior to the fire. Neither

regressions on dome size nor Wilcoxon's rank tests performed on three size-class groups of domes (<0.5 ha, 0.6–1.0 ha, >1.1 ha) indicated any effect of dome size on the changes observed in pre-fire versus post-fire mean height.

Trees which I estimated to have been alive just prior to the Deep Fire were larger in the centers of domes than at their edges; this trend also was observed among trees surviving the fire. Linear regressions were performed on tree heights from dome edges to centers, using both pre-fire heights and those of live trees one year following the fire. One year after the fire, regression coefficients for edge distance were nearly twice those for pre-fire heights (Table 2-2). Differential mortality according to size, and heterogeneous size distribution of trees within the dome, produced differences in fire effects on structure depending on the position within the dome. Mean heights of surviving trees were lower compared to pre-fire heights near dome edges, while those closer to the centers of most cypress domes increased (Figure 2-6).

Discussion

Dome Size, Severity, and Pondcypress Mortality

Contrary to expectations, there did not appear to be a noticeable attenuation of fire severity in larger cypress domes compared to smaller domes. A lack of dome-size effect on cypress mortality reinforces this conclusion. Although data on background mortality are not available (i.e., proportion of trees tagged that might have been dead prior to the fire), the occurrence of only two dead cypress trees among the initial 423 stems tagged immediately following the fire suggests that this rate is low. Our findings lead to the question of whether cypress domes in this region are too small for any size-related effects on fire severity to emerge. Another possibility is that in the case of long or persistent drought events, differences in microclimate between small cypress domes

and large ones are not sufficiently great to result in differential fire severity. However, important differences were evidenced in association with location within the domes. Severity was higher at dome edges than in the centers of domes, suggesting that location within the dome corresponded to differences in fuel availability, microclimate, and perhaps tree resistance.

While dome size appears not to make a difference in terms of fire effects in these isolated forested wetlands, tree size does matter: taller trees, or those with larger diameters, displayed greater survival in the Deep Fire regardless of their location in the dome or the depth of soil in which they occurred. While neither soil depth nor edge distance was correlated with severity or mortality, trees were larger in areas with deeper soil and toward the centers of domes. The tendency of larger trees to better survive fire is unsurprising because of the tendency of larger trees to possess thicker bark, shown to be protective against mortality from fire in several tree species (e.g., Ryan and Reinhardt 1988, Hengst et al. 1994). This result also may be due to the greater distance between the canopies of larger trees and the surface fire, limiting canopy scorch or foliage consumption during the burn.

Local soil elevation appeared to play about as great a role in determining cypress survival as did tree size. Trees occurring in areas with slightly lower soil elevations (as little as a few cm) were more likely to die in the year following the Deep Fire. While soil elevations tend to be lower (and thus hydroperiods longer) as one proceeds toward dome centers (MacPherson 1974), sufficient microtopographic variation appears to exist in these sites to allow variables associated with soil elevation to predict mortality while edge distance does not. One possible mechanism behind this observation may relate to

cypress rooting in organic soil. Total soil depth increases from dome edges towards centers, as does the thickness of the uppermost organic layer. While quite thin at edges, peat deposits may be a meter thick close to the center of a cypress dome; because anoxic conditions limit rooting depth of cypress, a large proportion of cypress roots will be found in the organic soil layer near the centers of domes that at their edges. Fires that occur under drought conditions and result in soil combustion (such as the Deep Fire) will cause damage to a greater proportion of roots in these deep organic soils than nearer the edge, where cypress rooted in sandy marl soils underlying the thinner organic layer will be better protected from combustion and heating. Longer hydroperiods found at lower elevations, usually no threat to mature cypress trees, may represent an additional stress to trees whose roots have been damaged by fire. Increases in hydrologic stress from flooding among root-damaged trees may be greater towards dome centers due to their increased hydroperiods and greater likelihood of experiencing damage from soil combustion. Allocation of stored energy reserves to the production of new leaves shortly following the fire may have prevented damaged trees from repairing damaged roots, perhaps contributing to the delayed mortality response seen here.

Why a substantial number of trees were able to recover foliage lost to the fire, only to succumb during the subsequent period of senescence (corresponding to the dry season, which in 2009-2010 was unusually wet), is unclear. The considerable proportion of tree mortality that occurred only after a season's growth following the fire may be due to the interaction of a number of factors. Explanations that invoke cambial or root damage do not seem to account for the months-long period during which these

trees held foliage and appeared to be recovering; also, no noteworthy instances of insect damage or disease to these trees were recorded in the initial post-fire survey, during the 2010 census, or through observations of unburned domes in the area. It may be that the initial post-fire foliage flush represented a stress response, and, after consuming crucial carbohydrate reserves during the dry season, trees succumbed to their fire-induced injuries in the cambium, fine root systems, or both. Delayed mortality following fire has been observed in pines (Thies et al. 2008) and in related baldcypress (Taxodium distichum var. distichum) following hurricanes (Keeland and Gorham 2009), with similar mechanisms proposed to account for tree death up to several years following disturbance. Trees in this study that died in the year following the Deep Fire were associated with higher overstory severity values in the centers of domes in which they occurred, indicating that a combination of bole damage and stress from canopy scorch at least partly explain the delayed mortality.

Two additional factors are likely to predict fire-caused mortality of pond cypress. First, the consumption of duff (decomposing litter), and associated fine roots, has been shown to be a determinant of mortality among longleaf pine (Pinus palustris) in fire-suppressed forests (Varner 2007, 2009); consumption of duff and upper-horizon sapric material is probably also a predictor of mortality (along with organic soil consumption) in desiccated cypress domes. However, the inability to accurately estimate soil and duff consumption due to a lack of pre-fire estimates of soil elevation or duff thickness, precluded use of this parameter in my analysis. Crown scorch and consumption, typically useful in predictions of fire-caused mortality among Western US conifers (Ryan and Amman 1994) as well as those in the southeastern US (e.g., Varner et al. 2007),

could not be accurately assessed in this study because the flush of cypress regrowth began to obscure crown scorch and consumption soon after the fire.

Fire Maintenance of Dome Structure via Topkill

One of the most compelling results of this study concerns the role of fire in reinforcing dome structure within the wetland landscape. The 10% of trees whose stems were killed, and which resprouted from basal or epicormic shoots, represent a commonly observed morphological characteristic of pondcypress known locally as "hatrack cypress" or "bonsai cypress." This topkill resulted in changes to the mean heights of surviving trees. I observed a significant relationship between pre-fire tree size and edge distance, with larger trees occurring further toward the centers of cypress domes. This finding is not new and has been discussed elsewhere (e.g., Mitsch and Ewel 1979, Ewel and Wickenheiser 1988), as have the proposed mechanisms underlying it such as longer hydroperiods, deeper soils, and increased nutrient availability (Coultas and Duever 1984).

Fire has been invoked as a factor in shaping cypress dome development as well (Kurz and Wagner 1953, Taylor and Rochefort 1981, Duever et al. 1984), based on the observation that small trees are more susceptible to mortality and topkill than large trees. However, this relationship has never been documented adequately. In this study, I observed a stronger relationship between tree size and edge distance following the fire than existed prior to the Deep Fire. These effects are illustrated in the mean heights of trees found at 5-m increments along our plots, proceeding from dome edges to their centers. The scatterplots of both values recall the characteristic profile that lends the cypress dome its local name, but the changes caused by fire to live tree heights changes according to distance. Towards the edges of domes, the trees are more

susceptible to topkill, and the mean heights of live trees are reduced one year following fire. At distances that correspond to the centers of medium- to large-sized domes, tree sizes are larger after the fire. Perhaps owing to deeper and more damage-resistant root systems or thicker bark among the tallest dome-center trees, smaller trees are more likely to be eliminated far from the edges of domes. This phenomenon results in an increase in the mean heights of surviving trees at distances of about 60–100 m from dome edges. Thus, while hydrology and nutrients may initiate the structural differences among trees in these isolated forested wetlands, these observations quantify for the first time the important role of fire in reinforcing the vegetation structure of these landscape features.

Figure 2-1. This circular cypress swamp approximately 2 ha in area displays the dome-shaped profile that lends these common landscape features their name. Pondcypress trees (*Taxodium distichum* var. *imbricarium*) in dome centers may reach heights of 20 m or more in soils a few meters deep; those toward the edge are far shorter due to thin soils and the influence of fire. Light-colored areas at periphery of dome are periphyton and marl; the surrounding forest is pine rockland with canopy of South Florida slash pine (*Pinus eliottii* var. *densa*).

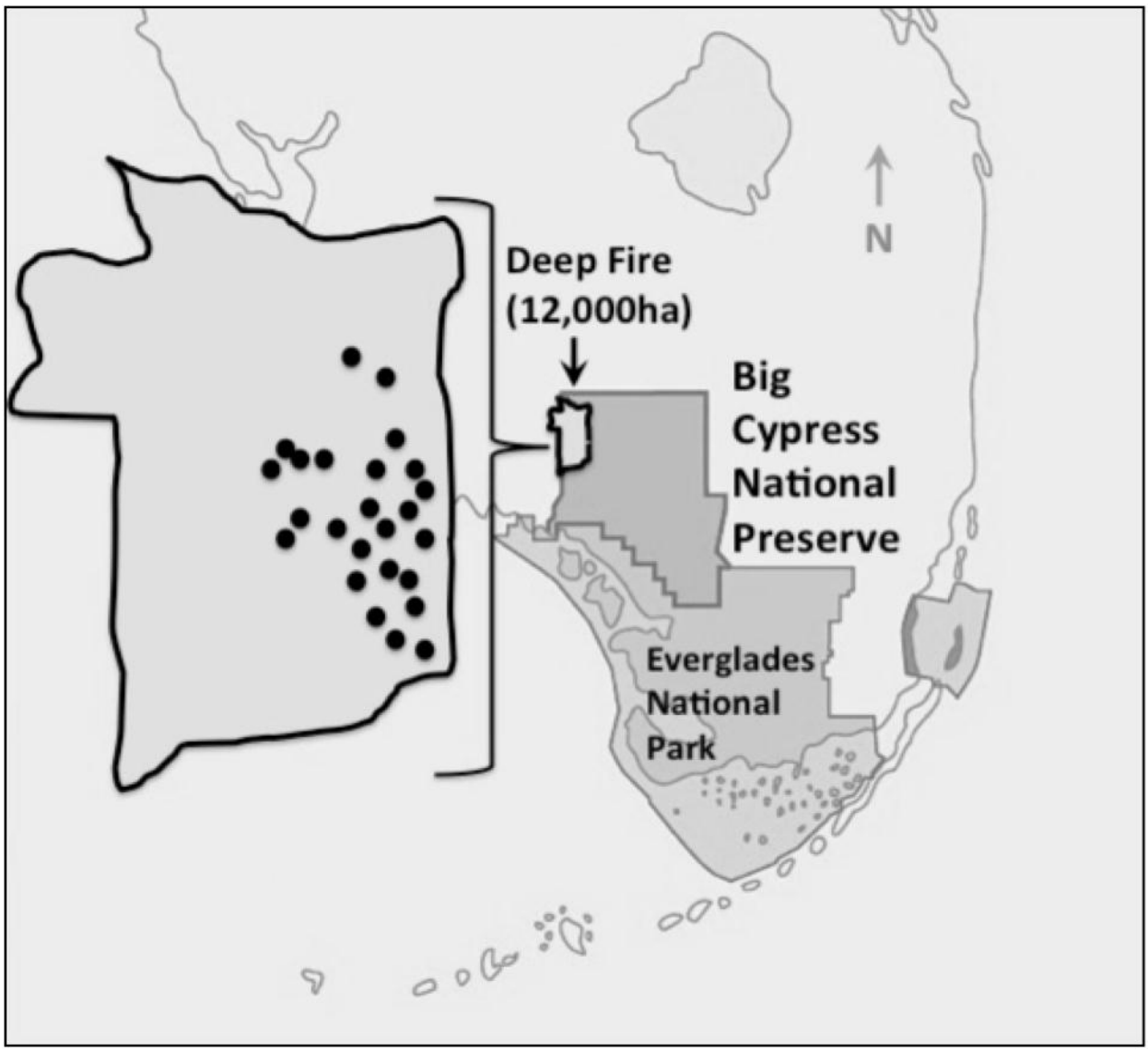

Figure 2-2. Big Cypress National Preserve, some 300,000 ha in area, is continuous with Everglades National Park in southern Florida. The Preserve was the site of the 12,000 ha Deep Fire in 2009; approximate locations of cypress domes in which sampling took place (n=25; inset) are shown here.

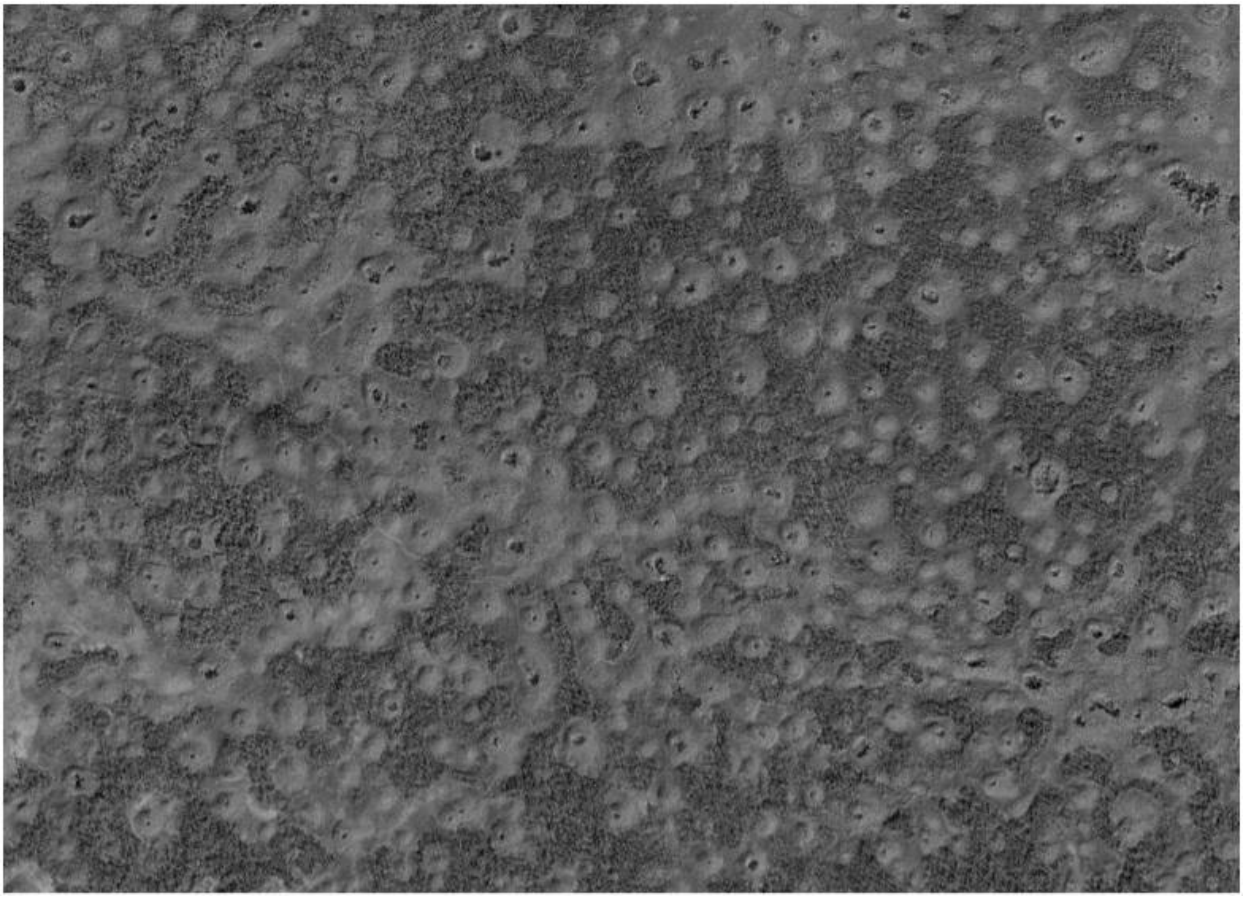

Figure 2-3. Rounded or circular cypress domes occur regularly among fire-prone pine forests in Big Cypress National Preserve. This representative satellite image of a 1200-ha portion of the Preserve illustrates the marshes (dark spots) found at the center of some domes.

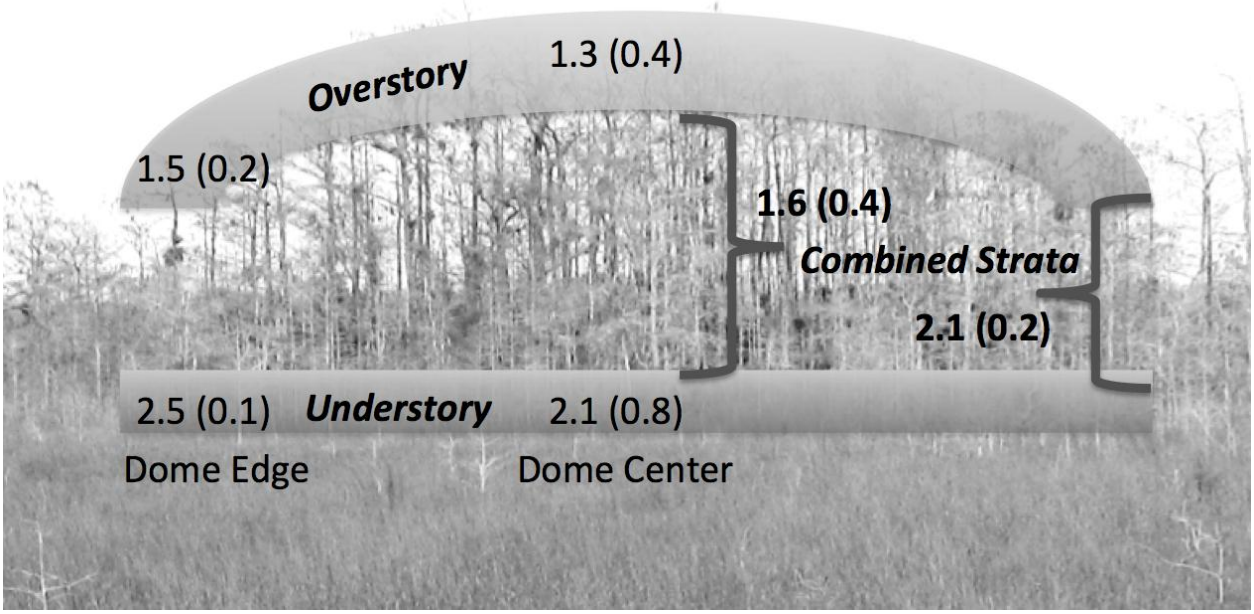

Figure 2-4. Fire severity was significantly lower at cypress dome centers compared to dome edges. This tendency was the case whether measured in overstory vegetation (canopy and subcanopy trees; $P < 0.05$), understory (shrubs and groundcover; $P < 0.05$), or all strata combined ($P < 0.01$). Fire severity was measured using a modified Composite Burn Index method (CBI, Key and Benson 2006), which returns values from 0 (unburned) to 3.0 (highly altered). Mean values (with variances in parentheses) are shown for the 25 domes measured in the study.

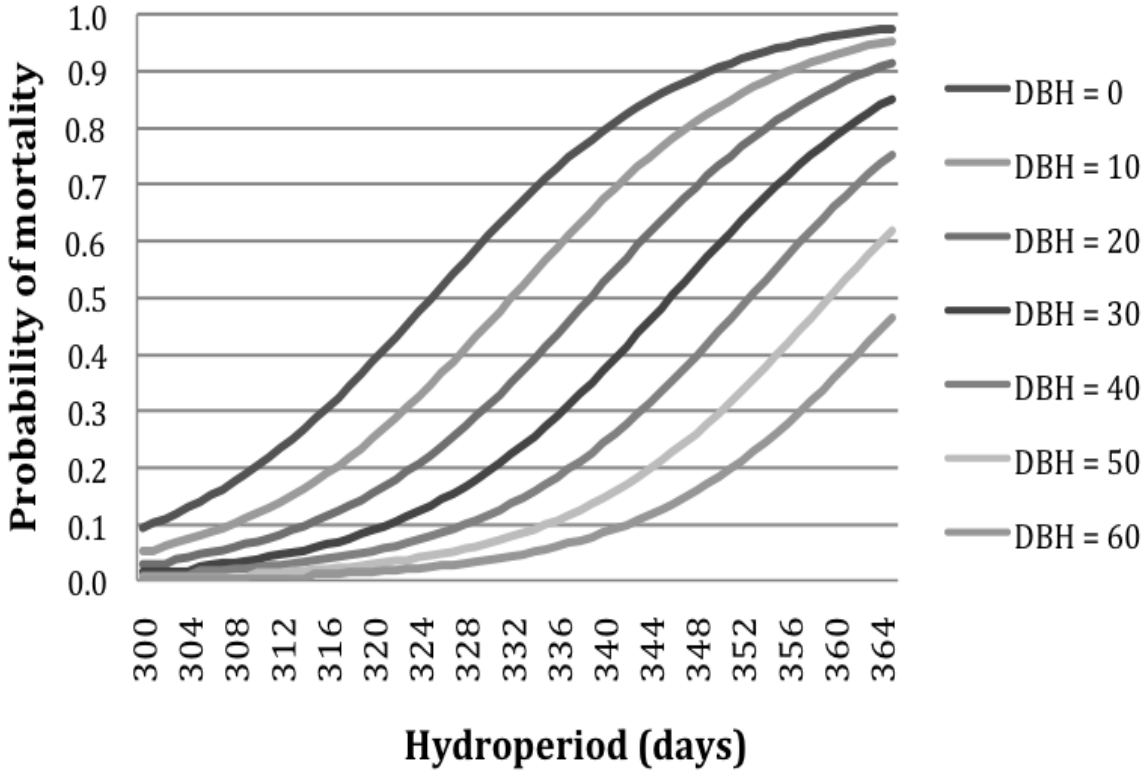

Figure 2-5. Predictions of best-performing logistic regression to describe probability of delayed-mortality response to drought-season fire in pondcypress. The model incorporates tree diameter at breast height (DBH in cm) and local hydroperiod.

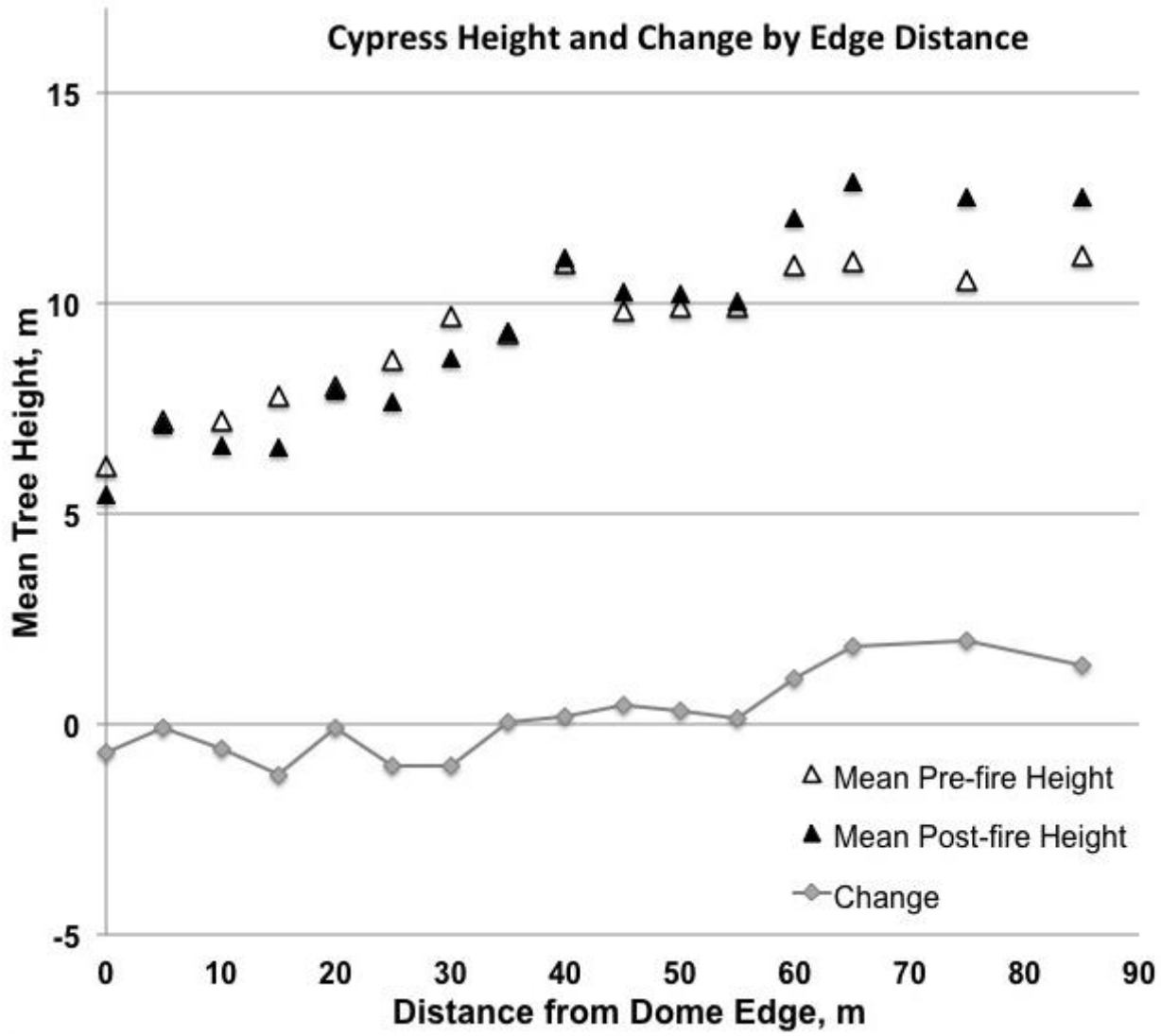

Figure 2-6. Mean heights of trees among all cypress domes in relation to dome edge, prior to fire and one year following fire. The mean decrease in live tree heights toward dome edges and increase in tree heights nearer dome centers indicates that a severe fire has exaggerated the characteristic structure of the domes in the study area.

Table 2-1. Logistic regression models predicting fire-caused pondcypress mortality. Elevation values were calculated for each tree measured based on water depth measurements benchmarked to USGS hydrographic data during landscape inundation.

Model	β_0	β_1	X_1	β_2	X_2	AIC	ROC
Height + Soil Elevation	14.5115	-0.1240	Height	-0.0575	Soil Elevation	421.4	0.701
DBH + Soil Elevation	13.8210	-0.0629	DBH	-0.0552	Soil Elevation	408.1	0.732

Notes: *β_0 is intercept; β_n are coefficients; X_n are model parameters; Soil elevation was calculated at the base of each tree measured; DBH = tree diameter at breast height; AIC = Alkake's information criterion; ROC = receiver operating curve. All regression coefficients differ significantly from zero at $p \leq 0.0001$.*

Table 2-2. Regression models describing tree size and location, pre- and post-fire.

