

MICROTOPOGRAPHICAL EFFECTS OF CLEARCUTTING OF *TAXODIUM-NYSSA*  
SWAMPS

By

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To my husband and best friend, Luke Gommermann, for years of love and support

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Abstract of Thesis Presented to the Graduate School  
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Hummock-hollow microtopography, common in *Taxodium-Nyssa* swamps of the Southeast Coastal Plain, may be an important indicator of forest wetland conditions following logging. Past studies have indicated the importance of these microtopographic features because many plant species germinate and establish preferentially on hummocks. Concern over clearcut logging in forested wetlands has prompted interest in evaluating the recovery of these systems following conventional and new logging practices. The objectives of this research were to: 1) characterize the microtopography in reference sites (in terms of prevalence, spatial organization, and elevated feature characteristics) and determine the degree to which conventional techniques (bottom logging) and new techniques (mat logging) alter microtopography; and, 2) to compare the relationships between vegetation and microtopographic position in both reference and logged swamps. Five second-growth reference swamps that were logged approximately 40-100 years ago, three bottom-logged sites logged 3-13 years ago, and two mat-logged sites logged 1-5 years ago were sampled. Elevations were recorded following a spatially-nested design in 30 x 30 m plots, and systematic surveys of vegetation and microtopographic position were conducted concurrently.

Thirty transects measuring elevations across skid trails (15 mat-logged, 15 bottom-logged) were also recorded. Reference swamps displayed clear bimodality in elevational histograms related to hummock and hollow topography, which was reduced in prevalence over 50% in recently mat and bottom-logged sites. Bottom-logged sites showed trimodality, which was due to the abundance of low ruts as well as remaining elevated features. Line transects also revealed lower elevations across bottom-logged skid trails as compared to mat-logged trails. Variograms indicate differences in horizontal spatial patterns between bottom-logged, mat-logged, and reference sites, with reference and bottom-logged sites exhibiting the highest sill, and bottom-logged sites the greatest range. Relative abundances of substrate types of elevated features differed between reference and logged sites, with root/soil features relatively more common in reference sites, and stump/soil and stump features more common in mat and bottom-logged sites. Total understory stem density and species richness were greater on elevated microsites than on the swamp bottom in both reference and logged sites. The woody vine and shrub functional groups exhibited the strongest preferences for elevated features. The results of this study indicate that both logging techniques diminished the prevalence of elevated microtopographic features as well as altered the relative abundance of their substrate types, while only bottom-logging created low elevations via deeper skid trail rutting. Vegetation is clearly linked to these features, which suggests their importance in swamp plant communities. Sampling soil elevations proved an effective tool for understanding changes in the vertical structuring of microtopography across sites.

## CHAPTER 1 INTRODUCTION

### ***Taxodium-Nyssa Swamps***

Swamps with an overstory dominated by cypress (*Taxodium distichum* var. *nutans* and var. *distichum*) and swamp tupelo trees (*Nyssa sylvatica* var. *biflora*) are found throughout floodplain and depressional areas of the Southeast Coastal Plain (Ewel, 1998). In Florida, they often occur as semi-isolated depressional features within a matrix of pine flatwoods or pine plantations (Ewel, 1998). Because hydroperiods of 10-12 months are characteristic of this forest association (Kellison and Young, 1997), decomposition of organic material is slow, allowing a thick organic-rich soil horizon to accumulate.

The forest floor of cypress-tupelo swamps often exhibits microtopographic relief (on the order of 0.5 - 1.5 m) that influences the hydrology, decomposition, and plant community structure of the forest community (Brown, 1972). Several studies have demonstrated the importance of topographic variability in swamps as providing a range of hydrologic conditions that encourages plant diversity and shapes vegetative structure (Anderson et al., 2009, Streng, 1989, Moser et al., 2007). In other studies, the presence of raised microtopographic features, specifically, has been shown to encourage woody plant regeneration (Titus, 1990, Huenneke and Sharitz, 1986) and enhance plant productivity (Jones et al., 2000). In many cypress-tupelo swamps, higher topographic positions support a dense shrub layer and a number of herbaceous species (Ewel, 1998).

Depressional cypress-tupelo swamps coincide with an exposed surficial aquifer (Crownover et al, 1995) and can affect regional hydrology by acting as groundwater

recharge areas, aiding in flood prevention in surrounding areas (Ewel, 1998) and influencing nitrogen and phosphorus dynamics (Walbridge and Lockaby, 1984). Water table fluctuations can result in periodic exposure of portions of the forest floor during crucial regeneration times for trees and other plant species. Almost all woody species in these swamps, including cypress and tupelo, require unflooded sites to germinate (Myers and Ewel, 1990).

Cypress-tupelo swamps are an important component of the larger landscape in which they reside for reasons beyond hydrology. The ecotone between cypress and hardwood swamps and upland forests are believed to be hot spots for wildlife diversity in Florida (Myers and Ewel, 1990). Cypress-tupelo swamps provide food and cover for numerous animal species-- especially amphibians, reptiles, and birds. Because they are often nestled within pine plantations, the swamps act as refugia for displaced wildlife after pine logging (Ewel, 1998).

Perturbations, including natural flooding, fire and hurricanes as well as logging play an important role in shaping the ecological trajectory of swamps. It is thought that cypress-tupelo swamps may be mostly dominated over time by regenerative processes that occur during recovery from minor or major perturbations (Odum and Ewel, 1984). Flooding is a frequent and mild pulse of energy that can affect plant regeneration and productivity as well as soil nutrient cycling. According to Myers and Ewel (1990), cypress-tupelo swamps may experience several fires per century, and these events undoubtedly shape the long term plant succession of these swamps and possibly even plant evolution. Also, when fire occurs during dry periods, the peat layer can burn, and it is thought that fire may be what limits the thickness of this layer (Ewel, 1998).

Hurricanes exert selective pressures on swamp vegetation (Putz and Sharitz, 1990), and logging drastically alters the condition of the swamp and may initiate changes in the type of ecosystem present. Interestingly, cypress-tupelo swamps are thought to be subclimax communities that are maintained by natural perturbations that prevent the encroachment of other, less adapted species (Gunderson, 1977).

### **Logging History**

Since the early 1800s, the logging industry in cypress-tupelo swamps has been an important component of the economy of southern states of the Coastal Plain (Ewel, 1998). It is estimated that most cypress-tupelo swamps in Florida have been selectively logged or clearcut at least one time for the valuable, rot-resistant heartwood found in old-growth cypress trees. The peak of cypress logging occurred in the early 1900s, followed by collapse due to lack of accessible old-growth trees and other economic constraints (Duryea and Hermansen, 1998). In the past few decades, there has been a resurgence of cypress logging in the second growth swamps, in part because of new or more profitable markets. For example, demand for cypress mulch for landscaping has risen such that as of 1996, 47% of harvested cypress wood was used to produce it (Duryea and Hermansen, 1998).

Today's common harvesting practice in cypress-tupelo swamps is to complete a seed-tree cut with the intention that natural regeneration will then occur (Ewel, 1998, pers. obs). Until recently, these operations used a technique known as "bottom-logging", where all harvesting equipment drove directly on the soil surface, causing soil rutting and destruction of tree stumps that may have otherwise sprouted. Also, during each operation, a large percentage of the swamp was affected by skid trails because deeply-rutted trails were routinely abandoned in favor of routes through untouched soils.

Bottom-logging has thus received much scrutiny by a number of groups, including non-governmental environmental organizations as well as the Environmental Protection Agency and the Division of Forestry. The result has been an impetus to develop alternative harvest strategies that may better protect water quality and otherwise better maintain the ecological integrity of southern swamps.

A number of alternative harvesting strategies are listed in the Florida Silvicultural Best Management Practices (BMP) Manual, which is an evolving document that includes guidelines for harvesting near riparian areas and in wetlands, road and culvert design, site preparation and logging techniques. This manual is the product of the Silvicultural BMPs program that was started by the Florida Division of Forestry in 1979 to improve ecosystem protection related to forestry operations. It is continually updated via a technical advisory committee that includes state, federal, university, industry and environmental representatives (Karels, 2009). In the spring of 2007, an alternative swamp logging technique, referred to as “mat-logging” (or “shovel-logging”) was incorporated into Florida’s silvicultural BMP manual for its purported reduced soil impacts. In this technique, logs are cut and laid down length-wise to create “mat trails”, and skidding traffic is then confined to these routes during the logging operation. However, the impacts of this technique relative to former methods like bottom-logging have not been quantified.

### **Logging Concerns**

There are a number of areas of environmental concern and uncertainty in cypress-tupelo swamp recovery after logging, including slow or undesirable vegetative succession, hydrologic alterations, physical and chemical changes in soils, and microtopographic changes. Cypress-tupelo swamps are characteristically slow to

regenerate to a desired vegetative composition (Kellison and Young, 1997) due primarily to the hindrance of woody plant regeneration under flooded conditions (Laderman, 1998) and secondarily to the paucity of advance regeneration at the time of harvest (Meadows and Stanturf, 1997). Also, while coppicing of both cypress and tupelo is common and seed production can begin as soon as two years after harvest (Ewel, 1998), long-term survival of sprouts and their contribution to the future forest canopy remains uncertain (Randall et al., 2005, Conner and Buford, 1998). A recent study found that the percentage of cut cypress stumps to have live sprouts ten years after clearcutting ranged from 10-41% in seven North Florida domes (Ricci, 2010). In a number of case studies, swamps quickly succeeded to dense shrubby cover following disturbance and subsequent tree regeneration was slow, unreliable, and tended to occur via cohort regeneration in years when conditions were dry and otherwise suitable (Dunn and Sharitz, 1987, Spencer et al., 2001). Cypress trees, in particular, have low seed viability and a narrow range of germination and establishment requirements, including open and unflooded conditions (Gunderson, 1977) and may only regenerate in large numbers when a number of criteria are simultaneously met.

While vegetation may be slow to recover after clearcutting of cypress-tupelo swamps, the impacts of logging on soils and hydrology have been found to be relatively minor and short-lived (returning to pre-logging conditions within 1-2 years) in a number of cases (i.e. Sun et al., 2001). The most commonly reported hydrologic change following logging in swamps is a temporary rise in the water table, presumably due to a decrease in evapotranspiration (Lockaby et al., 1997, Sun et al., 2000). This effect may be most pronounced when logging occurs during dry periods (Sun et al., 2000).

Changes in soil properties tend to be spatially variable across logged sites, with impacts concentrated near skid trails (Sun et al., 2001). In particular, soil bulk density may increase (Grace et al., 2006) and hydraulic conductivity decrease (Gardiner et al., 1994). Soil organic matter also commonly decreases after logging (Aust et al., 1991), which can be attributed to both higher soil temperatures (Trettin et al., 1996) driving higher rates of decomposition and a lack of organic inputs from vegetation.

While the soil and hydrologic impacts of logging cypress-tupelo swamps are relatively consistent and understood, considerable uncertainty remains regarding logging impacts on the land surface character, and, specifically, the microtopography. Perhaps the most influential stressor in swamp ecosystems is flooding, which is an obstacle to woody plant regeneration. Therefore, small topographic changes in these systems can have drastic consequences for vegetation. Microtopographic variability has been shown to influence plant regeneration (e.g., Titus, 1990) and productivity (Jones et al., 2000) in swamps. The soft, organic surface soils are susceptible to compaction by heavy harvesting vehicles (Casey and Ewel, 1998) and removal of logs may also abrade the surface. Therefore, alteration of this surface could substantially alter the rate and/or mode of recovery of the swamp after logging. The objectives of this study were to compare 1) the vertical structuring of microtopography, 2) the horizontal structuring of microtopography, 3) the raised microtopographic feature substrate composition and size distribution between mat-logged, bottom-logged and reference sites, 4) skid trail dimensions between mat-logged and bottom-logged sites, and 5) the relationships between vegetation and microtopographic position in reference and logged swamps.

## CHAPTER 2 IMPACTS OF LOGGING ON MICROTOPOGRAPHY IN *TAXODIUM-NYSSA* SWAMPS

### **Background**

Swamps with an overstory dominated by cypress (*Taxodium distichum* var. *nutans* and var. *distichum*) and swamp tupelo trees (*Nyssa sylvatica* var. *biflora*) are found throughout floodplain and depressional areas of the Southeast Coastal Plain (Ewel, 1998). In Florida, they often occur as semi-isolated depressional features within a matrix of pine flatwoods or pine plantations (Ewel, 1998). Because hydroperiods of 10-12 months are characteristic of this forest association (Kellison and Young, 1997), decomposition of organic material is slow, allowing a thick organic-rich soil horizon to accumulate. Microtopography and fluctuations in water depth (Odum and Ewel, 1986) act to create a spatial and temporal variety of hydrologic niches that allow for woody plant regeneration. In addition to natural stressors, anthropogenic disturbances such as logging and hydrologic modifications have historically had large impacts on cypress-tupelo swamps (Duryea and Hermansen, 1998).

Over the past 200 years, logging has been a pervasive disturbance, and most cypress-tupelo swamps in Florida and many across the southeast coastal plain have been selectively logged or clear-cut at least once for the valuable, rot-resistant heartwood found in old-growth cypress trees (Odum and Ewel, 1986). The peak of cypress logging occurred in the early 1900s, followed by collapse due to lack of accessible old-growth trees and other economic constraints (Duryea and Hermansen, 1998). In the past few decades, there has been a resurgence of cypress logging in second growth swamps, in part because of new or more profitable markets. For example, demand for cypress mulch for landscaping has risen such that as of 1996,

47% of harvested cypress wood was used to produce it (Duryea and Hermansen, 1998). Currently, an estimated 1.3 million ha of cypress-tupelo swamps are managed for timber across 13 states of the Southeastern U.S., and over half of the acreage occurs in Florida and Louisiana (USFS Forest Inventory and Analysis in Faulkner et al., 2009). A resurgence in cypress logging has renewed concerns about the impacts of this activity on ecosystem structure and function of these swamps.

In recent decades, swamp logging has been conducted using a method known as “bottom-logging”, where all harvesting equipment drove directly on the soil surface, causing soil rutting in skid trails (Figure 2-1) and destruction of tree stumps that may have otherwise sprouted. Also, during each operation, a large percentage of the swamp was affected by skid trails because deeply-rutted trails were routinely abandoned in favor of routes through untouched soils. Bottom-logging has thus received much scrutiny by a number of groups, including the Environmental Protection Agency, due to these impacts and concerns about their long-term effects. In the spring of 2007, an alternative swamp logging technique, developed by loggers and referred to as “mat-logging” (or “shovel-logging”) was incorporated into Florida’s Silvicultural Best Management Practice manual for its purported reductions in soil rutting (Karels, 2009). In this technique, logs are cut and laid down length-wise to create “mat trails”, and skidding traffic is then confined to these routes during the logging operation. After the operation is complete, all merchantable logs are removed from the skid trails (Figure 2-2). Today, this technique has all but replaced bottom-logging for most loggers. However, the impacts of this technique relative to former methods like bottom-logging

remain uncertain; perhaps most conspicuously, it is still not clear whether mat-logging techniques results in a reduction in soil surface rutting.

