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Herpetofauna Occupancy and Community Composition Along a Tidal Swamp Salinity Gradient

Sidney Thomas Godfrey
Clemson University, sidgodfrey7@gmail.com

HERPETOFAUNA OCCUPANCY AND COMMUNITY COMPOSITION ALONG A TIDAL SWAMP SALINITY GRADIENT

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Sidney Thomas Godfrey
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Accepted by:
Dr. Robert Baldwin, Committee Chair
Dr. Jamie Duberstein
Dr. William Conner
Dr. Hardin Waddle
Dr. William Bridges

ABSTRACT

Tidal swamps provide habitats for a variety of reptiles and amphibians (herpetofauna), but their community compositions in most tidal swamps are currently unknown. These swamps currently face a number of threats, such as saltwater intrusion, yet the impacts to herpetofaunal communities have not been assessed. Saltwater intrusions into the upper reaches of coastal rivers contribute to their salinity gradients, which can influence associated plant and animal communities. Our study assessed the reptile and amphibian diversity along a salinity gradient in the upper estuary of the Savannah River to further predictive capabilities regarding herpetofauna. Goals included: species inventorying; determining communities; examining microhabitat associations; and modeling reptile and amphibian occupancy to predict the impacts of salinity.

We conducted surveys in tidal swamps of the Savannah National Wildlife Refuge from March to June during 2016 and 2017 using a variety of methods. Our surveys detected 20 species: 8 amphibians and 12 reptiles. Community analyses failed to detect any patterns due to data sparsity. Species richness/diversity generally declined along the salinity gradient, but the drivers of the observed patterns were unclear and may be related to landscape-level mosaics of tidal wetland habits. Microhabitat associations were detected for two amphibian species via the occupancy analyses. Occupancy and regression analyses indicated that a number of species' occurrences were significantly influenced by soil salinity. Amphibian detections were uniquely related to water depth, pH values, and weather conditions. These results expand our understanding of amphibian and reptile species within an understudied, and threatened, wetland type.

DEDICATION

This manuscript is dedicated to my family, friends, and colleagues. Your love, support, encouragement, and insights have been invaluable to my development as both a person and a scientist. It has been a privilege to know each and every one of you. I would like to dedicate this work to the memory of David Wagner and Kyle Thomas. You may be gone, but you will never be forgotten.

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TABLE OF CONTENTS

Page

TITLE PAGE i

ABSTRACT ii

DEDICATION iii

ACKNOWLEDGEMENTS iv

LIST OF TABLES vii

LIST OF FIGURES viii

CHAPTER

I. INTRODUCTION 1

Tidal Swamps 2
Factors Influencing Tidal Swamps 4
Herpetofauna in Tidal Swamps 15
Factors Influencing Herpetofauna 18
Justification and Objectives 27

II. METHODS AND RESULTS 29

Study Site 29
Field Methods 31
Data Analyses 38
Results 41

III. DISCUSSION 73

Herpetofauna Occupancy 73
Study Design Limitations 80
Future Impacts to Tidal Swamp Herpetofauna 84
Future Research Topics 86
Conclusion 88

Table of Contents (Continued)

Page

APPENDICES 90

A: Species Inventory and Detection Data 91
B: Environmental Data 98
C: Morphometric Data 111
D: Bycatch Data 115

LITERATURE CITED 117

LIST OF TABLES

Table		Page
2.1	Study sites and sample plots	32
2.2	Environmental variables and measurement units	36
2.3	Top three selected occupancy analysis models	43
2.4	Estimated occupancy and detection probabilities	44
2.5	Top site covariate effect sizes	45
2.6	Top observation covariate effect sizes	46
2.7	Estimates of the proportion of sites occupied	47
2.8	Species detections and method efficiencies	50
2.9	Combined regression analysis results	56
2.10	Regression results (no groupings)	57
2.11	Regression results (year, site)	63
2.12	Regression results (year, site, month)	66
2.13	Regression results (year, site, plot)	69