Model	β_0	β_1	X_1	p ($\leq$)
DBH_PreFire $\propto$ DFE	15.1314	0.0538	DFE	0.05
DBH_PostFire $\propto$ DFE	14.8900	0.1045	DFE	0.001
Height_PreFire $\propto$ DFE	7.6737	0.0351	DFE	0.001
Height_PostFire $\propto$ DFE	6.6975	0.0626	DFE	0.001

Notes: *β_0 is intercept; β_1 is coefficient; X_1 is model parameter; DBH_PreFire = diameter of surviving trees measured immediately following the Deep Fire (99.5% of all trees in study plots); DBH_PostFire = diameter of surviving trees one year following fire; Height_PreFire = height of surviving trees immediately following fire (99.5% of all trees in study plots); Height_PostFire =height of surviving trees one year following fire. DFE = distance of tree from edge of cypress dome, measured in 5-m increments toward dome center.*

CHAPTER 3
HYDROLOGY AND FIRE REGULATE EDGE INFLUENCE ON MICROCLIMATE IN WETLAND FOREST PATCHES

Background

Edge effects in ecology are well accepted, and have been demonstrated across a variety of ecological systems and attributes (e.g., Harris 1988, Saunders et al. 1991). Among the numerous examples from forests ranging from the boreal (Schmiegelow and Mönkkönen 2002, Hamberg et al. 2009) to the neotropics (Laurance 1991, Laurance et al. 2000), the changing conditions from the edge of a patch toward its interior have been shown to affect animal populations (Paton 1994, Fletcher 2005) as well as plant populations (Gehrig-Downie et al. 2011, Obregon et al. 2011). While these relationships are explained by a number of factors that vary with the distance from the edge of a community or ecosystem edge (e.g., physical structure, and area of available habitat for animals; Margules and Pressey 2000), many components of edge effects are explained by changing microclimatic conditions.

Microclimate, or atmospheric conditions at a particular point on the landscape near the ground (Geiger 1965), influence a range of ecological processes (Meentemeyer 1978, Waring and Running 1998, McDonald and Urban 2005, Turner and Chapin 2005). Often, microclimate differences are studied between areas of contrasting vegetation communities, such as between forested patches and areas that have been cleared by logging or for road building (Asbjornsen et al. 2004). In the case of the former, clear changes have been observed in microclimate with increasing distance away from the edge of the interface of opening and forest, proceeding perpendicular away from the open area (Chen et al. 1993, Chen et al. 1995). In general, at increased distances from

an opening toward the interior of a forest patch[1], values and variances of temperature, humidity, and wind speed are attenuated (Vanwalleghem and Meentemeyer 2009). The reasons for these changes include decreased wind penetration into remnant forest, increased shading of soil and low vegetation strata, and decreased lateral diffusion of moisture to the atmosphere exterior to the forest patch.

In the same way that fragmentation results in changes to forest structure that affect microclimate attributes of resulting patches, other disturbance events that alter vegetation structure within a forest patch may exert control over edge effects on microclimate. Fire consumes standing live and dead biomass; and, by removing elements of forest structure and reducing forest canopy area (e.g., Cochrane et al. 1999), can increase insolation and air movement. Villegas et al. (2010) have shown seasonal effects on microclimate as conditions of canopy cover and evapotranspiration change substantially depending on leaf development and senescence. In addition to directly influencing microclimate, fire occurring in a forest patch may exert similar control over the influence of edge effect by reducing or eliminating those structural elements which attenuate microclimate with increasing distance from a patch edge.

Despite progress in understanding effects of edge distance (Chen et al. 1999) on microclimate (Vanwalleghem and Meentemeyer 2009), studies heretofore have been limited to terrestrial forests. Few studies have examined microclimate in wetland forests, and none have been published concerning edge effect and microclimate in these communities. Thermal mass of the water inundating a wetland or saturating its soil

1 For purposes of this discussion, “patch” should not be assumed to indicate a small fragment of forest or forest remnant, but rather any spatially-discrete unit of continuous forest regardless of size.

[2] Fire records for the area are unreliable; but lack of long-lived evidence of fire in domes such as charred areas on tree trunks, or dead/downed trees evidencing fire damage, indicated no recent fire activity.

[3] Comparisons of area measurements of depressions using hand-held WAAS (Wide Area Augmentation

would influence temperature (and certainly humidity), perhaps more so than the effects of canopy shading or attenuation of air mixing. Under these circumstances, hydrologic effects on microclimate could overwhelm the edge effects on microclimate that otherwise would be predicted under non-hydric conditions: in other words, edge effects on microclimate could be governed by a hydrologic “switch.”

In wetlands subject to strong seasonal variations in hydrologic regimes, might fires during droughts exert control over edge effects on microclimate? Could seasonal inundation likewise create hydrologic control over the occurrence of edge effects on microclimate? I sought to investigate whether either wildfire or inundation govern the occurrence of edge effects on microclimate in seasonally-inundated forest patches.

Hypothesized hydrologic control on edge-mediated microclimate variation leads to the following predictions:

1. Under non-inundated (e.g., drought) conditions, microclimate variation in wetland forest patches adjacent to nonforest communities would exhibit similar trends in response to patch and edge effect as those observed in terrestrial forests; i.e., attenuated temperatures and higher relative humidity with increasing distance from edges toward centers of patches.

2. Inundation degrades these relationships, resulting in a partial or complete loss of relationship between distance from edge (DFE) and microclimate.

3. Wildfire sufficient to cause substantial changes to vegetation structure results in losses of edge influence, resulting in higher temperatures and lower humidity among domes experiencing fire compared to unburned domes.

Hydrologic government of edge effect, if extant, could improve our understanding of the implications of severe droughts or future altered climate on wetland forest processes, particularly where issues of fragmentation or small patch size are concerned. Knowledge of fire impacts to microclimate and edge influence, meanwhile, may allow us to better forecast potential effects of future fires following wildfire events.

Materials and Methods

Study area

Big Cypress National Preserve in southwestern Florida USA (26° N, 81° W, Figure 3-1) covers 300,000 ha of low-relief landscape. There, upland forests of south Florida slash pine (*Pinus elliottii* var. *densa* [Little and Dorman]) and prairies primarily composed of muhlygrass (*Muhlenbergia capillaris* [Lam.]) occur adjacent to swamps dominated by pondcypress (*Taxodium distichum* var. *imbricarium* [Nutt.]), a deciduous conifer characteristic of long-hydroperiod wetland forests across large portions of the southeastern United States. Small swamp patches, called domes because of their structure, occur frequently across large areas of the preserve, providing the opportunity to investigate wetland forest processes in a landscape with generous replication of patches at a range of sizes. Mean annual precipitation of 1360 mm y^{-1} occurs primarily in the wet-season months of June – September (Duever et al. 1986). While the entire landscape experiences periodic inundation during periods of intense precipitation, standing water is generally confined during and shortly after the wet season to cypress swamps where soil elevations are lower than those in the surrounding landscape by 1 m or more (Table 3-1). Water infiltrates into the region's karst limestone after rains cease, and the shallow depressions in which cypress domes occur may become dry for 3 – 6 months during the late dry season (Ewel 1995).

As the first thunderstorms of the rainy season begin (usually in May), frequent lightning strikes occur on a landscape with plentiful available fuel. Naturally ignited wildfires occur frequently during this seasonal transition, with the pyrogenic vegetation of flatwoods and prairie communities readily carrying fire to the edges of swamps and domes. Dry conditions can permit sufficient fuel continuity to allow fire to enter these wetland forests, where understory vegetation such as sawgrass (*Cladium jamaicense* [Crantz]) may burn readily. During drought conditions, large ground fuels, accumulated duff, or even the peat soils themselves may ignite, resulting in severe fires. In May 2009, during a severe regional drought, the Deep Fire was ignited by lightning and burned 12,000 ha in the northwestern corner of the Preserve. The fire burned through all vegetation communities within its perimeter, including desiccated cypress domes which experienced moderate to severe fire effects and substantial (23.5% overall) tree mortality (Watts et al. 2012).

Experimental design and data collection

Using 2.5 m resolution images from SPOT (Satellite Pour l'Observation de la Terre) imagery from 2010 (geo-referenced and accessed via Google Earth, Google, Inc., Mountain View, CA), I selected 12 cypress domes in which to measure microclimate. Six domes were selected from within the perimeter of the Deep Fire, and visited prior to data collection to verify that they had experienced substantial effects from fire (i.e., evidence of soil consumption, overstory tree mortality, charring on trunks, etc.); the other six were selected from 0.5 – 1.5 km east of the fire perimeter, where

wildfire had not occurred in domes for several years[2], as a control. Within each treatment, domes were selected based on three selection criteria: shape (round, or nearly so); surrounding community (prairie or sparse savanna occurring adjacent to ~50% or more of dome edge); and size, estimated from satellite imagery[3]. Due to the replicated nature of the domes in the landscape, it was possible to select domes in the treatment area with sizes corresponding to those selected in the control area (Table 3-2).

At each circular dome, a transect was established from the center to the edge along an azimuth chosen based on the occurrence of prairie exterior to the dome, and a clearly-defined community edge. Sampling points were established at dome centers, edges, midway between the two locations, and exterior locations ca. 20 – 40 m beyond the dome edge along the transect. At each sampling point, a ventilated radiation shield housing a Lascar EL-USB-2 datalogger with thermistor temperature and capacitive humidity sensors (Lascar Electronics Ltd., Salisbury, UK) was affixed to the nearest cypress tree > 6 cm diameter at breast height (DBH). Sensors in domes were located on trees at 2.0 m in height and at a northern aspect; in external locations, sensors were placed on snags or isolated trees (Figure 3-2). Each sensor was programmed to record temperature and relative humidity readings at 30-minute intervals. Data collection was initiated in late December 2010 in order to reliably measure fire effects due to canopy

[2] Fire records for the area are unreliable; but lack of long-lived evidence of fire in domes such as charred areas on tree trunks, or dead/downed trees evidencing fire damage, indicated no recent fire activity.

[3] Comparisons of area measurements of depressions using hand-held WAAS (Wide Area Augmentation System) GPS (Global Positioning System) receivers found agreement within approximately 5% of those obtained from satellite images (data not shown).

changes from mortality among pondcypress, which occurred predominantly in the second growing season following the Deep Fire.

Data analysis

For comparisons of microclimate readings at locations within and exterior to domes, daily maximum temperature and minimum daily RH readings were compared using Tukey's W test (also known as Tukey's Honest Significant Differences (HSD) test); this procedure controls for additive error associated with multiple post-hoc comparisons (Ott 1993). To test for the presence of edge effects on microclimate, diurnal (between 0800h and 1900h US Eastern Standard Time) temperature and relative humidity measurements for a given sensor were compared with the readings taken exterior to the dome in which it occurred; this method normalized each dome's data against local external conditions, improving the ability to discern differences in microclimate based on edge distance. For temperature, differences in daily mean and daily maximum were calculated; for relative humidity, differences were calculated in daily mean and daily minimum. Additionally, vapor pressure deficit (VPD) – a measure of the difference between actual and saturation vapor pressure of water vapor in the atmosphere at a given temperature (Anderson 1936) was calculated as an ecologically meaningful index of organismal difficulty in maintaining water balance. To calculate VPD, saturation vapor pressure (ES) first was determined based on temperature, using the following equation:

$$ES = 0.6108 * e^{(17.27 * T / (T + 237.3))} \qquad 3\text{-}1$$

in which *e* is Euler's number, and T is temperature in Celsius. Then, actual vapor pressure (EA) was calculated thus:

$$EA = RH / 100 * ES \qquad 3\text{-}2$$

in which RH is relative humidity, and ES is saturation vapor pressure as calculated in Equation 3-1. VPD is then found by subtracting ES from EA (Allen et al. 2005).

To test for hydrologic and wildfire influence over edge effect, hydrologic condition (inundated or dry) and disturbance (burned or control) groups of temperature and humidity differences at the location of observation (edge, mid-transect, or center) using analysis-of-variance (ANOVA) or Kruskal-Wallis (K-W) tests if assumptions of normality or homoscedasticity (tested with Kolgorov-Smirnov and Levene's tests, respectively) were not met for a given variable in the test.

To compare edge effect in domes between the two treatments and in contrasting hydrologic conditions, linear regression was performed on temperature or relative humidity data normalized as described above (i.e., the difference between the reading at a particular location in the dome and the reading exterior to the dome), and the distance a given sensor was located from the edge of a dome (with edge locations assigned a zero-distance value). Linear regression analyses were performed separately on these temperature and relative humidity differences according to distance from dome edge. Additionally, linear regression was performed on VPD values to determine the varying response of this variable to distance from edge according to the different seasons and treatment. Relative strength of edge effects in each instance was compared using regression coefficients obtained for the distance component of regression models for each model (Sokal and Rolfe 1995). Analyses were performed using the software package R (R Development Core Team 2005).

Predicted relationships between distance from edge and temperature (negative) and humidity (positive) should be stronger during full canopy coverage than during

periods of canopy leaf senescence (Villegas et al. 2010). Therefore, although I collected data for periods of both canopy presence and leaf senescence (January – February 2011) to verify this prediction, analyses were performed only on data collected during periods when canopy leaves were present for the test of hydrologic influence on edge effect (i.e., April – May 2011 for dry conditions and August – September 2011 for inundated conditions). Wildfire control over edge effect was tested using data collected during the fire season when leaves were present (April – May 2011), since comparisons during periods of senescence likely would omit observation of an important effect of wildfire (i.e., the removal of canopy due to damage and mortality).

Results

During the sampling period (through October 2011), temperature and relative humidity varied by month. High temperatures (over 30 °C) were common from April until October but occurred in all months (Figure 3-3). Relative humidity measurements fluctuated more, probably due to the influence of precipitation events, (Figure 3-4), but monthly averages of RH and VPD (Figure 3-5) generally reflected seasonal hydrologic variation illustrated in hydrographs from Everglades Depth Estimation Network (EDEN, Telis 2006) located within the Preserve (Figure 3-6). During January through June, when no standing water was present in cypress domes, temperature in a given dome tended to decrease from the exterior community towards its interior, while relative humidity increased (Table 3-2).

As expected, temperature and humidity measurements differed for mid-transect and dome-center locations according to whether cypress trees carried leaves (t-tests on daily maximum temperature and daily minimum humidity by leaf status; $p < 0.001$ in

each instance). No effect of the azimuth of transects was observed on temperature or relative humidity for any of the season-treatment combinations.

K-W tests for temperature and relative humidity differences revealed effects of location for data collected under dry as well as inundated hydrologic conditions, in both control and post-wildfire locations ($p < 0.001$ in each of four tests on daily maximum temperature; $p < 0.001$ in each of four tests on daily minimum relative humidity). Post-hoc pairwise comparisons between locations within and exterior to domes indicated no significant differences in microclimate between dome edges and exterior communities, except among unburned domes during dry periods when edge maximum temperature readings were lower (Table 3-3). Mid-transect locations and dome edges exhibited significantly different maximum temperature and minimum RH regardless of fire status or hydrologic condition. Mid-transect and center microclimate did not differ during inundated conditions, but were significantly different during dry conditions (with the exception of maximum temperature in post-fire domes).

Linear regressions models fitted to values of normalized temperature and relative humidity differences by edge distance indicated larger coefficients for edge-distance terms for temperature and humidity during dry months compared to inundated months (Table 3-4). The differences observed in these coefficients for contrasting hydrologic conditions were substantially greater at burned sites compared to control (113% greater for dry than inundated in burned domes vs. 57% in control domes for temperature; 133% in burned domes vs. 19% in control domes for relative humidity; Figures 3-7, 3-8). Vapor pressure deficits were highest at dome edges for all four season/treatment categories (inundated-control, dry-control, inundated-burned, and dry-burned) and

decreased with increasing distance from dome edges toward interiors, with lower values for VPD during the wet season than dry season; similar coefficients were observed for control and burned locations for each season (Figure 3-9).

Among sensors located within domes (i.e., dome-center and mid-transect locations), temperature readings were similar except for the months of June – August, when domes within the Deep Fire perimeter experienced higher daily maximum temperatures (Kruskal-Wallis tests, $p < 0.05$; Figure 3-10). Differences between relative humidity observed at within-dome locations and external community locations were similar for burned and control treatments except during April, May, and July, when daily minimum RH readings were lower for control sites than for domes that had experienced wildfire two years prior to sampling (K-W test, $p < 0.05$ for each comparison; Figure 3-11).

Discussion

Edge Effects on Microclimate in Desiccated Cypress Swamp Patches

Compared to open vegetation communities or those with sparse tree canopies, all 12 instrumented cypress domes displayed lower temperatures and higher relative humidity within their community boundaries. The prediction of lowered temperature and higher humidity with increasing distance under dry (non-inundated) conditions was observed as measured by pairwise comparisons between mid-transect and dome-center locations, with the exception of daily maximum temperature measurements in burned domes (Table 3-3). Regression analysis further confirmed the positive relationship between the distance within a given dome at which a measurement was taken and the difference between microclimatic conditions at that location and those at the location exterior to the dome (Table 3-4).

Low values for the coefficients of determination resulting from regression of temperature and humidity on distance from edge indicated that only a small portion of the variance in values for microclimate were explained by edge distance (Sokal and Rolfe 1995). This is unsurprising: the variation among temperature readings over the two-month periods examined in the regression analysis would be affected by seasonal climatic trends; precipitation and frontal passages; and other events with the likelihood of affecting temperature readings to a much greater extent than the influence of edge effect. The objective of regression analysis in this instance was to determine whether edge effect exists and varies with inundation and following fire, not to construct comprehensive forest climate models. In this study the discernable effect of edge distance was present in all regression models to a significant degree, influencing temperature and humidity consistent with theory on edge literature (e.g., Forman and Godron 1986).

Hydrologic Influence on Edge Effect

Pairwise comparisons of microclimate conditions between adjacent sampling locations reveal fewer significant differences in maximum temperature or minimum relative humidity during inundation compared with drought conditions. Some differences in dome microclimate in relation to edge distance that were observed during dry periods, such as those between dome centers and locations halfway between centers and edges, disappear when wet-season inundation occurs. Inundation does not erase all predicted effects of forest patch interiors on microclimate, as illustrated by significant microclimate differences between edge and mid-transect locations during inundation (Table 3-3) as well as positive effects of edge distance on attenuation of microclimate under inundated conditions (Figure 3-7, Figure 3-8). However, the influence of edge

distance on temperature and humidity within domes is greatly reduced when standing water is present. Also, while the effect of increasing distance from dome edge toward interior on VPD is seen across all four combinations of season and treatment, VPD is lower at all edge distances during the wet season than the dry season (Figure 3-9). Thus, while there does not appear to be a “hydrologic switch” caused by the thermal influence of standing water overwhelming that of edge distance, there does appear to be substantial hydrologic control over the importance of edge effect on microclimate in wetland forest patches subject to fluctuating water levels.

Wildfire Control on Edge Effect

Cypress domes that had experienced moderate to severe fire two years prior to sampling were similar in microclimate to unburned domes during most months of the year. Exceptions were during the wet-season months of June – August, when maximum daily temperatures within domes were higher than those recorded in unburned domes. These findings of increased temperature within burned domes are consistent with expectations, but the observation of statistically significant differences during only three months of the study period offers little support of the hypothesized reduction in attenuation of microclimate within cypress domes. To the contrary, relative humidity values within burned domes were either similar or, in the case of three months (April, May, and July), greater than those in unburned domes. Also, the slope of regression lines describing the influence of edge distance on both temperature and humidity were greater for burned domes than unburned domes (although the differences observed under inundated conditions were much smaller than dry conditions). VPD showed the least difference in burned compared to unburned domes, with similar intercepts and

coefficients of determination during the dry season and nearly indistinguishable regression models during the wet season (Figure 3-9).

Decreased humidity and increased temperature were expected based on observed post-fire changes in understory due to substantial consumption (Figure 3-12) as well as delayed overstory tree mortality rates of 23.5% observed in a study following the Deep Fire (Watts et al. 2012). However, the observations of this study indicated nearly the opposite effect compared to predictions. One possible mechanism to explain similar microclimate and increased effect of edge distance despite a reduction in canopy cover due to tree mortality may be the rapid regrowth of understory (Figure 3-13), perhaps from increased light as well as nutrients mineralized due to the fire. Vigorous regrowth in the understory may substitute for overstory canopy to some degree in the attenuation of temperature by providing additional shade, while evapotranspiration from rapidly-growing vegetation may explain RH values similar to or greater than those in unburned locations. Finally, the increased influence of edge effect may be partly explained by the exaggeration of the characteristic dome-shaped structure due to wildfire in these communities (Watts et al. 2012): following fire in cypress domes, mean tree heights toward dome edges decrease due to topkill, while mean heights toward dome interiors increase due to higher mortality among shorter trees. If exaggeration of dome structure by fire results in a greater reduction of canopy cover near dome edges compared to dome centers, then changes in temperature and humidity at edges compared to centers of domes may become greater.

Despite the capacity of water to moderate local climate by absorbing and releasing thermal energy, flooded conditions do not overwhelm the influence of edge effect on

microclimate in cypress domes. However, while there appears to be no hydrologic "switch" that prevents the operation of edge influence when water levels are above the soil surface, inundation does substantially reduce the degree to which edge distance causes changes in temperature and relative humidity in cypress domes.

During dry periods when water levels retreat, wetland forest patches appear to be subject to the same influence of edge on microclimate as their upland counterparts. In forests where seasonal fluctuations leave wetland forests dry for extended periods (weeks to months), the implications of edge effects and fragmentation for management and conservation are similar to those encountered among upland forests. Even among wetlands that rarely experience desiccation, the occurrence of drought may have detrimental interactive effects with fragmentation on species that rely on conditions attenuated by distance from edge, such as some bromeliads and epiphytic plants (e.g., Muss 2001, Gehrig-Downie et al. 2011, Obregon et al. 2011).

An additional concern involves edge-related fragmentation effects in wetland forests subject to fire. Under dry conditions, wetland forests likely are subject to the same enhanced effects of wildfires when subjected to changes that increase the edge:area ratio, due to an effective decrease in edge distance within the remnant (Cochrane 2001). Numerous studies on the effects of fragmentation on microclimate, as well as dedicated studies concerning the interactive effects among fragmentation, structure, and fire effects (e.g., Cochrane and Schulze 1999), led to the development of positive-feedback models of fragmentation and fire (Lindenmayer et al. 2009). This positive-feedback model describes logging, fragmentation, or other activities that simplify the structure of a forest patch, as leading to increases in fire severity, intensity,

or frequency; changes in the fire regime help to maintain clearer understory and sparser overstory that further enhance favorability of microclimate for promoting fire behavior. In this study, the positive feedback model predicted increased temperature and decreased humidity following fire. Contrary to expectations, findings appeared to contradict the positive-feedback model of fragmentation and fire-promoting microclimate conditions.[4] Instead, post-fire changes to cypress domes appear neutral in their potential effects on the behavior of recurrent fire, or (in the case of increased RH) somewhat negative. Negative fire feedbacks have been observed in Amazonian forests (Balch et al. 2008), but are more likely due to changes in fuels than in microclimate as suggested by the findings of this study.

Further measurements to describe changes to vegetation structure, nutrient cycling, and productivity may elucidate the mechanisms behind the findings concerning post-fire changes in microclimate in cypress domes. Meanwhile, continued observations will improve our understanding of the dynamics of post-fire changes in edge influence on microclimate in these wetland forest patches, while detailed monitoring of hydrologic conditions and additional parameters will enable the modeling of microclimate in wetland forest patches under a variety of hydrologic conditions. These efforts are expected to improve the ability of resource managers to maintain the value of these valuable communities under predicted future scenarios of greater variability in climate and precipitation regimes.

[4] The changes to fuel availability and fuel loads following fire are of obvious importance to the behavior and effects of recurrent fires, but are outside the scope of the present study.

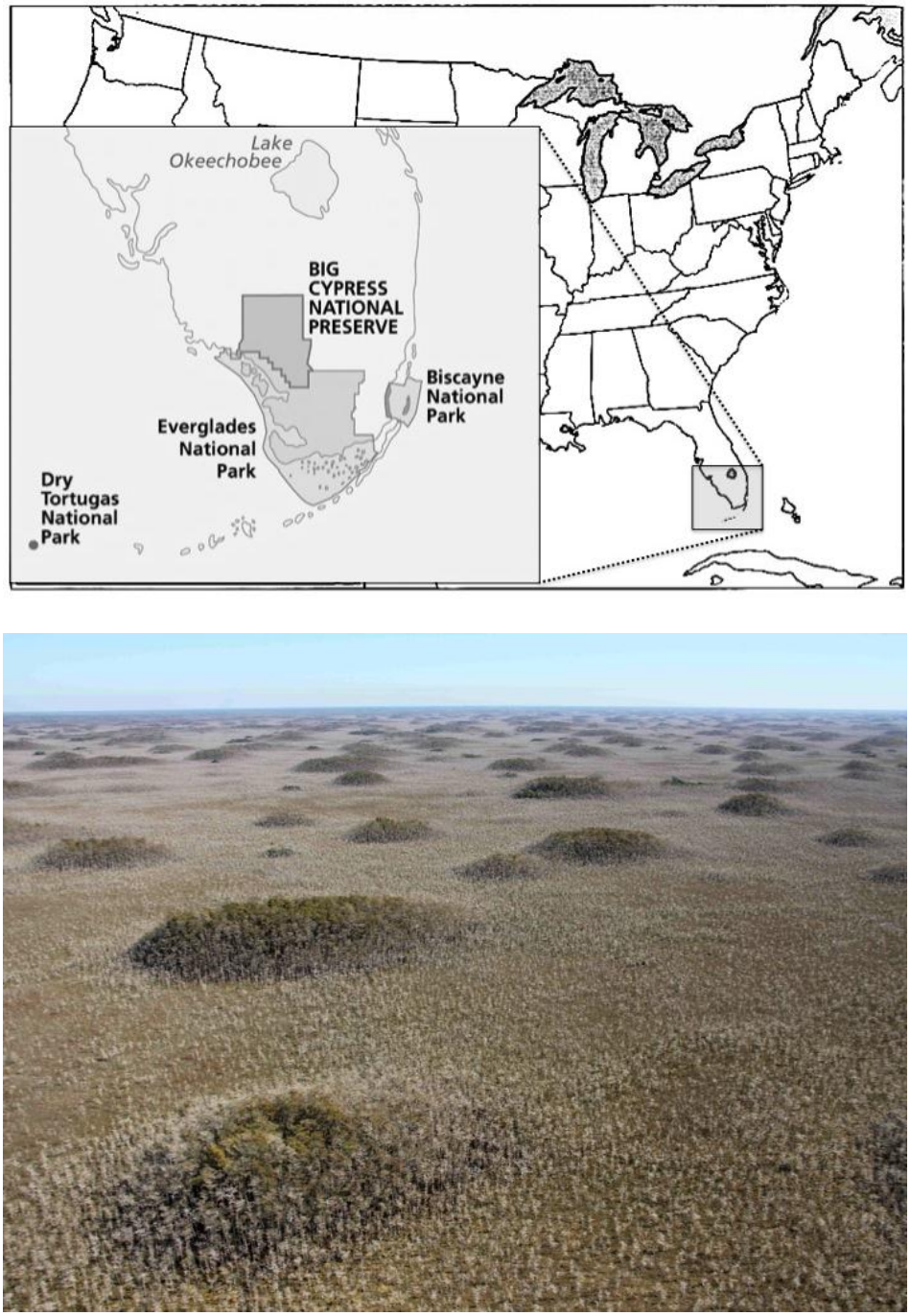

Figure 3-1. Big Cypress National Preserve, in southern Florida, USA, protects 300,000 ha in a low-relief area characterized by subtropical climate. Strong seasonal distribution of rainfall means that the region's many small depressional features become inundated during the rainy season from approximately July to December. Rapid infiltration through shallow soils into the limestone bedrock leaves many swamps dry for up to a few months per year.