Microtopographic variation characterizes the surface of many Southeastern swamps, and clearcut logging may alter this character. Importantly, microtopography has been linked to enhanced botanical diversity (Moser et al., 2007, Bukata and Sloan, 2002, Simmons et al., 2009) and fine root productivity (Jones et al., 2000), as well as having an influence over biogeochemical functions and hydrology. Additionally, elevated microsites have been shown to aid in seed entrapment (Bukata and Sloan, 2002), enhance wetland water storage and filtration capacity (Bukata and Sloan, 2002), affect nitrogen mineralization and cycling (Bruland and Richardson, 2005), and provide aerobic conditions and subsequently increase success of vesicular-arbuscular mycorrhizae (Cantelmo and Ehrenfeld, 1999). Consequently, microtopographic features may be useful as a metric for assessing the magnitude of physical damage or recovery after disturbance, and also for making predictions about the vegetative succession during recovery.

Cypress-tupelo swamps are often slow to recover vegetatively from disturbances, both natural and anthropogenic, as most woody plants require unflooded conditions for germination (Titus, 1990, Anderson, 2009), and many species, even those adapted to wetland conditions, grow optimally with some relief from flooding (Dickson and Broyer, 1971). Exacerbating the delay of arboreal regeneration are elevated water tables that can persist for months after logging due to decreased evapotranspiration (e.g. Sun et al., 2000) and soil compaction that can reduce local soil elevations and hydraulic conductivity, and increase bulk density (Gardiner et al., 1994, Grace III et al., 2006).

While the seeds of many wetland species can remain viable during prolonged submergence (Burns and Honkala, 1990) and cypress and tupelo readily sprout from coppice and can produce seed in under three years (Ewel, 1998), considerable uncertainty remains regarding long-term regenerative capacities of swamp trees (especially cypress) due to poor initiation of cypress sprouts over time (Ricci, 2010).

Microtopographic relief in swamp environments creates a variety of hydrologic niches that influence the vegetation dynamics following disturbance by providing microsites with different flooding regimes. Woody vegetation is often preferentially associated with the elevated microtopographic features due to differential seed dispersal and germination as well as growth restrictions caused by flooding (Titus, 1990, Bukata and Sloan, 2002). A recent study by Anderson (2009) highlighted the impacts of elevated microsites on the distribution of a woody shrub, *Itea virginica*. Though the adults of this species tolerate flooded conditions, they are almost always found on elevated microsites due to restrictions they faced as seeds and seedlings. This and other evidence suggests that microtopography can be important in determining vegetation patterns in swamps (Moser et al., 2007).

The arrangement and heterogeneity of microtopographic features across space may offer additional clues to the ability of a swamp to recover ecologically after disturbances. In other systems that contain biogenic microtopographic features, regular patterns have been observed, suggesting that scale-dependent feedbacks, which include local positive feedbacks, but negative feedbacks at greater distances are controlling the spatial distribution of ecosystem features. For example, the Everglades in South Florida have elongated high ridges and low sloughs that are regularly spaced

(Watts et al., 2010). In Siberia, peatlands have been shown to have a regular, maze-like series of ridges that support woody vegetation otherwise unsuccessful at colonizing inundated hollows (Eppinga et al., 2009). Evidence suggests that in both of these systems, higher evapotranspiration on ridges may be leading to higher nutrient concentrations on ridges, thus further enhancing productivity and evapotranspiration. This then leads to a paucity of nutrients at some distance, which perpetuates the hollow state. Thus, the arrangement of microtopographic features and measurements of disturbance effects on this may provide valuable information about the carbon dynamics of these systems. Also, the amount of topographic heterogeneity across horizontal space may allow for predictions of biotic recovery after logging based on the amount of physical complexity in the ecosystem.

In addition to size and configuration of microtopography, substrate composition and stability can also be important to predicting plant regeneration responses. Microsites that are composed of logs or other woody debris are not as stable as those of soil, roots or stumps and may be less likely to support long-term woody plant growth (Huenneke and Sharitz, 1990). Interestingly, plant species can be found preferentially with particular substrate types, suggesting that they benefit from particular characteristics of a substrate. For instance, in a South Carolina swamp, woody seedlings were found more often than expected on mucky substrates that were close to fixed objects, such as trees or roots, and were found less than would be expected on loose muck or muck that overlaid logs and/or branches (Huenneke and Sharitz, 1986). While emergent substrates can be ideal spots for seedlings, they may render adult trees more likely to be uprooted in storms, as was seen in perched *Acer rubrum* trees in a

South Carolina swamp after Hurricane Hugo (Putz and Sharitz, 1991). It has also been found that disturbance can alter the abundance of particular substrate types of microsites (Huenneke and Sharitz, 1986), which may influence the composition of the regeneration plant community.

A number of approaches have been used to quantify and characterize swamp microtopography. Commonly, mathematical measures of topographic heterogeneity such as vertical relief, rugosity (wrinkledness in a plane), tortuosity (ratio of over-surface distance to the straight line path), and surface roughness (frequency of microtopographic features along a transect) have been employed to quantify the degree of microtopography present (Bukata, 1999, Sloan, 1998, Moser et al., 2007). Others have tallied individual microtopographic features, including soil features as well as those composed of decomposing stumps, logs, roots and other elevated features, focusing on the abundance of these features, their suitability as germination sites, and plant preferences for particular features (Titus, 1990, Huenneke and Sharitz, 1986). This research draws from each of these approaches to allow for multiple comparisons of microtopographic characteristics across recently logged and reference sites.

The objectives of this study were to compare 1) the vertical structuring of microtopography 2) the horizontal spatial structuring of microtopography 3) the raised microtopographic feature substrate composition and size distribution between mat-logged, bottom-logged and reference sites; and, 4) skid trail dimensions between mat-logged and bottom-logged sites. These results may provide insight into the environmental soundness of two harvesting systems, as indicated by changes in microtopography and the potential for ecosystem recovery after logging.

## Methods

### Study Sites

Sites were located within backwater floodplain, strand, and depressional *Taxodium-Nyssa* swamps on industrial (agricultural/silvicultural) and federal lands in Alachua, Gilchrist, Bradford and Baker counties of North Central Florida between 29° 37' and 30° 15' N and 82° 9' and 82° 48' W (Table 2-1). This region's average annual precipitation is 1250 mm, with average annual high and low temperatures of 26.6°C and 14.2 °C (NOAA, 2010). Soils are very poorly drained fine sands and sandy loams (Monteocha and Mascotte series), very poorly drained fine sands with a mucky fine sand surface layer (Lynn Haven series) and very poorly drained mucks with loamy substratums (Pamlico series) (NRCS, 2010). Depth to water table for each of these series is zero inches, and each are found in depressions in the landscape. Pine plantations and isolated wetland features represent the main type of land use in the area (Table 2-1).

Tree canopies were most often dominated by *T. distichum* var. *nutans* and *N. sylvatica* var. *biflora*, with other species such as *Magnolia virginiana*, *Gordonia lasianthus*, and *Persea borbonia* sometimes common or even co-dominant in the canopy. Microtopographic relief had an elevational range of 0.75 - 1.4 m within each site.

Sampling occurred between January and May of 2010, during which monthly rainfall was near average and air temperatures were colder than average by 3.3°C in January through March (NOAA, 2010). In most sites, all soil except the raised microtopographic features was submerged in tannic water for the duration of the study.

In total, 5 reference swamps were sampled. The sites were chosen based on their similarity in species composition and hydrology to sampled logged sites and often were in close proximity (< 1 km) to the logged sites. Each of these sites exhibited evidence of a history of at least some selective logging within the past century. Truly “pristine” swamps that had escaped all logging and/or hydrologic modification are rare in North Florida. Basal areas exceeded 34.4 m<sup>2</sup>/ha in these sites, though it was difficult to measure accurately due to buttressing. The understory vegetation was characteristically dense and was often dominated by woody shrubs such as *Lyonia lucida* and *Itea virginica*, among others. Additionally, ferns, forbs and vines were also common in some sites.

Five recently logged sites were sampled, 2 of which had been mat-logged (1 and 5 years ago), and 3 of which had been bottom-logged (3,7 and 13 years ago). These sites ranged from having sparse or very young tree regeneration (basal area of 0.5-1.2 m<sup>2</sup>/ha) to dense regeneration of coppice and/or seedling recruits (basal area of 4.6-9.2 m<sup>2</sup>/ha).

## **Field Methods**

### **Water depths**

In each study swamp, I randomly located two 30 x 30 m sampling frames (except for “reference 2” which had 1 frame due to inaccessibility) in the central area of the swamps by satellite imagery. I divided each frame into four quadrants and randomly located two non-overlapping sampling stations in each quadrant, for a total of eight sampling stations per frame (Figure 2-3A). A sampling station consisted of 16 water depth measurements, four taken at random distances between 0.5 – 4 m along each cardinal direction from the center of the station (Figure 2-3B). When raised

microtopographic features were encountered at sampling points, their height above the water surface was recorded as a negative water depth. For each water depth measurement, I recorded its location as being in one of three categories: skid trail (in a rutted area where a skidder had driven), swamp bottom (flat, low, and often flooded soil surface) and raised microtopographic features (distinctly higher than the surrounding soil surface, often unflooded). The stratified locations of the sampling stations across a sampling frame ensured that an adequate number of point pairs were sampled for each lag distance to conduct a spatial autocorrelation analysis.

### **Skid trail transects**

To compare the impacts of the two logging methods, fifteen transects in two mat-logged sites (seven in a site logged one year ago and eight in a site logged five years ago) and fifteen transects in two bottom-logged sites (seven in a site logged seven years ago and eight in a site logged thirteen years ago) were traversed perpendicular to skid trails, with water depth measurements recorded every 0.5 m. Each transect extended for an additional 2-5 m beyond each trail edge. Trail edges were defined based on visual and elevational evidence present at the site.

### **Elevated microsite surveys**

A survey of elevated microsites was conducted in two reference sites, two mat-logged sites and two bottom-logged sites. A total of 291 randomly located features in reference, 134 in mat-logged and 128 in bottom-logged were surveyed. Each elevated feature within each plot was measured for maximum length and width and classified by type as follows: tree base - expanded bases of live trees with some litter accumulation (Figure 2-4), soil - predominantly organic and/or inorganic soil material (Figure 2-5), stump/soil - decomposing stump with substantial accumulations of litter and

decomposed organic material (Figure 2-6), roots/soil - exposed tree roots with substantial accumulation of litter and decomposed organic material (Figure 2-7), log - dead wood (Figure 2-8), stump - tree stump with little or no decomposed organics or litter associated with it (Figure 2-9), tip-up mound - root ball and associated soil from upturned trees (Figure 2-10), and slash debris - dense accumulation of coarse woody debris (Figure 2-11).

## **Data Analysis**

### **Water depths**

Water depths were converted to relative elevations by setting the deepest observation in each frame equal to zero, and then histograms of elevation were created for each. To model the data according to elevational clusters, the univariate model-based clustering feature of Mclust, a package for the statistical software R, was used to generate best fit models for the set of observations (128) in each sampling frame across all sites. For univariate data, two types of models were possible: equal variance and unequal variance. Upon model selection, Mclust then found the number of components (or normal distributions) that resulted in the best fit Bayesian Information Criterion (BIC) value, incurring a penalty that increased based on the number of components (Fraley and Raftery, 2006) (Appendix A).

To verify the presence of spatial autocorrelation within the sites, a maximum likelihood analysis (AIC) was used to determine if an exponential, spherical, or Gaussian spatial variogram model explained more variation among sites than a non-spatial model. Using a mixed model (proc mixed) in SAS statistical software, average sill, range, and nugget values for reference, mat, and bottom-logged sites were obtained. Variograms were then drawn based on these values and the most

appropriate spatial variogram model (previously obtained via AIC values). Correlograms were also constructed using GS+ software for each frame in order to compare spatial correlations for each site.

### **Skid trail transects**

Average skid trail depths, measured for each transect as the difference in elevation between on and off-trail measurements, were calculated for mat and bottom-logged sites and compared via the Student's t-test. Average skid trail widths were also compared via the Student's t-test. A composite skid trail profile was created by aligning all 15 transects from each logging treatment at the trail centers and obtaining an average elevation at each measurement point.

### **Elevated microsite surveys**

The size of each elevated microsite was estimated as the area (m<sup>2</sup>) of an ellipse. The median and interquartile range of microsite areas were calculated for each surveyed site. Features are characteristically steep-sided, so change in area with water level was assumed to be negligible for comparing general characteristics of elevated microsites across sites. For each substrate type, I tested for differences in sample proportions between each site treatment (reference, mat-logged, bottom-logged) ( $\alpha = 0.05$ ). The mean sizes of elevated features were compared between sites using the Bonferroni multiple comparison method in an ANOVA ( $\alpha = 0.05$ ) (Appendix B).

## **Results**

### **Water Depths**

#### **Vertical structure**

In reference sites, two elevational modes (bimodality) was the best fit model for seven of nine frames (Figures 2-12 and 2-13, Table 2-2). The other two frames were

trimodal and pentamodel. (Figure 2-13). In each of the nine reference frames, the highest elevational mode included a surprisingly consistent average of 22.6% ( $\pm$  1.671%) of observations for that frame in the model output. In each frame, this mode was composed almost entirely of observations whose topographic positions had been classified as “elevated microtopographic features” during field collection. Each bimodal reference frame also displayed a lower elevational mode that contained the majority of observations. For each frame, this mode was composed almost entirely of observations whose topographic position had been classified as “swamp bottom”. These bimodal results suggest that reference swamps are characterized by two elevational modes: the swamp bottom, and distinctly higher microtopographic features.

In mat-logged sites, bimodality was the best fit model in three of the four sampling frames, though one of the four frames was unimodal (Figure 2-14, Table 2-2). As seen in reference sites, the majority of the observations were found in the lower elevational mode, and a smaller proportion were found in the higher elevational mode. However, the higher elevational mode for mat-logged frames contained an average of only 10.6% ( $\pm$  4.345%) of the observations, which was lower than that of reference sites. The vast majority of observations in the higher elevational mode corresponded to field-classified “elevated microtopographic features”, whereas the observations in the lower elevational mode corresponded to both the “swamp bottom” and “skid trail” topographic positions. The decrease in the number of observations in the higher elevational mode (or, in one case, the absence of this mode) as compared to reference frames suggests a loss in the area of elevated microtopographic features relative to swamp bottom.

In bottom-logged sites, one frame was trimodal, two were quadramodal, and three were bimodal (Figure 2-15, Table 2-2). Five of the six bottom-logged frames had a high elevational mode composed of elevations classified as “elevated microtopographic features”; an average of 9.2% ( $\pm 1.362\%$ ) of observations were placed in this mode for these frames. Unlike mat-logged frames, four of the six bottom-logged frames also contained an additional low elevational mode comprised primarily of “skid trail” observations according to field classification. As in other sites, the majority of observations were classified as “swamp bottom” and were found in the largest elevational mode. These results suggest that bottom-logging results, not only in the loss of elevated microtopographic features, but the creation of deeply rutted areas that are distinctly lower than the swamp bottom. In comparing mat and bottom-logged frames, the proportion of observations making up the higher elevational mode of “elevated microtopographic features” was variable across logged sites, and did not appear to be a function of logging treatment and years since harvest.

