Research Article

Tree Island Response to Fire and Flooding in the Short-Hydroperiod Marl Prairie Grasslands of the Florida Everglades, USA

Pablo L. Ruiz[1*], Jay P. Sah[1], Michael S. Ross[1,2], and Adam A. Spitzig[1]

[1]Southeast Environmental Research Center, Florida International University, 11200 SW 8th Street, Miami, Florida 33199, USA

[2]Earth and Environment Department, Florida International University, 11200 SW 8th Street, Miami, Florida 33199, USA

*Corresponding author: Tel.: 001-786-205-1032; e-mail: plruiz.fiu@gmail.com

ABSTRACT

Within the marl prairie grasslands of the Florida Everglades, USA, the combined effects of fire and flooding usually lead to very significant changes in tree island structure and composition. Depending on fire severity and post-fire hydroperiod, these effects vary spatially and temporally throughout the landscape, creating a patchy post-fire mosaic of tree islands with different successional states. Through the use of the Normalized Difference Vegetation Index (NDVI) and three predictor variables (marsh water table elevation at the time of fire, post-fire hydroperiod, and tree island size), along with logistic regression analysis, we examined the probability of tree island burning and recovering following the Mustang Corner Fire (May to June 2008) in Everglades National Park. Our data show that hydrologic conditions during and after fire, which are under varying degrees of management control, can lead to tree island contraction or loss. More specifically, the elevation of the marsh water table at the time of the fire appears to be the most important parameter determining the severity of fire in marl prairie tree islands. Furthermore, in the post-fire recovery phase, both tree island size and hydroperiod during the first year after the fire played important roles in determining the probability of tree island recovery, contraction, or loss.

Keywords: fire, flooding, Google Earth, kml, marl prairies, NDVI, regime shift, skeleton islands, tree islands

Citation: Ruiz, P.L., J.P. Sah, M.S. Ross, and A.A. Spitzig. 2013. Tree island response to fire and flooding in the short-hydroperiod marl prairie grasslands of the Florida Everglades, USA. Fire Ecology 9(1): 38-54. doi: 10.4996/fireecology.0901038

INTRODUCTION

Under frequent fire return intervals, the integrity (i.e., structure, composition, and ecological function) of most fire-dependent terrestrial plant assemblages remains relatively intact. However, in the absence of fire, fire-dependent ecosystems like pine forest may succeed into hardwood forest or other climax type communities (Robertson 1953, Brown 1975, Duever 1984, Graham and Jain 2005). Likewise, salt marshes may shift towards buttonwood thickets (Schmidt *et al.* 2010); short-hydroperiod graminoid wetlands may transform into cypress swamps or mesic forests (Alexander and Crook 1984, Duever 1984); and semi-arid grasslands may shift toward mixed tree-grass systems or savannas (White and Loftin 2000).

In the above examples, plant assemblages are shown shifting from one alternative stable state to another via a unidirectional linear vector in response to long-term fluxes in the periodicity of a discrete singular driver, fire, in this case. Nature, however, is not that simplistic. Regime shifts, (i.e., large, abrupt, and deleterious long-term changes to the structure, composition, and function of a system or community, which may be permanent [Biggs *et al.* 2009]), sometimes occur quite quickly and follow non-linear pathways in response to the synergistic interactions of physical (e.g., weather, climate, fire, hydroperiod, etc.) and biological (e.g., inter- and intraspecific competition, disease, pest infestation, etc.) drivers co-occurring in time and space.

As physical drivers or perturbation events within the landscape, fire and hydrology often interact to shape the composition, structure, function, and spatial patterning of terrestrial and wetland plant communities (Olmsted and Loope 1984, White 1994, Lockwood *et al.* 2003). Fire, in particular, can be an important force in maintaining landscape heterogeneity by affecting nutrient cycling and productivity (Carter and Foster 2004), and both physical and chemical soil properties (Verma and Jayakumar 2012), and by suppressing the natural succession of plant assemblages towards an alternative stable state (White 1994, White and Loftin 2000). In turn, spatial and temporal variability in hydrology (i.e., flooding or droughts) can modify the intensity of fire and its overall effect on the landscape, as well as the capacity of vegetation to recover from it (Kozlowski 1997).

The synergistic interactions of fire and hydrology are known to have catastrophic long-term consequences on wetlands and uplands alike (Craighead 1984, Olmsted and Loope 1984), and can lead to regime shift. Flooding conditions immediately following a fire can transform productive wetlands into sparsely vegetated low-biomass pools or ponds with little or no resemblance to the pre-existing community (Olmsted and Loope 1984, Sah *et al.* 2012). Likewise, fires during drought conditions can burn into tropical hardwood hammocks or tree islands from adjacent pyrogenic communities (e.g., pine forest or graminoid prairies), and produce catastrophic results (Craighead 1984, Armentano *et al.* 2002).

In the Everglades, forested tree patches or tree islands are an integral component of the landscape and are generally considered climax communities. Tree islands, which are prominent features in both the short- and long-hydroperiod wetlands of the Everglades, provide a network of refuges for forest-dwelling plants and animals and perform important biodiversity and nutrient cycling functions (Gaines *et al.* 2002, Meshaka *et al.* 2002, Jayachandran *et al.* 2004, Hanan and Ross 2009, D'Odorico *et al.* 2011) and are highly susceptible to the effects of fire and prolonged flooding.

Tree islands in the short-hydroperiod marl prairies of the Everglades number in the thousands (Loope and Urban 1980) and range in size from a few square meters, consisting of three to five individual trees, to several hectares, with hundreds of stems. Species diversity, a function of tree island size and successional processes, is generally high and consists of a mixed-species assemblage of both tropical and temperate plant species, encompassing a broad range of hydrologic requirements, fire tolerances, and growth forms (Loope and Urban 1980, Snyder *et al.* 1990, Hanan *et al.* 2010). Regardless of size, the location of most marl prairie tree islands is predicated on the presence of a limestone bedrock outcrop that rises well above the marsh surface (Loope and Urban 1980). Among small ($\leq$100 m^2) tree islands, Hanan and Ross (2009) found the difference in elevation between the marsh and the top of the bedrock outcrop to be approximately 20 cm (Hanan and Ross 2009). On larger tree islands, the bedrock outcrop sometimes extends 60 cm to 122 cm above the prairie surface (Craighead 1984, Ruiz *et al.* 2011).

Sparsely vegetated bedrock outcrops are also commonplace within the marl prairie landscape (Hofstetter and Hilsenbeck 1980). These skeleton islands (Figure 1) have the same general species composition and underlying geologic structure as fully formed and densely vegetated tree islands. However, skeleton islands have little or no soil in which the native flora may germinate and root, or from which they may gather water and nutrients. As a result, vegetation cover is generally below 10 %, with most species rooted in cracks and fissures in the limestone bedrock. The natural history of these landscape features is currently unknown. It is possible that they are proto-tree islands or early nucleation sites from which new tree islands are emerging. Alternatively, however, they may be relic tree islands (Hofstetter and Hilsenbeck 1980, Gunderson and Snyder 1994) in a degradative state resulting from fires or other exogenous drivers.

Figure 1. Example of sparsely vegetated rock outcrop (skeleton island) common throughout the short-hydroperiod marl prairie grasslands of the Everglades, Florida, USA.

The deleterious effects of flooding on Everglades tree islands are well documented (Patterson and Finck 1999, Avineon 2002, Sklar *et al.* 2004, Hofmockel *et al.* 2008). However, the long-term effects of fire on tree island genesis, persistence, degradation, and loss within the marl prairies of the Everglades have yet to be properly studied. Likewise, much remains unknown regarding the interactive role that fire and hydrology (i.e., drought or flooding) have on tree island spatial patterns and metacommunity processes within this landscape.