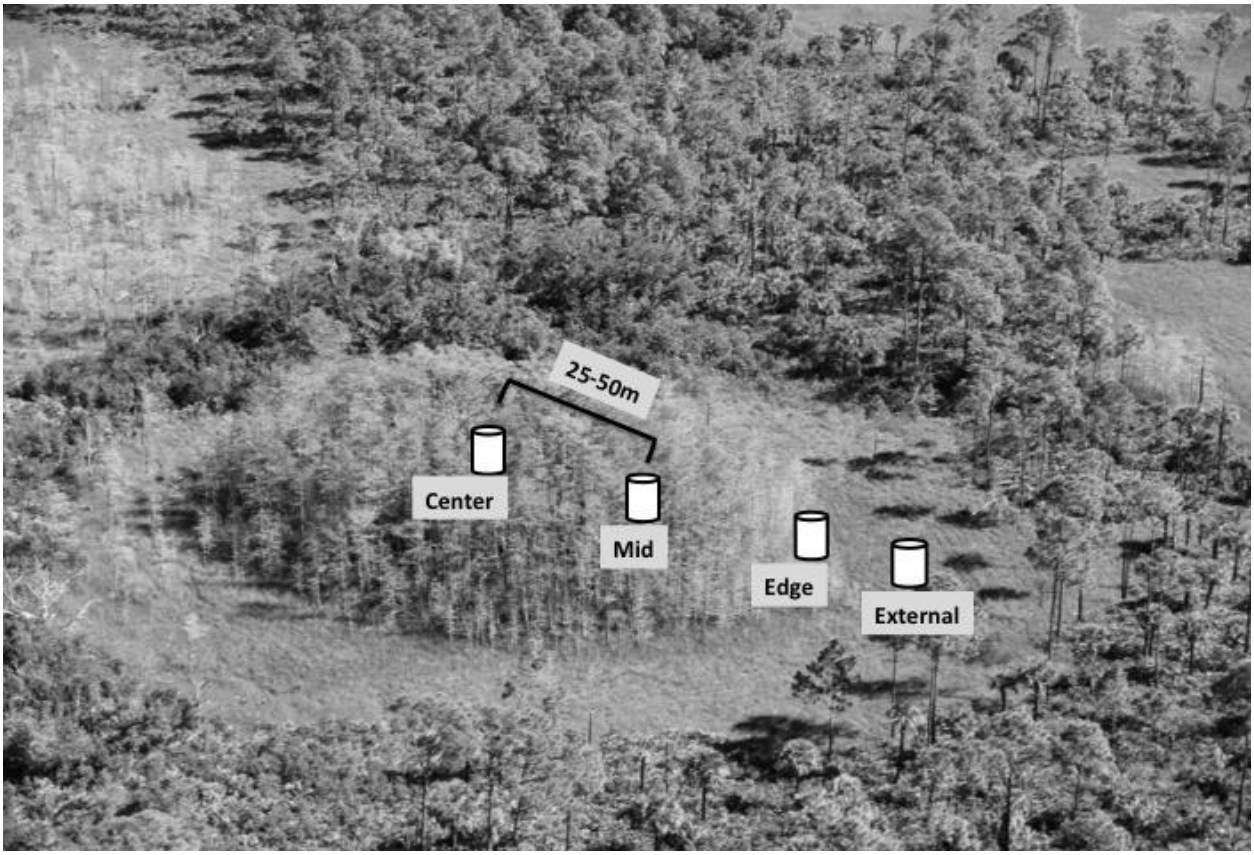

Figure 3-2. Schematic representation of sampling locations along a transect leading from center of a cypress dome to the external community. In the dome pictured above, sensors are located approximately 30 m apart, while external sensor is located 15 m outside of dome along a southwestern azimuth.

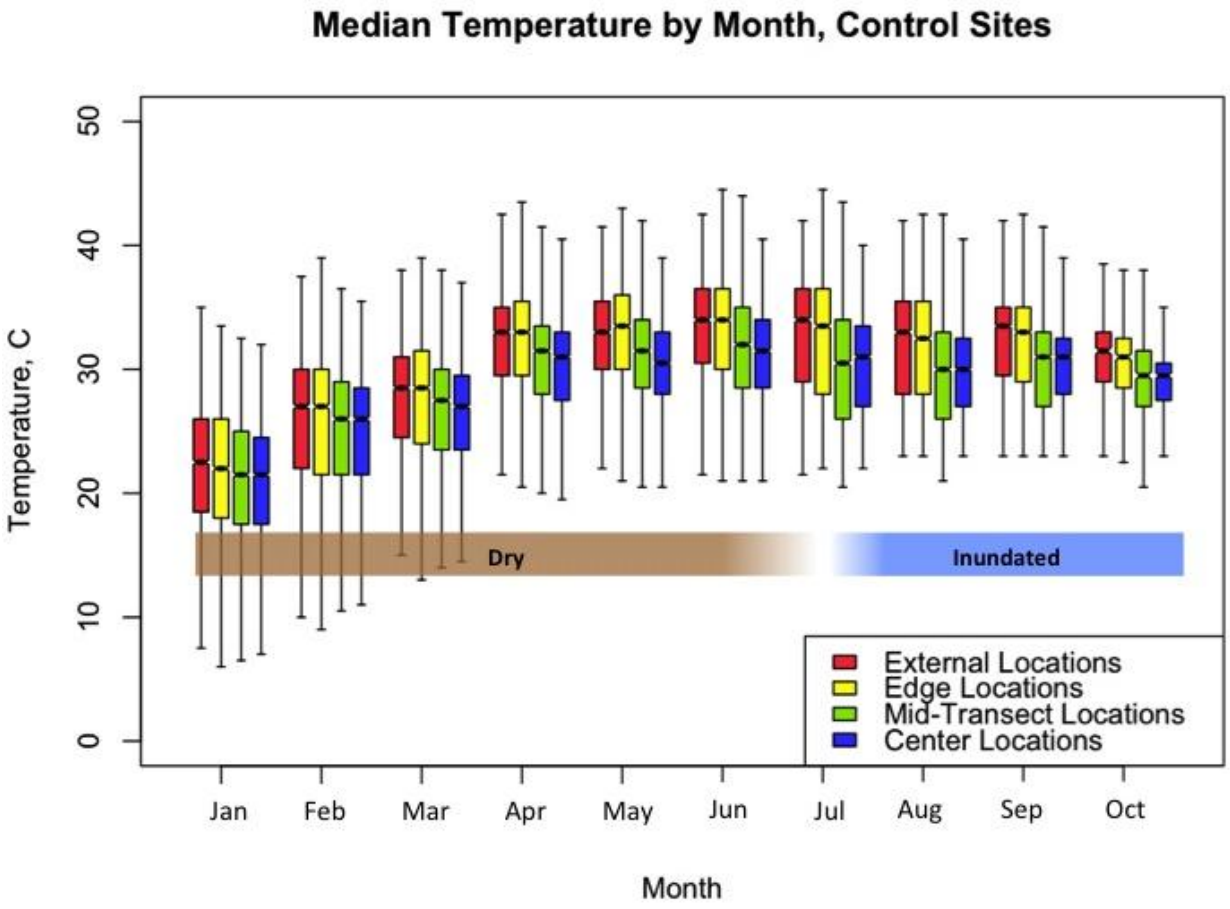

Figure 3-3. Boxplot of temperature readings collected at control (unburned) cypress domes by month, January – October 2011. Data are grouped by location at which readings were taken relative to a transect running from dome centers to external communities. Readings in the latter, usually graminoid prairie or sparse savanna, were taken 20 – 40 m outside of domes; mid-transect locations were located halfway between centers and edges. Boxes represent upper and lower quartile values; whiskers show ± 1.5 interquartile range. Notches at median values for each month indicate significant differences among non-overlapping groups (McGill et al. 1978); outliers not shown.

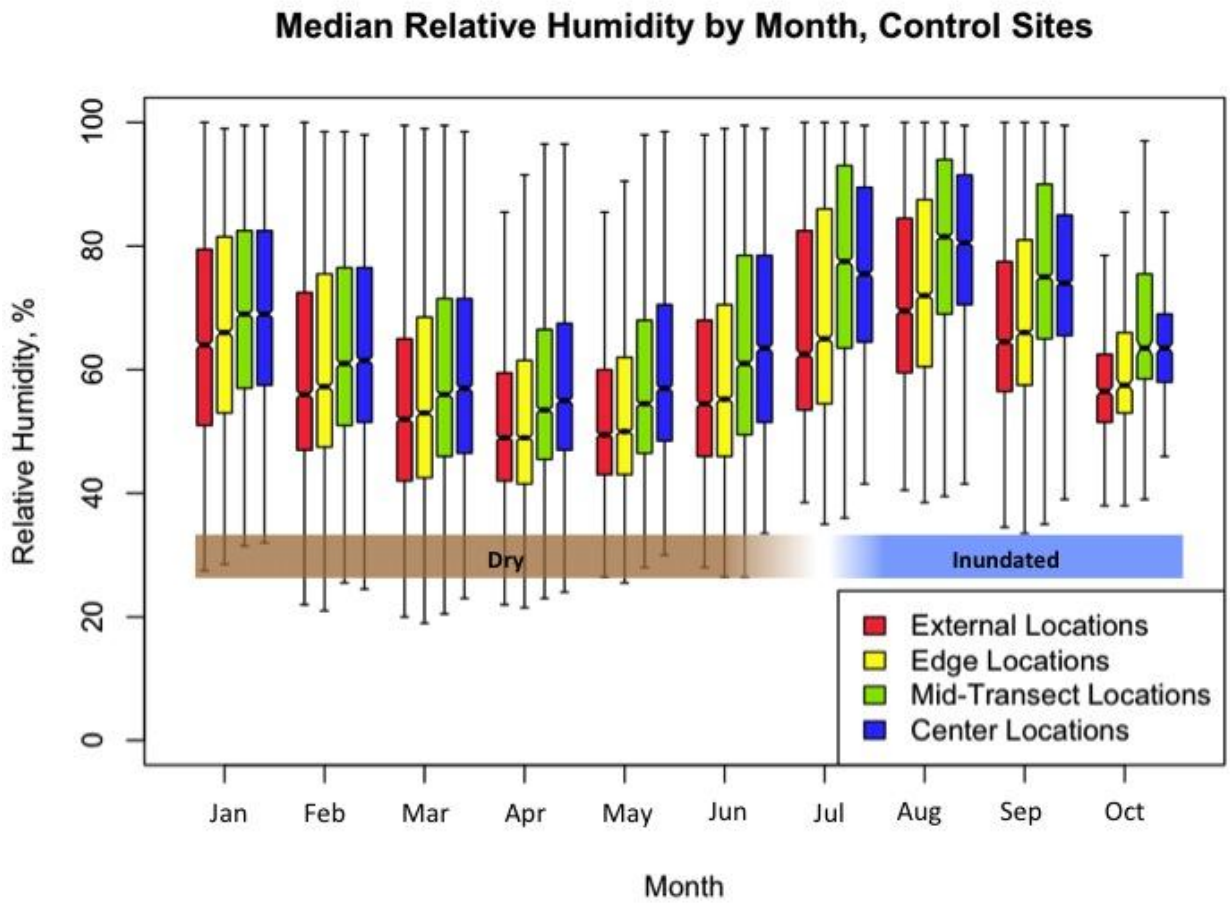

Figure 3-4. Boxplot of relative humidity readings collected at control (unburned) cypress domes by month, January – October 2011. Data are grouped by location at which readings were taken relative to a transect running from dome centers to external communities. Readings in the latter, usually graminoid prairie or sparse savanna, were taken 20 – 40 m outside of domes; mid-transect locations were located halfway between centers and edges. Boxes represent upper and lower quartile values; whiskers show ± 1.5 interquartile range. Notches at median values for each month indicate significant differences among non-overlapping groups (McGill et al. 1978); outliers not shown.

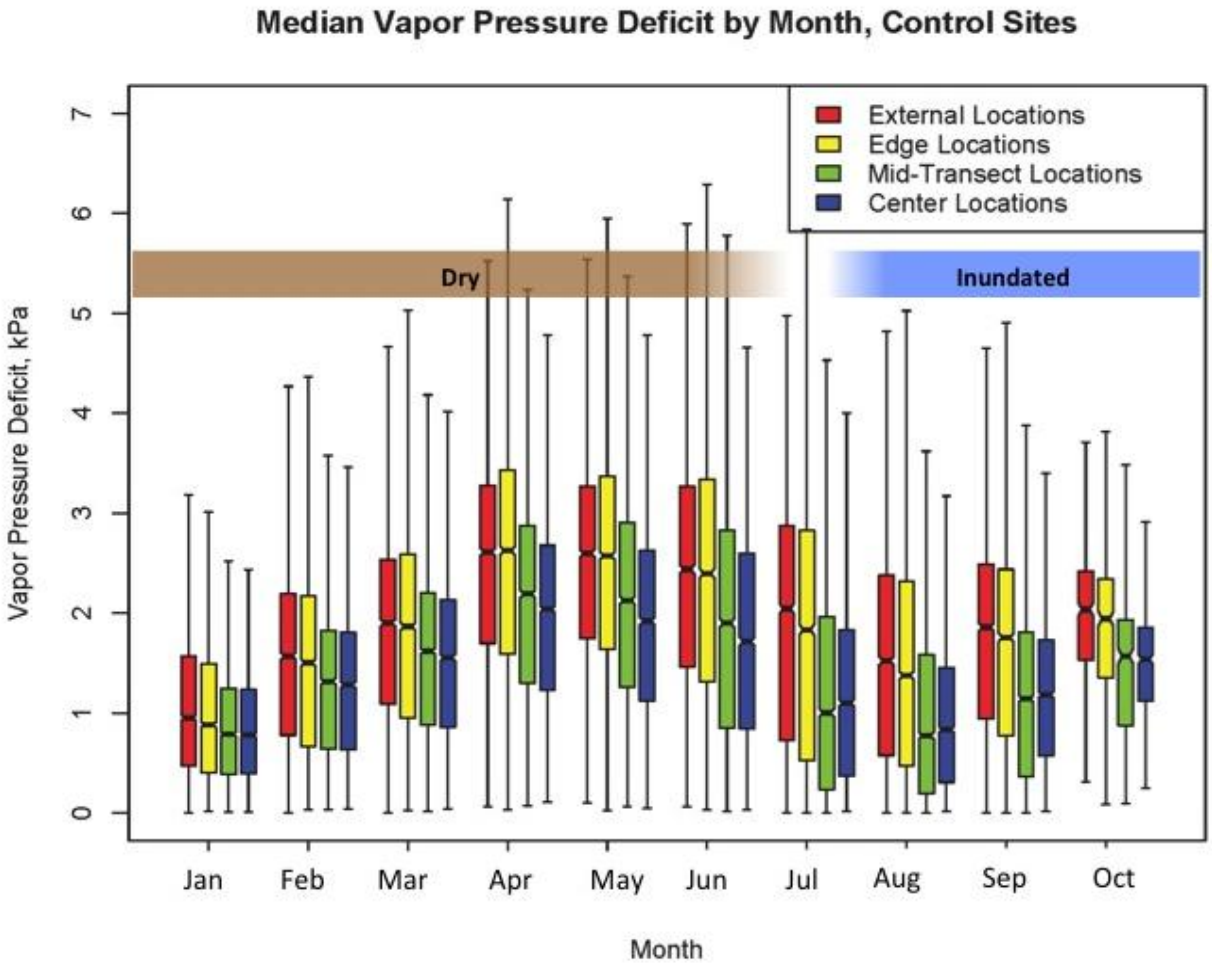

Figure 3-5. Vapor pressure deficit (VPD; Anderson 1936) at control (unburned) cypress domes by month, January – October 2011. Data are grouped by location at which readings were taken relative to a transect running from dome centers to external communities. Readings in the latter, usually graminoid prairie or sparse savanna, were taken 20 – 40 m outside of domes; mid-transect locations were located halfway between centers and edges. Boxes represent upper and lower quartile values; whiskers show ± 1.5 interquartile range. Notches at median values for each month indicate significant differences among non-overlapping groups (McGill et al. 1978); outliers not shown.

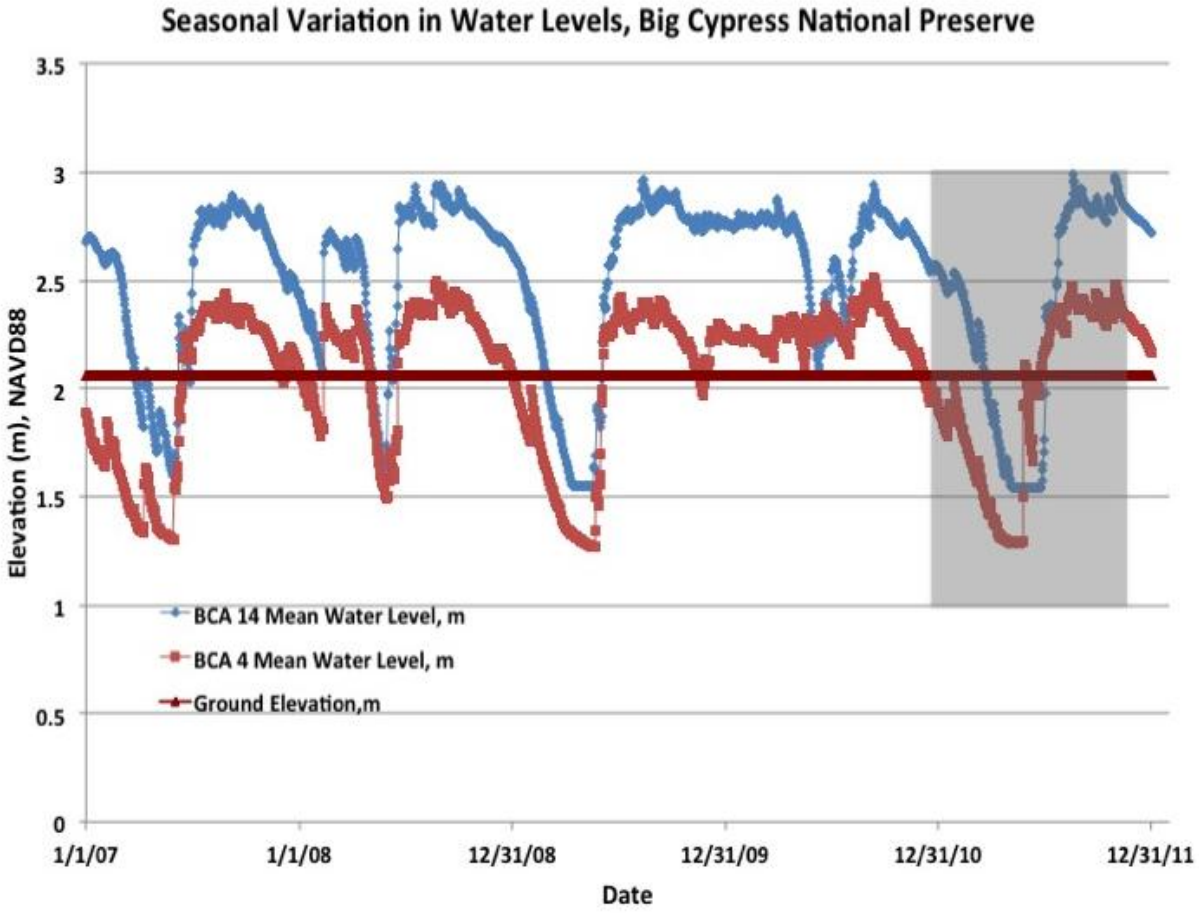

Figure 3-6. Data from two monitoring wells show the seasonal hydrologic fluctuation experienced in the region. Red and blue lines illustrate daily water table elevation in relation to average ground-surface elevation (brown line) adjacent to the stations. Shaded area of graph indicates microclimate sampling period. Readings shown are from Everglades Depth Estimation Network (EDEN; Telis et al. 2006) sensors located in the central portion of Big Cypress National Preserve

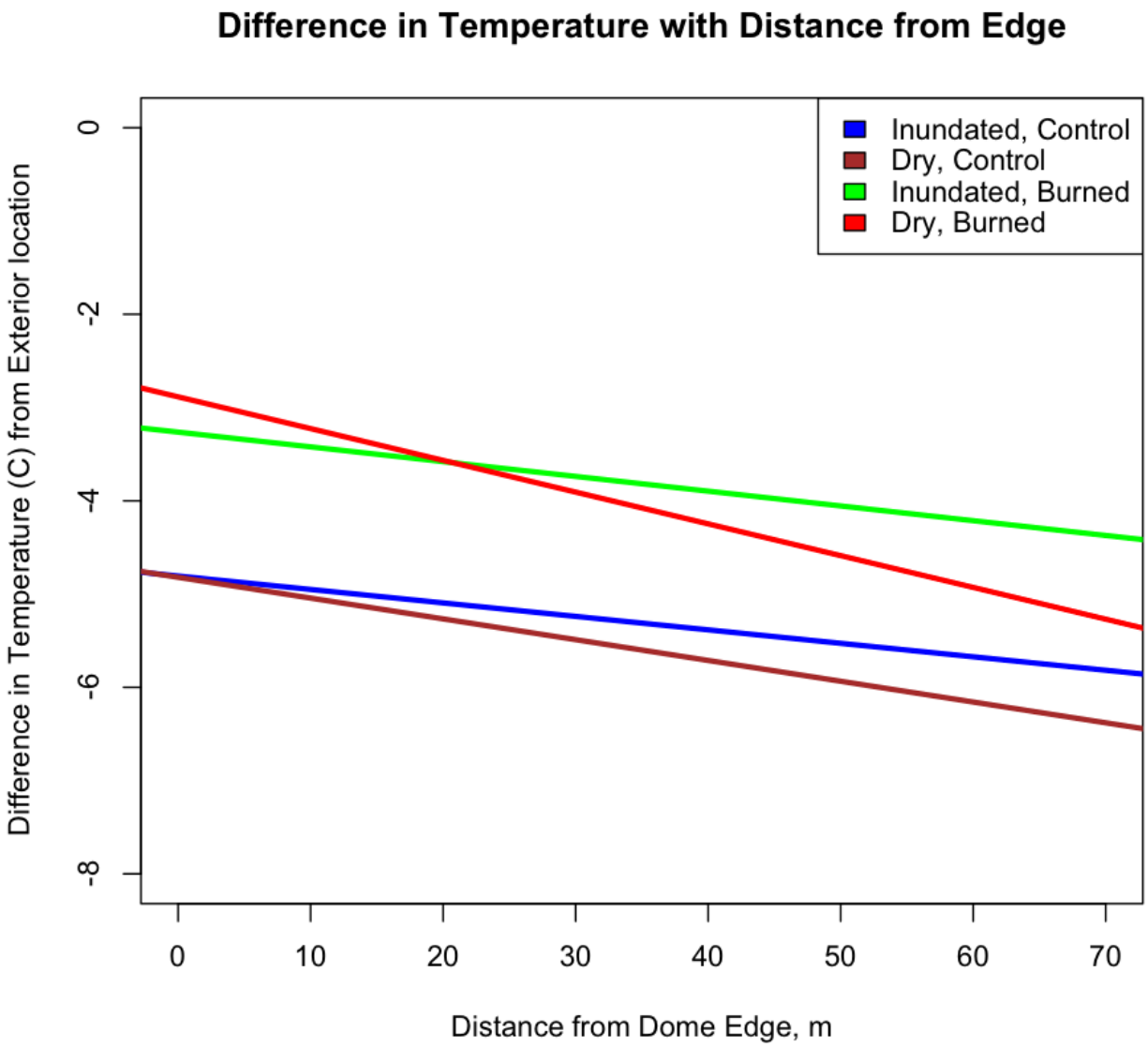

Figure 3-7. Regression models of within-dome temperature difference from exterior locations by distance for treatments, control vs. burned and inundated vs. dry.

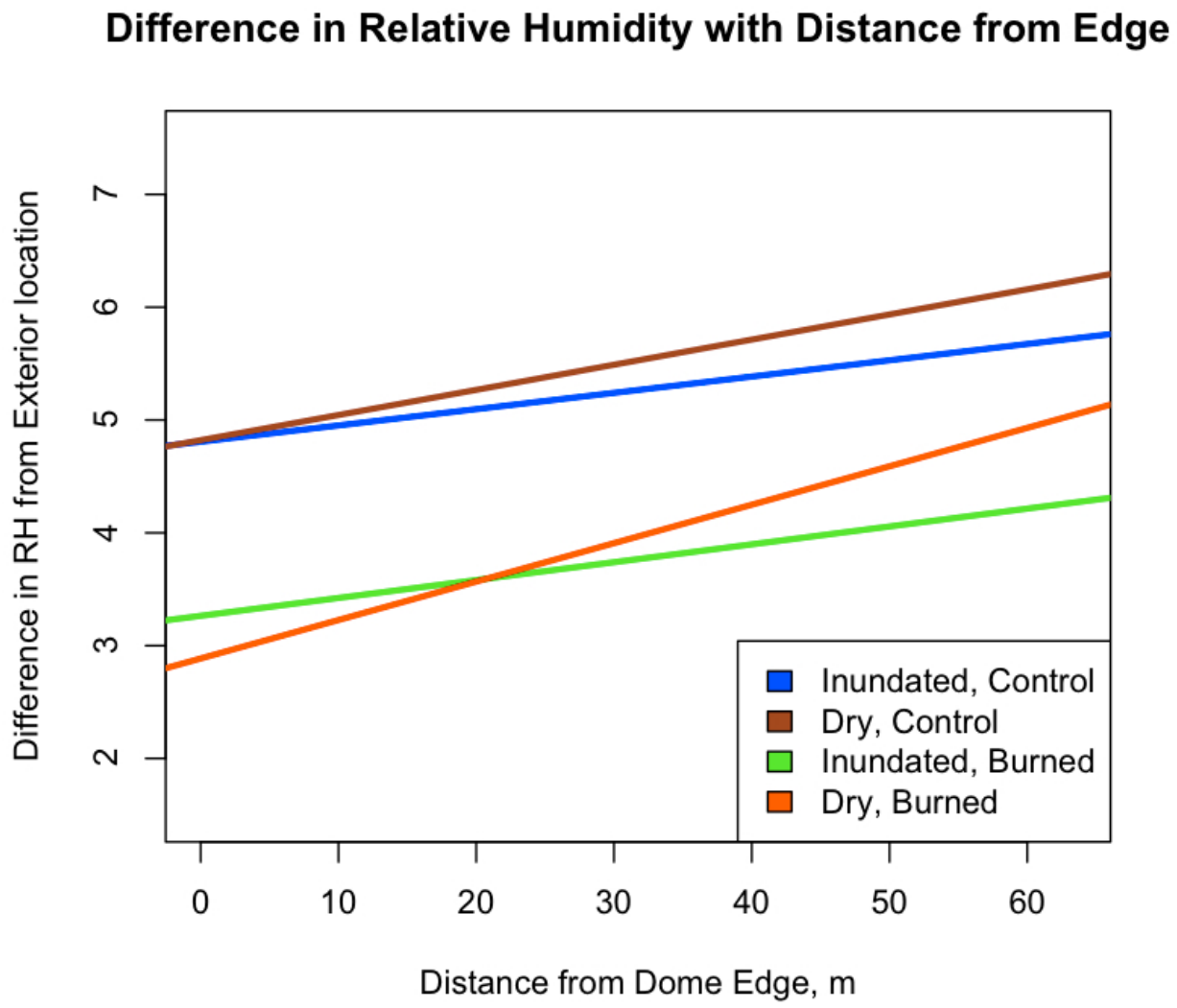

Figure 3-8. Regression models of normalized difference in relative humidity readings from exterior locations by edge distance for different treatments. For equation coefficients and intercepts, see Table 3-4.