### **Horizontal spatial structure**

The exponential spatial variogram model was consistently the best-fit model (lowest AIC value) for explaining the distribution of soil elevations for each site. Average experimental variogram parameters differed between reference, bottom-logged and mat-logged sites. Reference sites had the highest sill or variance ( $782 \text{ cm}^2$ ) relative to that bottom-logged sites ( $763 \text{ cm}^2$ ) and mat-logged sites ( $420 \text{ cm}^2$ ) (Figure 2-16). Bottom-logged sites exhibited the greatest range of spatial autocorrelation (501cm), while reference sites had a range of 200 cm and mat-logged sites had a range of 157 cm. All sites had low nugget variance, indicating that most of the variation in soil

elevations was explained by location in space. Correlograms revealed no consistent or strong patterns in microtopographic variance across sites.

### **Skid Trail Transects**

Skid trails resulting from bottom-logging operations were, on average 34.7 cm ( $\pm$  2.350) deep relative to the surrounding land, which was deeper than trails following mat-logging operations, which were 17.5 cm ( $\pm$  1.450) deep ( $p < .0001$ ) (Figure 2-17). Mat-logging and bottom-logging trails were not different in width, averaging 5.2 m ( $\pm$  0.332) m and 4.5 m ( $\pm$  0.276), respectively. Time since logging (up to 13 years) did not appear to effect the depth or width of skid trails.

### **Elevated Microsite Surveys**

#### **Substrate characteristics of elevated microsites**

The relative proportions of microtopographic feature substrate types varied between reference, mat-logged, and bottom-logged sites (Figure 2-18). In mat and bottom-logged sites, a lower proportion of features were root/soil (24.5% and 11.7%, respectively) as compared to 52% in reference ( $p < .0001$ ,  $p < .0001$ ). Though relatively uncommon in all sites, tip-up mounds were most prevalent in reference sites, comprising 2.9% of elevated features, were rarer in mat-logged sites ( $p = 0.0440$ ), comprising 0.5% of features (Figure 2-18B), and were not encountered in bottom-logged sites (Figure 2-18C). Stump microsites were rarer in reference sites (0.4%) than in mat and bottom-logged sites ( $p < .0001$ ,  $p < .0001$ ), comprising 15.2% and 30.5 % of microsites, respectively. Decaying stump/soil microsites were also proportionally more common in both mat-logged sites (43.2%) and in bottom-logged sites (50.0%) than in reference (31.5%) ( $p < .0001$ ,  $p < .0001$ ). Decaying log microsites and tree base microsites were only found in reference sites, making up 1.6% and 5.0% of elevated

features, respectively. Slash debris was only found in mat-logged sites and made up 6.1% elevated microsites. Differences between logging types included a greater proportion of stump (30%) and soil features (8%) in bottom-logged sites and a lower proportion of root/soil features (12%) than in mat-logged (15%, 3% and 25% respectively).

### **Size of elevated microsites**

The size distribution of microtopographic features varied from site to site, and no clear differences in the average size or the size range of these features were observed between reference and logged sites (Figure 2-19). Rather, size distribution and range appeared to be a function of proximity of sites to each other, regardless of logging history. For example, sites 4R (reference) and 5M (mat-logged 5 years ago) were located adjacent to one another in a backwater riverine swamp and had mean elevated microsite areas of 1.39 m<sup>2</sup> and 1.83 m<sup>2</sup>, respectively, which did not differ from one another, but differed from other sites that were compared. Similarly, sites 3R (reference) and 1M (mat-logged 1 year ago) were located adjacent to one another in the same depressional complex, and had mean elevated microsite areas that did not differ from one another (0.48 m<sup>2</sup> and 0.41 m<sup>2</sup>, respectively). Sites 7B (bottom-logged 7 years ago) and 13B (bottom-logged 13 years ago), though not adjacent, were within 5 km of each other as part of a contiguous, managed pine flatwood and swamp mosaic, and had mean elevated microsite areas that did not differ (0.63 m<sup>2</sup> and 0.85 m<sup>2</sup> respectively, alpha = 0.05), although they also did not differ from sites 3R and 1M.

## Discussion

### Microtopography in Reference Conditions

There was a striking similarity in the frequency and distribution of elevated microsites across reference stands measured in our study. Microtopographic features represented a distinct elevational state from the swamp bottom. Reference sites showed a strong bimodality in elevations, and except for one site (3R; Figure 2-12), the elevational distributions appeared quite similar. There was also a striking consistency in the proportion of observations in each elevational mode across all reference sites, with about 1/5<sup>th</sup> of all observations falling into the higher elevational mode. Interestingly, Bukata and Sloan (2002) predicted this to be the ideal proportion of elevated features in terms of productivity and water storage in a model developed based on Florida swamps. Swamp trees will organize over time to fill all canopy space, and this proportion of elevated features may correspond to the amount of adventitious and aerial root mass that the limited biomass of trees can produce considering continual losses due to organic matter oxidation. These features are biogenic, having formed directly from living plant tissues and from organic materials accumulated from the death of these tissues, and it is likely that environmental factors such as hydrology, nutrient inputs and disturbances govern the formation and maintenance of microtopographic features.

Elevational bimodality, which implies that there are two stable elevations, has been observed in a number of wetland ecosystems, from ombrotrophic peatlands in Siberia (Eppinga et al., 2008) to the Everglades marshes of South Florida (Watts et al., 2010). In these systems and likely in Southeastern swamps, short-range positive feedback between productivity and organic matter accretion cause the formation of elevated features (Eppinga et al., 2008). Higher elevations have higher productivity than

lower (Jones et al., 2000), which leads to accretion of organic materials, creating a positive feedback. By contrast, low elevations that experience prolonged flooding have lower productivity, which prevents the accretion of organic materials, thus perpetuating the low elevational state. In cypress-tupelo swamps, this mechanism may contribute to the formation of steep-sided and distinct microtopographic features, though further studies are needed to elucidate details of this process.

In contrast, results from our correlograms indicated no regular horizontal spatial patterning in microtopography across the landscape, which suggests a lack of strong negative productivity feedbacks at some distance away from elevated features, a prerequisite for the formation of spatial elevational patterns (Reitkert and Koppel, 2007). Regular spacing of elevated features, as seen in some peatlands (Eppinga et al., 2008) would be predicted only if the formation of elevated features effectively inhibited the formation of additional features for some distance. It is possible that weak, scale-dependent feedbacks are present, the self-organization of microtopographic features in swamps is a very gradual process, and only in remote swamps that have not experienced large disturbances for long periods of time would regular microtopographic patterns become detectable.

The spatial distribution of trees in swamps may also play a “top-down” role in determining the arrangement of elevated features as they nucleate the features. There is evidence from other Southeastern swamps that as trees become larger, they tend towards regularity in spacing, suggesting that old forests may be most likely to exhibit overall regularity in tree patterning (Good and Whipple, 1982). Spatial structuring of microtopography would also be predicted over time based on this mechanism. If this is

the case, the reference sites in this study may not be developed to this point since most were previously selectively logged or have experienced some degree of hydrologic modification. Additionally, selective logging opens the tree canopy and originates stump and log features, which may alter the natural arrangement of microtopography.

### **Impact of Logging on Microtopography**

Both mat-logging and bottom-logging alter the frequency and distribution of elevated microsites, though to varying degrees as compared to reference sites. Mat-logged sites appeared to have weaker bimodality as compared to reference sites, a much smaller number of observations in the higher elevational mode, and a smaller height difference over the swamp bottom than the corresponding mode in reference sites. This homogeneity in elevational ranges following mat-logging was also detected by the much smaller sill of the variograms as compared to reference sites. However, the relatively short range of spatial autocorrelation in both reference and mat-logged sites indicates that microtopographic variability occurs on the scale of individual trees in both types of sties. ,

Both mat and bottom-logging resulted in the loss of microtopographic features and/or in the height of these features. During harvest operations, uprooting of trees by heavy machinery and compression by skidder traffic has the potential to destroy microtopographic features. Additionally, dragging of logs may abrade microtopographic features as was seen in a study of Canadian peatlands where logging resulted in reduced heights of hummocks (Locky and Bayley, 2006). In the years following logging, additional losses in microtopographic features by decomposition could potentially result from a lack of carbon inputs and death of supporting tissues such as roots. Conversely,

some new elevated features are created during logging in the form of stumps and logs that are left after harvest and soil mounded by skidders, but the proportions of such sites is nevertheless much reduced due to logging. Temporary rises in the water table following logging may act to slow decomposition and thus protect remaining organic features.

Bottom-logging had similar impacts as mat-logging to the frequency and distribution of elevated microsites, though mat-logging appeared to minimize the impact of skid trails on the swamp bottom as compared to bottom-logging. In mat-logged sites, skid trail observations were always included in the lower elevational mode, indicating that, across frames, they were not sufficiently rutted to be clustered as a separate elevational mode from the swamp bottom. On the other hand, skid trails produced by bottom-logging were often substantially deeper than the swamp bottom, as evidenced by the trimodality of elevation modes due to a very low elevational mode classified separately from the swamp bottom. Interestingly, the sill of the variograms in bottom-logged sites were more similar to reference conditions than mat-logged sites. It may have been possible that the older bottom-logged sites have had more time to recover towards reference conditions. However, given the evidence of deeper skid trails as measured in the line transects and detected in the trimodality of elevational distributions, it is more likely that bottom-logged sites appear more similar to reference conditions due to the heterogeneity introduced by deeply rutted skid trails. This suggests that variograms provided only limited ecological information as overall heterogeneity measures did not necessarily correlate to improved site conditions.

### **Microsite Availability, Substrate Type, and Potential for Regeneration**

The loss of elevated microtopography following logging may impede recolonization by plant species that are the least tolerant of flooded conditions. For example, species such as *Ilex spp.* are often confined to the higher elevations in swamps and may be at a disadvantage, whereas other species such as *Cephalanthus occidentalis* and *Nyssa spp.* are found at lower elevations (Titus, 1990) and may be better suited to post-harvest conditions. Most shrubs are confined to elevated areas (i.e. Anderson et al., 2009); thus, the loss of these microsites may alter the structure of the vegetation in cypress-tupelo swamps by decreasing the sites for shrub regeneration. Cohort regeneration during periodic dry downs may be a means of tree canopy recovery in some swamps (Dunn and Sharitz, 1987). However, this was not observed in the studies, which generally were dominated by shrub, small tree and coppice regeneration. Mat-logging may offer an advantage over bottom-logging in the reestablishment of woody vegetation following logging by preventing the formation of deeply rutted, permanently flooded areas, though it remains to be seen if this will foster tree canopy recovery.

The substrate composition of microtopographic features is an important component of their quality for woody plant regeneration and survival. Studies have shown that woody seedlings in Southeastern swamps are distributed nonrandomly across microsite types, with stable substrates such as soil immediately adjacent to trees, aerial roots, and knees harboring more seedlings than expected given the abundance of these sites (Titus, 1990, Huenneke and Sharitz, 1986). This pattern may be due to uneven numbers of seeds arriving at these sites and/or higher germination and/or survival of seedlings at these sites. Long-lived plants such as trees may stand a

better chance at reaching maturity on sites that are not likely to float away, deteriorate, or erode. In contrast, vines and shrubs with shorter life spans are spread more evenly across substrate types and are found more often on less permanent substrates such as logs and stumps than trees (Titus, 1990). Tip-up mounds support greater amounts of *Rubus spp.* and *Vitis spp.* than would be expected given the abundance of these features in studied sites (Titus, 1990). A study of *Nyssa sylvatica* revealed each substrate type to present advantages and disadvantages for regeneration. While emergent sites such as stumps, knees, and tree bases had much higher rates of germination than lower microsites (28% vs. <1%), predation was also much greater in emergent sites (Huenneke and Sharitz, 1990). The ideal microsite is likely to be species-dependent and also contingent of a variety of environmental conditions including flooding regime, predators, competition and light conditions. Shifts in the composition of microtopographic features therefore has the potential to influence the succession of the plant community in swamps.

Live tree roots, including cypress knees, shallow root masses of tupelo and aggregations of “n-shaped” aerial tupelo roots appeared to be an important source of stable microtopographic features in reference sites that could potentially support tree regeneration. Stump/soil features were also common due to both natural tree death and perhaps stumps that remained from past selective logging operations, though these features are prone to decomposition and are perhaps more short-lived than live root features. The relative loss of root/soil features in both mat and bottom-logged sites, which is perhaps only due to the large increase in stump features, or possibly due to the loss of root features via uprooting during logging or slow deterioration due to death of

roots, indicates that the features that remain after logging may not be as stable or long-lived as those of reference sites. The creation of slash debris as a result of mat-logging could be due to the nature of the logging technique, which may cause more branches to be left in the vicinity of skid trails from the mats used to cover the trails. Alternatively, the slash debris, which likely decomposes relatively rapidly, may have been present only in mat-logged sites because they were younger in age than the bottom-logged sites.

### **Concluding Remarks**

Water depth surveys and subsequent creation of elevational histograms was an effective way to get a sense of the topographic variability at each site. This method is effective if vegetation is not too thick and if the area is mostly flooded. However, for dry sites, similar data can be collected via a laser-level and statia rod design (e.g. Bukata and Sloan, 2002). Skid trail transects proved an effective and easily interpreted method to assess soil rutting relative to the surrounding land surface, and a surprising level of detail was visible in composite transects, including individual tire tracks.

Bimodality in elevations, relatively high spatial variance and a short range of autocorrelation across reference sites highlights the presence of distinct, elevated microtopographic features at the scale of individual plants. These features may be maintained via positive productivity feedbacks and limited by continual carbon oxidation and discrete tree productivity, as evidenced by the similar prevalence of elevated observations across all reference sites. A lack of evidence for spatial patterning suggests a lack of strong negative distal feedback that would regulate elevated feature spacing. These features undoubtedly play an important role in shaping plant communities and promoting diversity and productivity in many cypress-tupelo swamps.

Reduced frequency and height of elevated microtopographic features and altered substrate compositions of these features that result from mat and bottom-logging have the potential to alter the ability of cypress-tupelo swamps to support tree regeneration and could alter biogeochemical cycling via changes in productivity and/or plant communities. Reductions in distinct, raised microtopography were often near 50% in recently clearcut sites, which could favor species that tolerate flooding and decrease regeneration of those who need dry ground for germination and/or growth. Because bottom-logging maintains overall microtopographic heterogeneity across space, it may actually support a relatively diverse plant assemblage in comparison to mat-logging. However, if site recovery toward historical conditions is desired, mat-logging, while causing a loss in microtopographic heterogeneity, may have equal or better potential to regenerate over time due the absence of deep skid trails. Specifically, mat-logging offers an advantage over bottom-logging by substantially reducing the depth of soil rutting, thereby avoiding long-term flooding in trails. This will encourage woody plant regeneration (including valuable timber trees), which is required of ongoing forestry operations under the Federal Clean Water Act. It is not clear yet if mat-logging provides a long-term advantage over bottom-logging for full ecosystem recovery. There has scarcely been enough time since mat-logging and even bottom-logging began across large areas to understand the long-term consequences; thus, it will be important to continue to track recovery of these ecosystems over greater time scales.