Under extreme drought and elevated fuel loads, fires can burn vigorously into tree islands, consuming soils, litter, and understory vegetation, as well as top-killing most, if not all, of the trees present, and damaging or destroying their root systems (Wade *et al.* 1980, Doren and Rochefort 1984, Rein *et al.* 2008). When such fires occur, they typically lead to significant soil loss and the exposure of the underlying limestone bedrock (Hofstetter and Hilsenbeck 1980, Taylor 1981, Doren and Rochefort 1984). Dramatic shifts in community structure and composition as well as tree island contraction or loss can occur if soil loss is enough to alter the hydrologic regime and flooding frequency of these tree islands because of an overall decrease in soil surface elevation (Zaffke 1983).

Anecdotal evidence suggests that tree islands within the marl prairie grasslands of the Everglades usually recover from a fire within several years (Loope and Urban 1980). However, very little is known about the successional sequence of tree islands following an intense fire and how post-fire flooding affects tree island resilience, (i.e., the ability of a system or community to absorb perturbations and reorganize while maintaining the same functions, structure, identity, and feedbacks [Folke *et al.* 2004]), or the time scale associated with its structural and compositional recovery.

Within this context, we coupled remote sensing and GIS techniques along with multiple logistic regression analysis to test two hypotheses regarding the interactive effects of fire and hydrology on post-fire tree island burned status and recovery. We hypothesized that: (H1) the likelihood of a tree island burning is dependent on 1) the marsh water table elevation during the fire, and 2) the size of the tree island; and (H2) the likelihood of a burned tree island recovering to its pre-fire, forested state is dependent on 1) the post-fire hydrologic conditions of the marsh, and 2) the size of the tree island.

METHODS

Study Area

This study was conducted within the perimeter of the Mustang Corner Fire in Everglades National Park, Florida, USA (Figure 2). The Mustang Corner Fire, which burned for almost a month in the spring of 2008, impacted 16 250 ha of environmentally sensitive marl prairie habitat between the northeastern edge of Shark River Slough and the eastern boundary of Everglades National Park (Figure 2). On 14 June 2008, when the fire was finally extinguished, aerial surveys indicated that significant portions of the landscape were devoid of all vegetation and that most tree islands experienced topkill of all trees and were left with little or no standing live biomass. Historically, lightning was the main source of fire ignition in the Everglades. However, during the last century or so, fires have increased in frequency and intensity due to human manipulation of the landscape for land reclamation and resource extraction, as well as to carelessness (Hofstetter 1984).

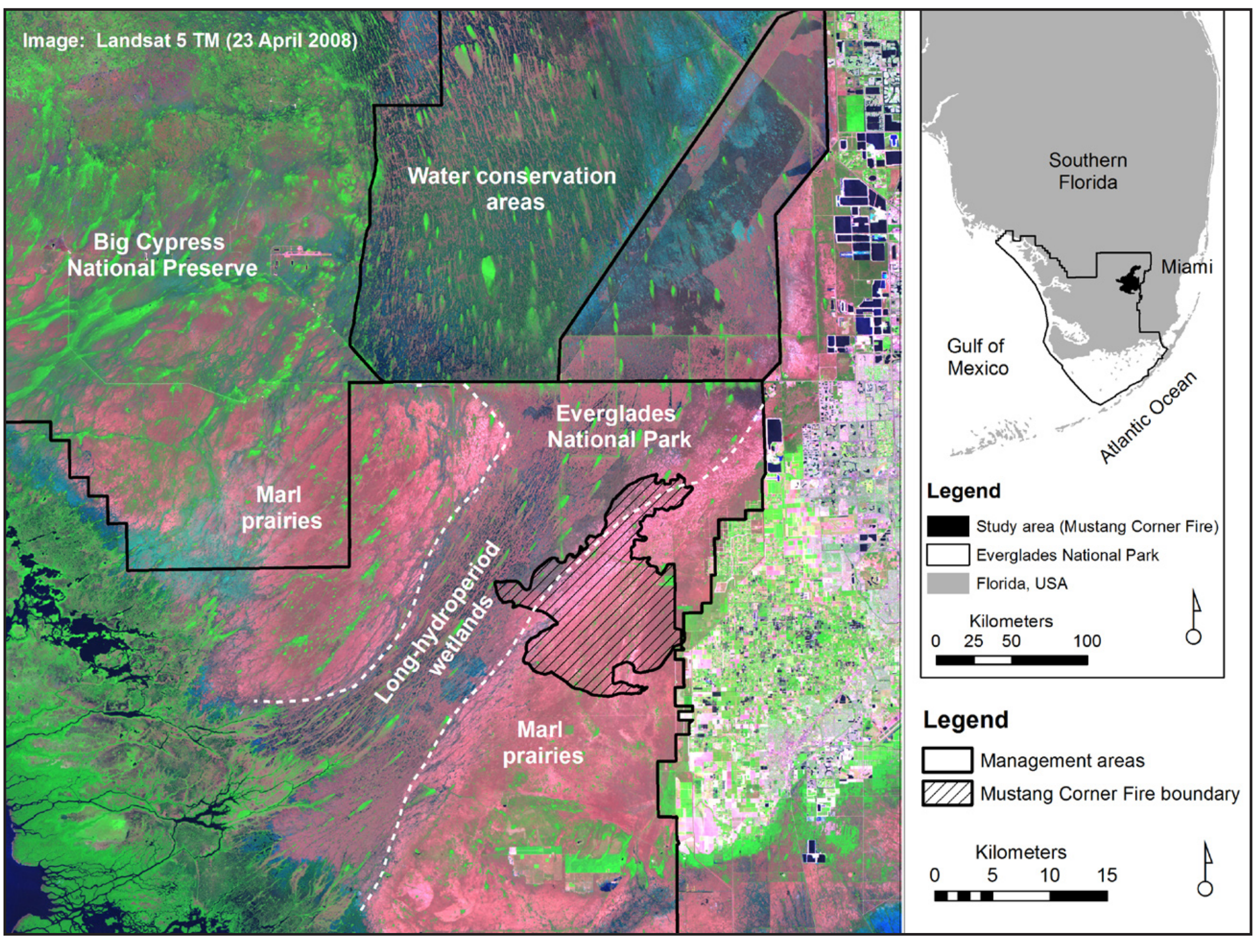

Figure 2. Mustang Corner Fire (2008) incident boundary within Everglades National Park, Florida, USA.

The marl prairies of the Everglades are typified by shallow calcareous soils with frequent exposures of limestone bedrock, high graminoid and herbaceous species diversity, and many tree islands (Loope and Urban 1980, Olmsted and Loope 1984, Hanan *et al.* 2010). The discontinuous annual period of inundation, hereafter referred to as "hydroperiod," within this grassland ranges between two and seven months (Lockwood *et al.* 2003, Ross *et al.* 2006) and is controlled by intra- and inter-annual variation in rainfall as well as water management decisions by the South Florida Water Management District and the United States Army Corps of Engineers. These two agencies administer and regulate the timing and volume of water delivery and hydroperiods within the Everglades by moving water through an extensive network of canals, levees, and water control structures, which have compartmentalized the current Everglades into distinct hydrologic units.

Remote Sensing

All tree islands (≥36 m^2) within and up to 500 m beyond the incident boundary of the Mustang Corner Fire (Figure 2) were identified, digitized, and populated into a geodatabase using ESRI® ArcMap™ 9.3 (ESRI 2009). The basemap used for the identification of tree islands consisted of a set of 2004 1 m resolution color infrared (NIR, Red, and Green) images. This image dataset corresponded to the regularly flown (about once every five to seven years) National Aerial Photography Program (NAPP) Digital Ortho Quarter Quadrangles (DOQQs). The DOQQs were enhanced using a low pass 3 × 3 kernel filter and spectrally calibrated in ERDAS Imagine 9.3 (Erdas 2008) to ensure spectral consistency between images.