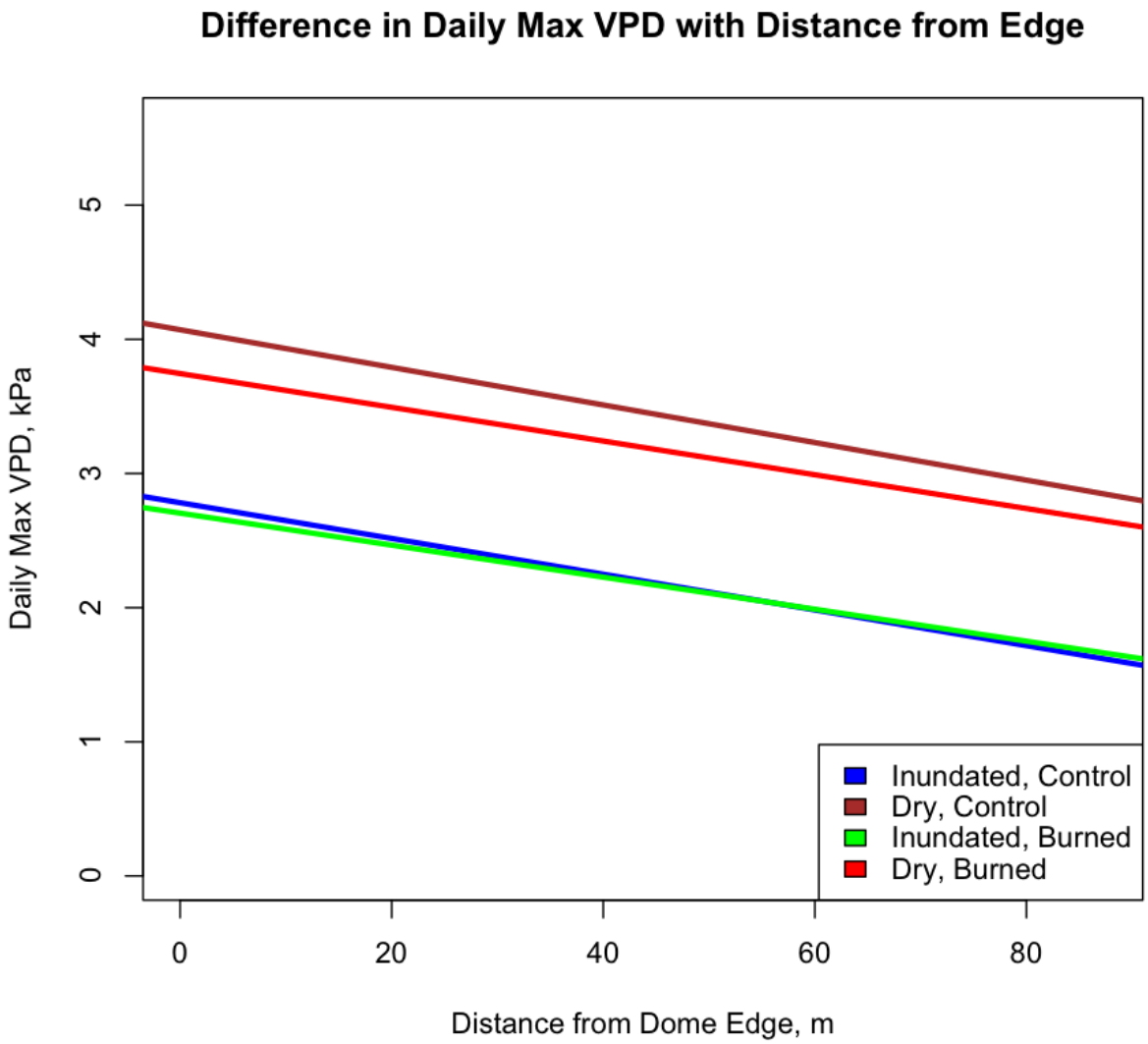

Figure 3-9. Illustration of regression models showing response of vapor pressure deficit (VPD) to increasing distance from dome edge under the four different season/treatment combinations.

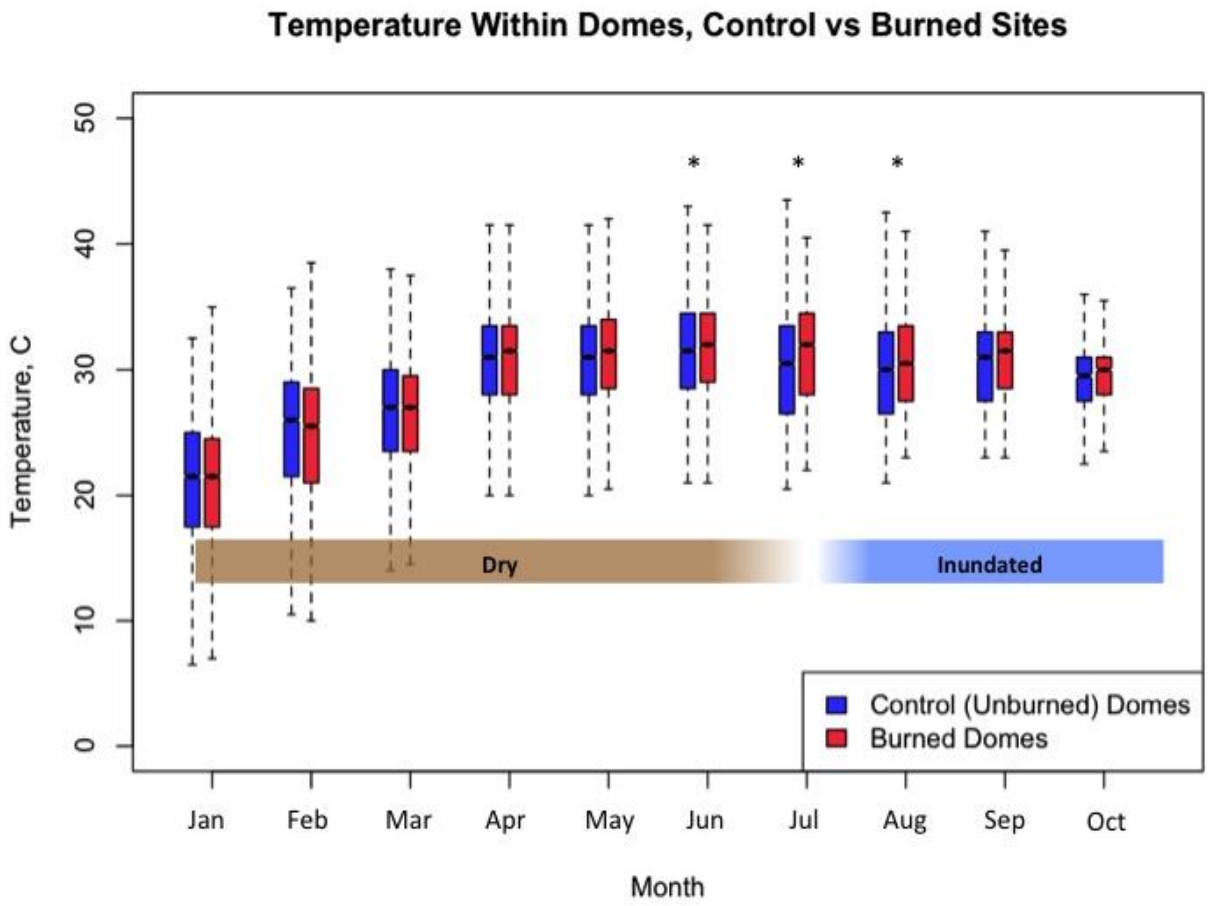

Figure 3-10. Boxplots of temperature readings collected at mid-transect or dome-center sampling locations within cypress domes by month, January – October 2011. Boxes represent upper and lower quartile values; whiskers show ± 1.5 interquartile range. Notches at median values for each month indicate significant differences among non-overlapping groups (McGill et al. 1978); outliers not shown. Asterisks (*) indicate significant differences in maximum daily temperature readings between treatments for a given month (Kruskal-Wallace test, $p < 0.05$).

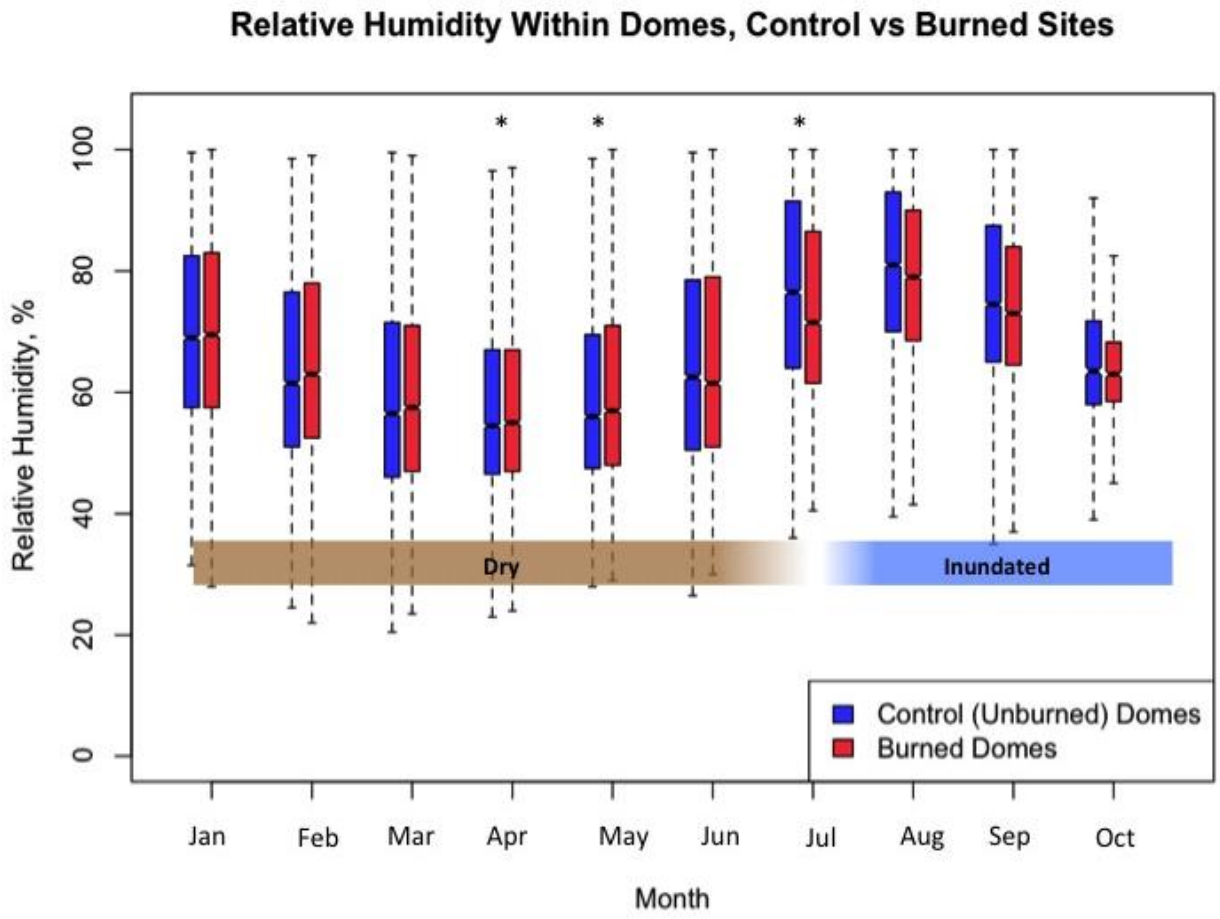

Figure 3-11. Boxplots of relative humidity readings at mid-transect or dome-center sampling location within cypress domes by month, January – October 2011. Boxes represent upper and lower quartile values; whiskers show ± 1.5 interquartile range. Notches at median values for each month indicate significant differences among non-overlapping groups (McGill et al. 1978); outliers not shown. Asterisks (*) indicate significant differences in minimum daily RH readings between treatments for a given month (Kruskal-Wallace test, $p < 0.05$).

Figure 3-12. In the months following the Deep Fire, interiors of burned cypress domes displayed simplified structure, and enhanced wind and insolation.

Figure 3-13. By two years following the Deep Fire, understory regrowth in burned domes was vigorous.

Table 3-1. Canopy leaf status and inundation for study sites by month, 2011.

Month	Leaf Status	Inundation Status
January	Off	Dry
February	Off	Dry
March	†	Dry
April	On	Dry
May	On	Dry
June	On	Dry
July	On	†††
August	On	Inundated
September	On	Inundated
October	†	Inundated
November	Off††	Inundated††
December	Off††	Inundated††

Notes: † Leafout began during March for most trees, but full canopies were not in place until the end of the month; similarly, senescence began in October but abscission was not complete until November. †† Data were unavailable for November and December. ††† Most domes inundated by mid-month.

Table 3-2. Mean and standard deviations for temperature and relative humidity observations in study domes, January – June 2011.

Dome Label	Sensor Nos.	Size, ha	Jan-June Mean Temp, RH Exterior	Jan-June Mean Temp, RH at Edge	Jan-June Mean Temp, RH at ¼ Diameter; Distance, m	Jan-June Mean Temp, RH at Center; Distance, m	Condition
T1	25 – 28	0.67	28.7 (0.1) °C 57.1 (0.3) %	28 (0.1) °C 59.6 (0.3) %	27.3 (0.1) °C 62.6 (0.2) %; 22.5 m	26.9 (0.1) °C 63.3 (0.3) %; 45 m	Control
T8	29 – 32	0.71	28.3 (0.1) °C 57.9 (0.3) %	28.8 (0.1) °C 58.4 (0.3) %	27.3 (0.1) °C 62.9 (0.3) %; 22 m	27.1 (0.1) °C 63.2 (0.2) %; 44.5 m	Control
T4	33 – 36	0.56	28.8 (0.1) °C 57.6 (0.3) %	28.6 (0.1) °C 58.5 (0.3) %	26.9 (0.1) °C 62.7 (0.3) %; 22.5 m	26.8 (0.1) °C 63.3 (0.2) %; 44.5 m	Control
T7	37 – 40	1.74	26.1 (0.1) °C 58.5 (0.4) %	29.3 (0.1) °C 57.3 (0.3) %	28.6 (0.1) °C 59.8 (0.3) %; 32 m	28.2 (0.1) °C 60.5 (0.3) %; 63.5 m	Control
T5	41 – 44	2.14	28.7 (0.1) °C 57.9 (0.3) %	28.7 (0.1) °C 59.2 (0.3) %	26.6 (0.1) °C 64.6 (0.3) %; 44 m	26.7 (0.1) °C 64.9 (0.3) %; 87.5m	Control
T6	45 – 48	1.77	29.3 (0.1) °C 56.3 (0.3) %	28.8 (0.1) °C 59.4 (0.3) %	28.3 (0.1) °C 61.1 (0.3) %; 30.5 m	27.2 (0.1) °C 63.1 (0.3) %; 61 m	Control
54	1 – 4	0.92	28.5 (0.1) °C 58.3 (0.3) %	27.7 (0.1) °C 60.8 (0.3) %	27 (0.1) °C 62.9 (0.2) %; 25.5 m	27.1 (0.1) °C 62.3 (0.3) %; 51 m	Burned
C2	5 – 8	1.87	28.2 (0.1) °C 59.5 (0.3) %	28.1 (0.1) °C 59.9 (0.3) %	27.9 (0.1) °C 60.5 (0.3) %; 32 m	26.8 (0.1) °C 63.9 (0.3) %; 64 m	Burned
C4	9 – 12	1.77	28.8 (0.1) °C 57.4 (0.3) %	28.8 (0.1) °C 57.4 (0.3) %	27.2 (0.1) °C 63.8 (0.2) %; 35.5 m	27.4 (0.1) °C 62.3 (0.2) %; 71 m	Burned
C3	13 – 16	0.59	28.3 (0.1) °C 59 (0.3) %	28.2 (0.1) °C 58.8 (0.3) %	28.2 (0.1) °C 60.1 (0.3) %; 21.5 m	28.1 (0.1) °C 60.9 (0.3) %; 42.5 m	Burned
C1	17 – 20	1.81	28.9 (0.1) °C 58.5 (0.3) %	28.2 (0.1) °C 60.6 (0.3) %	27.2 (0.1) °C 63.6 (0.2) %; 33.5 m	25.8 (0.1) °C 75.9 (0.3) %; 66.5 m	Burned
C5	21 – 24	0.59	28.1 (0.1) °C 60.6 (0.3) %	27.6 (0.1) °C 61 (0.3) %	27.4 (0.1) °C 63.1 (0.2) %; 20 m	27.8 (0.1) °C 61.7 (0.3) %; 40 m	Burned

Table 3-3. Results of pairwise comparisons among daily maximum temperature and daily minimum relative humidity values in contrasting hydrologic conditions for both treatments.

	Control (unburned) Domes				Burned Domes			
	Max. Temp		Min. RH		Max. Temp		Min. RH	
Comparison	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
Exterior – Edge	*	No	No	No	No	No	No	No
Edge – Mid	*	*	*	*	*	*	*	*
Mid – Center	*	No	*	No	No	No	*	No
Exterior – Mid	*	*	*	*	*	*	*	*
Exterior – Center	*	*	*	*	*	*	*	*
Edge – Center	*	*	*	*	*	*	*	*

Notes: Mid = midpoint of a transect extending from dome center to edge (i.e., positioned at ½ of radius); Wet = inundated conditions (i.e., observations from August – September); Dry = non-inundated conditions (i.e., observations from April – May); during both periods, canopy leaves were present. Tukey's W test ($\alpha = 0.01$) used for comparisons; an asterisk (*) indicates significant differences. Values for temperature were lower and humidity higher at the location closer to the center of domes.

Table 3-4. Linear regression of microclimate parameters by distance from community edge, control (i.e., unburned) sites.

Model	Season	Coefficient	Intercept	R^2
Daily Max ΔTemp ~ DFE, Control	Wet	0.014	4.81	0.02
Daily Max ΔTemp ~ DFE, Control	Dry	0.022	4.82	0.07
Daily Max ΔRH ~ DFE, Control	Wet	0.059	16.12	0.03
Daily Max ΔRH ~ DFE, Control	Dry	0.070	15.28	0.05
Daily Max ΔTemp ~ DFE, Burned Sites	Wet	0.016	3.26	0.04
Daily Max ΔTemp ~ DFE, Burned Sites	Dry	0.034	2.89	0.20
Daily Max ΔRH ~ DFE, Burned Sites	Wet	0.069	10.19	0.09
Daily Max ΔRH ~ DFE, Burned Sites	Dry	0.161	6.89	0.21

Notes: DFE = distance of a given location from the cypress dome edge (m); Daily Max ΔTemp and Daily Max ΔRH represent daily observations at which differences in maximum temperature (°C) or relative humidity (RH, %) are greatest between a given location within a dome (edge, mid-transect, center) and the reading recorded external to a given dome. Comparisons are for periods when canopy leaves were present (i.e., April – May for dry periods, August – September for inundated (wet) periods).

CHAPTER 4
ORGANIC SOIL COMBUSTION IN CYPRESS SWAMPS: MOISTURE EFFECTS AND LANDSCAPE IMPLICATIONS FOR CARBON RELEASE

Background

Extended droughts across large areas have contributed to headline-generating wildfires in recent years, including across large areas of North America (Mack et al. 2011, Leahy 2012) and Siberian Russia (Doyle 2010, Kramer 2010). Severe droughts can create conditions sufficient for wildfire to spread into areas normally inundated or too wet to support combustion, which often contain soils with high organic content (de Groot 2012). In addition to the flaming combustion associated with combustion of aboveground vegetation, ground fires can occur in which organic soils are consumed via smoldering combustion. The dynamics, controlling parameters, and consequences of ground fires are far less understood than their surface and aerial fire counterparts. Yet the ecological impacts posed by smoldering combustion to ecological processes as well as public health (Rappold et al. 2011) and safety (e.g., Abdel-Aty et al. 2011) are considerable, and may be expected to increase if ground fire activity grows in response to changing climatic conditions as predicted (IPCC 2007). Thus an improved understanding of factors influencing smoldering combustion, as well as expanding the study of ground fires to more ecosystems in which they occur, will be important in a future marked by increased occurrence of wildfire and so-called “megafires” (National Interagency Fire Center 2009).

In contrast to flaming combustion, which typically lasts a fraction of an hour at a given location, smoldering combustion is a flameless form of combustion that can persist for long periods (Ohlemiller 1995). Smoldering ground fires can continue in

organic soils, such as peat—soil developed from accumulated biomass (Joosten and Clarke 2002; Hurt et al. 2003)—for many days, or even months in cases such as Indonesia's anthropogenic Kalimantan peat fires in 1997 (Page et al. 2002, Usup et al. 2004) and the naturally ignited fire in Georgia's Okefenokee Swamp (burning in "muck" soils from 28 April 2011 until at least February 2012; Florida Times-Union 2012). Despite typically lower temperatures for smoldering combustion compared to flaming combustion (500 – 700 °C versus 1500 – 1800 °C; Rein et al. 2008), smoldering fire persistence can eventually transfer more heat to surrounding soils and plants than flaming combustion, and can produce significant ecological effects both because of the long residence time and their occurrence in the rooting zone (Rein et al 2008), where plants have few adaptations to withstand fire. Sustained smoldering can occur in peat soils with far higher moisture content than those which would support flaming combustion in other fuel classes. Peat formed by accumulated Sphagnum spp., for example, may display persistent smoldering even at a moisture content above 120% (Frandsen 1997), and McMahon et al. (1980) found Florida organic soils to support smoldering at moisture levels of 135%.

The combination of heating, direct consumption of roots embedded in organic soils, and organic soil loss to combustion (Figure 4-1) can result in significant damage and mortality to trees (Hartford and Frandsen 1992, Stephens and Finney 2002). In landscapes with low topographic relief, soil-consuming fires also may produce significant hydrologic consequences. Where subtle changes in elevation can significantly affect hydroperiod, vegetation communities or wildlife species may experience change due to the change in soil elevation from ground fires (Cook and

Ewel 1992, Watts et al. 2012). Ground fires could change the volume of depressional isolated wetlands, with hydrologic consequences for the surrounding landscape: given a set amount of water delivered to a landscape via precipitation or overland flow, greater depressional storage volume may provide increased water availability proximate to basins, while limiting availability to higher-elevation areas of landscape.

Implications of ground fires extend beyond local scales. Peat soils represent accumulation of plant biomass over many decades to centuries or longer, as flooded or otherwise anoxic conditions have retarded their decomposition. Ground fires may release far more carbon to the atmosphere than fires that consume standing vegetation alone (Langmann and Heil 2004). Existing efforts to quantify the potential for carbon sequestration on public lands as a means of mitigating anthropogenic CO2 emissions (e.g., Depro et al 2008, Failey and Dilling 2010) will further increase interest in soil-consuming fires among managers who may be charged with preventing them or accounting for their effects on ecosystem carbon pools.

Future climate change scenarios predict drought events of greater severity and frequency in many areas, including those with the potential for ground fires to occur (Running 2006, Liu et al. 2010). Despite studies of ground fire effects and behavior in Indonesian forests (Page et al. 2002), Canadian peatlands and boreal forests (Benscoter et al. 2011), and a handful of North American ecosystems (Reardon et al. 2007), many additional peat-based ecosystems (i.e., those occurring on soils with > 30 cm of peat, Page et al. 2011) exist and are susceptible to ground fires. Our understanding of fire effects in these peat systems is nearly nonexistent. One example of regionally important ecosystems with peat soils in the southeastern U.S. and portions

of Mexico are swamps dominated by cypress trees (genus *Taxodium*). Cypress swamps have long hydroperiods that promote development of organic soils, but occasionally experience severe droughts that expose them to the occurrence of ground fires as frequently as every 100 – 150 years (Snyder 1991). The widespread occurrence of small (<10 ha) circular-shaped cypress swamps amid upland communities with frequent fire regimes provides ample potential ignition sources, making these embedded ecosystems good models for increasing our understanding of smoldering combustion and its consequences.

Vegetation structure, soil elevation, and severity of drought-condition wildfire in cypress swamps are influenced by landscape position, edge effects, and swamp size (Watts et al. 2012). Compared to their edges or adjacent upland communities, locations toward the centers of cypress swamps are cooler, more humid, and slightly lower in elevation, with taller and larger-diameter trees (Watts 2012). The biophysical consequences of these spatially explicit factors—higher humidity, lower temperature, and decreased insolation due to larger canopies (Kira et al. 1969)—would appear to influence soil moisture, and therefore peat fuel availability and combustion (although increased evapotranspirative losses from larger trees may counteract predicted differences). Lower elevations toward centers of domes act as physical sinks for water and nutrients, and increased hydroperiods limit decomposition due to longer periods of anoxic soil conditions. Thus while landscape and structural factors might lead to the expectation of increased soil moisture toward the centers of desiccated swamp patches, nutrient-driven productivity increased and anoxia-limited decomposition may lead to higher biomass accumulation and levels of soil organic carbon (SOC) content with

increased distance from swamp edges (but see Burns 1984 for a conflicting view). Together, these factors may oppose one another in affecting the degree to which distance from swamp edge impacts peat fuels consumption in depressional cypress ecosystems.

This study investigates SM and SOC effects on smoldering combustion in extracted samples of peat from cypress swamps, and predicts consequences to soil carbon pools and modeled local hydrologic factors. Specifically, I address the following questions and predictions:

1. What are the influences of SM, mineral, and SOC content on degree of combustion of peat found in Florida cypress swamps? I predicted a strong negative influence of SM on depth of combustion and SOC combustion, and a positive influence of SOC on depth of combustion.

2. How do SM, mineral, and SOC values change according to swamp size, edge distance, and depth? Is it possible to use predictive relationships among SM and/or SOC values and soil consumption to determine whether potential combustion could vary according to landscape position within the swamp?

3. What are the implications of soil-consuming fires for release of SOC at the landscape scale?

Materials and Methods

Study Site

In a low-relief, carbonate platform region of southern Florida USA, Big Cypress National Preserve comprises 300,000 ha, and contains many hundreds of distinct wetland forest patches dominated by pond cypress (*Taxodium distichum* var. *imbricarium* [Nutt.]; Figure 4-2). These elongated strands and circular or teardrop-

shaped patches (the latter technically fens) tend to be separated by higher-elevation communities of slash pine (*Pinus elliottii* var. *densa* [Little and Dorman]) flatwoods or transitional pine rocklands, or graminoid prairies dominated by muhly grass (*Muhlenbergia capillaris* [Lam]) or sawgrass (*Cladium jamaicense* [Crantz]). These flatwoods or prairie communities typically experience natural or anthropogenic prescribed fires every 2-6 years (Abrahamson and Hartnett 1990, Snyder et al. 1990), with the former type occurring most often during the onset of the region's rainy-season thunderstorms in the late spring. Precipitation drives regional hydrology, which follows a strongly seasonal pattern: with frequent inundation and occasional sheetflow occur during the wet summer months during which 70% of rainfall occurs (Duever et al. 1986), followed by a dry season and retreat of water levels below the surface in all but the lowest elevations within marshes and swamps. Long hydroperiods allow buildup of a layer of organic matter in the form of fibric peat that can exceed 1 m in thickness over the region's calcareous soils in the centers of small depressional wetlands—called domes because of their characteristic structure, probably dictated primarily by hydrologic and edaphic factors (Kurz and Wagner 1953) and exaggerated by mortality and topkill from fires (Watts et al. 2012)—and 2 m in thickness in larger strands or slough-swamps (Duever et al. 1986). During drought conditions, the peat accumulated within cypress swamps may dry sufficiently to support combustion (Ewel 1995).

Mineral soils in the region are derived from shallow Tamiami and Fort Thompson carbonate rocks of Pleistocene age. The resulting calcareous mineral soils contain ca. 20% insoluble material (primarily quartz; A. Watts and J. Martin, *unpublished data*). In upland communities adjacent to cypress swamps these soils are very thin, often

occurring only within crevices in exposed carbonate rock. Despite very shallow landscape relief (ca. 5 cm/km mean north-south bed slope), these soils occur in thicker deposits in the bowl-shaped depressions in which cypress domes occur. Over these mineral soils lies accumulated organic matter, which may occur as histic epipedon near edges of swamps or fibric peat in thicker deposits, which are still quite shallow in comparison with peats from boreal regions or some areas of the tropics (e.g., Page et al. 2011). An abrupt transition typically exists between organic and mineral horizons, yet quartz sand and carbonate particles occur in the soil profile due to bioturbation and sediment transport from surrounding uplands (although contribution from the latter is likely minor due to minimal transport velocities). These mineral inclusions in the peat profile would be expected to exert a negative influence on combustibility, as described by Frandsen (1987) and Reardon et al. (2007).