The styles used in this document are called paragraph styles. Paragraph styles are used to format the entire text within a paragraph. To apply a style, follow these instructions:

Table 2-1. List of study sites. (\*Basal areas were estimated > 34.4 m<sup>2</sup>/ha for reference sites, however, accurate measurements could not be made due to buttressing.)

Site #	treatment	yrs since logging	Landscape position	Surrounding land use	Basal area (m <sup>2</sup> /ha)	County	Location
1R	Reference	NA	depression	residential/agriculture	--	Alachua	29°37'43.60"N, 82°17'54.14"W
2R	Reference	NA	Strand	national forest/wetlands	--	Baker	30°15'27.30"N, 82°24'30.40"W
3R	Reference	NA	depression	pine plantation/wetlands	--	Alachua	29°46'2.13"N, 82°13'7.35"W
4R	Reference	NA	backwater floodplain	pine plantation/river floodplain	--	Bradford	29°50'8.89"N, 82° 9'30.92"W
5R	Reference	NA	depression	pine plantation/wetlands	--	Alachua	29°47'7.95"N, 82°16'8.54"W
1M	Mat-logged	1	depression	pine plantations/wetlands	0	Alachua	29°45'57.88"N, 82°12'53.16"W
5M	Mat-logged	5	backwater floodplain	pine plantations/river floodplain	1.0	Bradford	29°50'26.23"N, 82° 9'13.21"W
3B	Bottom-logged	3	depression	pine plantations/wetlands	0.8	Alachua	29°46'50.77"N, 82°16'0.92"W
7B	Bottom-logged	7	depression	pine plantations/wetlands	3.4	Gilchrist	29°47'26.29"N, 82°48'33.91"W
13B	Bottom-logged	13	depression	pine plantations/wetlands	5.9	Gilchrist	29°48'12.55"N, 82°47'14.76"W

Table 2-2. BIC values for unimodal, bimodal and trimodal models generated by the Mclust package. "Components" indicates the number of elevational clusters in the best fit model.

site	sampling frame	model variance	components	unimodal	bimodal	trimodal
Reference 1	1	equal	2	-1271.0	<b>-1206.0</b>	-1215.3
Reference 1	2	equal	2	-1255.0	<b>-1232.5</b>	-1242.5
Reference 2	1	unequal	2	-1088.0	<b>-1052.9</b>	-1058.5
Reference 3	1	unequal	5	-893.0	-849.3	-849.3
Reference 3	2	equal	3	-900.5	-882.9	<b>-880.6</b>
Reference 4	1	unequal	2	-1180.0	<b>-1138.1</b>	-1145.0
Reference 4	2	equal	2	-1185.0	<b>-1165.1</b>	-1174.9
Reference 5	1	unequal	2	-1158.5	<b>-1105.3</b>	-1119.1
Reference 5	2	equal	2	-1236.0	<b>-1204.2</b>	-1213.0
Bottom-logged 3	1	unequal	2	-1011.0	<b>-980.7</b>	-991.8
Bottom-logged 7	1	unequal	2	-1143.5	<b>-1136.3</b>	-1136.6
Bottom-logged 7	2	equal	4	-1161.0	-1158.0	-1120.0
Bottom-logged 13	1	unequal	4	-1257.0	-1213.4	-1216.8
Bottom-logged 13	2	equal	2	-1163.2	<b>-1162.9</b>	-1165.0
Mat-logged 1	1	unequal	2	-1157.0	<b>-1089.1</b>	-1097.0
Mat-logged 1	2	equal	1	<b>-1140.0</b>	-1145.2	-1149.0
Mat-logged 5	1	equal	2	-1101.9	<b>-1099.8</b>	-1107.0
Mat-logged 5	2	equal	2	-1072.0	<b>-1053.9</b>	-1060.9



Figure 2-1. Skid trails created during bottom-logging operations A) 10 yrs ago and B) 12 yrs ago.

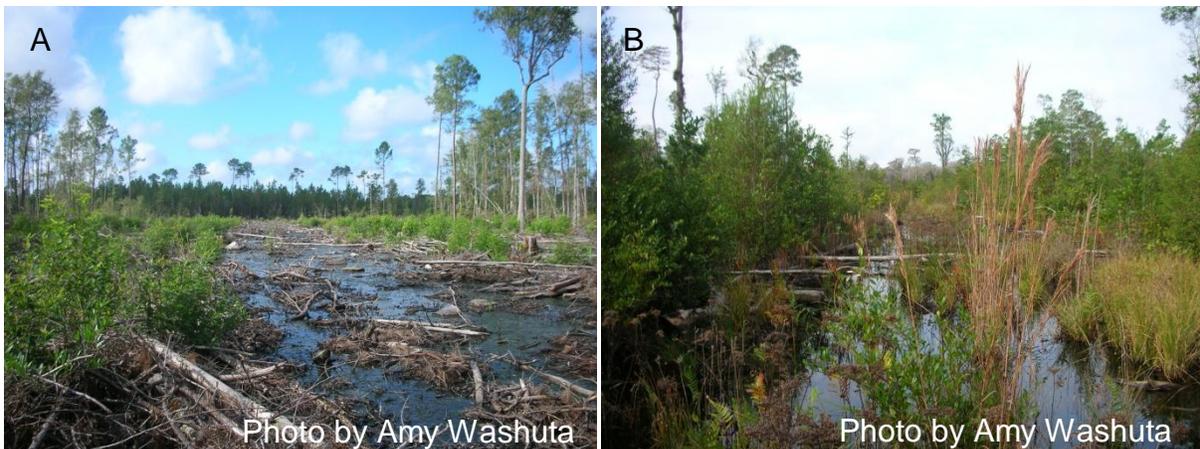


Figure 2-2. Skid trails created during mat-logging operations A) 1 yr ago and B) 5 yrs ago.

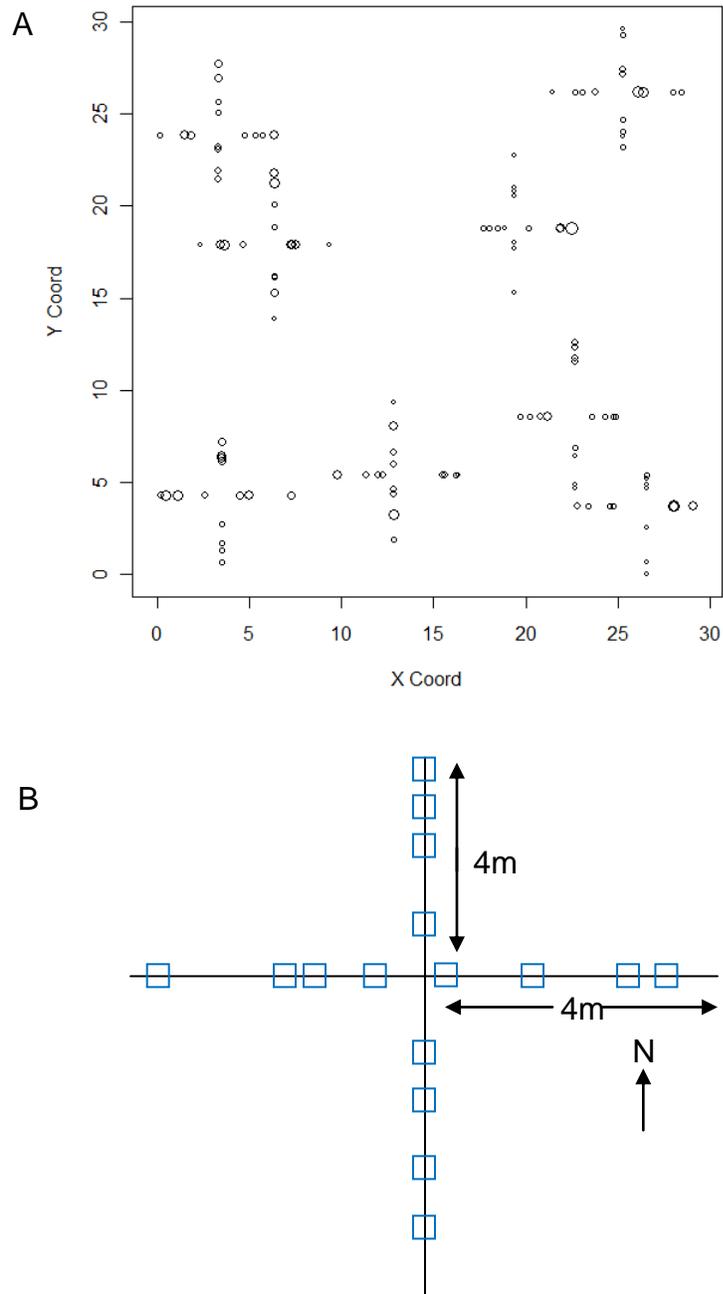


Figure 2-3. A) A water depth sampling scheme for one 30x30m frame and B) An example sampling station within the frame with 16 sampling points distributed in four cardinal directions.



Figure 2-4. A tree base microtopographic feature.



Figure 2-5. A soil microtopographic feature.



Photo by Amy Washuta

Figure 2-6. A stump/soil microtopographic feature.

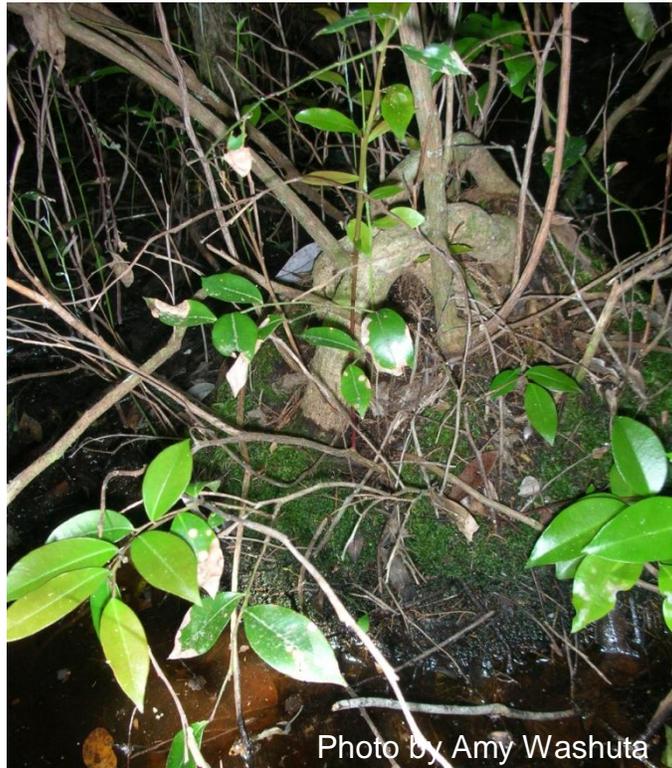


Photo by Amy Washuta

Figure 2-7. A root/soil microtopographic feature.



Photo by Amy Washuta

Figure 2-8. A log microtopographic feature.



Photo by Amy Washuta

Figure 2-9. A stump microtopographic feature.



Figure 2-10. A tip-up mound microtopographic feature.



Figure 2-11. A slash debris microtopographic feature.

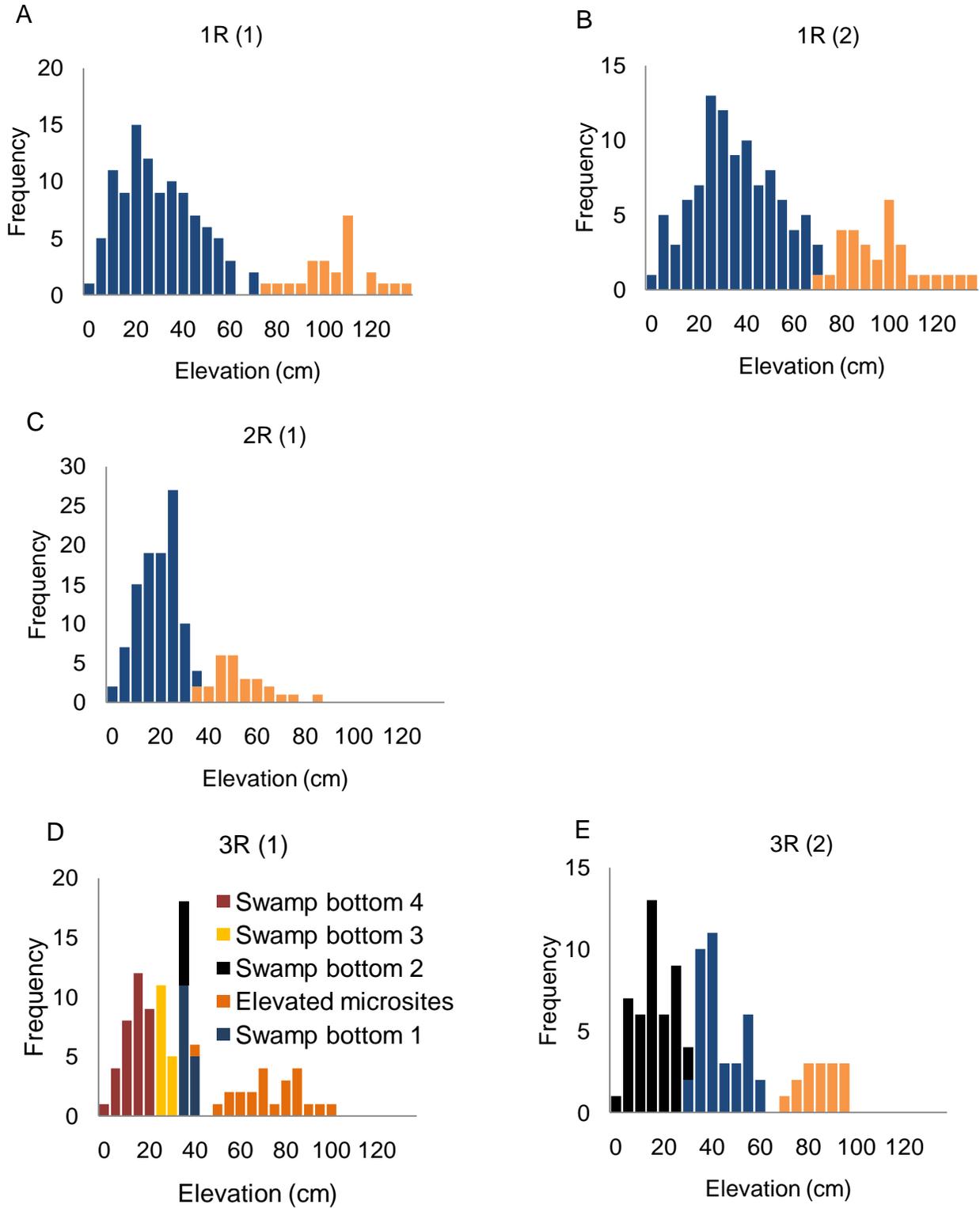


Figure 2-12. Elevational histograms for frames in three reference swamps. Shades indicate elevational modes modeled by the Mclust package (R software).