Following the image enhancing process, the Normalized Difference Vegetation Index (NDVI) was calculated for each DOQQ in ESRI® ArcMap™ 9.3. The NDVI is considered an excellent predictor of photosynthetic activity or vigor and productivity within a landscape (Wang *et al.* 2003, Weiss *et al.* 2004, Warren and Metternicht 2005). It has been used widely to estimate vegetation cover, leaf area index, and biomass among other vegetation canopy biophysical parameters (Weiss *et al.* 2004). The NDVI is derived as follows:

$$NDVI = \frac{(R_{NIR} - R_{red})}{(R_{NIR} + R_{red})} \quad (1)$$

where R_{NIR} and R_{red} represent spectral reflectance in the near-infrared (λ ~ 0.76 µm to 0.90 µm) and red (λ ~ 0.62 µm to 0.74 µm) portions of the electromagnetic spectrum, respectively.

The resulting NDVI raster consisted of pixels for which values ranged between −1.0 and +1.0 (Figure 3). In general, positive NDVI

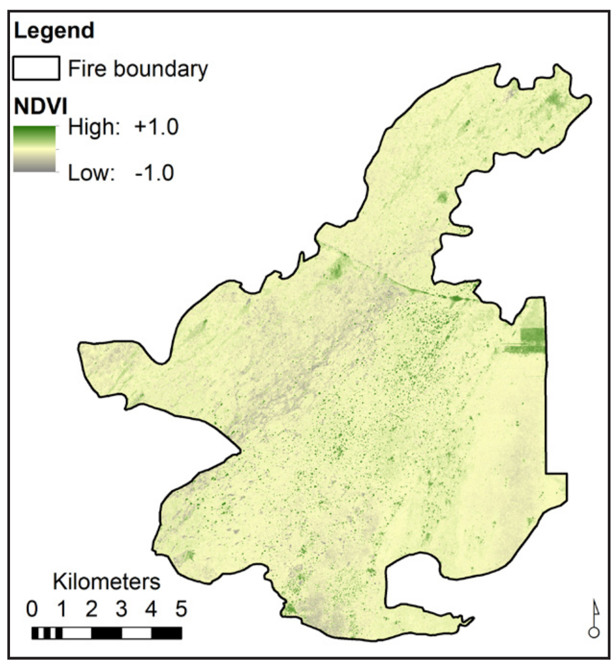

Figure 3. 2004 Normalized Differenced Vegetation Index (NDVI) map used to identify and map tree islands within the boundary of the Mustang Corner Fire (2008), Everglades National Park, Florida, USA.

values are associated with vegetated areas (e.g., grasslands, forests, or agricultural fields), while values ≤0 are associated with non-vegetative surfaces like bare soil or water (Jackson and Huete 1991, Weiss *et al.* 2004).

Based on this general relationship and empirical examination of all of the images, a minimum threshold NDVI value of 0.35 was chosen to characterize all tree islands within the study area. Using this value as a cutoff, all raster pixels with an NDVI value <0.35 were classified as marsh (i.e., 0) while those with values ≥0.35 were classified as tree islands (i.e., 1). The resulting binary rasters were mosaicked and clipped to include all areas within the Mustang Corner Fire and a buffer of 500 m around it. This product was then exported to a shapefile and the area of each tree island object was examined. All tree island objects of total area <36 m^2 were reclassified as marsh, since this size was the minimum resolution that allowed tree island objects to be identified with a high degree of certainty in the 2004 imagery. Next, the entire 22 528 ha tree island-marsh mosaic was visually inspected in order to identify improperly classified tree island objects ≥36 m^2 (e.g., agricultural fields, woody plants growing along roads, or sawgrass strands). During this final QC/QA phase, tree island objects that exhibited gross boundary errors or other anomalies were manually edited.

The post-fire status of tree islands was assessed using color infrared aerial photographs taken in April 2009, nearly a year after the Mustang Corner Fire. This image dataset consisted of ~30 cm spatial resolution aerial imagery taken with a Microsoft UltraCamX frame-based digital camera as part of the Comprehensive Everglades Restoration Plan (CERP) Restoration Coordination and Verification (RECOVER) vegetation mapping project (RECOVER 2006).

Using NDVI as an indicator of post-fire vegetation regrowth and cover, we created an NDVI raster using the 2009 CERP imagery and the pre-fire tree island boundaries as the analysis mask within the spatial analysis tool in ESRI® ArcMap™ 9.3. Consequently, we only calculated NDVI for those pixels that fell within the pre-fire boundary and ignored all other regions (i.e., the marsh).

Spectral variability in airborne-acquired imagery, due to external conditions and changes in technology, makes it difficult, if not impossible, to directly compare temporal differences in spectral indices such as NDVI. As a result, a new tree island NDVI threshold value was determined empirically, for the 2009 imagery, by evaluating different NDVI ranges that best duplicated the pre-fire tree island shape created from the 2004 DOQQs for tree islands known to have been unaffected by the Mustang Corner Fire. The new NDVI threshold value for the post-fire tree island objects was determined to be 0.25 for all 2009 images. Pixels with NDVI values <0.25 were classified as non-vegetated or burned (i.e., 0), while pixels with NDVI values ≥0.25 were classified as vegetated or not burned (i.e., 1). The resulting new raster was exported to a shapefile and the post-fire tree island area was calculated.

To assess the immediate impact of the Mustang Corner Fire, individual tree islands were classified based on their change in area between 2004 and 2009. Those that had a total area decrease of <30 % were classified as unburned, otherwise they were considered to be burned. The burned tree island class was further subdivided into two subclasses. Tree islands that had total area decreases of between 30 % and 99 % were classified as burned with signs of recovery, while tree islands with 100 % loss of tree island area were classified as burned with no signs of recovery.

Three-year (2011) post-fire recovery was determined by exporting the burned with no signs of recovery classified tree islands (i.e., those tree islands that burned in the fire but showed no signs of recovery one year later) into a Google Earth kml file (Google, Inc. 2012*a*). The kml file was then opened in

Google Earth v6.1 (Google, Inc. 2012*b*) and the spectral signature for each of these islands was reevaluated visually and reclassified as burned with signs of recovery if there was any sign of greenness or vegetative regeneration within the tree island boundary. The date of the Google Earth imagery used was 26 March 2011.

Data Analysis

For each tree island, we calculated the following tree independent variables: water table, hydroperiod, and tree island size.

Water table represented the elevation of the water table relative to the ground surface of the marsh (i.e., the difference between the marsh water surface elevation and the ground elevation), in meters, on 17 May 2008, three days after fire ignition. The depth of the water table on 17 May 2008 was available from the Everglades Depth Estimation Network (EDEN 2008), which estimates water depth throughout the freshwater Everglades from stage data at a network of water level recorders and ground elevation from the USGS Digital Elevation Model (EDEN 2008). We included water table as a predictor in our analyses on the assumption that the higher the water table near a tree island, the less likely it was to burn, because elevated soil moisture in both marsh and tree island would likely impede the advance of fire through the island (Craighead 1984).

Hydroperiod represented the discontinuous number of days in a year that an area is inundated (>0 cm). This variable was calculated by using the EDEN network data (EDEN 2008) for a one year period between 17 May 2008 and 16 May 2009. Our assumption for hydroperiod was that burned tree islands in persistently flooded areas would show little to no recovery when compared to burned tree islands in non-flooded areas, because post-fire flooding would hinder post-fire macrophyte germination and regrowth by inhibiting root growth as well as shoot and leaf development (Kirkman and Sharitz 1994, White 1994, Kozlowski 1997, Snyder and Hilton 2012).