Sample Collection and Combustion

In May and June 2011, near the end of a historic drought and active wildfire season in the region, we collected 14 cylindrical, monolithic samples of fibric peat profiles from cypress domes within the Preserve for lab combustion experiments (Figure 4-3, 4-4). Samples were collected by cutting a ca. 20 cm-diameter circle into the soil profile, and inserting a waxed-cardboard tube until the encompassed profile included the extent of organic-derived soil.[5] Intact cores were then excavated with a shovel, protected in vapor-barrier containers, and transported on ice to a cold room where they were stored at 1 – 2 °C pending combustion. The position of each sample within a

[5] Actual diameter of samples varied according to interior dimensions of cardboard tubes, which measured 18.5 – 21.0 cm in diameter.

circular pondcypress dome was recorded, and the distance to the edge of the community recorded.

The day prior to combustion, these peat monoliths were removed from cold storage to allow equalization to ambient lab temperature (24 °C), which was set to match within 1 – 2 °C of diurnal temperatures found in soils during sample collection. Monoliths were placed in aluminum trays and the waxed-cardboard sleeves removed. We assessed soil moisture by collecting subsamples from each monolith collected at three depth ranges: 0 – 10 cm, 11 – 20 cm, and 21 – 30 cm. The 10 cm stratifications were determined based on the preponderance of small roots to approximately this depth, and following the methods of Reardon et al. (2007). Samples were then dried to constant weight at 70 °C; subsequently, these subsamples were combusted in a muffle furnace at 500 °C for 8 hours to determine loss on ignition (LOI), the relatively low combustion temperature being preferred in the instance of soil with significant calcareous mineral content, as higher temperatures could introduce error due to mineral content contributions. Change of organic carbon content based on furnace or smoldering combustion was calculated using the equation

$$SOC = (0.40 \pm 0.01 * LOI) + (0.0025 \pm 0.0003* LOI) \quad 4\text{-}1$$

where SOC = soil organic carbon (expressed as percent), and LOI = loss on ignition (Craft et al. 1991); i.e., the loss of mass in an oven-dried soil sample subjected to complete combustion.

Vertical sides of the cylindrical monoliths were wrapped in a layer of 8cm fiberglass insulation; in addition to supporting sides of the sample and preventing collapse during combustion, the insulation reduces convective and radiative heat loss

during combustion and better simulate *in situ* conditions (Reardon et al. 2007, Benscoter et al. 2011). Wrapped samples were placed outside in a wind-sheltered location on a day when forecast conditions conformed to those typically found in their parent locations near the end of the dry season, which is the typical wildfire season (i.e., 32 – 34 °C, 30% – 40% relative humidity, calm wind). The ignition source for smoldering experiments was an electric heating element in a half-loop shape, with 500W output (sufficient to initiate smoldering combustion in pilot experiments). The element was situated with the terminal portion embedded 4 – 5 cm into the soil profile (approaching the depth limit for sustained smoldering in duff, Miyanishi 2001) along one side of the sample, and the remaining portion angled above the sample surface (Figure 4-5). This arrangement simulated both the initiation of smoldering combustion via radiative heat transfer from flaming combustion (i.e. passage of the flame front through aerial fuels), as well as propagation of the smoldering front through the soil matrix (Rein et al. 2009) or via embedded solid fuels and conductive heat transfer (e.g. branches, roots). Current was applied to heating elements for 5 minutes to simulate the approximate burnout time of small branches which may serve as combustion vectors (and based on the Benscoter et al. (2011) study in boreal sphagnum peat), after which time they were carefully removed.

Post-Combustion Processing And Data Analysis

After samples had finished burning and had cooled, they were returned to the lab where they were weighed to determine mass loss due to combustion. Volume loss was calculated by determining change in height based on five averaged measurements of the post-combustion soil surface, based on pilot experiments indicating that combustion was not uniform in depth across the entire face of the monolith. To measure height of

the resulting organic matter constituting the soil surface as opposed to the top of the resulting ash layer (which may be multiple centimeters thick depending on soil mineral content but which is highly porous and friable), a force of 1.5 N over a 1 cm^2 area was applied using a weighted dowel. Measurements of SM and OC content obtained for each sample for three profile depth ranges, and pre-fire volumetric measurements of monolithic soil samples, were used in conjunction with dry bulk density measurements at corresponding depths to estimate SOC storage within each soil profile "layer." SOC loss due to smoldering combustion was calculated using sample mass loss and measurements of SM and OC from the three 10 cm-thick "layers" analyzed from each monolith sample. Regression analyses were performed using data from the monolith combustion to determine relationships, if any, between combustion depth or volume or mass loss and hypothesized predictor variables of soil moisture at various depths (Sokol and Rolfe 1995, p. 455). Models were compared using Akaike's corrected information criterion (Burnham and Anderson 2002, Crawley 2007) to compare model performance.

To permit characterization of SM under typical field conditions and organic carbon content in relation to landscape position and profile depth, a second set of 134 samples were collected from 34 cypress domes. Samples were collected at a variety of distances from community edges and at four depths (0 – 5 cm, 6 – 10 cm, 11 – 15 cm, and 16 – 20 cm) at each location. To reduce possible diurnal effects on soil moisture, all samples were collected during a 3-hour period (1200-1500) on two subsequent days during which temperature and humidity profiles were nearly equal, and precipitation had not occurred for at least one month prior to sampling. Upon collection, samples were placed

in vapor-barrier bags and transported on ice to a laboratory where they were analyzed for field moisture content (i.e., weighed, then oven-dried at 70 °C to constant weight and weighed again). These samples were then burned in a muffle furnace at 500 °C for 8 hours to determine organic matter loss. Change of organic carbon content was calculated using equation 4-1. To determine whether soil moisture values or SOC content varied according to position with respect to patch edge (i.e., edge, center, or halfway between the two), landscape position was used as the basis for comparisons of these variables at each of the four depths sampled. Due to the presence of unequal sample sizes (e.g., some locations at edges were not sampled to 20 cm depth due to a lack of soil), Dunnett's (1980) modified Tukey-Kramer multiple pairwise comparison tests were used; these tests account for unequal variance and sample size. Implementation of this procedure was facilitated by the DTK package in program R (R Development Core Team 2005). Next, regression analyses were performed to determine the degree to which edge distance and profile depth predicted soil moisture or organic carbon content. Models developed from the combustion experiment were used to estimate the potential for carbon release and soil surface height changes given the snapshot of soil moisture values obtained from these samples.

Landscape Extrapolations

Finally, a third set of volumetric core samples (N = 21) collected from a subsample of cypress domes were sectioned at 5 cm increments to determine bulk density and porosity for subsequent estimation of soil physical properties. To estimate potential implications for carbon storage and emissions, soil physical properties and relationships between combustion and variables measured in these experiments were extrapolated to the Big Cypress landscape. For this purpose, individual measurements were made of

spatial attributes for three separate landscape blocks representative of community mosaics where fire-dependent upland ecosystems are juxtaposed with depressional wetland patches underlain by thick peat soil. Each block measured 1.5 x 1.5 km (225 ha), containing a total of 165 distinct patches (Figure 4-6). Heads-up classification (Wolf and Dewitt 2000) of 2.5 m resolution images from SPOT (Satellite Pour l'Observation de la Terre) was used for remote measurements of the sizes of individual domes based on community edges. Ground-truth testing using Wide Area Augmentation System (WAAS) enabled GPS in this area (Watts et al. 2012) indicated high degree of accuracy (90 – 95%) of this method in both measurement of the area of landform depressions and in the co-occurence of easily-discernable community boundaries with organic soils of ca. > 5 cm thickness. SOC on a per-m^2 basis for Big Cypress peat, based on monolith and volumetric samples, was used to estimate SOC at the landscape scale using remote measurements of dome area. C release from smoldering was scaled to the landscape using these values and emissions modeled using results obtained from smoldering experiments and mean SM values at upper and middle soil layers found among the from the 134 field-moisture samples.

Results

Monolith Sample Combustion

The 14 monolith soil samples ranged from 20 – 39.5cm in pre-fire height. Subsample analysis indicated highly variable field soil moisture values, from a minimum of 36.4% in the upper 10 cm to a maximum of 268% at a depth of 11–20 cm in one sample. Pearson's correlation test performed on SM values observed at 0-10 cm depths and 11–20 cm depths found little relationship between the two (0.158), although SM at 11–20 cm was highly correlated (0.760) with SM at depths of 21–30 cm. Calculated

SOC content as a percentage of profile-layer mass ranged from 4.75% to 36.25% (Table 4-1).

Smoldering combustion, initiated by the electric heating element, generally proceeded simultaneously outward from the element as well as downward, although these observations were not quantified by measurements. None of the predictor variables (soil moisture, SOC content, or mineral content), regardless of depth at which they were measured, were statistically significant predictors of soil consumption as measured by change in soil-surface height. When soil consumption due to smoldering was measured by SOC loss normalized to area, the best-fit regression model indicated significant negative relationships between soil moisture and consumption ($P < 0.01$). Addition of the soil moisture at depths of 11 – 20 cm, while not itself a parameter with significant predictive power, provided the best-fit model (Figure 4-7):

$$SOC^* = -9.66 \cdot SM0\text{-}10 - 5.75 \cdot SM11\text{-}20 + 9897.8 \qquad 4\text{-}2$$

Where SOC* represents SOC consumed, expressed as $kg \cdot m^{-2}$, and SM0-10 and SM11-20 are soil moisture values observed at depths of 0 – 10 cm and 11 – 20 cm, respectively.

Landscape Position, Soil Properties, and Landscape Extrapolations

A total of 134 samples from 34 cypress domes were collected to establish relationships between soil moisture and SOC. Soil moisture and SOC values displayed high variance, and groups of samples from a given depth did not differ significantly in moisture or OC content depending on where along the radial dome transect they were collected. Regression modeling indicated a significant predictive relationship between a given sample's distance from the dome edge (i.e., toward the dome's center) and soil moisture values found in the upper 10 cm of soil ($P < 0.01$; Figure 4-8).

Values of soil moisture down the soil profile found from these samples in the upper 10 cm of soil (mean 105.8%, s.d. 60.8) and in the layer at 11 – 20 cm deep (mean 82.2%, s.d. 50.4), and the best-fit model of SOC consumption based on monolith combustion, allowed estimations of potential SOC loss under scenarios of observed soil moisture values across the landscape (Table 4-2). Given the range of observed soil moisture conditions, and variance in estimations introduced by varying peat depth and moisture by landscape position modeled peat SOC combustion are predicted between 2.78 and 5.55 kg m^2 (with a value of 4.18 kg m^2 based on sample means) in the peat soils of cypress domes. Based on the landscape area comprised of peat soils, widespread fires that ignited soils under these conditions of soil moisture could release large quantities of SOC during smoldering combustion.

Discussion

Although expectations of this study were that smoldering consumption in peat soil could be represented by height change and predicted by soil moisture or inorganic mineral content (Frandsen 1987, 1997), this study could not establish a relationship between these predictor variables and depth of burn. This finding may have been due to variations in physical properties such as bulk density and porosity among upper layers of soil samples, which can affect smoldering due to impacts on heat transfer and air flow. These variables were not measured in the monoliths collected for combustion, and future studies should attempt to incorporate them to determine their relative influence on peat smoldering. While an effort was made to collect samples that did not contain large roots or embedded coarse woody fuels (i.e., larger than approximately 25 mm diameter), their undetected presence in samples could have contributed to the formation of combustion vectors and (once consumed) air pipes (Rein et al. 2008) causing

variation in combustion depth. Additionally, mineral content for 21 – 30 cm layers was near the limit for sustained smoldering combustion in organic soils, particularly given the moisture values observed. The combination of mineral and moisture content for the 11 – 20 cm layers also was near this lower limit (J. Reardon, personal communication); under these marginal conditions it may be that the measured changes in soil surface incorporated sufficient uncombusted mineral ash that depth of burn measurements were decoupled from organic matter combustion. Findings from this study do refine our understanding of the moisture levels at which cypress peat will experience smoldering combustion, however: five samples underwent sustained smoldering at moisture levels above 150%. The wettest sample displayed 9cm of combustion depth despite a moisture content of 250%. It is worth noting that observed SM values in the upper layer of soil samples bore little correlation to those at lower depths: factors such as plant rooting depths and evaporation are likely to be among the explanations for this unexpected observation.

Soil organic carbon released due to smoldering combustion was predicted by soil moisture content in the upper 10 cm of soil samples, with SM at depths of 11 – 20 cm improving regression model performance without itself being a significant predictor. This finding may have been due to the majority of samples experiencing consumption only of the upper 10 cm of soil (and an additional two samples with combustion depths of 11 – 12 cm, where moisture levels may have resembled those in the upper layer). SOC content could provide an alternative means of assessing combustion in soils where variations in soil physical properties cause problems for estimating soil height change in situ. Additionally, estimating combustion effects more explicitly in terms of SOC loss

may help to reduce some of the uncertainties related to scaling issues that result from landscape-wide studies of smoldering. For example, rather than assuming a homogeneous depth of burn across a large burned area in order to estimate C emissions (e.g., Page et al. 2002) and then deriving C emissions from those parameters, known or inferred pre-fire soil data—even estimates available from remote-sensing assets, such as drought index, or SM estimates based on weather information—could assist in refining assessments of the carbon impact of large peat fires. Combining spatially-explicit estimates of important determinants of combustion such as SM and SOC with values for mineral content and peat texture, of they are known , would be a particularly valuable improvement over previous scaling attempts.

Soil moisture values in the upper 10 cm of soil profiles, a significant predictor of SOC release, increased with increasing distance from the edge of a wetland forest patch toward its center. This landscape position trend was weak, however, with no significant difference found based on whether a given sample originated in the center of a cypress dome, at its edge, or midway between. Therefore a weak edge distance effect may present some problems for scaling up C emissions from smoldering combustion across the landscape, where the center portions of larger patch sizes may mitigate the effects of drought (the extent to which this effect may depend on soil elevation is unclear). However; the snapshot of soil moisture values observed in this study may permit a first-order approximation of the potential for C release from smoldering combustion in the cypress peat soils of the study area's patchy landscape. On a given day when moisture conditions display similar means to those observed among the set of

134 field-moisture samples, C release potential from smoldering combustion of soils alone is modeled at a normalized 4.18 kg m^{-2} in cypress domes.[6]

This estimate is not without errors associated with landscape scaling of laboratory measurements, particularly due to the heterogeneous nature of fire events (and especially ground fires). However, this figure may be conservative in its estimation for a number reasons: first, samples were collected as far as practical from trees, in order to avoid problems of sample collection caused by the presence of large roots close to trees. Because litter and duff often collect in greater amounts close to the bases of trees, it is likely that samples collected from these locations would possess greater depths of low-mineral peat; including such estimates in an analysis would probably increase estimates of combustion potential at larger spatial scales. Also, Rein et al. (2008) describe areas closer to trees as likely to experience higher levels of soil consumption, due to the withdrawal of water by roots (and see Figure 4-1). Also, soil samples for landscape-level SM estimations were collected in late April, and the study area remained under a drought for nearly two more months. The potential for soil consumption would be considerably higher as the dry season approached its end; indeed, the 2011 Jarhead Fire (14,000 ha) entered every cypress dome within the fire perimeter, in some cases consuming >1m of accumulated peat. The widespread presence of coarse woody debris (Figure 4-4), which can serve as ignition vectors, was not considered in this study. When these fuels are ignited by passing flame fronts and transition to smoldering, they can promote the initiation of smoldering. Then, as they are

6 The region's calcareous mineral soils also contain vast quantities of inorganic C. During combustion above approximately 900 °C the mineral structure of calcite and aragonite of carbonate minerals begins to break down, releasing inorganic C (Heiri et al. 2001); however, during the lower temperatures associated with smoldering combustion, mineral C is likely to be retained and liberation of mineral C should be minimal.

reduced to ash (often relatively quickly compared to surrounding peat), the channels they leave behind can become air conduits to support continued smoldering. While the ignition method (conductive heat transfer for an extended period) provided some simulation of this phenomenon, the contribution of these transitional fuels to smoldering and its maintenance should be considered in future studies. Finally, the conversion rate used in this study for calculating SOC for cypress peat soils (approximately 41%) is somewhat conservative compared to estimates of carbon concentration for various peat soils in studies surveyed by Page et al. (2011), which frequently exceed 50%.

Additional sources of uncertainty in this study include the inability of laboratory methods to replicate certain behaviors observed in smoldering of organic soils and peats. The progression of smoldering downward, sometimes leaving a thin upper layer of soil completely unconsumed, has not been reproduced in laboratory studies (G., Rein, personal communication). Likewise, the highly variable nature of combustion depths observed in many instances remain to be quantified in a spatially explicit manner. Because of the vast amount of carbon contained in these fuels, improving scaled estimates of combustion of organic soils and peats through the use of such estimates would reduce uncertainties associated with extrapolating to the extent of large burned areas. Also, the fate of combustion products is unaccounted for in this and most other studies of organic soil smoldering. While the majority of carbon from smoldering peat is converted to atmospheric CO2 and CO, some emissions have been reported to reside in soils following combustion (e.g., Massman et al. 2010), while other organic carbon species may be formed and precipitated into unburned soil particles. An improved understanding of the partitioning of combustion products of organic soils

would be a valuable addition to future estimates of atmospheric emissions from smoldering fires.

The approach described herein for estimating SOC loss from smoldering arrives at mean consumption of 4.2 kg m^{-2} in cypress swamps based on conservative estimates of peat depths away from the bases of trees; also carbon concentration estimates are at the low end of values used for peats, while values for soil moisture used in estimating potential combustion are probably higher than those found nearer the end of the region's dry season. Even with these conservative parameters, the consumption of SOC from smoldering in cypress peats in this study is estimated to be considerably higher than the 3.2 kg m^{-2} consumption estimated in boreal organic soils such as Canadian Sphagnum peat (B. Benscoter, personal communication).

Globally, organic soils and peats may store as much as 6.1×10^{17} g of terrestrial C, representing between one-fifth and one-third of the planet's terrestrial organic carbon (Gorham 1994, Page et al. 2011). This is approximately the same mass of C as that contained in Earth's atmosphere, despite peatlands occupying only 3% of its surface. Effects of fires in these ecosystems are of concern due to their potential for enormous carbon release to the atmosphere: Kasischke et al. (2005) estimated annual C emissions from boreal forest and peat soils to be $1.1 – 2.1 \times 10^{12}$ g, for example. The contribution from smoldering combustion to global releases of terrestrial carbon to the atmosphere may increase under scenarios of warming and drying climatic conditions (Gorham 1991, IPCC 2007). The implications for contributions of peat fires to the global carbon cycle and global warming scenarios are even more striking when one considers that smoldering combustion in peats may consume carbon that has accumulated over a

period of hundreds to thousands of years, in comparison to carbon release during flaming combustion of fuels that have accumulated in aboveground biomass much more recently (i.e. years to decades, generally).

The role of soil moisture in determining the release of C from smoldering in cypress peat soils is of particular importance in regard to the global impact of ground fires. Even ground fires that are small in area have the potential for large carbon emissions, especially in some larger cypress swamps where peat deposits may reach 3m. Seasonally variable hydrology found in the range of many cypress swamps and tropical peatlands places large quantities of soils at the threshold of availability for smoldering combustion during dry seasons and droughts. Because drought conditions also are a driver of large fires (Slocum et al. 2010), emissions from smoldering combustion in deep organic soils may display a geometric response to drought severity as fire size and spread through deeper layers of the soil profile. Increasing the challenges to managers tasked with dealing with such fires are the large volumes of water required to change soil moisture values at intermediate depths (e.g., beyond 20 cm and increasing moisture to > 250%), which makes the effects of droughts on the potential for smoldering combustion long-lasting and resilient to precipitation.

While smoldering fires in organic soils usually do not pose the immediate danger to life or property characteristic of some so-called “megafire” events such as the 2009 Black Saturday fires in Australia (Adams and Attiwill 2011), their effects are chronic at local and global scales. Impacts to human health and safety, and the possibility that ground fires may contribute measurably to and interact with global climate change, make these events worthy of increased research to improve our understanding of their

effects and management. Attention from the public and policymakers on “megafire” phenomena of recent years should likewise be drawn not only to dramatic wildfire events, but also directed at future scenarios of smoldering mega-fires which can involve ancient carbon and climatic effects.

In the future, improved sampling methods allowing for the continuous monitoring of soil-moisture content in relation to atmospheric and hydrologic conditions may improve our ability to observe changes in the potential for smoldering combustion in peat soils such as those found in cypress swamps. Additionally, accounting for the generation of pyrolyzed carbon (also known as “bio-char”) may increase our knowledge of the ecological impacts and carbon-dynamics implications of smoldering fires, since pyrolyzed C may alter soil chemical properties (e.g., by increasing cation-exchange capacity, Liang et al. 2006) and reduce turnover times due to its recalcitrance (Certini 2005). Methodological improvements to capture the spatial variability in smoldering combustion, which can vary widely across even small areas, will improve estimates of emissions as well as understanding of the ecological effects from smoldering fires. While many of these effects are commonly understood to be deleterious, in some cases peat-consuming fires may be beneficial for management objectives. One example of the latter is the lowering of accumulated soil heights during drought-condition ground fires to form deep pockets which can serve as refugia for wildlife or their aquatic prey during future dry periods. In southern Florida, these dry-season refugia may be important for wood storks (*Mycteria americana*) and the Florida panther (*Felis concolor coryi*), both of qhich are endangered (Cox et al. 2006, Fleming et al. 1994). Such an understanding of the ecological role of ground fires is needed as society determines whether certain

potential ecological benefits are outweighed by the considerable negative human and environmental impacts of these slow-motion megafires.

Figure 4-1. Consumption of peat can cause severe damage to trees by the removal of soil from the root zone. Additional effects of geomorphic change due to fire may be significant in areas of low topographic relief where these soils occur, as in this marsh in Putnam County, Florida USA.

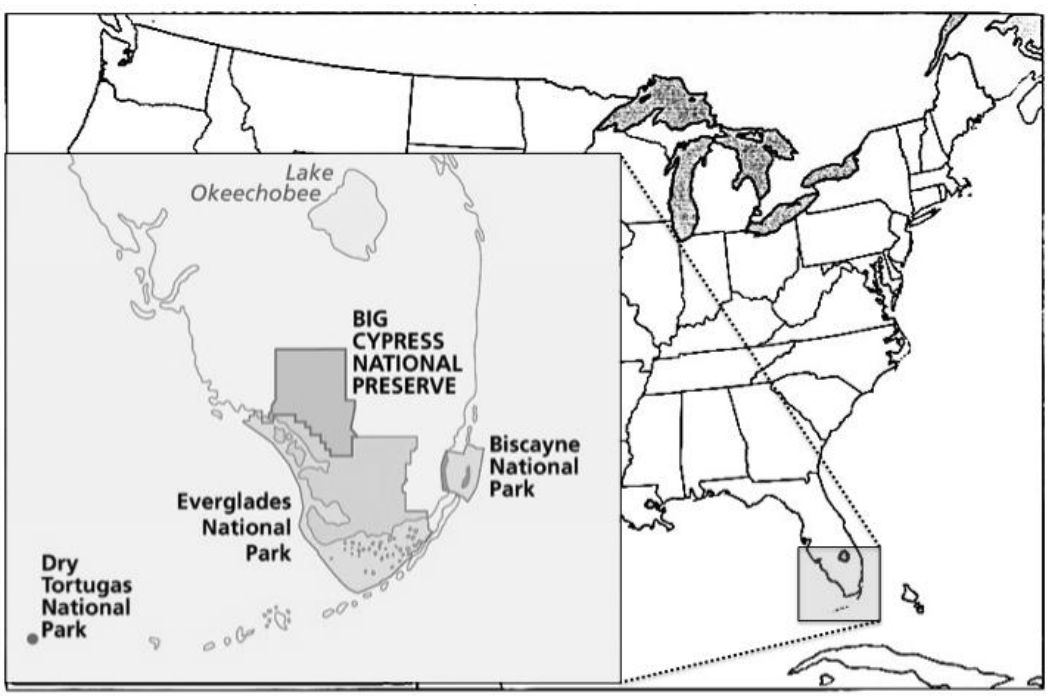

Figure 4-2. Big Cypress National Preserve in southern Florida comprises 300,000 ha containing a range of upland and wetland communities. These communities include swamps of various sizes dominated by pondcypress (*Taxodium distichum* var. imbricarium). Numerous cypress swamps are apparent due to their dome-like canopy shapes; the surrounding landscape is comprised of frequently-burned slash pine flatwoods. This configuration is typical of large areas of the Preserve.

Figure 4-3. Each peat monolith collected from within cypress domes for combustion was 20 cm in diameter and ranged from approximately 20 cm to 40 cm in height. This typical sample illustrates the preponderance of small roots in the upper 10 cm of the profile.

Figure 4-4. Typical cypress dome interior during severe drought conditions, showing the widespread occurrence of coarse woody debris. Branches from cypress, whose wood is famously resistant to decay, become incorporated into the upper layers of peat and can serve as ignition vectors for smoldering when ignited by passing flame fronts. Thickness of litter layer near the bases of cypress trees often is somewhat thicker compared to locations a few m away, where sampling was conducted in order to minimize inclusion of large roots.

Figure 4-5. The monolith sample collected from a pondcypress (*Taxodium distichum* var. *imbricarium*) swamp after ignition by an electric heating coil.

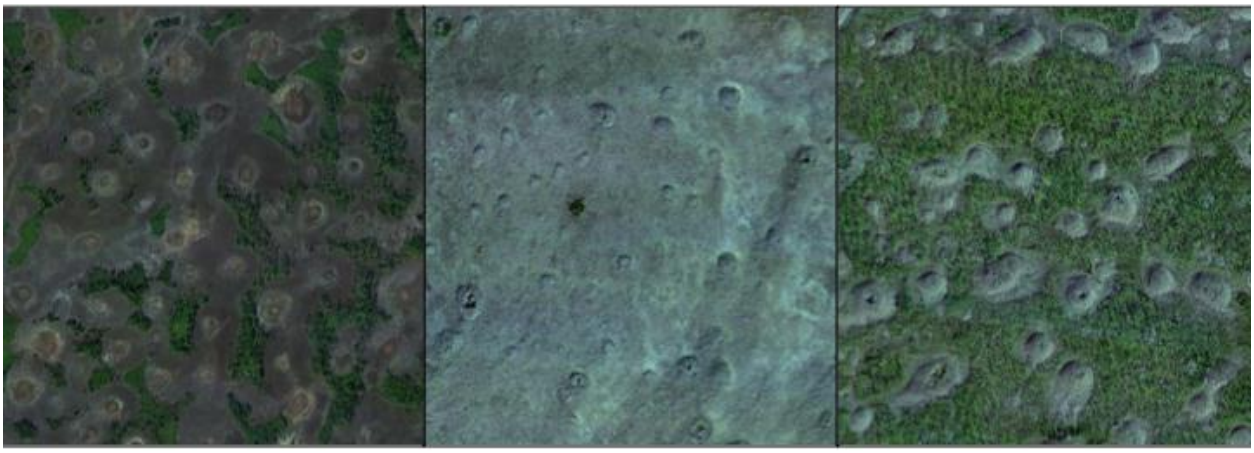

Figure 4-6. Three square, 225 ha blocks representative of landscape configurations within Big Cypress used for landscape-scale extrapolations. SPOT imagery viewed with Google Earth (Google, Inc., Mountain View, California, USA). From left to right: “Deep Lake” sampling block (26º 4', 81º 14'; “DL” in Table 4-2), “Low Site” block (25º 55', 80º 58'; “LS”), “Raccoon Point” block (26º 0', 80º 56', “RP”).