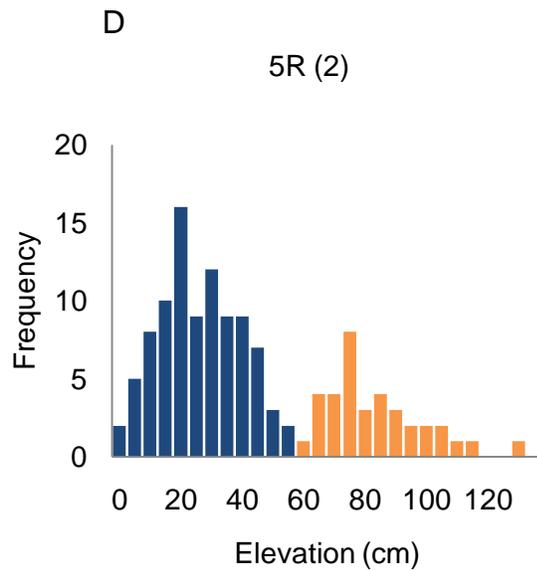
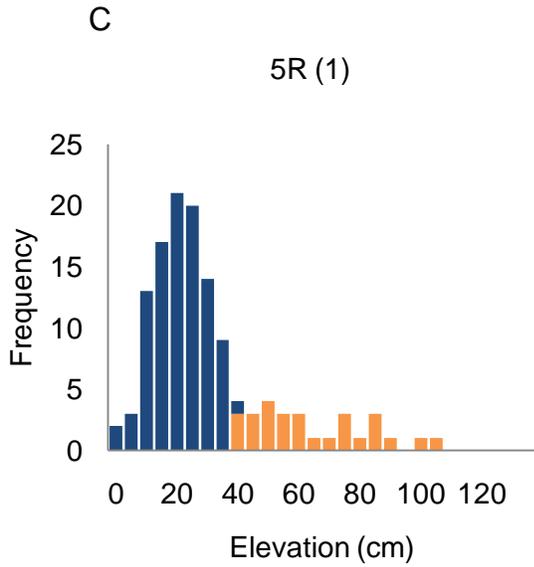
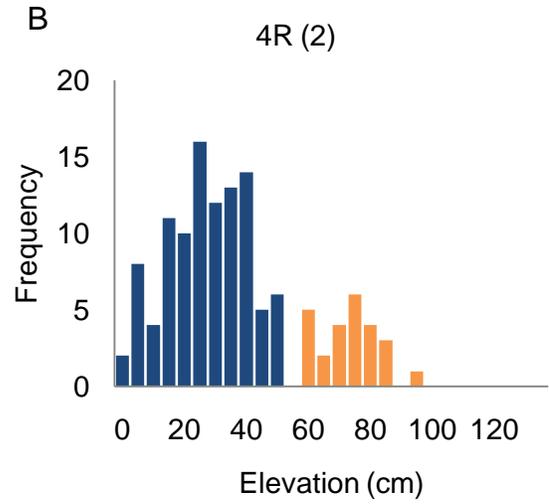
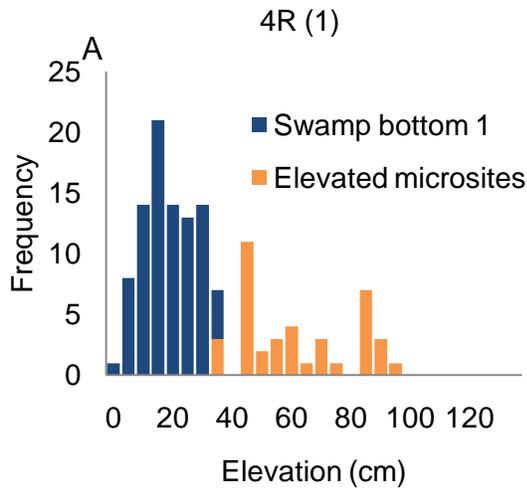


Figure 2-13. Elevational histograms for frames in reference swamp 4R (A and B) and 5R (C and D). Shades indicate elevational modes modeled by the Mclust package (R software).

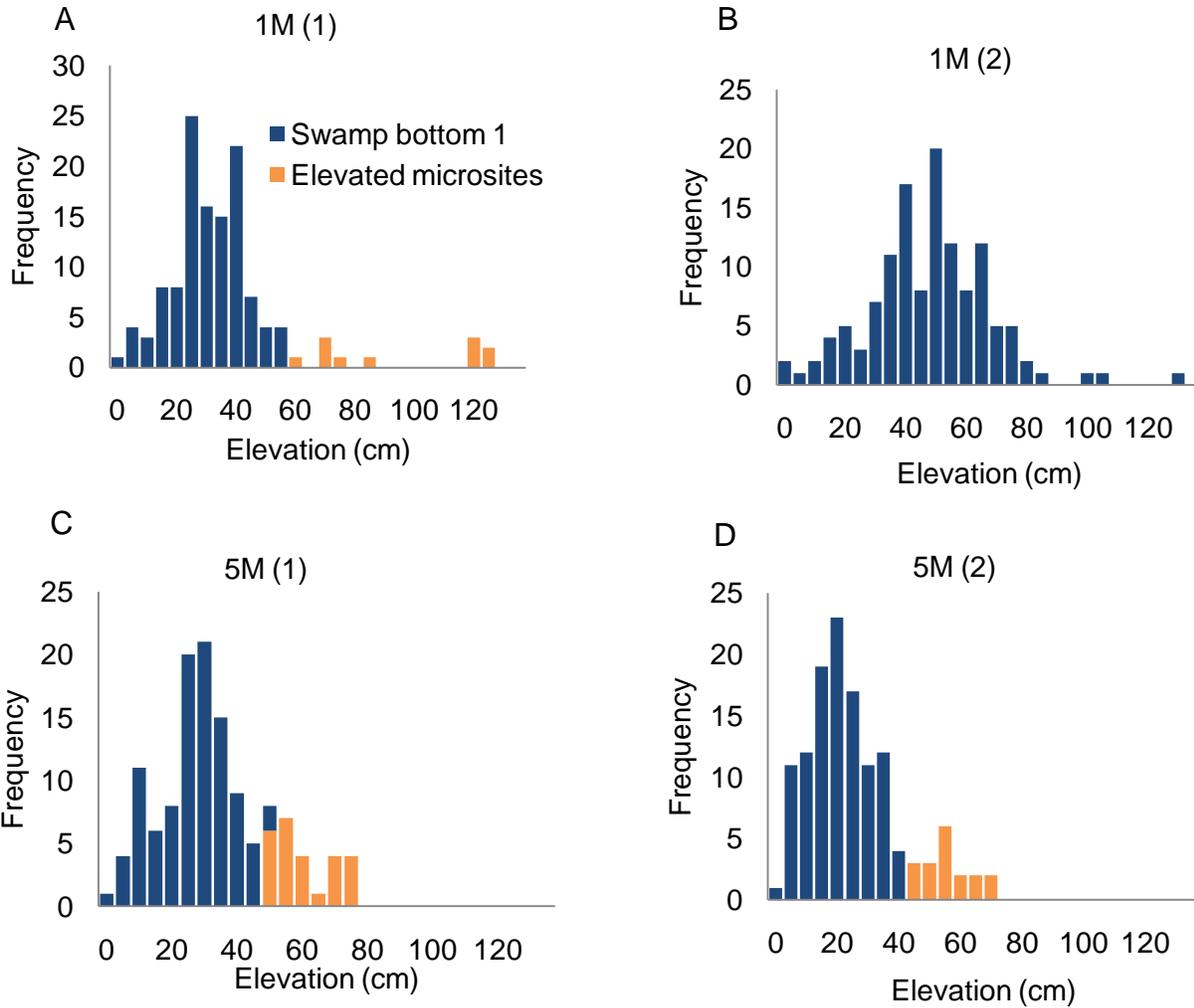


Figure 2-14. Elevational histograms for swamps mat-logged 1 year ago (A and B) and 5 years ago (C and D). Shades indicate elevational modes modeled by the Mclust (R software).

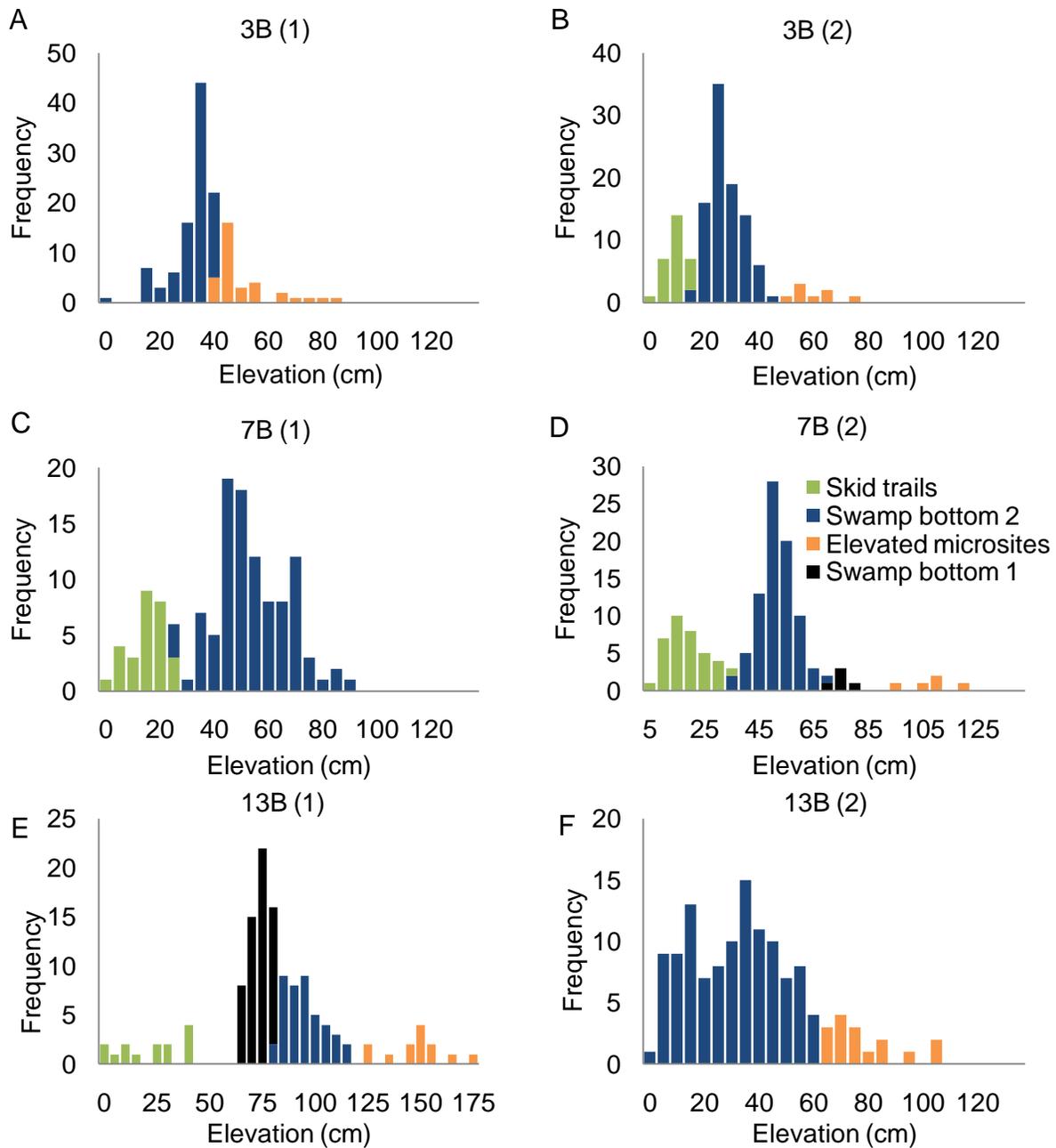


Figure 2-15. Elevational histograms for swamps bottom-logged 3 years ago (A and B), 7 years ago (C and D), and 13 years ago (E and F). Colors differentiate elevational modes modeled by the Mclust package (R software).

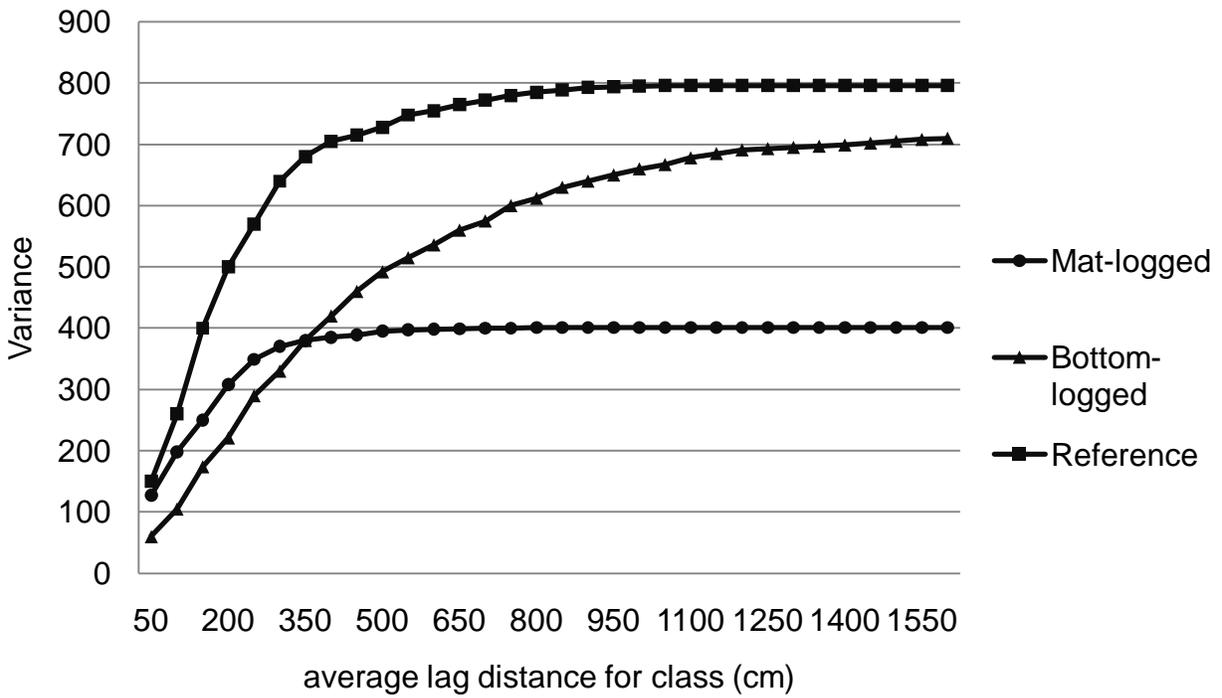


Figure 2-16. Exponential theoretical variograms modeled after the composite variogram parameters for all mat-logged, bottom-logged and reference sites.