Tree island size represented the area of each tree island. We expected that the size of a tree island might affect both the probability of burning and recovery, (i.e., larger tree islands might be less likely to burn completely because of the buffering effects that dense, moist, broad-leaved vegetation has on fire behavior and fuel consumption [Pyne *et al.* 1996, Sah *et al.* 2006]). In these islands, the spatial heterogeneity in vegetation moisture, cover, and density could lead to a heterogeneous fire effect with many unburned areas within the tree island (Olmsted and Loope 1984). In contrast, small tree islands are more likely to experience high fire severity. Tree island size might also influence post-fire recovery. Rapid regrowth should occur on larger burned tree islands, since recovery might be enhanced by the resources from within the tree island itself, (e.g., root sprouts, locally-derived propagules, and offshoots from surviving trees [Robertson 1953]), rather than external seed sources, which would be more typical of smaller tree islands. Tree island size was normalized using a natural log (ln) transformation.

The probabilities of a tree island burning (H1) or recovering (H2) following the Mustang Corner Fire were analyzed through multiple logistic regressions implemented in the "glm" function in the R statistical package ver. 2.13.1 (R Development Core Team 2011). This type of regression analysis utilizes one or more predictor variables to calculate the occurrence probability of a binary event, in this case tree island post-fire burned status (not burned vs. burned) and recovery (recovering vs. no recovery), by fitting a logistic function to observed conditions. In this type of regression analysis, an automated model selection procedure (stepwise regression) that selects a subset of the best predictors is commonly used. However, acknowledging the limitations of stepwise regression (Whittingham *et al.* 2006), we used an alternative approach, in which we developed models with all possible subsets of potential predictors. We ranked the models based on the Akaike Information Criterion (AIC), and tested for significant differences between each pair of models using a χ^2 test with one degree of freedom on their residual deviance (i.e., the difference between null and model deviance). The model that had the lowest AIC and differed significantly from all other models was selected. We used the Wald χ^2 test statistic to assess the significance or importance of the predictor variables or parameters within the model. The best predictive model for post-fire tree island burned status (H1) (i.e., not burned vs. burned) was:

$$P(m) = \frac{1}{(1 + e^{\wedge}(-(\beta_0 + \beta_1\, WT + \beta_2 A)))} \quad (2)$$

where *P(m)* is the probability of a tree island burning during a fire as a function of water table (*WT*) and tree island size (*A*). For the post-fire burned tree island recovery probability (H2) (i.e., not recovering vs. recovering), the best model was:

$$P(m) = \frac{1}{(1 + e^{\wedge}(-(\beta_0 + \beta_1 A + \beta_2\, HP)))} \quad (3)$$

where *P(m)* is the probability of a tree island that completely burned showing signs of recovery three years after fire as a function of tree island size (*A*) and hydroperiod (*HP*).

Furthermore, we used a collinearity diagnostic procedure, the variance inflation factor (VIF), to examine collinearity or correlation between the independent variables (water table, hydroperiod, and tree island size). The VIF values calculated for both models (1.32 and 1.10) were far below the value (2.5) above which collinearity is considered problematic in multiple logistic regression analysis (Allison 1999).

RESULTS

Tree Island Demography and Spatial Patterning

No more than 7412 tree islands of varying sizes and shapes were identified and mapped within the perimeter of the Mustang Corner Fire. The total tree island area mapped was 430 ha, or about 2.7 % of the total area affected by the fire. Median and mean tree island size was approximately 281 m^2 and 580 m^2, respectively, and ranged from 36 m^2, the minimum mapping unit (mmu), to a maximum of 63 827 m^2 (~6.4 ha). Tree islands <1000 m^2 (0.1 ha) in size accounted for approximately 86 % of the total number of tree islands mapped, but only about 44 % of the total tree island area within the fire perimeter (Figure 4). In contrast, large tree islands, those >10 000 m^2 (1.0 ha), accounted for approximately 0.3 % of the total number of tree islands mapped and represented approximately 8 % of the total tree island area mapped (Figure 4). Expressed as a kernel density function, tree island density ranged from zero to three tree islands per hectare, representing a heterogeneous landscape with highest tree island densities concentrated within an NNE-SSW strip midway across the area (Figure 5).

Hydrology

Hydrologic conditions in the marsh at the time of ignition in mid May, the typical changeover from dry to wet season in south Florida, were exceptionally dry following a 30 day period that saw no substantial precipitation. On average, the water table at fire inception was −0.647 m ± 0.007 m (S.E.) from the surface of the marsh and ranged from −1.844 m to 0.292 m within the study area. These values indicate that there was little or no standing water in most of the area at the time of fire ignition (Figure 6). The post-fire hydroperiod in the marsh during the first year averaged 129 days and ranged between 0 days and 326 days.

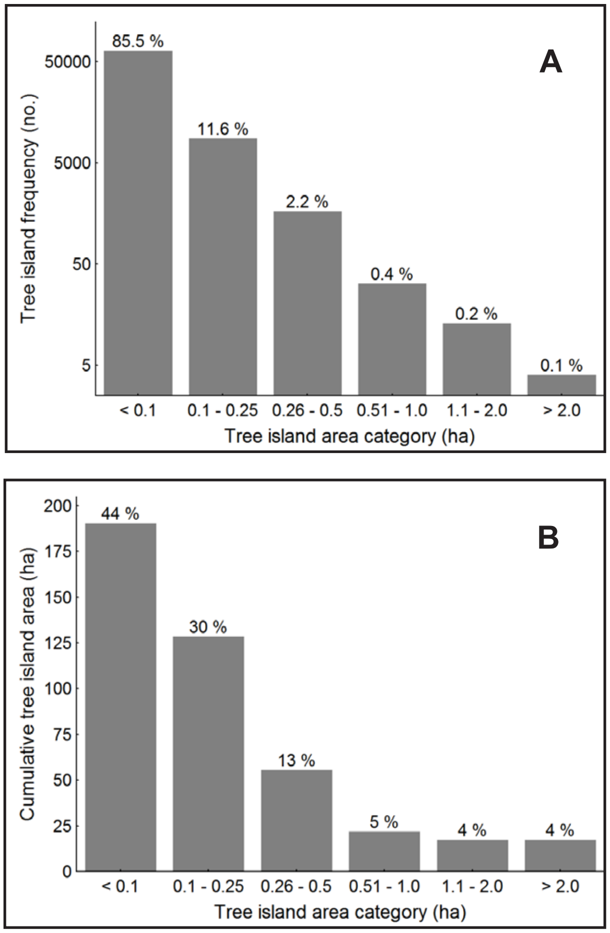

Figure 4. Frequency of tree islands (A) and cumulative area (B) by size classes within the Mustang Corner Fire incident boundary (2008), Everglades National Park, Florida, USA.

Post-Fire Tree Island Burn Status and Recovery

Of the tree islands identified within the Mustang Corner Fire boundary, 88% (6518) were classified as having totally or partially burned as a result of the fire (Figure 7). As expected, the probability of a tree island burning was negatively correlated to water table and tree island size (Table 1). Not surprisingly, the position of the water table at the time of the Mustang Corner Fire appears to be the major factor determining whether a tree island burned (i.e., the probability of a tree island burning increased as the distance between the tree island surface and water table position increased). On

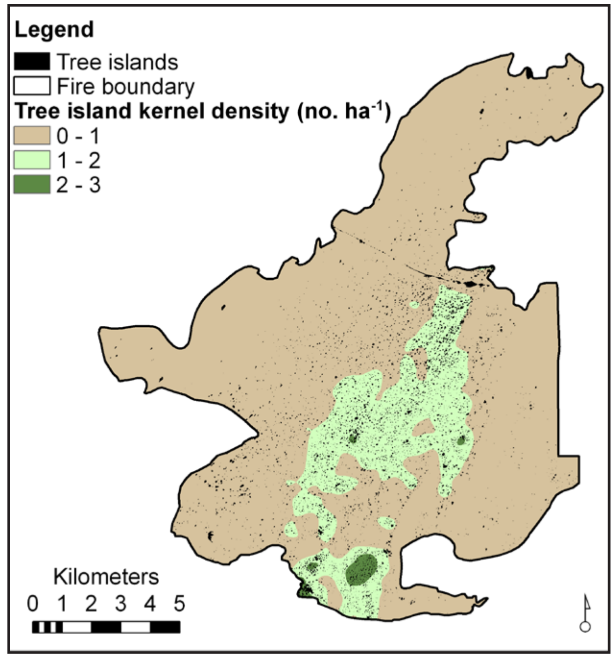

Figure 5. Tree island kernel density map (2004) showing the distribution of tree islands within the marl-prairie grasslands of the Everglades. A total of 7412 tree island are mapped within the boundary (16 250 ha) of the Mustang Corner Fire (2008).