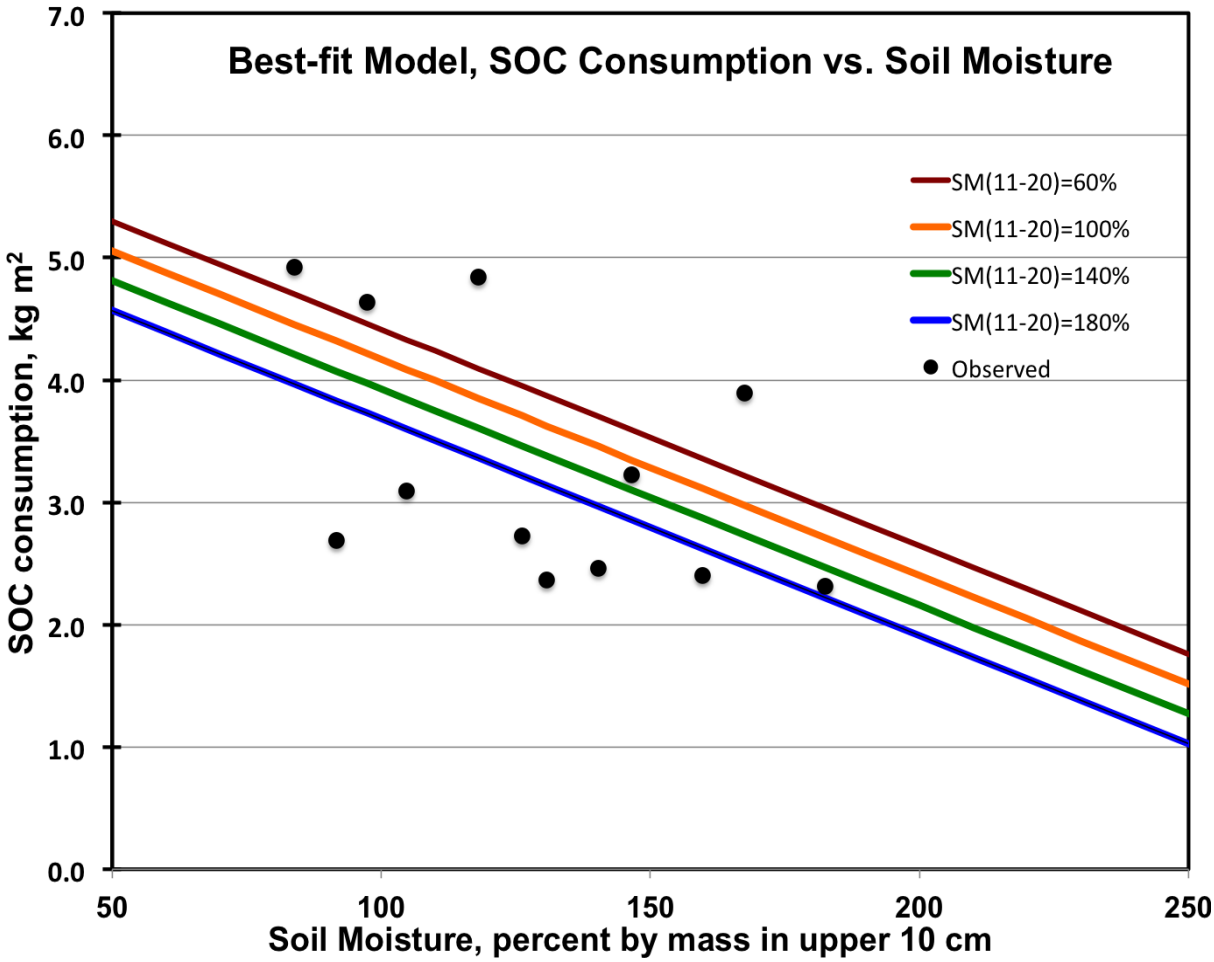

Figure 4-7. Best-fit general linear model predicting carbon emissions from cypress peat soils (in kg m^2), incorporating soil moisture at 0 – 10 cm and 11 – 20 cm. Predictions are shown for four realistic values of soil moisture in the 11 – 20 cm soil layer. Observations from the 14 monoliths from the study also are shown (in blue).

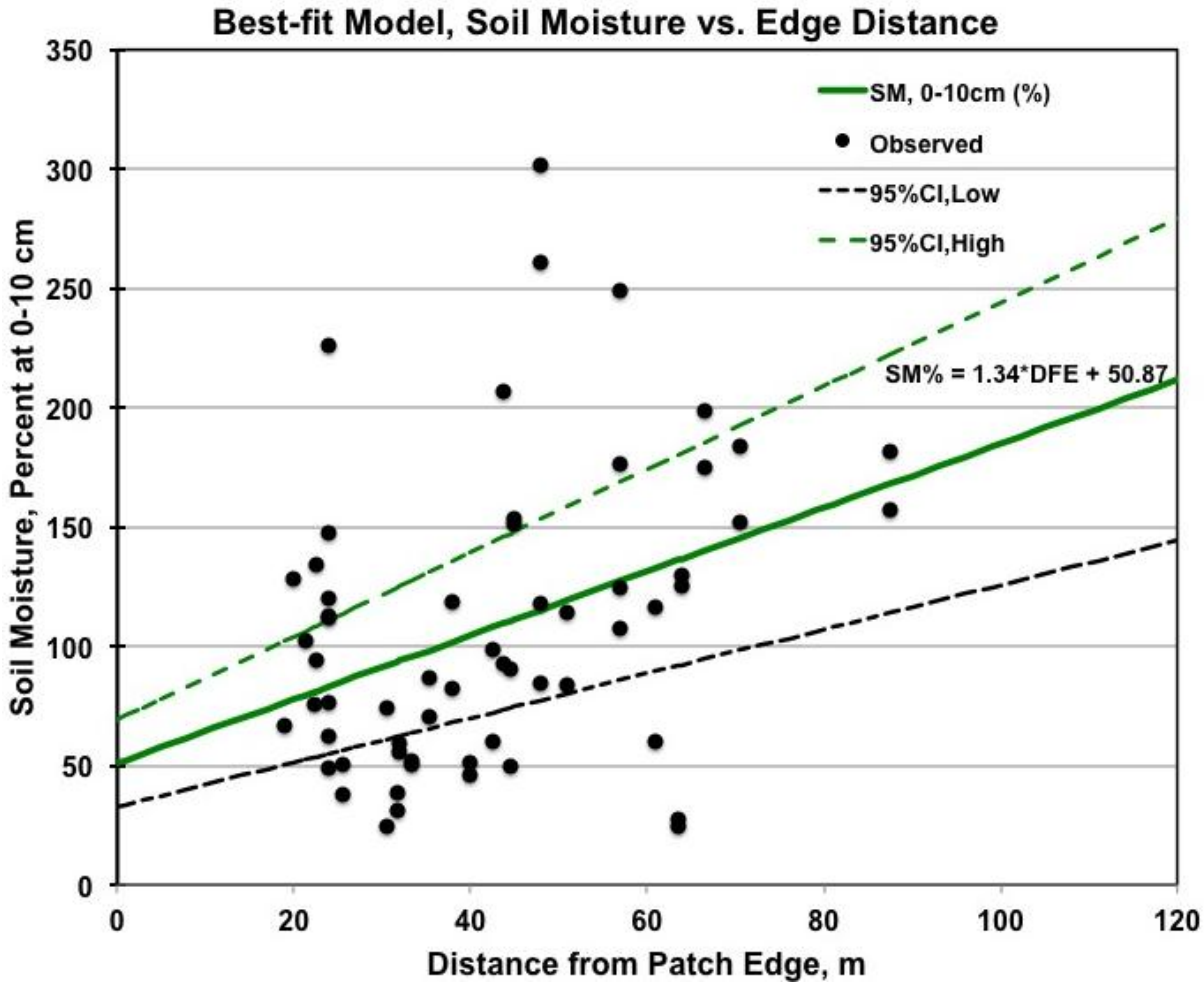

Figure 4-8. Best-fit generalized linear model describes soil moisture in upper 10 cm of soil as a function of distance from patch edge. Upper and lower 95% confidence bands shown in dashed green and black, respectively. In the model equation, SM% = percent soil moisture; DFE = distance from edge (i.e., moving toward patch center), in meters.

Table 4-1. Soil moisture values and estimated organic carbon content for three portions of soil profiles, and overall combustion depth and normalized organic carbon loss for the 14 monolith soil samples.

Soil Profile Depth	SM, %	SOC, %	Mineral Content, %	Combustion Depth, cm	SOC Loss, g cm^{-1}
0 – 10 cm	131.2 (51.4)	29.8 (6.7)	22.7 (9.8)		
11 – 20 cm	134.9 (58.1)	19.7 (7.7)	51.2 (19.1)		
21 – 30 cm	96.2 (36.3)	13.1 (8.6)	67.4 (21.3)		
Overall				8.9 (5.2)	0.785 (0.092)

Notes: SM: soil moisture content, % mass; SOC: soil organic carbon content, % mass; OC Loss cm^{-1}: calculated loss of SOC due to combustion, normalized to a cm^{-1} basis. Values reported are means, with standard deviations in parentheses.

Table 4-2. Estimated area of peat soils in three 225 ha landscape blocks, based on ground-truthed remote measurements of individual community patches. Potential consumption of SOC due to smoldering combustion in peat soils is calculated for each landscape block given mean soil moisture values observed at 0 – 10 cm and 11 – 20 cm depths from 134 samples, using soil monolith combustion model (Equation 4-2).

Landscape Block	Number of Cypress Domes	Mean (s.d.) Dome size, ha	Depression area, ha (%)	Mean Estimated SOC Consumption, Mg
DL	60	0.47 (0.31)	28.11 (12.5%)	1175.0
LS	45	0.25 (0.35)	11.02 (4.9%)	460.6
RP	60	0.58 (0.42)	34.89 (15.5%)	1458.4

Notes: "Depression area" is measured area of depressions estimated to contain combustible, shallow peat soils within each landscape block; area is expressed as estimated area in ha and percent of the total 225-ha area of landscape blocks.

CHAPTER 5
EVIDENCE OF BIOGEOMORPHIC PATTERNING IN A LOW-RELIEF KARST LANDSCAPE

Background

Ecological Pattern

The geologic record has long been recognized as a repository of evidence of prehistoric environmental conditions that shaped composition and morphology of sedimentary formations. More recently, the action of biota has been considered as a factor shaping geomorphology (Corenblit et al. 2011). Biological activity has been observed to influence the structure and arrangement of landform in a variety of ways across many ecosystems; the most familiar examples may include weathering of rock to form soil in terrestrial ecosystems (Sterfinger 2000, Brady and Weil 2008) and the accretion of biotically-precipitated carbonate to form reefs in shallow marine systems (Spencer and Viles 2002). Ecological investigations have expanded beyond the unidirectional “ecological engineer” concept, which focuses on the effects species have on the physical environment (Jones et al. 1997), to include reciprocal effects among organisms and the geomorphology of their environment (Corenblit et al. 2008).

Increased attention to the bidirectional nature of biota-landform interactions led to the expansion of studies beyond biotic influence on geomorphic structure, to the spatial arrangement of landforms and aggregations of species (Cutler 2011). Descriptions of non-random plant distributions have been made for a number of locations around the world (Prentice and Werger 1985, Pancer-Koteja et al. 1998, Lefever and Lejeune 1997), leading to investigations of mechanisms behind the emergence of ecological pattern (Rietkerk and van de Koppel 2008; Figure 5-1). Mechanistic explanations have been offered for spatial self-organization and resulting patterns in mussel beds in the

Netherlands (Van de Koppel et al. 2008), the Florida Everglades (Larsen and Harvey 2011), and xeric shrublands (Klausmaier 1999). Many of these explanations invoke the concept of scale-dependent feedback, which promotes resource availability at close spatial proximity with the effect of long-range inhibition (Rietkerk and van de Koppel 2008). These so-called reciprocal feedbacks act to promote clustering of biotic communities, and the development of relatively sparse areas in the zone of negative feedback (Corenblit et al 2011). The variety of ecosystems in which patterning has been observed and linked to plausible mechanistic explanations may lead an observer to the suspicion that wherever a spatial pattern is observed in the distribution of vegetation on a landscape, such reciprocal feedbacks may be at work.

Patterning Expressed on Landform Elevation

Vegetation patterning in the Everglades region of Florida USA, and its loss with hydrologic modification of this emblematic fen, has been described by Watts et al. (2010), who relate water depth to peat formation and organic-matter decomposition rates in areas of the Florida Everglades that exhibit strong spatial patterning. There, high-elevation sawgrass (*Cladium jamaicense* [Crantz]) ridges and open-water sloughs experiences different rates of productivity and respiration, yet landscape pattern is maintained via relatively balanced rates of net ecosystem productivity in both communities. In this example, the soil surface underlying the vegetative cover is formed directly as a result of biotic action. The focus of observations and predictions, then, have been expanded beyond remotely-observed vegetation patterns, to soil topography, and even to the underlying mineral-soil or bedrock geomorphology and the influences thereon of biotic processes (e.g., Corenblit et al 2008).

Other examples exist of landforms of geologic origin that are receptive to the imprint of biotic-process signatures. Limestone bedrock in karst systems, for example, may be subject to dissolution as respired carbon dioxide from roots and organic matter mineralization is dissolved in water that contacts, or is transported to, the soil-bedrock interface. Biotically-mediated carbonate dissolution, along with the action of acidified rainwater, is one proposed mechanism for the formation of depressional wetlands in areas with low topographic relief and shallow limestone bedrock (Odum 1984):

$$H_2O + CO_2 + CaCO_3 \rightarrow Ca^{++} + H^{+} + HCO_3^{-}$$

Small depressions attract and hold rainwater, which promotes locally increased plant activity (and therefore respiration), reducing pH via increased dissolved CO_2. As a result of these positive feedbacks among dissolution, water storage (and attraction), productivity, and pH, these depressions may eventually become landscape features such as marshes, or small swamps.

Cohen et al (2011) theorize biotically-mediated bedrock dissolution that extends to a landscape scale on a low-relief karst platform to the west of the Everglades in southwestern Florida. As depressions grow, the dissolution site at the interface of water and bedrock grows simultaneously outward and downward. Surface flow of water toward depression centers carries precipitated marl and insoluble overburden particles from the limestone matrix. Biotically-mediated carbonate dissolution is ultimately limited by the amount of water delivered to the landscape by precipitation and overland flow, and becomes concentrated in local depressions. As these depressions form and attract water from surrounding areas, the coupled reciprocal feedbacks to carbonate dissolution are formed, resulting in a prediction of uniform spacing of dissolution

features (as opposed to random, or clustered, spacing) across a landscape. It follows that, because a point on the landscape is predicted to lie either within a zone of positive feedbacks to biotic limestone dissolution or in an area where negative feedbacks (specifically low inundation period) discourage dissolution, we should expect the statistical distributions to be multimodal; i.e., means should occur clustered around a "high-elevation" value and a "low-elevation" value. The conceptual models of these processes lead to predictions of landform distribution on the landscape in three dimensions both in spatial distribution and in the statistical distribution of elevations of bedrock and soil (Figure 5-2).

Test Landscape: Big Cypress National Preserve

To the west of the Everglades region, Big Cypress National Preserve (Figure 5-3) exhibits arrangement of vegetation features that appear distributed at regular intervals (Figure 5-4). Throughout the preserve, the carbonate rocks of the Tamiami and Fort Thompson formations are at or very near the land surface. These Pleistocene deposits are relatively thin (ca. 20 m) and highly permeable, contain moderate (ca. 20%) insoluble residual material (principally quartz), and are bounded below by a thick clay confining unit. Extremely shallow relief (mean bed slope from north to south is ca. 5 cm/km) and abundant rainfall lead to prolonged periods of surface inundation, particularly in numerous circular depressions that are immediately evident in aerial imagery. Because the geologic formations under BICY are slightly mounded in relation to the surrounding landscapes (the central Everglades to the east, Everglades National Park to the south), the terrestrial and wetland systems are entirely rain-fed, and thus driven by strong seasonality, with ca. 70% of rainfall occurring between June and September (Duever et al. 1986). Vegetation in the preserve responds strongly to subtle

variation in elevation, with marked shifts in community composition and primary production evident over less than a meter of local surface relief. In higher elevation settings, pine rockland and hardwood hammock communities dominate, while cypress domes dominated by pond cypress (*Taxodium distichum* var. *imbricarium* [Nutt.]) and marshes are found in the landscape depressions. Of particular relevance to this work is the strong visual evidence of non-random spatial organization of these depressional wetlands; specifically, the depressions appear to be spatially overdispersed (i.e., distributed more uniformly than expected by chance; Diggle 2002) and remarkably consistent in size.

Because the quantity of water delivered to this landscape is limited, the aggregated volume of dissolution-formed depressions also is limited. The reciprocal feedbacks (locally positive with respect to dissolution, but distally negative) proposed by Cohen et al. (2011) result in the prediction of nonrandom distribution (i.e., self-organized biotic structuring) of depressional features in this flat landscape with shallow limestone bedrock. Given these predictions, a given point on such a landscape should fall either into one of these depressional basins, or far enough beyond the zone of influence that dissolution feedbacks are decoupled. In the latter case, a lack of biotically-influenced limestone dissolution will generally lead to a reduced “background” rate of limestone dissolution from dissolved CO_2 in precipitation or flood events (but water will be drawn from these locations toward lower-elevation depressions, reducing the amount of time available for these reactions to take place in higher-elevation zones). Locations within the zone of positive feedbacks will experience increased dissolution rates.

Within the zone of positive feedback dissolution proceeds; however, the presence of water in basins may promote the formation of an additional negative feedback to further downward dissolution. First, if transport of dissolved carbonate is inhibited, the rate of dissolution reactions would be slowed as the chemical reaction proceeds toward equilibrium. Second, limited oxygen availability beyond threshold depths inhibits the generation of metabolically-derived hydrogen ions. If the availability of water to the landscape changed, these feedbacks would be altered. For example, a water table far below the surface may prevent the formation of negative local dissolution feedbacks, resulting in ever-deeper dissolution features (e.g., *cenotes* found in Yucatan, Mexico). Conversely, increased hydroperiod may decouple the locally-positive, distally-negative feeedbacks posited to produce patterned occurrence of depressions. At a location on the landscape with longer hydroperiod, then, one would expect to encounter weaker landscape pattern, and fewer or smaller depressions.

Biotic Signature Obfuscation

A major obstacle to the detection of biotic-process signature in geomorphology is the obfuscating effects of other processes. In areas with high topographic relief, minor changes to topography from erosion by regular precipitation (or major ones from irregular floods) may be sufficiently great in magnitude or rate to overwhelm gradual and subtle biotic effects. Conversely, in landscapes that lack regular precipitation or surface water flow, water limitations may reduce biotic processes so much that slow abiotic processes such as aeolian sediment transport or erosion may reduce biotic-process signatures. In other words, patterning emerges when the “organizing” process is more strongly expressed on landform than the “disorganizing” process. Weerman et al. (2011) describe such an instance, in which top-down controls (diatom grazing by benthic

herbivores) can reduce the strength of the organizing feedback so much that the pattern disappears altogether because the disorganizing feedback (tidal smoothing of the mud) becomes dominant.

The dissolved calcium created via dissolution hot-spots in the Big Cypress landscape may be removed by water flow, or precipitated with other reactants or with the dissolved carbonate. In fact both of these occur: infiltration carries calcium-saturated water downward to a shallow aquifer, while occasional inundation during the rainy season allows low-velocity sheet flow to remove quantities of solute away from the system. Alternatively, the reduced extent of dry-season inundation and uptake of dissolved CO_2 by periphyton (which results in supersaturation of Ca^{++} ions) causes deposition of calcium carbonate as marl.

Anoxic conditions and water saturated with respect to calcite ($SI_{cal} > 0$) found at depth in depression centers decouple the positive dissolution feedback, leading to a buildup of material that is composed of reprecipitated aragonite, and accumulated organic matter. Material also is transported from higher-elevation areas. Thus, just as ecohydrologic conditions produce reciprocal feedbacks to form patterned landscapes, contemporary geomorphic processes can act contrary to biogeochemical processes to obscure imprints of the latter on bedrock under a “smoothed” mantle of soil. As a result, we should expect to see elevation bimodality expressed more strongly in the bedrock of a landscape experiencing these processes, compared with observations of soil-surface elevation.

Predictions

In this study, I tested the predictions that reciprocal feedbacks would lead to patterned distribution of depressions in the Big Cypress landscape as well as

bimodality of landform elevation. I used land-cover information from satellite imagery, and measurements of landform and bedrock elevation, to address the following predictions concerning reciprocal-feedback biotic process influences on the geomorphic record, and the relative ratio of ecohydrologic signal to abiotic noise, in a low-relief karst-platform landscape:

1. The hypothesis of locally-positive, distally-negative feedbacks operating on a low-relief karst landscape (Cohen et al. 2011) leads to a prediction of nonrandom, or patterned, spatial distribution of depressional landform features:

1a. Spatial analysis of depression features should indicate their even distribution in two dimensions, instead of clustering or random distribution.

1b. The patterned nature of depressional landform features also should be reflected in a third dimension: landform elevation. Correlograms of elevations and distances should reveal periodicities that roughly correspond to the areal size of depressional wetlands.

2. Measurements of landform elevations should reflect the prediction that areas tend to be included in attractor domains for the local-positive solution feedbacks, or excluded (i.e., subject to distal-negative feedbacks). Therefore, elevations should be distributed in a bimodal manner, with either low-elevation (depression) or high-elevation means.

3. The signature of biotically-mediated dissolution feedbacks will be seen more strongly in elevation measurements of underlying bedrock than in measurements taken of soil-surface elevation. Therefore:

3a. Bedrock elevation measurements will display greater bimodality than soil-surface elevations.

3b. Differences between local means from elevation distributions (i.e., “high-elevation” vs. “low-elevation” means) should be greater for measurements of bedrock elevation than for measurements of the overlying soil surface.

3c. Measurements of soil thickness will increase as bedrock elevation decreases, reflecting a “smoothing” influence of water erosion and overburden (or precipitate) translocation.

Material and Methods

Data Collection

Within the Preserve I selected three square, 1.5 km x 1.5 km plots in which to measure patterning of landform features, elevation, and soil thickness (Figure 5-5). Sampling sites were chosen which represented typical configurations of common communities within the Preserve. I utilized 2.5 m resolution images from SPOT (Satellite Pour l’Observation de la Terre) imagery from 2010 (geo-referenced and accessed via Google Earth, Google, Inc., Mountain View, CA) to locate the sampling blocks. The round shapes of depressional features (Figure 5-3) also facilitated measurement of depression area from satellite images, as well as determination of centers of circular depressions. In two of the sampling blocks (LS and RP), the boundary of depressional features was defined as the outer extent of the nearly monotypic communities of pondcypress. In the third sampling block (DL), depressions were occupied by marsh communities instead of forest patches; here, the boundary between prairie dominated by muhly grass (M*uhlenbergia capillaris* Lam.) and marsh composed primarily of sawgrass (*Cladium jamaicense* Crantz), cattail (*Typha domingensis* Pers.), or emersed

obligate wetland species (e.g., fire flag, *Thalia geniculata* Lin.) was counted as the depression boundary. In both cases species were chosen based on 1) their characteristic occurrence in wetlands of the region, 2) ease of identification from satellite imagery as signals of depressions, and 3) their ubiquity among all depressions in the sampling blocks in which they occurred. Comparisons of area measurements of depressions using hand-held WAAS (Wide Area Augmentation System) GPS (Global Positioning System) receivers found agreement within approximately 5% of those obtained from satellite images (unpublished data). Estimations of depression centers using ground-based methods were found to be unreliable and logistically problematic.

I visited sampling blocks during August–October 2011, late in the region's rainy season when seasonally high water tables inundated most of the local landscape. Within each block, 40–70 spatially-randomized sampling points were selected as the center of a sampling cluster in which 5 measurements of soil and bedrock elevation were made (one in each cardinal direction at random distances of 1–25 m, and one at the center). Soil elevation measurements were accomplished by measuring water depth, and benchmarking to nearby USGS Everglades Depth Estimation Network (Telis 2006) sites; low flow permitted benchmarking of known-elevation EDEN measurements to yield elevations of soil surface (Watts et al. 2010, Watts et al. 2012). Steel tile probes (Forestry Suppliers, Inc., Jackson, MS USA) were used to measure depth to bedrock and thickness of soils; benchmarking to EDEN gauges yielded elevations of bedrock. Where sampling points were exposed above the water table, a surveyor's level (Johnson Level and Tool, Mequon, WI USA) enabled benchmarking to nearby inundated areas.

Data Analysis

The widely-used K-function (Ripley 1979, Perry et al. 2006) was also calculated for corroboration of the test for CSR. K-function is regarded as a second-order analysis because it compares variance (i.e., second-order moment) of nearest-neighbor distances. From nearest-neighbor distances of N observed points, values of a scaled distance metric, L(*d*), are compared against expected values *d* and a confidence interval of random permutations of N points within a hypothetical study area of the same size and shape. Observed values of L(*d*) above the confidence interval indicate point clustering, while observed L(*d*) below the confidence interval indicate overdispersion.

Spatial autocorrelation measurements of landform elevation may assist in detecting scale-dependent feedbacks (Rietkerk and van de Koppel 2008, Eppinga et al. 2008). I used GS+ software (Gamma Design Software LLC, Plainwell, MI USA) to calculate and construct correlograms with lag spacing (*h*) of 10m and a range of 500m, and angular tolerance of 22.5°, for soil surface elevation and elevation of underlying bedrock for sets of measurements made from each site.

Bimodality of landform elevation distribution was assessed by comparing goodness-of-fit of a single-normal model and a mixed-normal model of observed soil-surface and bedrock elevations (Wolfe 1970); Bayes's Information Criterion (BIC) values for each model provided a means for comparing each model and testing the hypothesis of bimodal elevation distribution. Model selection and comparison were performed using the software program R (R Development Core Team 2005).

Results

Spatial Pattern Analysis of Depressions

Heads-up classification of satellite imagery was verified by field observations of 45–60 landform depressions in each of the three 225ha sampling blocks (shown in Figure 5-5). Depressions were mostly under 1ha in size, and comprised 11% – 28% of the area of the sampling blocks. Positive z-scores above 1.96 were observed for the distribution of depression centers in all sampling blocks (Table 5-1). K-function analysis indicated that observed values of L(*d*) were below 95% confidence interval minima of expected values at distances of approximately 150m at the Raccoon Point site, and 200m for the Low and Deep Lake sites (Figure 5-5).

Soil and Bedrock Elevation

Elevation measurements of soil surface ranged from 233 cm in depressions of the Raccoon Point site to 384 cm at the Deep Lake site. Underlying limestone bedrock reached a maximum elevation of 361 cm and a minimum of less than 72 cm (the latter in 9 observations of >500 due to equipment limitations), in both cases at the Deep Lake site.

Correlograms of elevation measurements indicated significant positive spatial autocorrelation at close distances for both soil and bedrock elevations at both sites ($P < 0.05$ for all cases). Significant negative autocorrelation was observed at increased distances for Deep Lake and Raccoon Point bedrock measurements ($P < 0.05$); in both cases, alternating positive and negative autocorrelations occurred with pseudoperiodicity roughly corresponding to mean depression diameters estimated from satellite imagery (Figure 6). Among soil elevations at both sites, alternating positive and negative spatial autocorrelation was apparent, but did not appear as closely related to

estimated depression sizes. Both bedrock and soil-surface elevations at the Low site displayed significant positive autocorrelation, although no relationship with vegetation signatures of landform size were apparent.