LIST OF FIGURES

Figure Page

1.1 Plant community transition of tidal swamps along a soil salinity gradient 2

2.1 Map of the Savannah River and Savannah National Wildlife Refuge 33

2.2 Map of study sites and sample plots 34

2.3 Herpetofauna richness and diversity 53

2.4 Regression (no groupings) 58

2.5 Regression graphs (no groupings) 59

2.6 Regression graphs (no groupings) 60

2.7 Regression graphs (no groupings) 61

2.8 Regression graphs (no groupings) 62

2.9 Regression graphs (year, site) 64

2.10 Regression graphs (year, site) 65

2.11 Regression graphs (year, site, month) 66

2.12 Regression graphs (year, site, month) 67

2.13 Regression graphs (year, site, month) 68

2.14 Regression graphs (year, site, plot) 70

2.15 Regression graphs (year, site, plot) 71

2.16 Regression graphs (year, site, plot) 72

CHAPTER ONE

INTRODUCTION

Coastal wetlands generally include marshes, swamps, mangroves, and other coastal plant communities, though no precise or widely agreed upon definition for coastal wetlands exists (Blankespoor et al. 2012). There have been serious declines in coastal wetlands (Nicholls 2004; Hoozemans et al. 1993). The causes of coastal wetland loss are diverse, complex, often interrelated, and site-specific (Blankespoor et al. 2012). One growing threat to coastal wetlands is salinization, which is tied to a variety of causes (Herbert et al. 2015). Salinization causes changes in the physical and chemical characteristics of the environment, which can result in shifts in wetland vegetation types (Herbert et al. 2015). Salinization impacts coastal freshwater wetlands by causing a transition of freshwater swamp or marsh into oligohaline or brackish marsh habitat, with a subsequent decrease in species diversity and changes in ecosystem function (Figure 1.1; Herbert et al. 2015). These impacts have been documented in a number of coastal wetlands both in the United States and abroad (Herbert et al. 2015). However, the impacts to the fauna of these wetlands are poorly documented, and, in some cases, the faunal communities are unknown.

Figure 1.1: Tidal swamps along a gradient of increasing soil salinity (clockwise from top left: ~0.1 parts per thousand soil salinity to ~0.9 parts per thousand soil salinity) in the Savannah National Wildlife Refuge, South Carolina, USA.

Tidal Swamps

Tidal freshwater forested wetlands (herein referred to as ‘tidal swamps’) are one of the wetland vegetation communities that constitute coastal wetlands. Tidal swamps occupy over 200,000 hectares of the United States’ coastal areas and range from Maryland to Texas (Field et al. 1991, Doyle et al. 2007). They typically occur in freshwater conditions (< 0.5 parts per thousand (ppt) salinity) from the upstream edge of tidal influence to the downstream boundary with oligohaline marsh (0.5 to 4 ppt salinity; Odum et al. 1984). Trees in tidal swamps die if exposed to chronic salinity levels of 2 ppt or greater (Hackney et al. 2007). The dominant plant species usually include swamp

tupelo (*Nyssa biflora*; Walter), baldcypress (*Taxodium distichum*; Rich) and water tupelo (*Nyssa aquatic*; Linnaeus), with a variety of shrub and herbaceous understory depending on salinity levels and canopy cover (Odum et al. 1984, Duberstein et al. 2014).

Tidal swamps of the southeastern United States are located in shallow floodplains that maintain saturated soils due to tidal fluctuations (Duberstein and Kitchens 2007). These floodplains contain raised areas called hummocks that vary from 1 to 10 m^2 in size and may possess several trees and some shrubs (Duberstein and Conner 2009). The base elevation of the floodplain, known as the hollows, are usually bare mud with herbaceous marsh vegetation (Day et al. 2007). Hummocks are limited on their upstream extent by areas that are tidally inundated (Rheinhardt 2007) and on their downstream extent by areas that maintain freshwater conditions (Noe et al. 2013).

When compared to non-tidal swamps, tidal swamps have smaller tree diameters but greater tree densities (Anderson et al. 2013). They also have more litter fall and more small coarse woody debris (< 7.62 centimeters), but less large coarse woody debris (> 7.62 centimeters; Anderson et al. 2013). Shrub cover is also higher in tidal swamps (Anderson et al. 2013). Tidal swamps soils are also more productive, yet more inundated than non-tidal swamps due to tidal subsidies (Findlay et al. 2009, Anderson and Lockaby 2011). This concept is supported by the lack of seasonality in nutrients, which suggests that they are subsidized by the tides (Findlay et al. 2009). There are no differences in tree growth or survival between swamp types (Krauss et al. 2009a), and there are no differences in nutrient cycling rates or plant nutrient concentrations (Verhoeven et al. 2001).