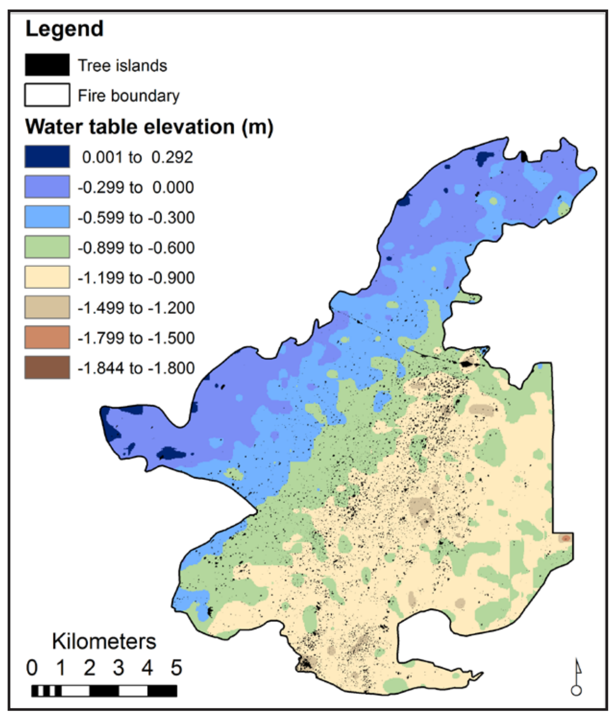

Figure 6. Mean marsh water table elevation within the Mustang Corner Fire incident boundary on 17 May 2008, three days after fire ignition.

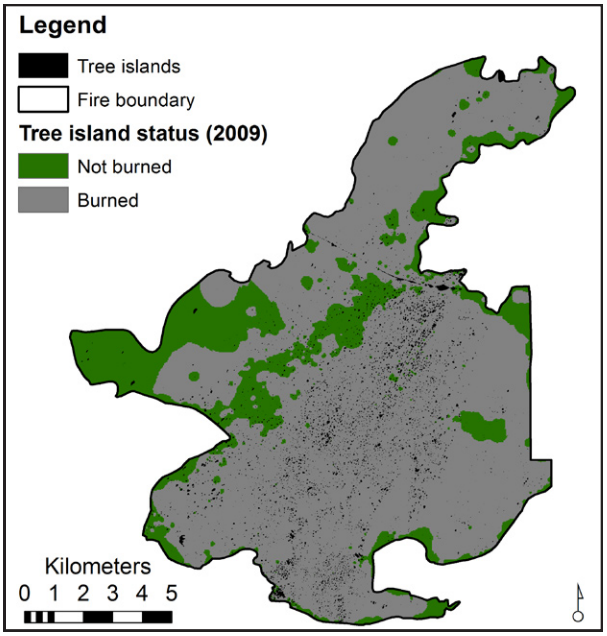

Figure 7. One year (2009) post-fire status of tree islands following the 2008 Mustang Corner Fire.

average, the marsh water table elevation was approximately 30 cm higher near non-burned tree islands (−0.665 m ± 0.009 m) than burned tree islands (−0.943 m ± 0.002 m). The size of the tree island, while significant, was less important than water table in predicting tree island burned status (Table 1).

Seventy-six percent (4933) of all tree islands that burned showed some early signs of recovery during the first year (2009). However, even three years after the fire (2011), about 4% of all the tree islands that initially burned showed no signs of recovery (Figure 8). To our surprise, tree island size, not hydroperiod, was the strongest predictor of post-fire tree island recovery (Table 2). The likelihood of post-fire recovery was positively affected by tree island size but negatively affected by hydroperiod. Post-fire recovering tree islands were, on average, several hundred square meters larger than non-recovering tree islands, 600 m^2 vs. 100 m^2, respectively, while mean marsh hydroperiods were 31 days longer on tree islands with no signs of recovery (153 days) than on tree islands showings signs of recovery (122 days).

DISCUSSION

Our analysis of the effects of the Mustang Corner Fire on tree islands revealed a direct relationship between pre- and post-fire hydrology and the probabilities of burning and recovery. More specifically, the multiple logistic regression models indicate that the elevation of the marsh water table at the time of a fire was the most important parameter in determining whether a tree island burned or not (Table 1), and that tree island size and post-fire hydroperiod both influenced the post-fire recovery of marl prairie tree islands (Table 2).

Both multiple logistic regression models provide a framework by which resource managers and ecologists can assess and determine the potential risk that a fire could have on tree islands within the marl prairies of the Everglades by examining three easily derivable variables (i.e., pre-fire water table, post-fire hydroperiod, and tree island size). Water table elevation and post-fire hydroperiod can both be manipulated, to some extent, by resource managers, and knowledge of their interactions with fire can be used to formulate and imple-

Table 1. Coefficients of the multiple logistic regression of tree island post-fire burned status (2008), not burned vs. burned.

Variable	Coefficient (ß)	S.E.	Wald statistic	Significance	Exp (ß)
Intercept	−0.696	0.276	6.371	<0.001	0.499
Water table (m)	−5.228	0.198	693.871	<0.001	0.005
Tree island ln (area, ha)	−0.209	0.042	24.812	<0.001	0.812

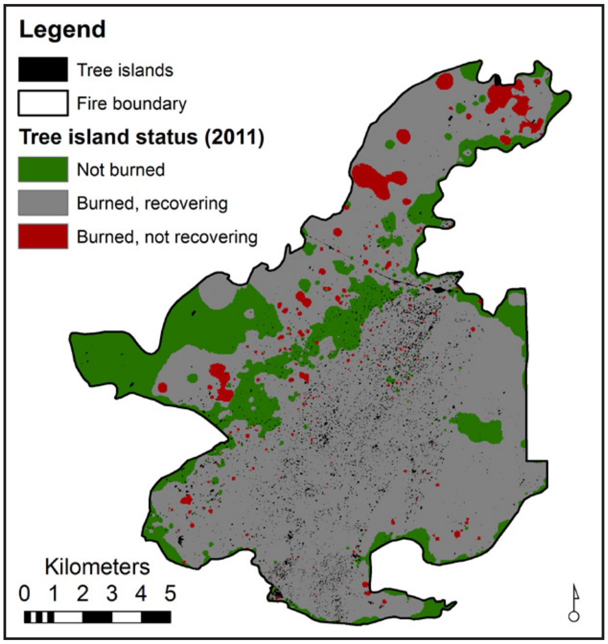

Figure 8. Three-year (2011) post-fire mosaic of tree islands successional state following the 2008 Mustang Corner Fire.

ment fire management plans. A hypothetical fire management plan could include a schedule of the rate, volume, and timing of water needed for delivery into a region to quickly raise the water table to a level that either prevents a fire from occurring or diminishes its overall effect on the landscape once ignited. Managers, however, need to be careful in implementing such a plan because of possible adverse repercussions. For example, if the rate and volume of water used to manage the fire leads to the post-fire flooding of burned tree islands, managers might find that their efforts to mitigate the effects of a fire and protect tree islands could result in the inability of burned tree islands to recover because they became flooded immediately after the fire and post-fire regeneration was inhibited.