Bimodality and Elevation Differences

Although distributions of elevation measurements of soil and bedrock were skewed (Figure 7), comparison using BIC scores indicated that best-fit models of landform elevation observations described bimodal distributions in all cases except for soil-surface elevation at Raccoon Point (Table 2). There, the best-fit model predicted a unimodal distribution. At all three sites, bimodal distributions were more strongly evident in limestone bedrock elevation observations than for soil-surface measurements. Difference in means between higher-elevation vs. lower-elevation modes were greater for bedrock than for soil elevations at both Deep Lake (120.7 cm vs. 25.6 cm) and the Low sampling locations (71.6 vs. 9.2 cm).

Soil Thickness Measurements

The layer of soil overlying limestone bedrock was typically thinnest at the highest bedrock elevations observed. At each site, upland vegetation communities generally occurred on thin layers of soil, with bare limestone outcrops common in the transitional pine rockland communities found at the Raccoon Point site. Long-hydroperiod, low-elevation pondcypress swamps and marshes occurred on deeper soils characterized by sandy, calcareous clay or granules under an organic horizon (histic or fibric epipedon, muck or peat). Depth of bedrock surface was strongly correlated with thickness of this soil layer at all three sites (Figure 5-8).

Discussion

H1: Regular Spatial Distribution of Depressions

The results from nearest-neighbor analysis and K-function tests for CSR indicated that in each of the three sampling blocks, depressions were distributed evenly about the landscape, as opposed to randomly or in a clumped arrangement. These results were based on observations of characteristic vegetation communities from remote images, essentially using vegetation as a proxy for landform. However, ground-truthed vegetation community classification corresponded well to both soil and underlying bedrock elevation measurements (Figure 5-9), indicating good support for using such methods. Additionally, field measurements indicated alternating positive and negative autocorrelations for bedrock and soil (though to a lesser extent for the latter). That these apparent periodicities in autocorrelation tendencies correspond with approximate boundaries of vegetation communities further indicates their utility for estimating landform depression occurrence across areas too large to intensively sample. Investigations of vegetation pattern routinely utilize remote estimates of community boundaries (e.g., van der Heide et al. 2010, Franz et al. 2012), but this study indicates the utility of remote vegetation measurements as geomorphologic proxy.

Hydrology is the most commonly invoked explanation for patterning in vegetation, whether from the standpoint of limitation (Scanlon et al. 2007), control over relative rates of ecosystem productivity and respiration (Eppinga et al. 2009, Sullivan et al. 2011), or direct hydrodynamics (van der Heide et al. 2010). Additional factors are proposed (usually tied to hydrology) that include the transport and concentration of nutrients (Rietkerk et al. 2004, Kefi et al. 2010) or sediment (Larsen and Harvey 2011). Our findings of depression overdispersion (indicated by vegetation and corroborated

with direct measurements) are consistent with predictions of reciprocal ecohydrologic feedbacks as described by Cohen et al. (2011) that involve hydrologic dissolution of limestone bedrock. No other mechanism offers a parsimonious explanation for the even pattern of landform distribution on this landscape.

H2: Bimodality of Landform Distributions

Elevations of limestone bedrock measured at randomized sampling locations tended toward either local-relative high or low elevations, as indicated by the bimodality in their distribution. That these elevation measurements clustered around either of two means also supports hypothesized ecohydrologic dissolution mechanisms that are locally self-reinforcing, yet also inhibitory of carbonate dissolution distally of low sites where dissolution processes are thought to occur (Odum 1984). While this study follows other investigators in examining elevation bimodality (e.g., Watts et al. 2010), these results may be the first documentation of findings consistent with self-organization in biotic systems imprinted in the geomorphic record. If further supported by biogeochemical evidence, this would represent an instance of particularly long-lived niche creation.

Bimodal tendency was most pronounced at Raccoon Point, where the highest proportion of the sampling area occupied by vegetation communities characteristic of depressions (15.5%) made capturing these areas more likely. Yet the propensity of elevations to fall near a “low” or “high” elevation mode was clear even at the Low sampling site, with relatively rare occurrence of depressional vegetation communities (< 5% of the area of the sampling unit). The visual contrast between the prevalence of depressions at the Raccoon Point and Deep Lake sites, and their sparse arrangement at the Low site, may be due to differences in hydrology due to elevation: mean bedrock

elevations at the Low site (297 cm) are substantially higher than those at the Deep Lake site (254 cm) or the Raccoon Point site (209 cm). Although a lack of knowledge about the age of the landform depressions in this region (and therefore the relative sea level, but also particularly the region's freshwater hydrology) reduces our ability to advance an explanation, it is reasonable to suppose that given the sites' geographic proximity and otherwise geological similarity, elevation-driven hydrologic differences may have driven biogeomorphologic evolution to arrive at subtly different expressions of the same feedbacks.

H3: Biotic Signature Smoothing in Soil versus Bedrock

For the Low and Deep Lake sampling sites, soil-surface elevation measurements also displayed bimodal distributions, but with less difference between local-relative low- and high-elevation modes. These distributions (and the unimodal distribution suggested by BIC score comparisons of best-fit models at Raccoon Point) indicate the action of unilateral (as opposed to reciprocal) processes that act to unite divergent means—particularly since the soils overlie bedrock with widely-separated elevation modes. These processes are due to formation of soil in depressions at greater rates than at higher elevations; differential rates would be due to accumulation of insoluble particles (e.g., sand) from dissolved carbonate matrix in depressions, as well as sediment transport and solute reprecipitation, plus organic matter accumulation due to net productivity differences at different elevations. The result of these processes is a gradual obfuscation of ecohydrologic imprint on geomorphology via landscape smoothing. The opposition of pattern-generating biota-environment interactions and abiotic processes (e.g., erosion) have been described (Francis et al. 2009, Corenblit et al. 2011) for riverine systems and demonstrated at small scales in a costal mudflat

(Weerman et al. 2011). We likewise propose hydraulic sediment transport as the abiotic process in opposition to patterning enabled indirectly by the water itself; however, in the instance of Big Cypress, these processes appear to have produced effects at relatively massive local scales and over a vast spatial extent.

Observations of the spatial arrangement of depressional features in these sites revealed clear evidence for their occurrence in nonrandom, even intervals. The use of vegetation communities identified from satellite imagery as proxy for depressions was validated by correlograms of alternating positive and negative autocorrelation of field elevation measurements at distances approximating their observed sizes. This evidence for nonrandom distribution of depressions in a carbonate-platform landscape supports the hypothesis that rainwater acidified by ambient atmospheric CO_2 and products of respiration acts directly on limestone bedrock. Further corroborating the hypotheses of reciprocal ecohydrologic feedbacks are bimodal distributions of landform elevation, detectable even where the depressional component of the landscape occupies less than 5% of its area. These dissolution processes likely proceed at very slow rates relative to the lifespans of the species whose members participate in their creation, and this study provides a compelling example of a system in which biogeomorphologic change can proceed and persist at far longer timescales than was traditionally accepted (Corenblit et al. 2011). Further studies to investigate dissolution by hypothesized biotic and abiotic processes, and the rates and fates of solute transport, will deepen our mechanistic understanding of biogeochemical activity on biological formations at large spatotemporal scales and extents.

I observed patterned distribution of landform depressions even in areas where I anticipated either randomized distribution of depressions, or too few depressions to determine their distribution. Long periods of dissolution acted to produce localized basins in the carbonate bedrock. Simultaneously, processes of soil formation and transport proceeded more rapidly at low elevations in this landscape, tending to obfuscate the imprint of pattern-generating processes on the geomorphic record. Pattern may occur where it is unexpected based on casual observations of the soil surface, based on our comparisons of soil elevations with those of underlying limestone.

These findings are initial evidence of reciprocal feedbacks operating directly on bedrock, in opposition to processes at the soil surface. These opposing suites of pattern-generating and smoothing forces will vary in their relative influences, depending on many factors (Figure 5-10). Where smoothing forces diametric to those generating landform pattern may occur, seeking evidence of pattern in landscape components less subject to them—such as bedrock, mineralogy, or elsewhere—may yield new evidence for patterned landscapes and the processes that generate them.

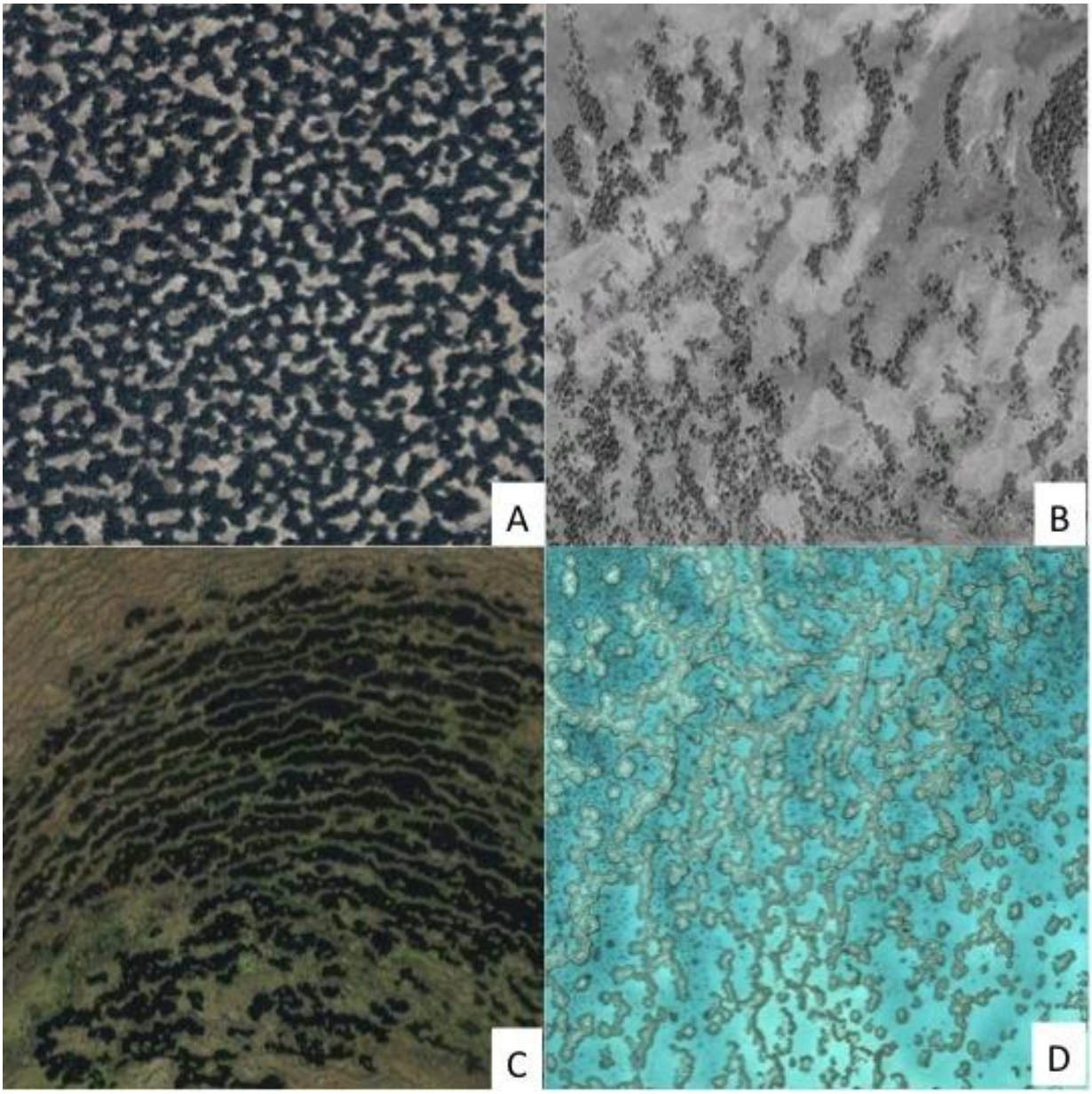

Figure 5-1. Patterned arrangements of organisms can be observed across the globe. Examples range from arid systems such as “tiger bush” in Niger (A) and ribbon forest in the USA (B) to patterned peatland in Finland (C) and Australia’s Bunker Reef (D). Images accessed using Google Earth (Google, Inc., Mountain View, CA); individual image sources: GeoEye (A); US Geological Survey (B); Digital Globe (C, D); all images used with permission.

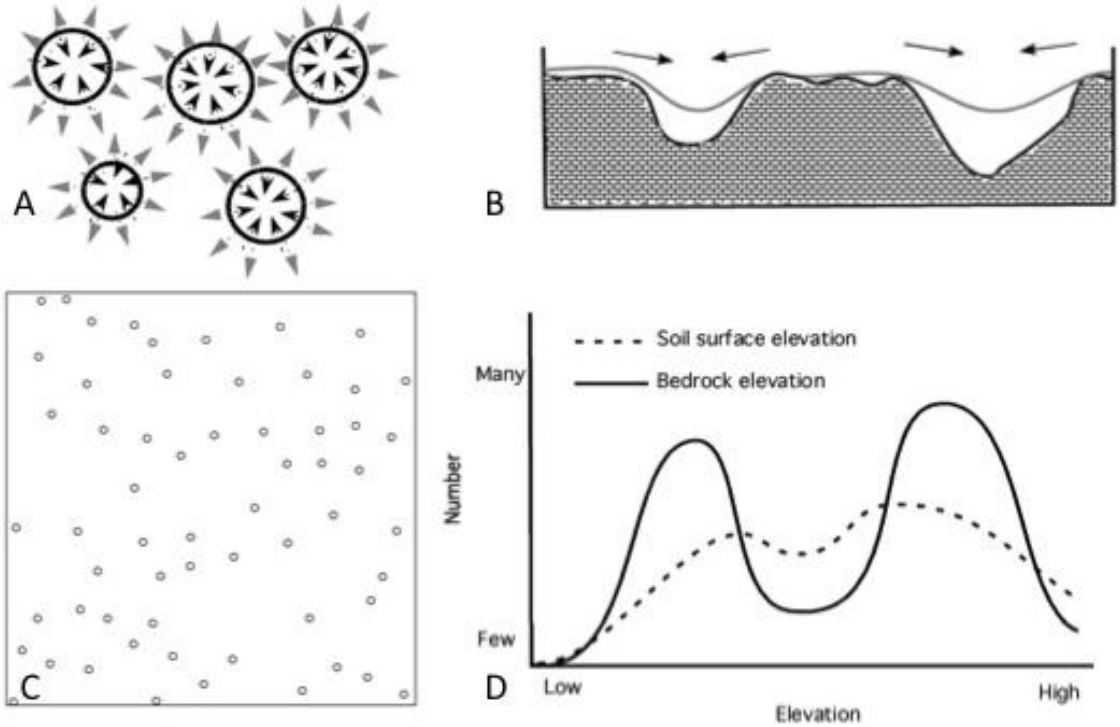

Figure 5-2. Schematic representation of the action of ecological feedback to produce patterns in limestone karst. A) In karst landscapes, landform-biota interactions may be observed in three dimensions as dissolution processes driven by biotic respiration and of acidic rainfall act on bedrock, such as aragonite or carbonate bedrock. B) Re-precipitation of solute, deposition of insoluble sediment from the bedrock matrix, or hydrologic transport into solution basins causes the buildup of a mineral soil layer over the underlying bedrock. Primary productivity causes the buildup of organic matter at a much more rapid rate than dissolution proceeds. The overburden mantle is thus more easily “smoothed” by biotic production and abiotic transport processes than the bedrock. C) These reciprocal feedbacks should lead to the formation of depressions in a karst-platform landscape with regular spacing (illustrated), as opposed to randomly spaced or clustered distributions of these features. D) In a patterned karst landscape where these processes operate, we should see bedrock elevation measurements approximate a bimodal distribution of either low-elevation sites (i.e., those within the spatial extent of positive-feedback dissolution processes), or high-elevation sites (those within the “distal-negative” feedback domain). If “smoothing” processes are operative, elevation of the overlying soil should display lower bimodality.

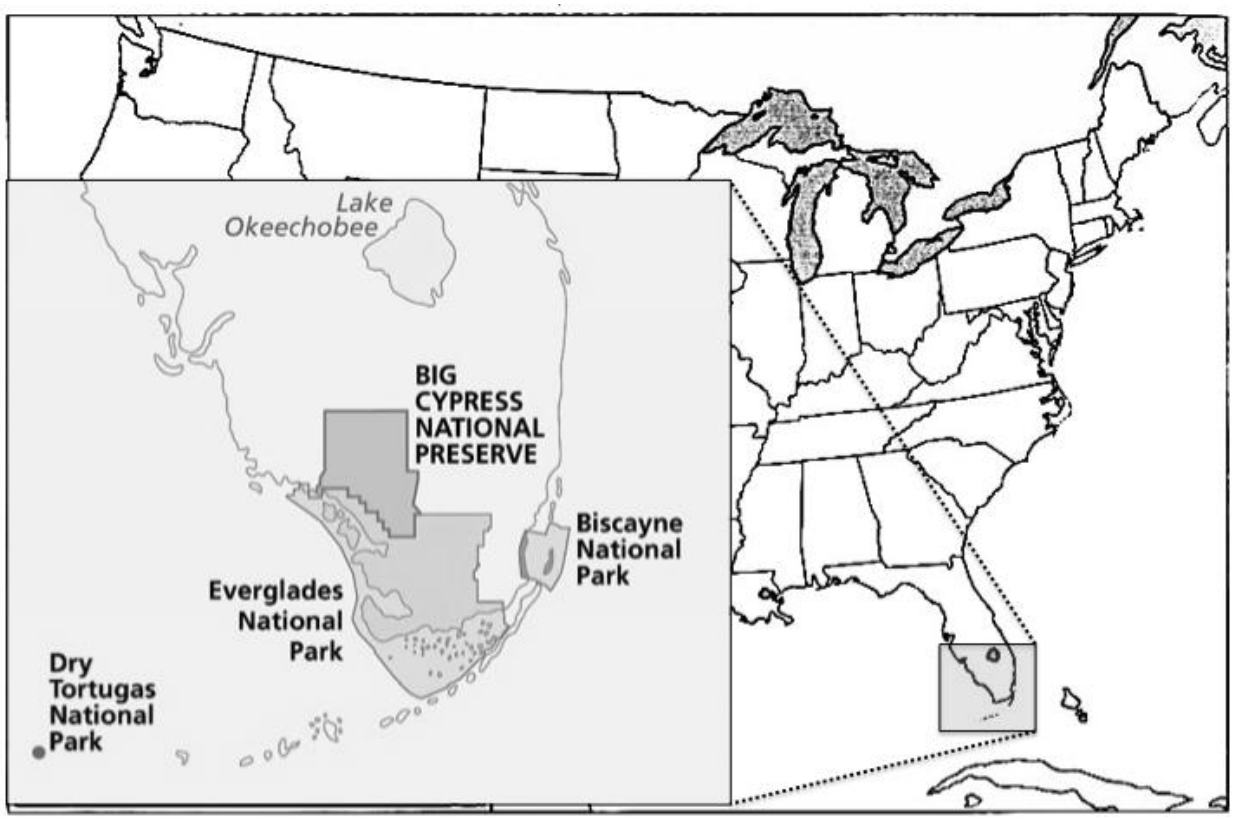

Figure 5-3. Big Cypress National Preserve occupies 300,000ha in southern Florida, USA, contiguous with Everglades National Park.

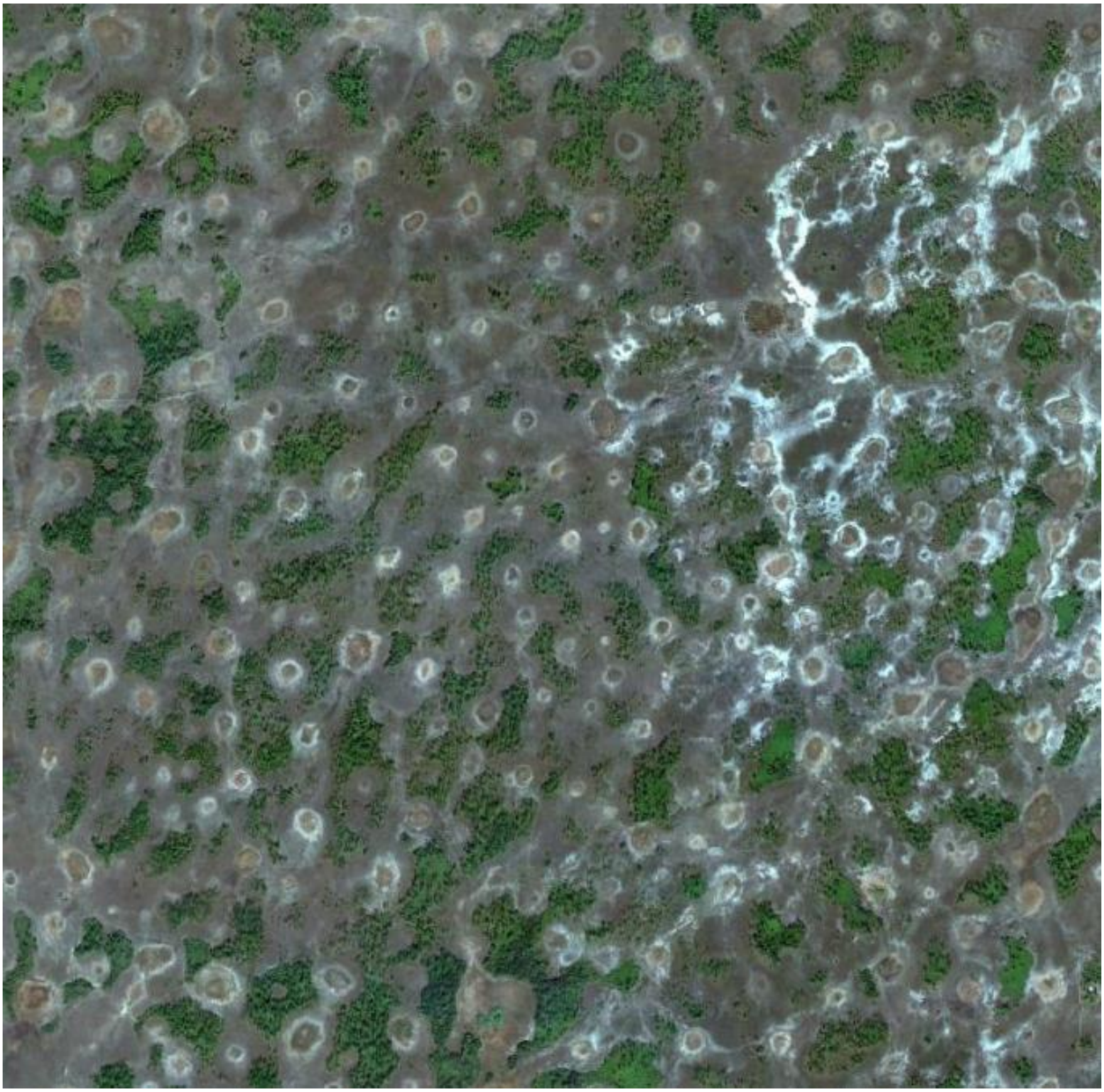

Figure 5-4. Illustration of the circular depressional wetlands characteristic of Big Cypress and elsewhere in undisturbed portions of southern Florida. This SPOT image from Google Earth (Google, Inc., Mountain View, CA USA) shows a 3km^2 area from the central portion of the Preserve.

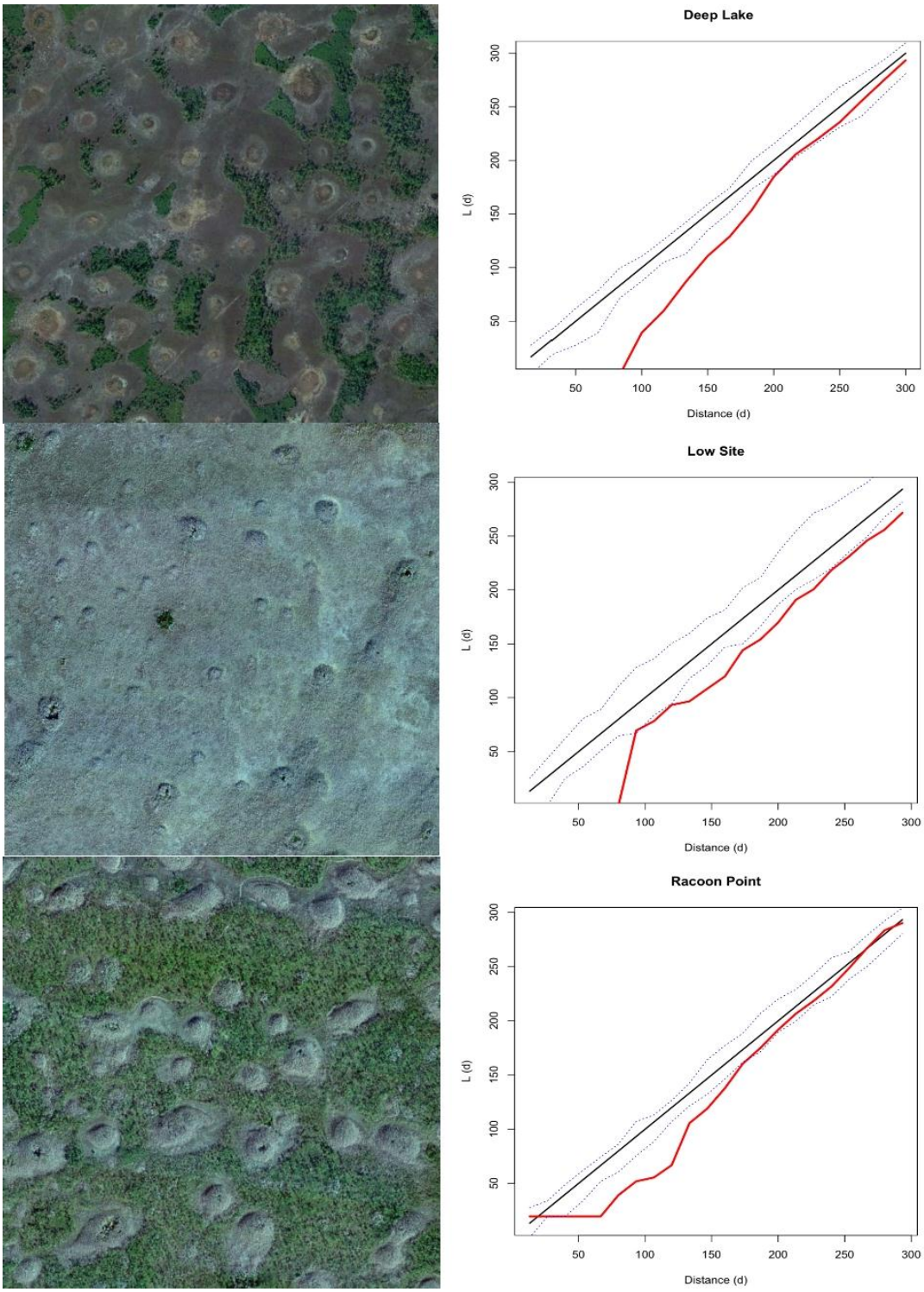

Figure 5-5. Images of sampling locations with their respective K-function plots. Shown are observed values of L(*d*) (red line), expected values (black line), and 95% confidence intervals for expected values at varying distances among sets of points representing centers of depressional landscape features. Images courtesy Google Earth (Google, Inc., Mountain View, CA USA).