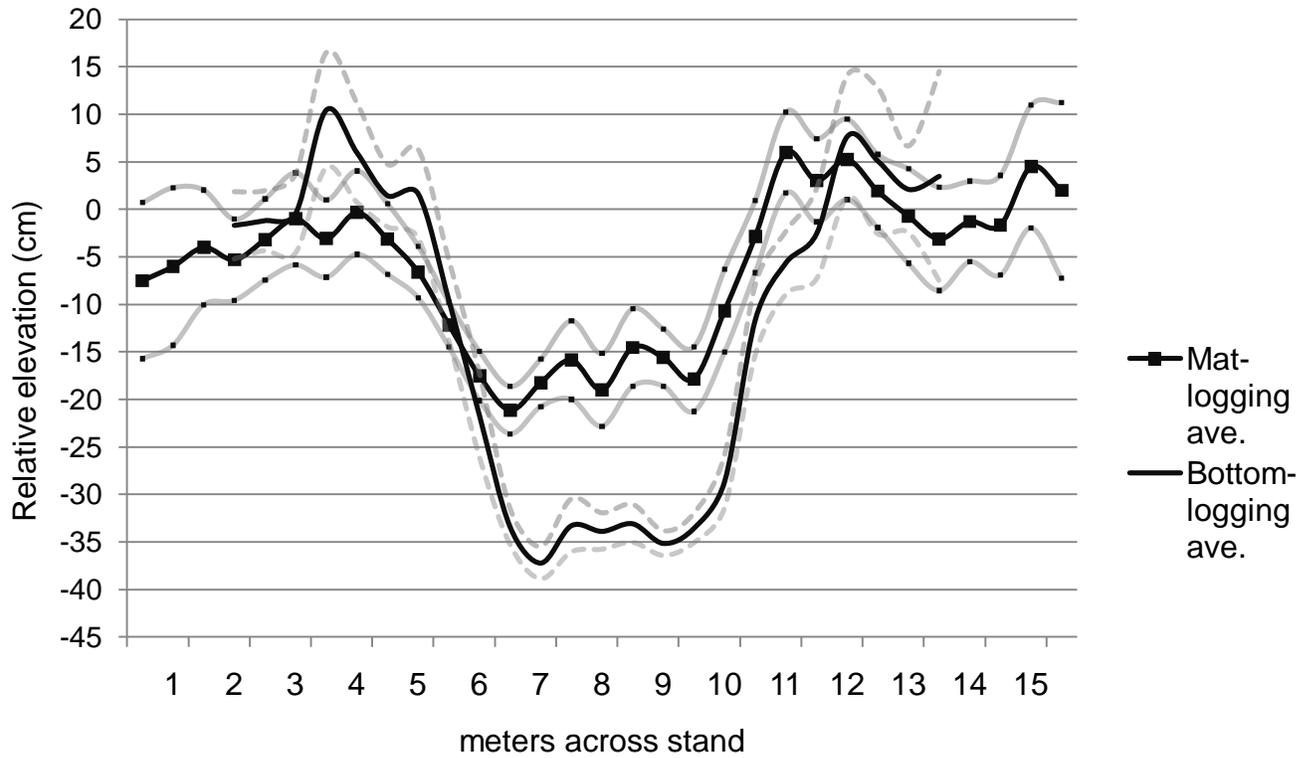


Figure 2-17. Composite transects showing average elevations in 15 transects across mat-logging skid trails and 15 transects across bottom-logging skid trails. 95% confidence envelopes are shown with each composite transect. Transects are superimposed so that the average off-trail elevations for mat and bottom-logging trails are equal.

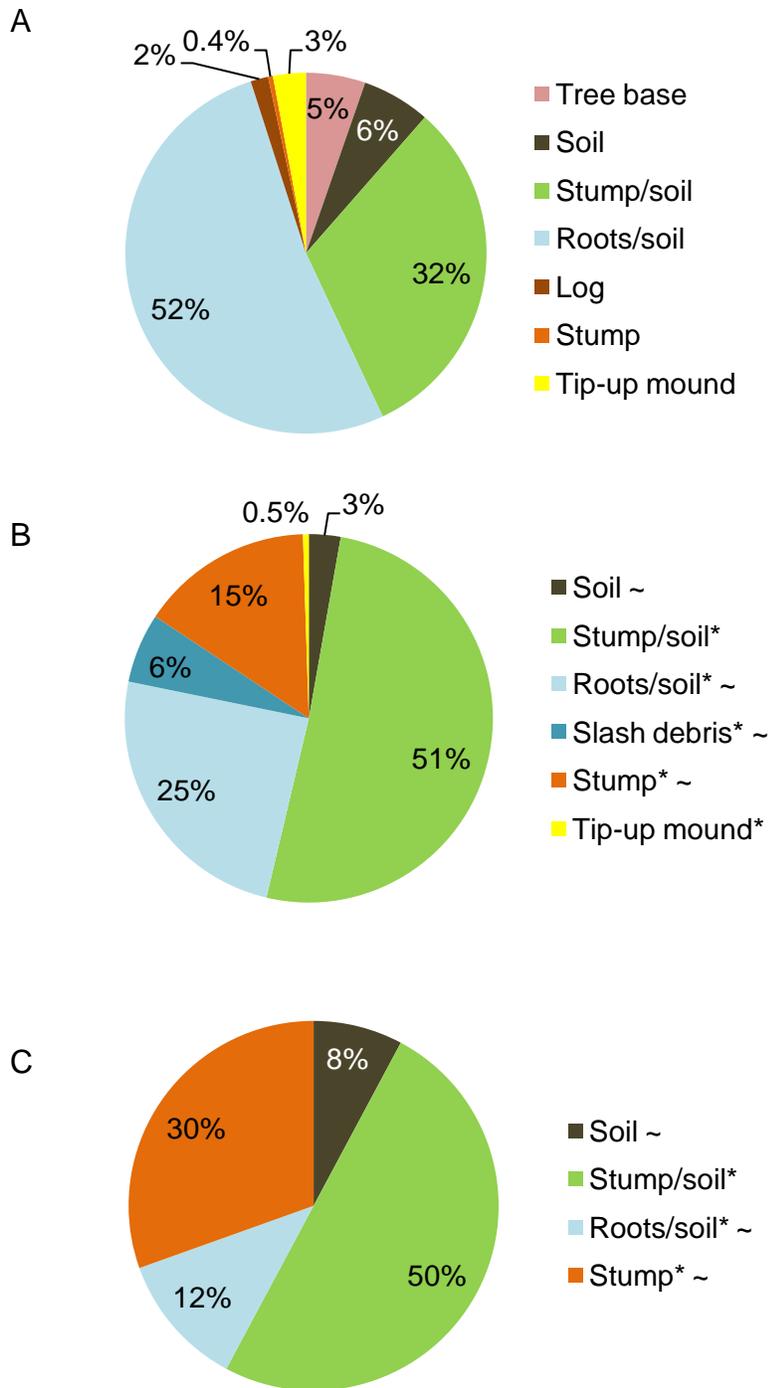


Figure 2-18. The relative proportions of various microsite substrate types in A) reference swamps, B) mat-logged swamps and C) bottom-logged swamps, with (\*) indicating a difference in proportion from reference swamps, and (~) indicating a difference in proportion between mat and bottom-logged swamps at  $\alpha = 0.05$ .

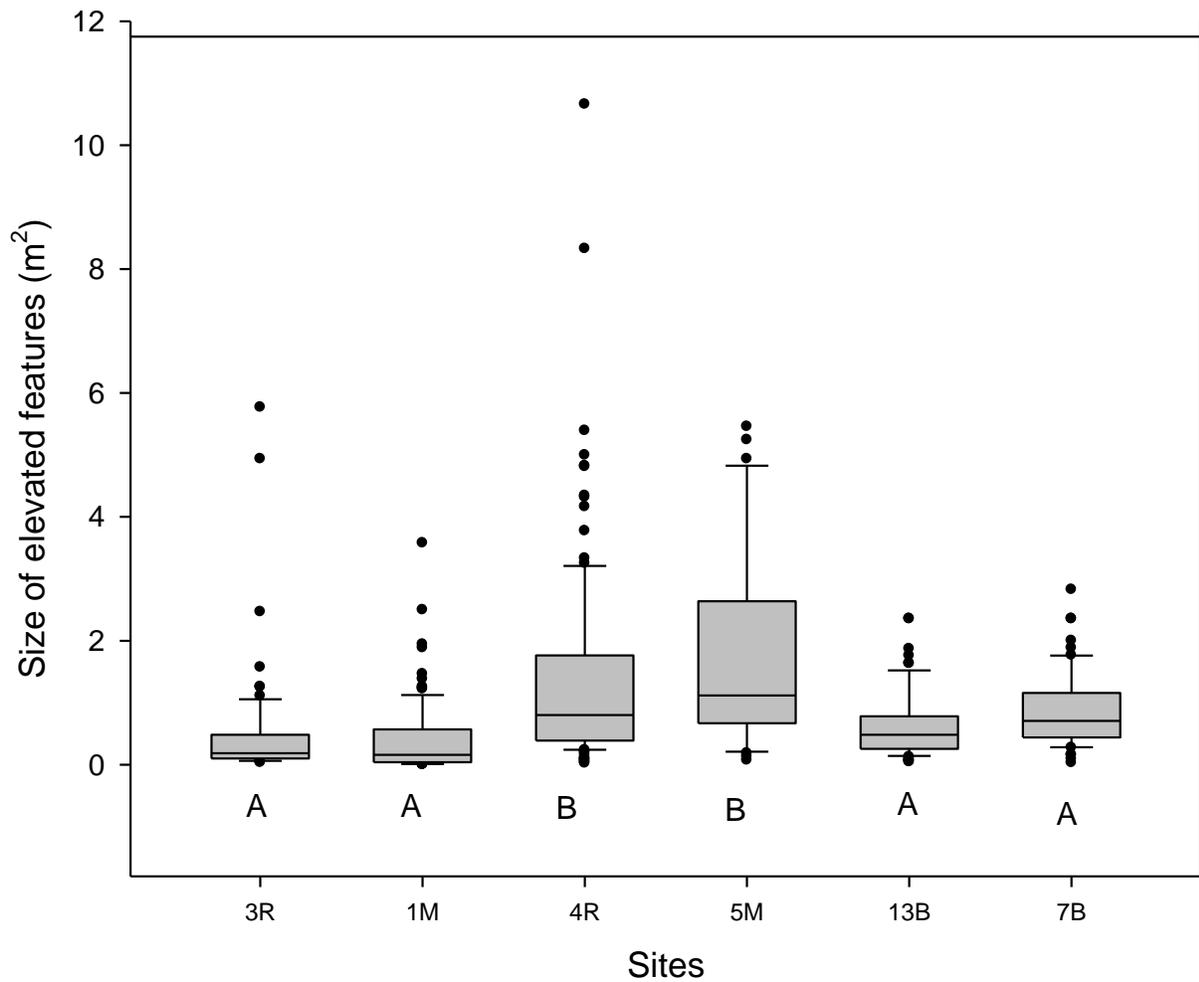


Figure 2-19. Boxplots indicating the minimum, maximum, mean, interquartile range and outliers for the area (m<sup>2</sup>) of elevated microtopographic features across six study sites. The mean feature size of sites labeled “A” differ at  $\alpha = 0.05$  from sites labeled “B”.

CHAPTER 3  
RELATIONSHIPS BETWEEN VEGETATION AND MICROTOPOGRAPHIC POSITION  
IN REFERENCE AND CLEARCUT *TAXODIUM-NYSSA* SWAMPS

**Background**

Flooded conditions pose problems for terrestrial woody plants as they greatly reduce oxygen available to the roots and allow a build-up of toxins that would normally be degraded under aerobic conditions. Also, this reducing environment can alter the form in which nutrients exist and thus affect their availability to plants (Conner and Buford, 1998). Even the most flood-tolerant species, such as cypress (*Taxodium distichum*) and tupelo (*Nyssa spp.*) have been shown to perform better in wet, but aerated conditions than under anaerobic saturation such as that found on swamp bottoms (Dickson and Broyer, 1971). These species, as well as most other woody plants that thrive in swamps, cannot generally germinate in submerged soils (Myers and Ewel, 1990, Titus, 1990). Disturbances such as clearcutting in these swamps are often followed by slow regeneration due to the hindrance of woody plant germination and establishment in flooded conditions (Laderman, 1998) and can exacerbate flooding due to decreased evapotranspiration (Sun et al., 2000), making microtopographical highs potentially important regeneration microsites in these swamps.

In addition to flooding, to the paucity of advance regeneration at the time of clearcutting may contribute to slow regeneration of desired woody species (Meadows and Stanturf, 1997). Also, while coppicing of both cypress and tupelo is common and seed production can begin as quickly as two years after harvest (Ewel, 1998), long-term survival of sprouts and their contribution to the future forest canopy remains uncertain (Randall et al., 2005, Conner and Buford, 1998). A recent study found 10-41% of cut cypress stumps to have live sprouts ten years after clearcutting in eight North Florida

domes (Ricci, 2010), and early studies revealed survival rates between 17-23% for cypress stump sprouts (Conner et al., 1986). In a number of case studies, swamps quickly succeeded to dense shrubby cover following clearcutting or thermal effluent wastewater loading, but subsequent tree regeneration was often slow, unreliable and tended to occur via cohort regeneration in years when conditions were dry and appropriate (Dunn and Sharitz, 1987, Spencer et al., 2001). Cypress trees, in particular, have low seed viability and a narrow range of ideal germination and growth requirements, including open and unflooded conditions (Gunderson, 1977) and may only regenerate in large numbers in when a number of criteria are simultaneously met.

Microtopographic variability provides a variety of hydrologic niches for plants and is likely a key structural component regulating the recovery of cypress-tupelo swamps. The microtopography in many southeastern swamps has an elevational range on the order of 0.5-1.5 m (Titus, 1990), with elevated features rising above a lower swamp bottom. Substrate conditions on elevated microtopographic features differ from that of the swamp bottom in that they are more aerobic, potentially more productive (Jones et al., 2000), harbor more arbuscular mycorrhizae structures (Cantelmo and Ehrenfeld, 1999), and potentially contribute disproportionately to ammonification and nitrification (Bruland and Richardson, 2005). Also, microtopographic features have been shown to influence the distribution of swamp plant species over the life cycle of the plants. Woody seedlings are often preferentially associated with elevated features (Titus, 1990, Anderson, 2009) due to factors including differential seedfall, seed trapping, germination and survival across microsites (Schneider and Sharitz, 1988, Titus, 1991). Individual plant species can show strong preferences for a particular and often unique elevational

range, with many woody and rare species favoring elevated microsites (Vivian-Smith, 1997, Simmons et al., 2009, Titus, 1990). For example, in a study of woody seedlings in a Florida floodplain swamp, *Ilex cassine*, *Vaccinium elliotii*, and *Lyonia lucida* were found at mean elevations about 20 cm higher than that of *Cephalanthus occidentalis*, *Taxodium distichum* and *Diospyros virginiana* (Titus, 1990). In general, early successional species have been shown to exhibit wider tolerance ranges for microtopographic positions in comparison to later successional species, which often thrive in narrower elevational ranges (Simmons et al., 2009). Beyond individual plant species, microtopographic heterogeneity has been correlated to enhanced botanical diversity in both observational and experimental wetland studies (Vivian-Smith, 1997, Moser et al., 2007, Sloan, 1998), and in particular, elevated features harbor greater plant diversity than lower elevations (Bukata and Sloan, 2002, Bukata, 1999, Simmons et al., 2009).