Within the fire boundary, we observed a 30 cm difference in mean marsh water table depth between unburned (–0.665 m) and burned (–0.943 m) tree islands at the time of the fire. This finding is consistent with that of Craighead (1984) who found that water table depths greater than –0.60 m tended to exclude fires from hardwood hammocks while values less than –0.60 m led to severe hardwood hammock fires. Craighead's (1984) observations, while representative of large well-developed hardwood hammocks embedded in a pine forest matrix, parallel our findings on the importance of pre-fire hydrologic conditions in determining post-fire effects on marl prairie tree islands within the Everglades.

In contrast, Snyder and Hilton (2012) noted that in marl prairies that flooded immediately after burning, the mortality of *Morella cerifera* (Linnaeus) Small, a shrub common to Everglades tree islands, was significantly higher than in prairies in which post-fire flooding was delayed by several weeks. Snyder and Hilton (2012) attributed the increase in the mortality of *M. cerifera* within flooded prairies to flooding-induced anoxia of belowground parts, which prevented the top-killed *M. cerifera* shrubs from resprouting. Our post-fire observations of tree island fire effects following flooding suggest that the relationship between post-fire flooding and post-fire woody plant mortality is not just limited to individual

Table 2. Coefficients of the multiple logistic regression of tree island post-fire recovery status (2011), not recovering vs. recovering.

Variable	Coefficient (ß)	S.E.	Wald statistic	Significance	Exp (ß)
Intercept	–3.146	0.445	12.576	<0.001	0.043
Tree island ln (area, ha)	1.466	0.092	207.492	<0.001	4.330
Hydroperiod (day)	–0.007	0.001	36.651	<0.001	0.993

woody stems within a landscape, as Snyder and Hilton (2012) documented, but to tree islands, as well.

The difference in post-fire hydroperiod in the marsh between recovering and non-recovering tree islands was approximately one month. Slightly higher hydroperiods appear to have created anoxic conditions at the root base of surviving top-killed trees that 1) hindered the regrowth and development of root systems damaged in the fire, and 2) prevented resprouting from basal or root apical meristems. Consequently, recovery has been slow or absent on tree islands affected by post-fire flooding and extended hydroperiods. On the few tree islands where limited recovery was observed, the recovery was marked by the presence of flood-tolerant graminoids, sedges, and ferns, as well as by perennial woody shrubs with no regrowth of the woody vegetation that once proliferated and defined these tree islands (Figure 9). The combined interactions of fire and flooding have resulted in a regime shift towards a more marsh-like community (Figure 9). As a result, it is very difficult to continue thinking of these burned tree islands as "tree islands" since they no longer support any trees and fail to provide the same ecological function commonly associated with tree islands (e. g., nutrient cycling or roosting and foraging habitat for animals). However, assuming successional processes are allowed to proceed with little or no interference, and the core environmental conditions (i.e., soil depth and surface elevation) within these former tree islands remains intact, these highly degraded tree islands might eventually succeed back into a healthy, ecologically functioning tree island. The temporal scale associated with such recovery is currently unknown but it is likely to take several decades (Loope and Urban 1980), if not longer. The many rock platforms or skeleton islands (Figure 1) that are present within this landscape bear testament to the ultimate fate of many of these burned tree islands.

Based on our remote sensing observations, it appears that large tree islands tend to recover much faster than smaller islands after fire. While we collected no environmental data to explore this relationship, it is likely that the

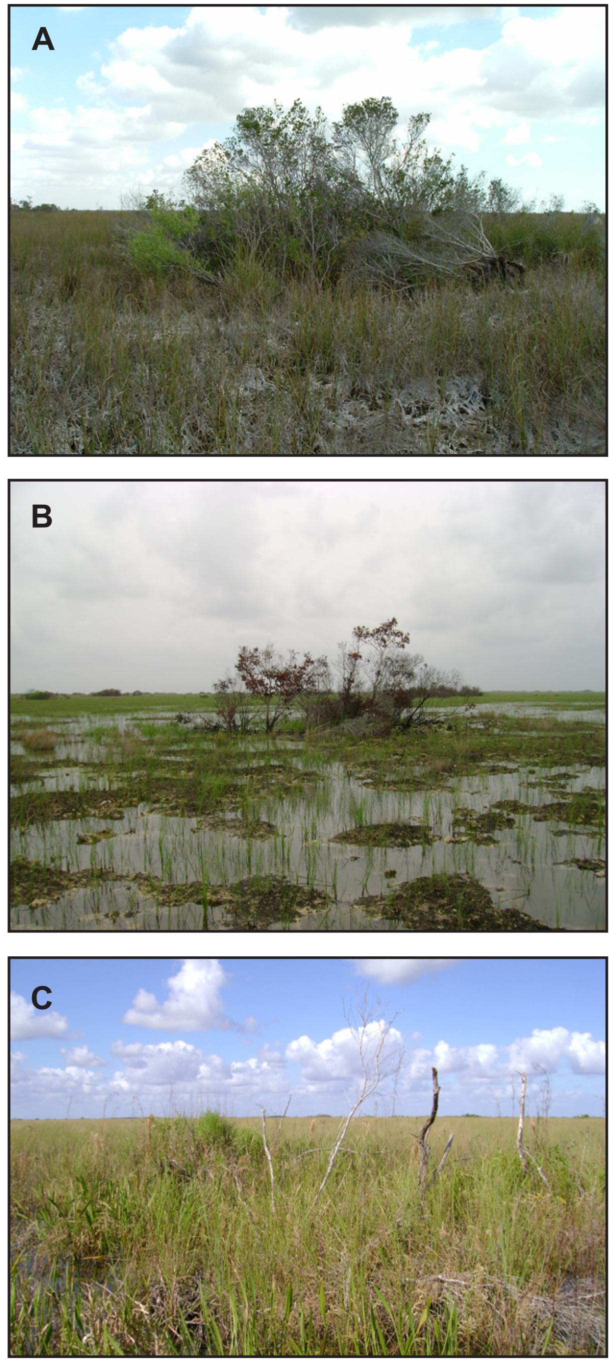

Figure 9. Photographs of a small but typical tree island found within the Mustang Corner Fire boundary: (A) 27 months pre-fire, (B) one month post-fire, and (C) 43 months post-fire. Note the loss of trees and the abundance of herbaceous and graminoid species before and after fire.

spatial heterogeneity in soil moisture, fuel load, and vegetation that one would expect to find in larger tree islands (Olmsted and Loope 1984), as well as a higher diversity of species with unique fire and hydrologic tolerances, is likely to result in many unburned or minimally impacted microsites within larger tree islands. Consequently, larger tree islands have a better chance than smaller islands of mitigating fire effects by self-recruiting new stems from a local cache of surviving trees or root sprouts. On small islands, fire effects are likely to be more homogenous and severe, and the recruitment of new stems will be more dependent on external seed sources from unburned neighboring tree islands. As a result, post-fire recovery in these smaller tree islands is likely to be slow and dominated by short-lived herbs, ferns, and tree species (e.g., *Pteridium aquilinum* [L.] Kuhn var. *caudatum* [L.] Sadeb., *Trema micrathum* [L.] Blume, *Baccharis* spp., *Solanum erianthum* D. Don, and *Carica papaya* L.) (Loope and Urban 1980, Olmsted and Loope 1984). Furthermore, recovery on these smaller tree islands is likely to be slow and hampered by additional perturbation events, which could lead to further degradation, and the potential colonization of invasive-exotic species like *Schinus terebinthifolius* Raddi (Brazilian pepper), *Melaleuca quinquenervia* (Cav.) S.T. Blake (punktree), and *Casuarina* spp. (Australian pine; Loope and Urban 1980).

CONCLUSION

Within the marl prairie grasslands of the Everglades, the combined effects of fire and hydrology can lead to significant shifts in tree island composition, structure, and function. Depending on soil moisture (i.e., the elevation of the water table), fire severity, and post-fire hydroperiods, these effects can vary spatially and temporally throughout the landscape, pushing tree island ecosystems from one state (forested) to another (unvegetated, or covered by herbaceous vegetation). Furthermore, frequent fire under drought conditions may exacerbate soil loss within tree islands, leading to lower tree island elevations and thus making tree islands much more susceptible to the effects of post-fire flooding, (e.g., soil anoxia, which may inhibit or prevent the re-sprouting of top-killed trees from basal or root apical meristems). This negative feedback mechanism may ultimately contribute to the degradation, contraction, and permanent alteration of tree islands under frequent and severe perturbation cycles.