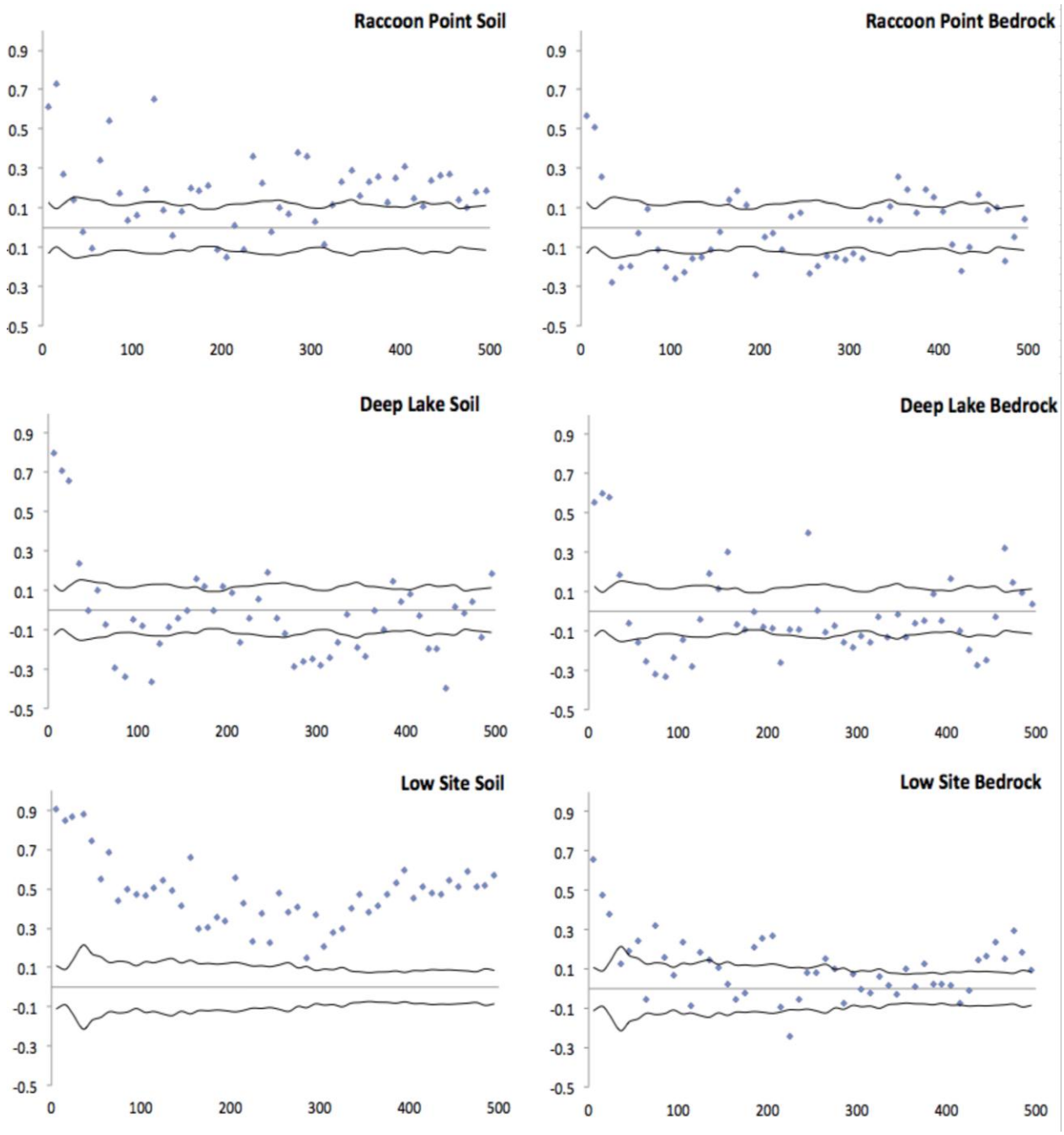

Figure 5-6. Correlograms showing spatial autocorrelation values (y-axis) of soil and limestone bedrock elevation measurements. Analyses shown include lag distance of 10 m and range of 500 m. Solid black lines indicate 95% confidence intervals at increasing distance in meters (x-axis); cross-correlation values are represented by gray dots.

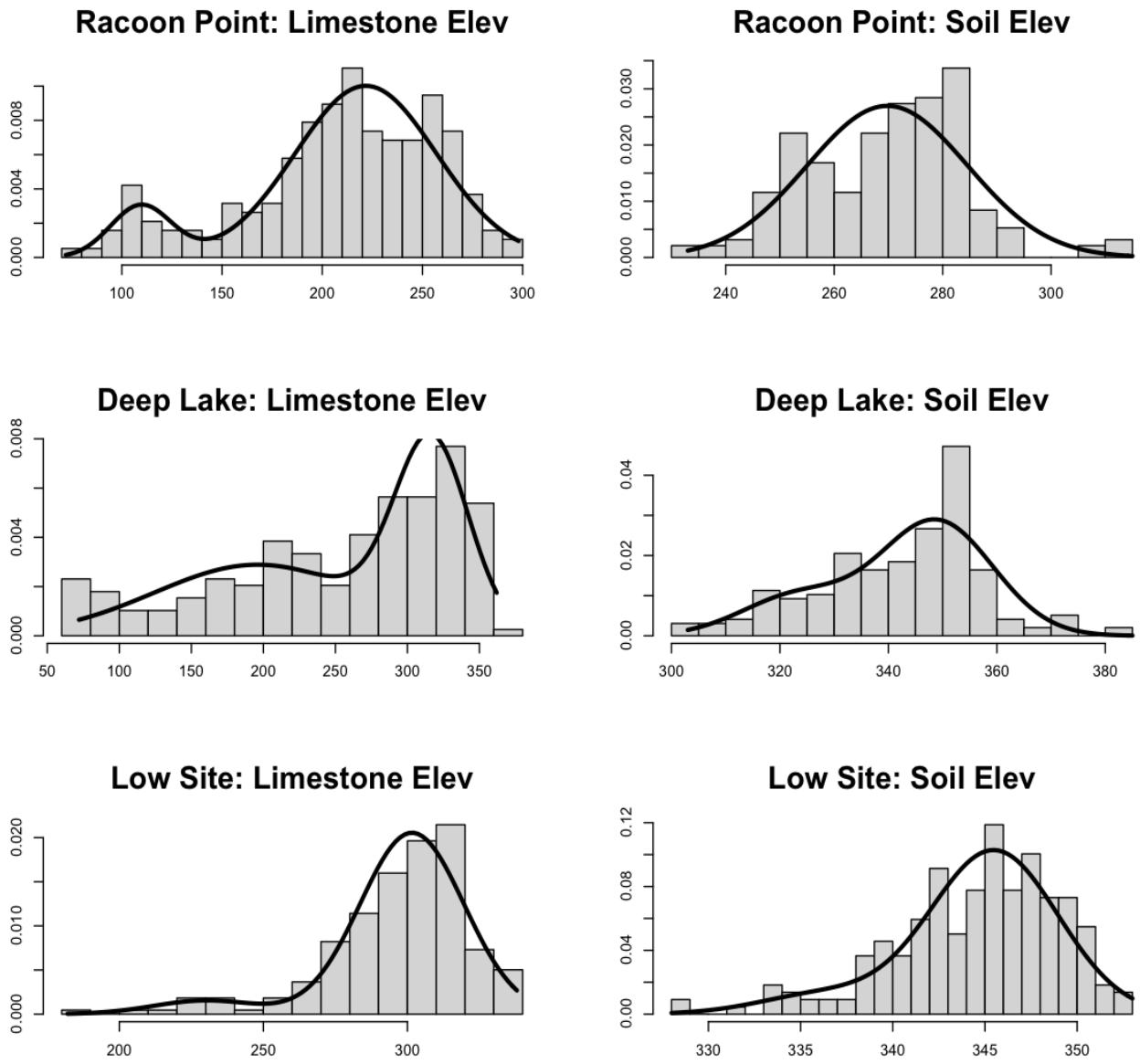

Figure 5-7. Best-fit models of elevation chosen by BIC scores (black line) superimposed over distributions of observations. Models indicate bimodal distribution in all cases except for Raccoon Point soil elevations, which were unimodal. Bimodality is strongly evident in limestone bedrock elevation at Raccoon Point and Deep Lake sites.

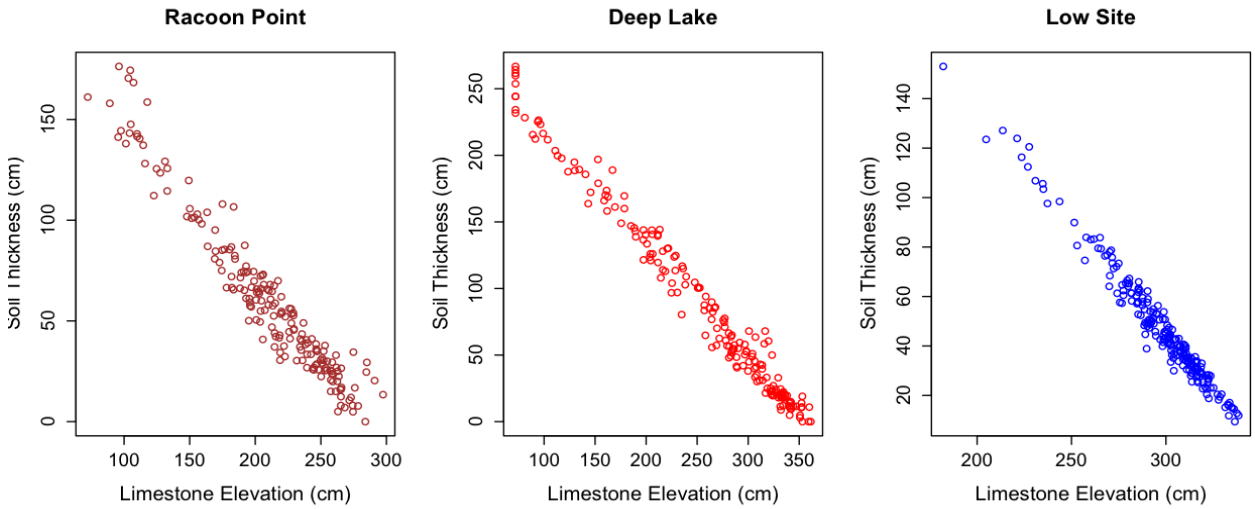

Figure 5-8. Thickness of soil was greatest at the lowest bedrock elevations observed in all three sampling locations. Soils became thinner at locations with decreasing bedrock depth. Elevation of limestone bedrock are in cm above mean sea level. R-squared values for linear-regression models of these relationships (not shown) are 0.93 for Raccoon Point; 0.97 for Deep Lake and Low Site ($P < 10^{-15}$ in each case).

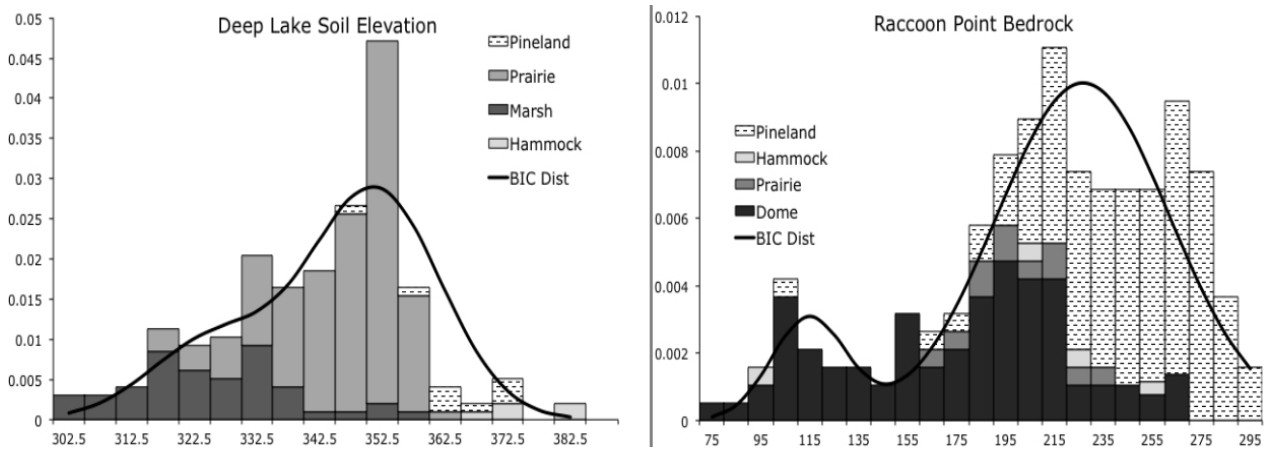

Figure 5-9. Distributions of vegetation communities observed for various soil (left) and bedrock (right) elevations at two sampling locations. “Dome” refers to patches of wetland forest dominated by pondcypress (*Taxodium distichum* var. *imbricarium*), regionally referred to as cypress domes. Black line is the best-fit model of landform elevation distribution, chosen by Bayes’ Information Criterion (BIC) score.

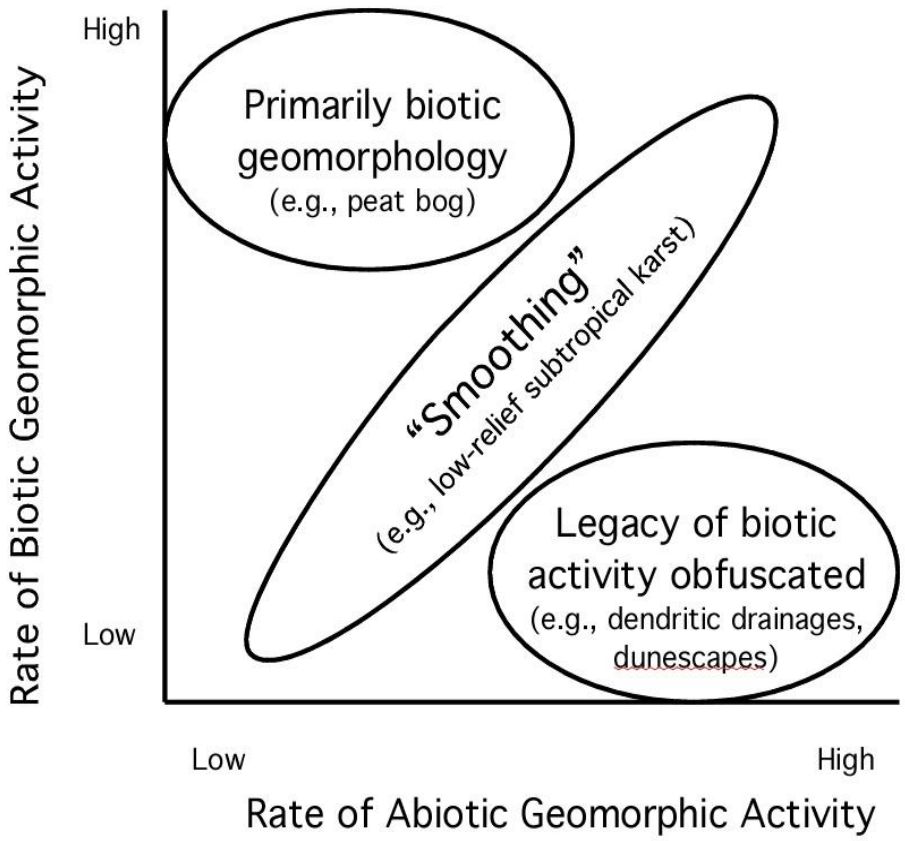

Figure 5-10. Landscapes where the pattern generated by a combination of biotic and environmental factors is easy to see may have low relative rates of abiotic geomorphic activity. Examples include patterned bogs and fens, where low topographic relief leads to dominance of biotic processes over erosional forces. Conversely, erosion due to high relief or frequent disturbance may overwhelm biotic signals on landform. Between the two extremes are situations in which the landform is receptive to biotic or ecohydrologic activity, as well as opposing forces which tend to obfuscate these signals.

Table 5-1. Characterization of the depressional landscape features observed in three 1.5 km x 1.5 km landscape sampling blocks. While average depression size and percentage of landscape occupied by depressional features varied, nearest-neighbor analysis indicated nonrandom, even distribution of landform depressions.

Site Name	Number of Depressions	Mean (s.d.) Depression size, ha	Mean (s.d.) Depression dia., m	Depression area, ha (%)	Z-score
DL	60	0.47 (0.31)	74 (24)	28.11 (12.5%)	6.351*
LS	45	0.25 (0.35)	50 (25)	11.02 (4.9%)	3.469*
RP	60	0.58 (0.42)	81 (29)	34.89 (15.5%)	4.302*

Note: *DL = Deep Lake; LS = Low Site; RP = Raccoon Point; *indicates significant overdispersion (i.e., regular or even spatial distribution, as opposed to random or clustered distribution),* $\alpha \leq 0.05$.

Table 5-2. Means and standard deviations for best-fit models of bedrock and soil surface elevation and soil thickness based on BIC comparisons.

Site	Measurement	Model Parameters (BIC best-fit model)				
		X_1	X_2	σ_1	σ_2	q
Raccoon Point	Bedrock Elevation	109.6	221.7	15.2	35.2	0.12
	Soil Surface Elevation	269.8	NA	14.8	NA	1.00
	Soil Thickness	47.0	132.3	23.8	23.8	0.84
Deep Lake	Bedrock Elevation	196.0	316.7	71.8	71.8	0.52
	Soil Surface Elevation	323.3	348.9	10.3	10.3	0.26
	Soil Thickness	32.7	139.2	20.5	20.5	0.48
Low Site	Bedrock Elevation	230.0	301.6	18.1	18.1	0.07
	Soil Surface Elevation	336.3	345.5	3.5	3.5	0.11
	Soil Thickness	43.2	108.9	16.8	16.8	0.93

Notes: *X_1 is mean at the first mode for bimodal distributions (or where greater maximum BIC values indicated unimodal model was more appropriate); X_2 is mean of second mode for bimodal distributions; σ_1 and σ_2 are standard deviations of first and second (if applicable) distributions; q is weight of first distribution; NA = not applicable (e.g. in cases of unimodal model offering better fit).*

CHAPTER 6
CONCLUSION

The landscape of southern Florida is a land of fire and water, and understanding the effects of these processes is prerequisite to achieving an understanding of the remaining relationships among organisms and their environment there. The studies presented here advance understanding of a few key components of the Big Cypress ecosystem, with some broader applicability elsewhere that wetlands experience periodic fire.

The first chapter describes mortality of a characteristic tree species, pondcypress, (*Taxodium distichum* var. *imbricarium*), in response to a wildfire that occurred under drought conditions of historic severity. Initially, the objectives of the study were to document mortality trends, to detect delayed mortality responses, and to determine which factors might predict pondcypress death due to fire. While these objectives were met and provide the first quantitative description of environmental contributions to mortality in the species, the role of fire in shaping vegetation at larger scales also was described. Through differential mortality depending on position and tree size, fire exaggerates the characteristic dome-shaped profile of these landscape features. Hydrology has been known for some time to affect dome structure, and now fire is strongly implicated as well.

The juxtaposition of moist, shady cypress domes with graminoid prairies or sparse-canopied pinelands and dwarf-cypress savannas provided the opportunity to test microclimate responses to edge and, given the hydrology and occurrence of wildfire, the effects of fire and water on microclimate as well. A hypothesized role of fire in promoting warmer, drier conditions within cypress domes would have suggested a positive-

feedback cycle in which fire history influences future fire behavior and effects. That these hypotheses were not supported by observations may be due to vigorous regrowth of vegetation in the two years following the Deep Fire. Significant edge effects on microclimate (both temperature and humidity) were observed, but these were far stronger during the dry season than during inundated conditions. There appears, then, not to be a hydrologic “switch” that turns edge effects on and off; however, hydrology does appear to exert substantial control over microclimate.

Hydrology intuitively affects soil moisture; and, just as fuel moisture affects fire intensity and rate of burn, so moisture in organic soils affects their potential for smoldering combustion. The lab-based smoldering combustion study in Chapter 3 provided the first information on soil moisture effects in smoldering combustion of cypress peat, and indicated the possibility of smoldering at surprisingly high moisture content. A conservative scaling-up approach was used to estimate the potential for carbon release both on a small unit-area (i.e., m^2) scale, within the extent of organic soils within a cypress dome, and at the larger landscape scale where the isolated occurrence of these domes within nonflammable marl soils and carbonate bedrock was considered. The former analysis indicated that, even at moisture levels found well before the height of the dry season, smoldering combustion in cypress peat soils may release more carbon to the atmosphere per unit area than did the infamous Kalamantan peat fires of the late 1990s.

The striking appearance of the Big Cypress landscape from the air or space strongly suggests that cypress domes occur at regularly-spaced intervals—an observation that, if true, would beg for an explanation. Earlier work has suggested a

mechanism which could result in patterning; and Chapter 4 provided empirical measurements of patterning as well as observations of landform elevation consistent with proposed ecohydrologic feedbacks which could produce regularly-spaced dissolution basins in low-relief carbonate bedrock. This was the first study of its kind to describe the biogeochemical footprint of an ecosystem in bedrock morphology at such a large spatial scale and extent. Additionally, comparisons of bedrock and soil elevation showed the obfuscating influence of erosional processes on patterned distribution of depressions, which were more clearly evident in bedrock elevation than in soil elevation. These investigations contribute evidence implicating vegetation structure and hydrology (both directly and indirectly) in producing geomorphic change and landscape pattern.

These four studies—fire influence on vegetation, vegetation influence on microclimate, soil moisture on smoldering, and pattern and ecohydrologic processes—are diverse in their examination of structure, process, and scale. They are superficially united primarily by geographic location. While this unity may appear the result of convenience, the succession of questions arose as I came to know the region better, and to comprehend the wealth of ecological questions begging to be addressed. Among the remarkable characteristics of the Big Cypress is the replication of wetland forest patches, which occur in a range of sizes in staggering numbers across hundreds of square miles. This feature alone would make the landscape an ideal setting for observational studies, even if Preserve policies would prevent manipulative experiments.

Yet beyond the superficial, the relationship of these studies lies in the relative influences of fire and hydrology at Big Cypress and other locations where hydrologic

variability in wetlands may result in vulnerability to fire. These relationships are illustrated in the influence diagram illustrated in Figure 6-1, which related known or intuitive relationships among fire, hydrology, and ecosystem and landscape characteristics with those investigated in the studies undertaken in this dissertation. Chapter 1 provided the first quantitative evidence for the role of fire in reinforcing the structure of pondcypress domes. Chapter 2 investigated a hypothesized role of fire and inundation in controlling the expression of edge effect, with implied feedback to wildfire. Chapter 3 described soil moisture influence on smoldering combustion (a form of wildfire, albeit one lacking much drama), and Chapter 4 suggests ecohydrologic feedbacks (including combined effects with vegetation structure) that alter geomorphology and produce pattern.

Much additional work remains to be done relating episodic fire to regular inundation and their interactive expression in this fascinating mosaic landscape. For example, the possibility exists that wildfire, by consuming organic soil in the depressional basins of cypress domes, may create increased storage volume at the landscape scale. Implications of this possibility are longer hydroperiods in the centers of domes (already suggested by the open-water marsh centers of some domes), and shorter hydroperiods in adjacent uplands as their lower elevation more effectively draws water from nearby areas. Thus it may be that wildfire, at least smoldering combustion during severe droughts, may affect local and landscape-scale hydrology during subsequent wet periods. Changes in soil chemistry and nutrient cycling due to consumption of peat, shown in other ecosystems, may alter nutrient cycles in domes following fires as well. Whether the conversion of peat to ask and the accompanying

pulse of mineralized nutrients persists in the highly-buffered pore water of lower soil layers remains to be investigated, but it is conceivable that such events could affect vegetation growth and soil respiration. If either were the case, the enhanced production of acidic byproducts of metabolism could affect dissolution rates of carbonate bedrock as well and suggest ecopyrologic influence on geomorphology.

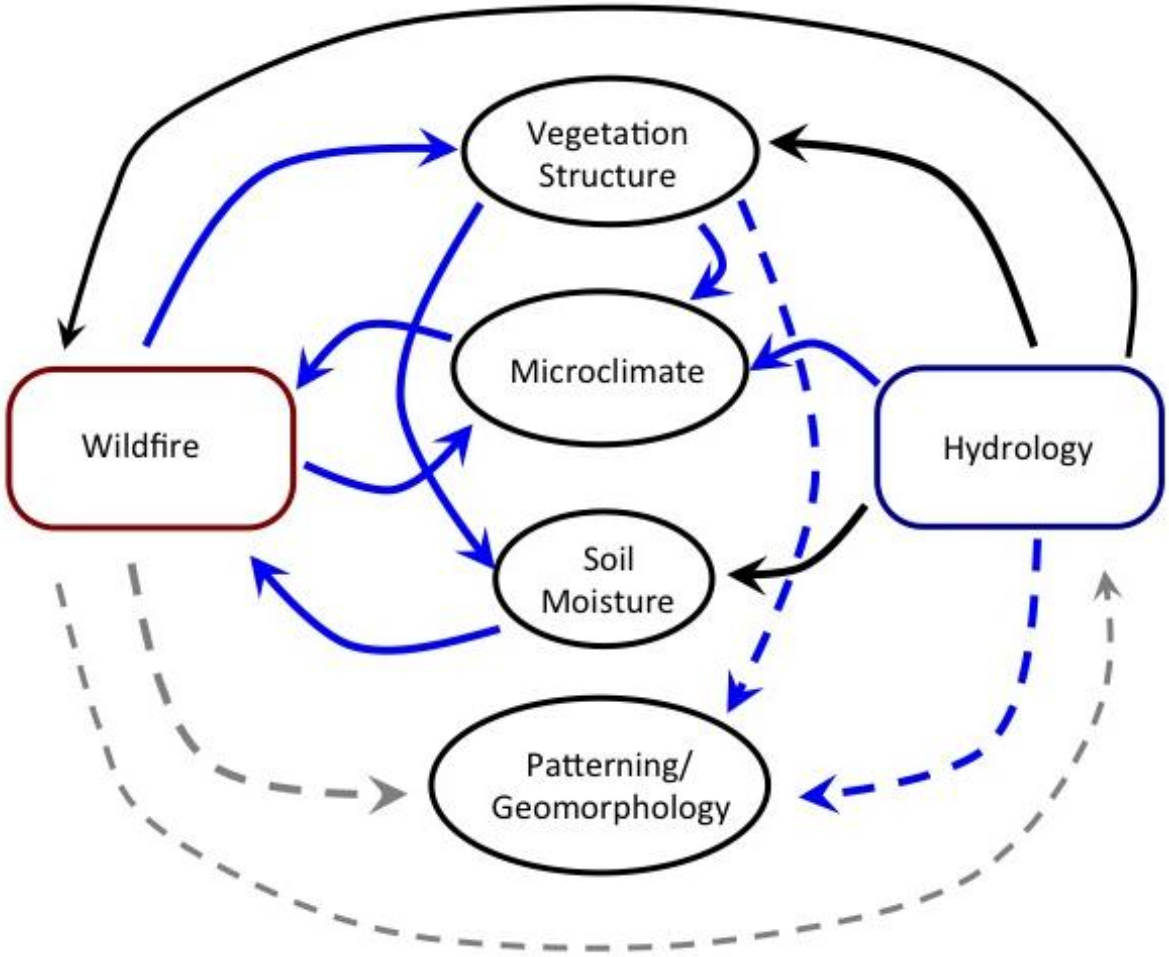

Figure 6-1. The four studies presented in this dissertation added to our understanding of relationships among fire, hydrology, and ecosystem and landscape characteristics. Black arrows represent relationships that have been previously investigated or are clearly understood *a priori*; blue solid arrows represent relationships investigated in the preceding four chapters. Dashed blue arrows represent relationships that are suggested by findings (both in Chapter 4), and dashed gray arrows represent relationships proposed here based on study findings and worthy of future investigation.

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BIOGRAPHICAL SKETCH

Adam Watts is native to the Coastal Plain Southeast, where he appreciated ecology long before learning of the field of academic study and was interested in fire long before knowing it can be governmentally condoned. As an undergraduate at Emory University, Watts majored in biology and ecology and learned the mountain trails and whitewater streams of the Piedmont. Chasing after a desire to study ecological restoration, he completed a M.S. degree in interdisciplinary ecology at University of Florida investigating the use of fire and mechanical means in restoring Florida dry prairie. Watts also served as a Peace Corps Volunteer in Guinea, and coordinated University of Florida's unmanned aircraft program prior to beginning his doctoral work.