Not all plant species have the same relationship with microtopographic features in swamps. These features are biogenic, and some species play a role in their creation, while others simply take advantage of their existence as suitable germination sites. The tree and shrub species that contribute to the formation of microtopographic features can be thought of as autogenic ecosystem engineers that modify the elevation of soil by virtue of their own morphology (Jones et al., 1994). These species undoubtedly alter the distribution and movement of resources in swamps, which can affect entire communities of organisms and overall ecosystem functioning (Gilad et al., 2004). Still, little is known about the nature and extent of these effects in southern swamps.

Given the important relationships between microtopography and swamp plant communities, it follows that microtopography plays an important role in the ability of these systems to regenerate after disturbance (Bukata and Sloan, 2002), and conversely, the regeneration of some key species may be important in the recovery of microtopography after disturbance. Characteristically slow regeneration of swamps after clearcutting (Kellison and Young, 1997) makes understanding limitations to regeneration of particular interest. Diminished prevalence and height of microtopographic features has been observed following clearcutting (Locky and Bayley, 2006), which may delay subsequent development of microtopography (Bukata and Sloan, 2002). Additionally, the creation of soil ruts from heavy skidding equipment during harvest may further reduce the suitable sites for woody plant regeneration.

The first objective of this study was to compare the relationships between the density and diversity of plant species and microtopographic position in both reference and clearcut swamps. The second objective was to determine the relationships, if any, between the size of individual trees of various species and microtopographic position in reference swamps. The results provide insight into the differences in plant composition and density between microtopographic highs and lows in sites with open and closed tree canopies and allow for regeneration predictions based on site microtopography.

## **Methods**

### **Study Sites**

Sites were located within backwater floodplain, strand and depressionnal *Taxodium-Nyssa* swamps on industrial and federal lands in Alachua, Gilchrist, Bradford and Baker counties of North Central Florida between 29° 37' and 30° 15' N and 82° 9' and 82° 48' W (Table 3-1). Average annual precipitation is 1250 mm, with average

annual high and low temperatures of 26.6°C and 14.2°C (NOAA). Sampling occurred in April and May of 2010, during which rainfall was near average and air temperatures were warmer than average by 1.1°C (NOAA, 2010).

Soils were very poorly drained fine sands and sandy loams (Monteocha and Mascotte series), very poorly drained fine sands with a mucky fine sand surface layer (Lynn Haven series) and very poorly drained mucks with loamy substratums (Pamlico series) (NRCS, 2010). Depth to water table for each of these series is zero inches, and each are found in depressions in the landscape. Pine plantations and isolated wetland features represent the main type of surrounding land use (Table 3-1).

### **Reference sites**

Six reference swamps were sampled in all, 3 were sampled for the understory vegetation analysis and 5 were sampled for the tree and elevated microsite surveys (Table 3-1). The sites were chosen based on their similarity in species composition and hydrology to sampled logged sites and often were in close proximity to the logged sites. Each of these sites exhibited evidence of a history of minor to moderate incomplete or selective logging within the past century. Truly “pristine” swamps that had escaped all logging and/or hydrologic modification could not easily be found in North Florida. Each of the 5 reference sites were similar in that they were all dominated by a small suite of canopy trees that included primarily *Nyssa sylvatica*, *Taxodium ascendens*, and *Taxodium distichum*, and secondarily *Gordonia lasianthus*, *Magnolia virginiana*, and *Persea borbonia*. The understory vegetation was characteristically dense and shrubby and was often dominated by *Lyonia lucida* and *Itea virginica*, among others. Additionally, ferns, herbs and vines were also common in some sites.

Microtopographic relief had an amplitude of 0.75 - 1.4 m within each site. Distinct elevated microsites formed by tree roots, stumps and soil and litter accumulations covered an average of 22.6% ( $\pm 1.671\%$ ) of the swamp floor. In most sites, all soil except the raised microtopographic features was submerged in tannic water for the duration of the study.

### **Logged sites**

Four sites that were recently clearcut were sampled, 3 of which were sampled for the understory vegetation analysis (Table 3-1). Tree and elevated microsite surveys were conducted in all 4 sites. These sites ranged from having sparse or very young tree regeneration (Basal areas of 0.5-1.2 m<sup>2</sup>/ha) to dense regeneration of coppice and/or seedling recruits (Basal area of 4.6-9.2 m<sup>2</sup>/ha). Elevated microsite features covered an average of 9.9% ( $\pm 2.854\%$ ) of the ground surface.

### **Field Methods**

#### **Understory vegetation**

In each of 6 study sites, either 10 or 20 1m<sup>2</sup> plots on elevated microsites and 10 or 20 1m<sup>2</sup> plots on the swamp bottom were randomly located, for a total of 80 plots across 3 reference sites, and 80 plots across 3 recently logged sites. Due to lack of accessibility to some sites, sampling across sites was unequally replicated. In each plot, the number of stems of each shrub, vine and forb species and the number of tree seedlings were recorded. For multi-stemmed shrubs such as *Lyonia lucida*, every stem was counted individually. Percent cover was estimated for graminoids.

#### **Tree surveys**

In randomly located 5m radius plots, 1042 trees were sampled across 5 reference sites, and 742 trees were sampled across 4 logged sites. For each tree, species, DBH

(diameter at breast height) and microsite association (on the swamp bottom or associated with an elevated microsite) were recorded.

## **Data Analysis**

### **Understory vegetation**

All plant species that were encountered (Appendix C) were grouped into 5 functional groups: graminoids, forbs, woody vines, shrubs, and tree seedlings. Using general linear mixed models (proc glimmix in SAS 9.2), a test for the fixed effects of microtopographic position (swamp bottom or elevated microsite), site treatment (reference or logged) and the interaction between these two explanatory variables on the response variables of stem density or percent cover and plant species richness was performed for each plant functional group and for all species combined. Site and plot were entered into each mixed model as random effects. Differences in plant functional group richness or density between microtopographic position and site treatment were evaluated at  $\alpha = 0.05$  (Appendix D).

### **Tree surveys**

I tested the distribution of trees against the percent that would be expected on hummocks. Specifically, a chi-squared test was performed to compare the proportion of individuals of each tree species found with elevated microsities against the null hypotheses of 22.6% for reference and 9.9% for logged, which were the average swamp area composed of elevated microsities in each treatment and thus the expected proportions. This test was done for the seven most commonly encountered tree species, pooled across reference and then across logged sites. Differences between the null hypotheses were evaluated at  $\alpha = 0.05$ .

To determine whether relationships between tree species and microsite were related to tree size, observations were divided into DBH classes so that each class had the same number of trees. The percentages of trees in each DBH class associated with elevated microsites were calculated. Linear regressions were used to examine the relationship between tree DBH and likelihood of elevated microsite association, with DBH class as the independent variable and % elevated microsite association the dependent variable. This was done for the five most common trees (excluded *Persea spp.* and *Pinus elliotii* because their sample sizes were not adequate for the analysis).

## **Results**

### **Understory Vegetation**

#### **Species richness**

Across sites, overall species richness was higher on elevated microsites ( $2.95/m^2$ ) than on the swamp bottom ( $0.73/m^2$ ) ( $p < .0001$ ). There was no effect of site treatment (reference vs. logged). On elevated microsites, the species richness of forbs ( $0.50/m^2$ ), woody vines ( $0.48/m^2$ ), shrubs ( $1.48/m^2$ ), and tree seedlings ( $1.48/m^2$ ) were greater than on the swamp bottom across sites ( $p = .0069$ ,  $p < .0001$ ,  $p < .0001$ ,  $p < .0001$ , respectively) (Figure 3-1). The relationships between topographic position and species richness for these groups were similar between reference and logged sites. Graminoid species richness did not differ with topographic position ( $p = 0.1429$ ), though an interaction effect ( $p = 0.0041$ ) indicated that there was greater divergence in species richness with topographic position in logged sites than in reference sites.

#### **Stem density**

On elevated microsites, the stem density of forbs (ave.  $2.09/m^2$ ), woody vines (ave.  $1.68/m^2$ ), shrubs (ave.  $14.03/m^2$ ), and tree seedlings (ave.  $1.81/m^2$ ) were greater

than on the swamp bottom across sites ( $p = .0025$ ,  $p = .0310$ ,  $p < .0001$ ,  $p < .0001$ ,  $p = .0088$ , respectively) (Figure 3-2). There were no differences between site treatments. Shrub stem densities were more divergent between elevated microsites and the swamp bottom in logged sites than in reference sites (interaction effect  $p < .0001$ ). Forbs, woody vines and tree seedlings did not have interaction effects between topographic position and site treatments, indicating that the relationship between topographic position and stem density was similar across all sites.

### **Tree Surveys**

For all tree taxa analyzed, a greater proportion were found in association with elevated microsites than would be expected under a random distribution, given the proportion of the swamp comprised of these microsites in both reference and logged sites (all  $p$  values  $< .0001$ ). In reference sites, 44% of *Nyssa sylvatica* var. *biflora* ( $n = 561$ ), 67% of *Taxodium distichum* var. *nutans*. ( $n = 55$ ), 71% of *Persea* spp. ( $n = 21$ ), 77% of *Magnolia virginiana* ( $n = 132$ ), 91% of *Ilex* spp. ( $n = 124$ ), 95% of *Gordonia lasianthus* ( $n = 138$ ), and 100% of *Pinus elliotii* ( $n = 7$ ) were found on elevated microsites. Similarly, in logged sites, 59% of *Nyssa sylvatica* var. *biflora* ( $n = 76$ ), 74% of *Taxodium distichum* var. *nutans*. ( $n = 182$ ), 93% of *Persea* spp. ( $n = 75$ ), 46% of *Magnolia virginiana* ( $n = 13$ ), 82% of *Ilex* spp. ( $n = 184$ ), 69% of *Gordonia lasianthus* ( $n = 127$ ), and 61% of *Pinus elliotii* ( $n = 75$ ) were found on elevated microsites.

Interestingly, *Taxodium distichum* var. *nutans* showed a strong, positive relationship between DBH class and likelihood of elevated microsite association (Figure 3-3,  $R^2 = 0.7296$ ), and that for *Nyssa sylvatica* var. *biflora* produced an  $R^2$  value of 0.7934. A strong relationship was not seen for *Magnolia virginiana* ( $R^2 = 0.3911$ ), *Ilex* spp. ( $R^2 = 0.0143$ ), or *Gordonia lasianthus* ( $R^2 = 0.1457$ ).

## Discussion

Species richness and stem densities of vegetation were generally much greater on elevated microsites than on the swamp bottom regardless of recent logging history. For most plant growth forms, the relationship between topographic position and the richness and density of vegetation was similar in logged and reference sites, indicating the importance of topographic position to plant communities in swamps in varying successional stages.

Trees were preferentially associated with elevated microsites rather than swamp bottoms, likely because these elevated sites act as safe sites for capture of seed rain, germination, and establishment. For some species, particularly those that have limited flood tolerance (i.e. *Magnolia virginiana* (Burns and Honkala, 1990)), it is likely that elevated microsites are most suitable for their germination and/or establishment and thus influence adult distributions, as was seen in a study of an *Itea virginica* population which was almost entirely confined to elevated microsites due to limitations in early life stages (Anderson et al., 2009). In a North Florida swamp study, seed rain was found to be lower on the swamp bottom than on elevated microsites (Titus, 1991). Elevated microsites may serve as important flooding refugia for some species that might not otherwise thrive in swamp ecosystems, and are likely important regeneration sites after logging disturbance.

The positive relationship between tree size and proportion of trees found with elevated microsites in both *Nyssa sylvatica* and *Taxodium spp.* may indicate that 1) those individuals that start on elevated microsites have greater survival and/or growth over time than those that start on the swamp bottom and/or 2) as individuals grow, they create new elevated microsites. There is some evidence that being located on an

elevated topographic position can enhance productivity in swamps (i.e. Jones et al., 2000), which supports the first hypothesis. However, because these two tree species are among the most flood tolerant in the Southeast United States, it seems unlikely that they would have difficulty thriving under swamp bottom conditions over time to the point that all aged individuals would be those that began on elevated microsites. Both of these species produce aerial roots (knees in cypress trees) as they age if growing in flooded conditions, which could contribute to the accumulation of organic material around their bases. Additionally, *Nyssa* trees produce a taproot and a swollen base up to the mean high water level and an accompanying proliferation of exposed roots immediately around their bases (Burns and Honkala, 1990). The facilitation of elevated microsite formation by *Nyssa* and *Taxodium spp.* may be important to the structure and composition of swamp plant communities. Thus, after clearcutting, the recovery of these species may be important to the recovery of other plant species.

### **Concluding Remarks**

The relationships between understory vegetation, tree communities and topographic positions in Southeastern swamps vary by species and undoubtedly are complex. What is clear is that there is an intimate relationship between elevated microtopographic features and many plant groups, especially woody species in both clearcut and reference swamps. The biogenic nature of elevated topographic features means that their formation is governed by the production and decomposition of organic materials and by the growth characteristics of swamp species. Some plant species contribute to the formation of elevated microsites via specialized roots while others indirectly contribute via leaf litter inputs, and simultaneously, some species are simply utilizing existing features for their own benefit. More research is needed to better

understand the role of various plant species in the formation (or deterioration) and utilization of elevated microsites. This information will be particularly useful for predicting the recovery of swamp ecosystems following disturbances.

Table 3-1. List of study sites.