ACKNOWLEDGMENTS

This research project was funded by Everglades National Park (ENP) under Cooperative Agreement H5297050027. We would like to thank J. Sadle from ENP, and V. Engel currently at the USGS, for their support in funding the project; K. Rutchey and T. Schall for providing the 2009 CERP imagery; and Everglades National Park Fire and Aviation Management Office for flight following and logistical support. Furthermore, we would like to thank the anonymous reviewers of this manuscript for their comments and suggestions. This material was developed in collaboration with the Florida Coastal Everglades Long-Term Ecological Research program under National Science Foundation Grant No. DBI-0620409 and is contribution number 596 from the Southeast Environmental Research Center at Florida International University.

LITERATURE CITED

Alexander, T.R., and A.G. Crook. 1984. Recent vegetational changes in southern Florida. Pages 199-210 in: P.J. Gleason, editor. Environments of south Florida: present and past II. Miami Geological Society, Coral Gables, Florida, USA.

Allison, P.D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Inc., Cary, North Carolina, USA.

Armentano, T.V., D.T. Jones, M.S. Ross, and B.W. Gamble. 2002. Vegetation pattern and process in tree islands of the southern Everglades and adjacent areas. Pages 225-282 in: F.H. Sklar and A. van der Valk, editors. Tree islands of the Everglades. Kluwer Academic Publishers, Boston, Massachusetts, USA.

Avineon. 2002. Vegetation change detection 1950s to 1990s for tree islands of WCA3, summary report. Report to the South Florida Water Management District, 22 November 2002. Clearwater, Florida, USA.

Biggs, R., S.R. Carpenter, and W.A. Brock. 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. Proceedings of the National Academy of Sciences of the United States of America 106(3): 826-831. doi: 10.1073/pnas.0811729106

Brown, J.K. 1975. Fire cycles and community dynamics in lodgepole pine forest. Pages 429-456 in: D. Baumgartner, editor. Management of lodgepole pine ecosystems: symposium proceedings. Washington State University, Pullman, USA.

Carter, M.S., and C.D. Foster. 2004. Prescribed burning and productivity in southern pine forests: a review. Forest Ecology and Management 191: 93-109. doi: 10.1016/j.foreco.2003.11.006

Craighead, F.C., Sr. 1984. Hammocks of south Florida. Pages 191-198 in: P.J. Gleason, editor. Environments of south Florida: present and past II. Miami Geological Society, Coral Gables, Florida, USA.

D'Odorico, P., V. Engel, J.A. Carr, S.F. Oberbauer, M.S. Ross, and J.P. Sah. 2011. Tree-grass coexistence in the Everglades freshwater system. Ecosystems 14: 298-310. doi: 10.1007/s10021-011-9412-3

Doren, R.F., and R.M. Rochefort. 1984. Summary of fires in Everglades National Park and Big Cypress National Preserve, 1981. South Florida Research Center Report SFRC-84/01. Everglades National Park, Homestead, Florida, USA. <http://www.nps.gov/ever/naturescience/upload/SecureTRSFRC84-01.pdf> Accessed 15 December 2012.

Duever, L.C. 1984. Natural communities of Florida's rocklands. Palmetto 4: 8-11.

EDEN [Everglades Depth Estimation Network]. 2008. South Florida Information Access (Sofia). <http://sofia.usgs.gov/eden>. Accessed 15 December 2012.

ESRI [Environmental Systems Resource Institute]. 2009. ARCMap 9.3.1. ESRI, Redlands, California, USA.

Erdas, Inc. 2008. Erdas Imagine 9.3. Erdas, Inc., Norcross, Georgia, USA.

Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C.S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35: 557-581. doi: 10.1146/annurev.ecolsys.35.021103.105711

Gaines, M.S., C.R. Sasso, J.E. Diffendorfer, and H. Beck. 2002. Effects of tree island size and water on the population dynamics of small mammals in the Everglades. Pages 429-444 in: F.H. Sklar and A. van der Valk, editors. Tree islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Google, Inc. 2012*a*. KML 2.2 support. <https://developers.google.com/kml/documentation/>. Accessed 15 December 2012.

Google, Inc. 2012*b*. Google maps/google earth apis terms of service. <http://code.google.com/apis/maps/terms.html>. Accessed 15 December 2012

Graham, R.T., and T.B. Jain. 2005. Ponderosa pine ecosystems. Pages 1-32 in: M.W. Ritchie, D.A. Maguire, and A. Youngblood, technical coordinators. Proceedings of the symposium on ponderosa pine: issues, trends, and management. 18-21 October 2004, Klamath Falls, Oregon. USDA Forest Service General Technical Report PSW-GTR-198, Southwest Research Station, Albany California, USA.

Gunderson, L.H., and J.R. Snyder. 1994. Fire patterns in the southern Everglades. Pages 291-305 in: S.M. Davis and J.C. Ogden, editors. Everglades: the ecosystem and its restoration. St Lucie Press, Delray Beach, Florida, USA.

Hanan, E.J. and M.S. Ross. 2009. Across-scale patterning of plant soil-water interactions surrounding tree islands in southern Everglades landscapes. Landscape Ecology 25: 463-476. doi: 10.1007/s10980-009-9426-9

Hanan, E.J., M.S. Ross, P.L. Ruiz, and J.P. Sah. 2010. Multi-scaled grassland-woody plant dynamics in the heterogeneous marl prairies of the southern Everglades. Ecosystems 13: 1256-1274. doi: 10.1007/s10021-010-9386-6

Hofmockel, K., C.J. Richardson, and P.N. Halpin. 2008. Effects of hydrologic management decisions on Everglades tree islands. Pages 191-214 in: C.J. Richardson, editor. The Everglades experiments: lessons for ecosystem restoration. Springer, New York, New York, USA. doi: 10.1007/978-0-387-68923-4_8

Hofstetter, R.H. 1984. The effects of fire on the pineland and sawgrass communities of southern Florida. Pages 465-476 in: P.J. Gleason, editor. Environments of south Florida: present and past II. Miami Geological Society, Coral Gables, Florida, USA.

Hofstetter, R.H., and C.E. Hilsenbeck. 1980. Vegetational studies of the east Everglades. Final report to Metropolitan Dade County, Miami Florida. Part of the East Everglades Resources Planning Project. Metropolitan Dade County, Miami, Florida, USA.

Jackson, R.D., and A.R. Huete. 1991. Interpreting vegetation indices. Preventive Veterinary Medicine 11: 185-200. doi: 10.1016/S0167-5877(05)80004-2

Jayachandran, K., S. Sah, J.P. Sah, and M.S. Ross. 2004. Characterization, biogeochemistry, pore water chemistry, and other aspects of soils in tree islands of Shark Slough. Pages 29-40 in: M.S. Ross and D.T. Jones, editors. Tree islands in the Shark Slough landscape: interactions of vegetation, soils, and hydrology. Final report to Everglades National Park, September 2004. Southeast Environmental Research Center, Florida International University, Miami, USA.

Kirkman, L.K., and R.R. Sharitz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina Bays in South Carolina. Ecological Applications 4: 177-188. doi: 10.2307/1942127

Kozlowski, T.T. 1997. Response of woody plants to flooding and salinity. Tree Physiology Monograph 1: 1-29.

Lockwood, J.L., M.S. Ross, and J.P. Sah. 2003. Smoke on the water: the interplay of fire and water flow on Everglades restoration. Frontiers in Ecology and the Environment. 1: 462-468. doi: 10.1890/1540-9295(2003)001[0462:SOTWTI]2.0.CO;2

Loope, L.L., and N.H. Urban. 1980. A survey of fire history and impacts in tropical hardwood hammocks in the east Everglades and adjacent portions of Everglades National Park. South Florida Natural Resource Center Report T-592. Everglades National Park, Homestead, Florida, USA. <http://www.nps.gov/ever/naturescience/upload/SecureTRT-592.pdf>. Accessed 15 December 2012.

Meshaka, W.E., R. Snow, O.L. Bass, and W.B. Robertson. 2002. Occurrence of wildlife on tree islands in the southern Everglades. Pages 391-427 in: F.H. Sklar and A. van der Valk, editors. Tree islands of the Everglades. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Olmsted, I.C., and L.L. Loope. 1984. Plant communities of Everglades National Park. Pages 167-184 in: P.J. Gleason, editor. Environments of south Florida: present and past II. Miami Geological Society, Coral Gables, Florida, USA.

Patterson, K., and R. Finck. 1999. Tree islands of the WCA3 aerial photointerpretation and trend analysis project summary report. Report to the South Florida Water Management District. Geonex Corporation, St. Petersburg, Florida, USA.

Pyne, S.J., P.L. Andrews, and R.D. Laven. 1996. An introduction to wildland fire. John Wiley and Sons Inc., New York, New York, USA.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing. <http://www.R-project.org>. Accesses

RECOVER. 2006. CERP Monitoring and Assessment Plan (MAP): part 2, 2006 Assessment strategy for the monitoring and assessment plan. Restoration Coordination and Verification Program, US Army Corps of Engineers, Jacksonville District, Jacksonville, Florida, USA; and South Florida Water Management District, West Palm Beach, Florida, USA.

Rein, G., N. Cleaver, C. Ashton, P. Pironi, and J.L. Torero. 2008. The severity of smouldering peat fires and damage to the forest soil. Catena 74(3): 304-309. doi: 10.1016/j.catena.2008.05.008

Robertson, W.B., Jr. 1953. A survey of the effects of fire in Everglades National Park. National Park Service, Homestead, Florida, USA.

Ross, M.S., J.P. Sah, P.L. Ruiz, D.T. Jones, H.C. Cooley, R. Travieso, F. Tobias, J.R. Snyder, and D. Hagayari. 2006. Effect of hydrology restoration on the habitat of the Cape Sable seaside sparrow. Report to Everglades National Park, 25 March 2006. Southeast Environmental Research Center, Miami, Florida, USA. <http://www2.fiu.edu/~serp1/projects/capesable/2005_CSSS_Annual_Report.pdf>. Accessed 15 December 2012.

Ruiz, P.L., J.P. Sah, M.S. Ross, D.L. Rodriguez, and A.M. Lambert. 2011. Monitoring of tree island conditions in the southern Everglades: the effects of hurricanes and hydrology on the status and population dynamics of sixteen tropical hardwood hammock tree islands. Report to US Army Engineer Research and Development Center, 18 January 2011. Southeast Environmental Research Center, Miami, Florida, USA.

Sah, J.P., M.S. Ross, J.R. Snyder, S. Koptur, and H. Cooley. 2006. Fuel loads, fire regimes and post-fire fuel dynamics in the Florida Keys pine forests. International Journal of Wildland Fire 15(4): 463-478. doi: 10.1071/WF05100

Sah, J.P., M.S. Ross, P.L. Ruiz, and J.R. Snyder. 2012. Fire and flooding interactions: vegetation trajectories in the southern Everglades marl prairies, Florida, USA. Page 509 in: The 9th INTECOL international wetlands conference: wetlands in a complex world. Conference abstracts, 3-8 June 2012, Orlando, Florida, USA. University of Florida, Gainesville, USA. <http://www.conference.ifas.ufl.edu/intecol/Abstracts.pdf>. Accessed 15 December 2012.

Schmidt, P.M., R.A. McCleery, R.R. Lopez, N.J. Silvy, and J.A. Schmidt. 2010. Habitat succession, hardwood encroachment and raccoons as limiting factors for Lower Keys marsh rabbits. Biological Conservation 143: 2703-2710. doi: 10.1016/j.biocon.2010.07.016

Sklar, F., C. Coronado-Molina, A. Gras, K. Rutchey, D. Gawlik, G. Crozier, L. Bauman, S. Hagerthy, R. Shuford, J. Leeds, Y. Wu, C. Madden, B. Garrett, M. Nungesser, M. Korvela, and C. McVoy. 2004. Chapter 6: ecological effects of hydrology. Pages 6(1)-6(58) in: G. Redfield and F. Nearhoof, editors. 2004 Everglades Consolidated Report. South Florida Water Management District, West Palm Beach, Florida, USA.

Snyder, J.R., A. Herndon, and W.B. Robertson. 1990. South Florida rockland. Pages 230-277 in: R.L. Myers and J.J. Ewel, editors. Ecosystems of Florida. University of Central Florida Press, Orlando, USA.

Snyder, J.R., and W.T. Hilton. 2012. Mass mortality of hardwood shrubs after a single fire in seasonally flooded prairie. Page 511 in: The 9th INTECOL international wetlands conference: wetlands in a complex world. Conference abstracts, 3-8 June 2012, Orlando, Florida, USA. University of Florida, Gainesville, USA. <http://www.conference.ifas.ufl.edu/intecol/Abstracts.pdf>. Accessed 15 December 2012.

Taylor, D.L. 1981. Fire history of fire records for Everglades National Park, 1948-1979. South Florida Research Center Report T-619. Everglades National Park, Homestead, Florida, USA. <http://www.nps.gov/ever/naturescience/upload/SecureTRT-619.pdf>. Accessed 15 December 2012.

Verma, S., and S. Jayakumar. 2012. Impact of forest fire on physical, chemical and biological properties of soil: a review. Proceedings of the International Academy of Ecology and Environmental Sciences 2(3): 168-176.

Wade, D., J.J. Ewel, and R. Hofstetter. 1980. Fire in south Florida ecosystems. USDA Forest Service General Technical Report SE-17. Southeast Forest Experimental Station, Asheville, North Carolina, USA.

Wang, J., P.M. Rich, and K.P. Price. 2003. Temporal responses of NDVI to precipitation and temperature in the central Great Plains, USA. International Journal of Remote Sensing 24: 2345-2364. doi: 10.1080/01431160210154812

Warren, G., and G. Metternicht. 2005. Agricultural applications of high-resolution digital multispectral imagery: evaluating within-field spatial variability of canola (*Brassica napus*) in Western Australia. Photogrammetric Engineering and Remote Sensing 71: 595-602.

Weiss, J.L., D.S. Gutzler, J.E.A. Coonrod, and C.N. Dahm. 2004. Long-term vegetation monitoring with NDVI in a diverse semi-arid setting, central New Mexico, USA. Journal of Arid Environments 58: 249-272. doi: 10.1016/j.jaridenv.2003.07.001

White, C.S., and S.R. Loftin. 2000. Response of 2 semiarid grasslands to cool-season pre-scribed fire. Journal of Range Management 53(1): 52-61. doi: 10.2307/4003392

White, P.S. 1994. Synthesis: vegetation pattern and process in the Everglades ecosystem. Pages 445-458 in: S.M. Davis and J.C. Ogden, editors. Everglades: the ecosystem and its restoration. St Lucie Press, Delray Beach, Florida, USA.

Whittingham, M.J., P.A. Stephens, R.B. Bradbury, and R.P. Freckleton. 2006. Why do we still use stepwise modeling in ecology and behavior? Journal of Animal Ecology 75: 1182-1189. doi: 10.1111/j.1365-2656.2006.01141.x

Zaffke, M. 1983. Plant communities of water conservation area 3A; base-line documentation prior to the operation of S-339 and S-340. Technical memorandum. South Florida Water Management District, West Palm Beach, Florida, USA.