Site #	treatment	Yrs since logging	Landscape position	Surrounding land use	County	Location
1R	Reference	NA	depression	residential/agriculture	Alachua	29°37'43.60"N, 82°17'54.14"W
2R	Reference	NA	strand	national forest/wetlands	Baker	30°15'27.30"N, 82°24'30.40"W
3R	Reference	NA	depression	pine plantation/wetlands	Alachua	29°46'2.13"N, 82°13'7.35"W
4R	Reference	NA	backwater floodplain	pine plantation/river floodplain	Bradford	29°50'8.89"N, 82° 9'30.92"W
5R	Reference	NA	depression	pine plantation/wetlands	Alachua	29°47'7.95"N, 82°16'8.54"W
6R	Reference	NA	lacustrine backwater floodplain	conservation/pine plantation pine plantations/river floodplain	Alachua	29°41'0.51"N, 82°14'5.04"W
1L	Logged	5			Bradford	29°50'26.23"N, 82° 9'13.21"W
2L	Logged	0.5	depression	pine plantations/wetlands	Alachua	29°46'50.77"N, 82°16'0.92"W
3L	Logged	7	depression	pine plantations/wetlands	Gilchrist	29°47'26.29"N, 82°48'33.91"W
4L	Logged	13	depression	pine plantations/wetlands	Gilchrist	29°48'12.55"N, 82°47'14.76"W

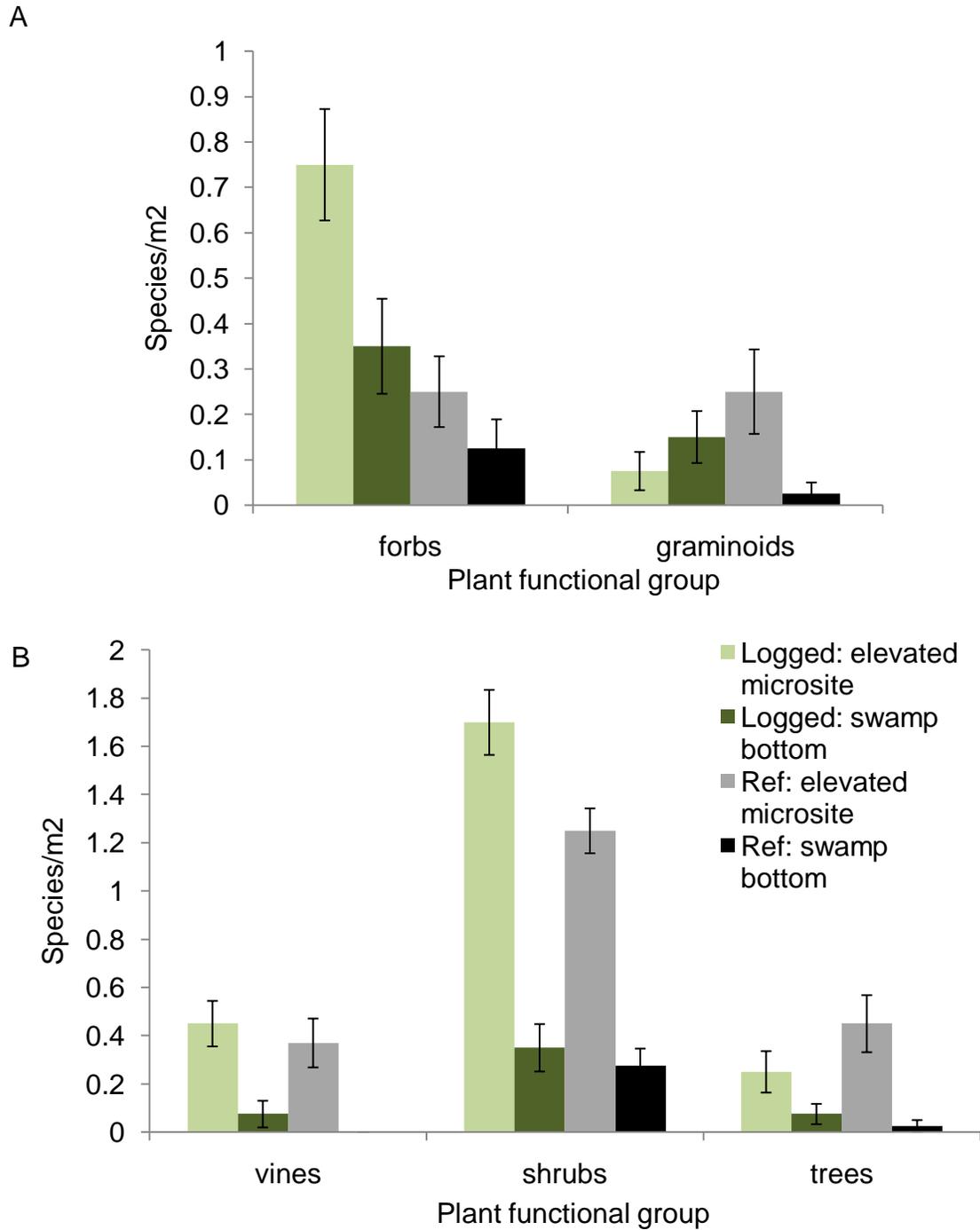


Figure 3-1. Average vegetation richness of A) forbs and graminoids and B) woody vines, shrubs and tree seedlings per m<sup>2</sup> on elevated microsities versus the swamp bottom in logged sites and reference sites.

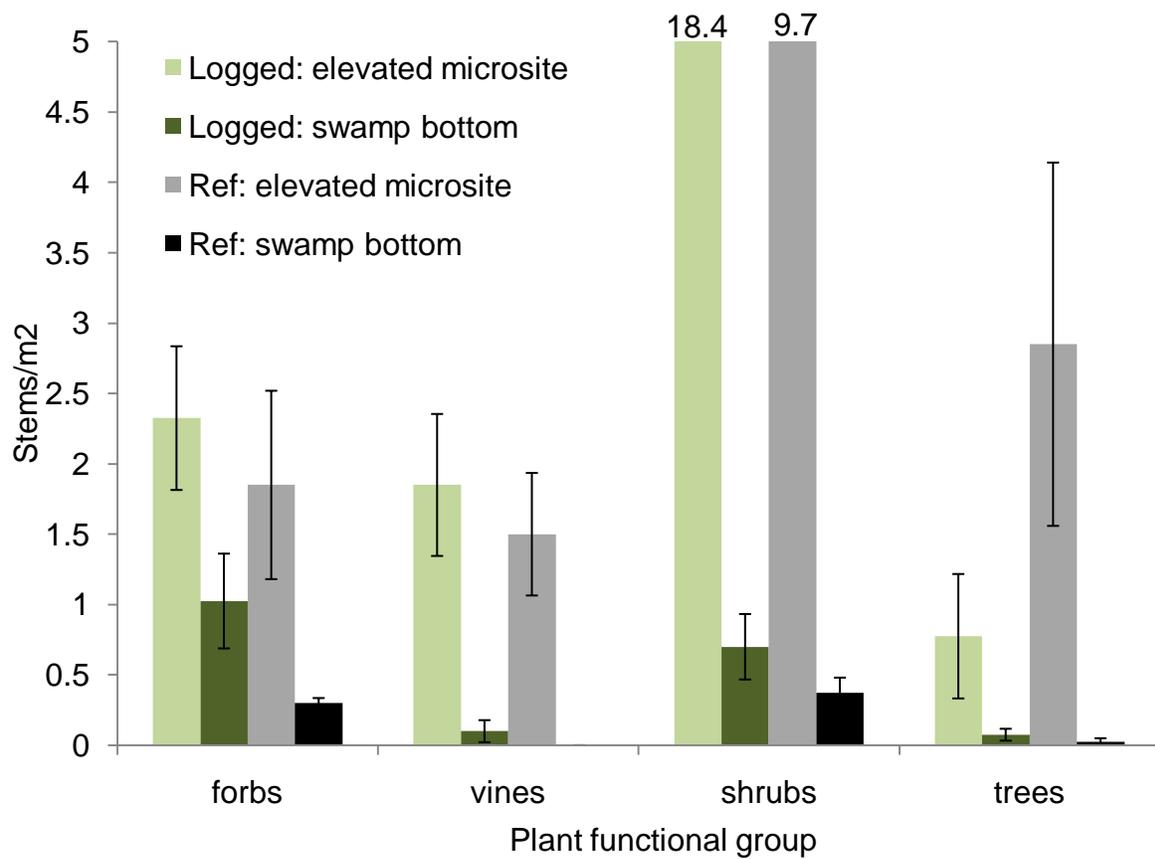


Figure 3-2. Average plant stem density of forbs, woody vines, shrubs and tree seedlings per m<sup>2</sup> on elevated microsities versus the swamp bottom in logged sites and reference sites.

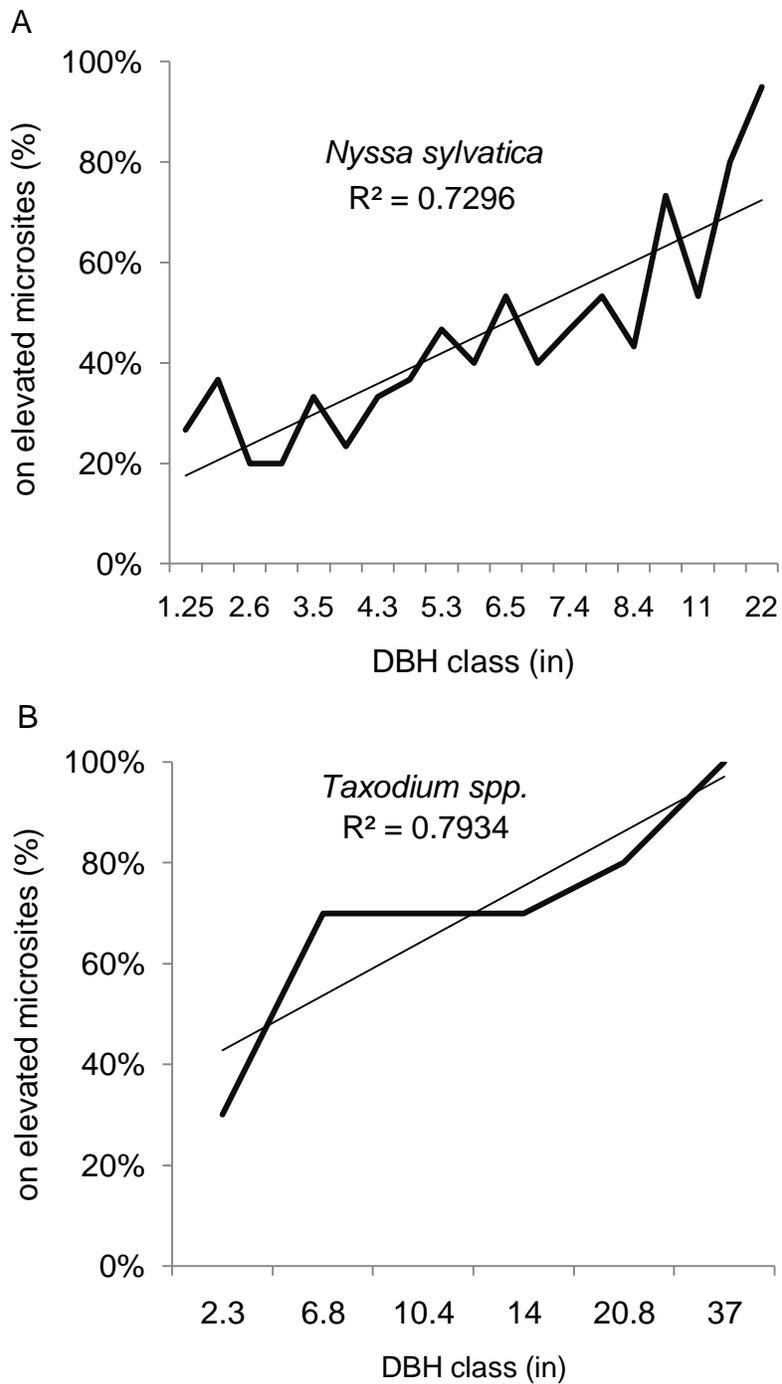


Figure 3-3. The proportion of A) *Nyssa sylvatica* (n=30 per DBH class) and B) *Taxodium spp.*(n=10 per DBH class) individuals growing on elevated microsites as a function of DBH in reference sites.

APPENDIX A  
EXAMPLE R CODE FOR HISTOGRAM CLUSTERING ANALYSIS

```
>Library (mclust)
>Bradfordref2=read.table('Bradfordref2.txt')
>fit=Mclust(Bradfordref2)
>plot(fit,Bradfordref2)
>print(fit)
> Bradfordref2BIC=mclustBIC(Bradfordref2)
> Bradfordref2Summary=summary(Bradfordref2BIC, data=Bradfordref2)
> Bradfordref2Summary
> Bradfordref2Mclust=Mclust(Bradfordref2)
> plot(Bradfordref2Mclust, Bradfordref2, legendArgs = list(x = "bottomleft"))
> Bradfordref2BIC=mclustBIC(Bradfordref2)
> plot(Bradfordref2BIC)
```

APPENDIX B  
SAS CODE FOR ELEVATED MICROSITE SIZES ANALYSIS

```
data size;  
input site size;  
datalines;  
3 0.678535303  
3 0.166549574  
(ETC).  
run;
```

```
proc glm data=size;  
class site;  
model size=site;  
means site /bon;  
lsmeans site/pdiff;  
run;
```

APPENDIX C  
LIST OF SPECIES FOR UNDERSTORY VEGETATION SURVEYS

Species	Reference Sites			Harvested Sites		
	R3	R4	R6	L2	L3	L4
<i>Acer rubrum</i>		x	x	x		
<i>Andropogon glomeratus</i>						x
<i>Carex spp.</i>			x			x
<i>Cephalanthus occidentalis</i>	x		x			
<i>Crinum americanum</i>			x			
<i>Cyrilla racemiflora</i>					x	x
<i>Dulichium arundinoceum</i>				x		
<i>Eupatorium capillifolium</i>				x		
<i>Gordonia lasianthus</i>	x			x		
<i>Hydrocotyle bonariensis</i>			x			
<i>Ilex cassine</i>	x	x		x	x	x
<i>Ilex myrtifolia</i>				x		
<i>Itea virginiana</i>	x		x	x	x	x
<i>Lachnanthes caroliniana</i>				x		
<i>Leucothoe racemosa</i>						x
<i>Liquidambar styraciflua</i>			x			
<i>Lyonia ligustrina</i>				x		
<i>Lyonia lucida</i>	x	x	x	x	x	x
<i>Magnolia virginiana</i>	x	x		x		
<i>Morella cerifera</i>		x		x	x	
<i>Osmunda regalis</i>			x			
<i>Persea borbonia</i>	x	x				
Poaceae			x			
<i>Quercus nigra</i>			x			
<i>Rubus spp.</i>			x		x	
<i>Saururus cernuus</i>			x	x		
<i>Smilax spp.</i>	x	x		x	x	x
<i>Taxodium ascendens</i>				x		
<i>Toxicodendron radicans</i>			x	x	x	
<i>Vitis rotundifolia</i>		x				
<i>Woodwardia areolata</i>				x		
<i>Woodwardia virginica</i>	x	x		x	x	x

APPENDIX D  
SAS CODE FOR UNDERSTORY VEGETATION ANALYSIS

```
Data veg1;
input site replication treatment $ loggedcond $ totalspecies;
datalines;
1      1      H      R      1
1      2      H      R      2
1      3      H      R      2
(ETC).
run;

ods rtf;
ods graphics on;

proc glimmix data=veg1 plots=all;
class site treatment replication loggedcond;
model totalspecies= treatment loggedcond treatment*loggedcond;
random site(loggedcond) replication(treatment*loggedcond);
Lsmeans treatment loggedcond treatment*loggedcond / pdiff;
Lsmeans treatment*loggedcond / plots=mean(CL join sliceby=treatment);
run;
ods rtf close;
```

(this procedure was repeated for each plant grouping of interest)

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## BIOGRAPHICAL SKETCH

Amy Washuta was raised in Stuart, Florida amongst well-watered lawns and planted palms. She became interested in natural science after she enrolled in an introductory geology class while studying fine arts at the University of Florida. She went on to graduate with her bachelor's degree in geology from the University of Florida in 2007.

After working with an environmental education program in Big Cypress National Preserve for a semester in 2008, she began graduate studies in Landscape Architecture at the University of Florida. A year later she shifted her graduate focus to Interdisciplinary Ecology in order to study her beloved cypress swamps more closely, working toward a Master of Science degree.