Despite what is currently known about tidal swamps, they remain relatively understudied because of their location in coastal river transitional zones (Odum et al. 1984, Odum 1988); access to interior portions of these swamps is difficult. Collaborative research on tidal swamps began in 2004 to improve our understanding of these ecosystems and factors influencing their distribution (Krauss et al. 2009c). Early research focused on measuring carbon cycling, ecosystem productivity, and hydrological and biogeochemical characteristics along transects in Louisiana, Georgia, and South Carolina (Krauss et al 2009c). Recent studies include sites in Virginia, Maryland, and Florida (Krauss et al. 2009c), yielding insights about microtopographic features (hummocks) and the impacts of climate change (Krauss et al. 2009c; Duberstein and Conner 2009, Duberstein et al. 2013). Wildlife studies to date are relatively sparse and have focused on river alteration impacts on invertebrate, fish, mammal, or bird populations (Hall et al. 1991, Winn and Knott 1992, Van Den Avyle and Maynard 1994, Winger et al. 2000).

Factors Influencing Tidal Swamps

Tidal swamps, similar to non-tidal swamps, are primarily influenced by changes in hydrology and cyclical disturbances such as hurricanes. Tidal swamps are also strongly influenced by tidal fluctuations, sediment and nutrient deposition, salinity, and microtopographic features. Droughts and human alterations (i.e., dams, flow alteration, and water diversions) to coastal rivers directly influence tidal swamps through changes to sediment transport and freshwater flows. Climate change and sea level rise (SLR) are expected to negatively impact tidal swamps in the future, leading to the inland migration

and/or destruction of these wetlands. Tidal swamps of the southeastern U.S. have experienced a number of man-made alterations and conversions over the past several centuries, which include: rice agriculture, the creation of canals for drainage and navigation, and swamp logging (Doyle et al. 2007, Lockaby 2009). More recent alterations include massive water control structures, such as tide gates, and increasingly deeper shipping channels. These factors, both natural and anthropogenic, influence tidal swamps and simultaneously influence each other.

Hurricanes

Historically, South Carolina experienced an average of one hurricane every 7 years (Dukes 1984). However, South Carolina has experienced three hurricanes during the past three years, and a similar rate could continue with climate change (Webster et al. 2005). Hurricanes can be largely positive disturbances for tidal swamps which move sediments and nutrients, increase rainfall, and create habitat heterogeneity, though there may be some short-term negative impacts (Conner et al. 1989, Wilson et al. 2006, Cahoon 2006, Morton and Barras 2011). Hurricanes can alter plant communities by elevating soil salinities, especially in low-slope or flat terrain (Conner et al. 2012). This may open the understory to shrub and herbaceous vegetation growth, although some herbaceous plants may be suppressed by saltwater intrusion (Conner et al. 2012). Natural and relatively unaltered wetlands are generally less impacted than modified systems (Conner et al. 2012). A tidal swamp in the Maurepas Swamp area of southeastern Louisiana had almost all of its midstory trees damaged or removed by Hurricanes Katrina and Rita during 2005

in low basal area, degraded stands. However, the effects were negligible once basal areas were at or above 30 $meter^2$/hectare (Shaffer et al. 2009). Tidal fluctuations likely influence the scale of hurricane impacts by mediating the duration and extent of storm surges as well as the redistribution of shifted nutrients and organic material.

Tidal Fluctuations

Tidal swamps exhibit hydrological transitions from streamside areas to back swamps via reductions in the magnitude and frequency of tidal flooding, which increases biological diversity (Anderson and Lockaby 2012). Water levels in tidal swamps can maintain a constant range for most of the year, except during high river flows (Anderson and Lockaby 2012). High flows dampen tidal influences (Anderson and Lockaby 2012), which could change community structure if maintained over longer time periods. Tidal connectivity and levels of soil organic matter influence tidal swamp forest communities (Pasternack 2009). Plant communities may also be influenced via tidal forcing of ground water, which can follow tidal patterns (Rheinhardt and Hershner 1992, Duberstein and Kitchens 2007). However, Rheinhardt and Hershner (1992) found that mean groundwater depth, not surface flooding, was the main driver of tree species composition in a tidal swamp in Virginia. Tidal fluctuations are also an important driver of water depths and salinity (Schile et al. 2011), which can have ramifications for sediment and nutrient deposition.

Sediment and Nutrient Deposition

Sediment and nutrient deposition rates in tidal wetlands can double along the transition from tidal swamps to oligohaline marsh (Ensign et al. 2014, Noe et al. 2016). Current sediment deposition rates in some tidal wetlands are 3 to 9 times higher than deposition rates for the past 150 years (Noe et al. 2016). Salinization increases nutrient mineralization fluxes, which can affect soil accretion and wetland elevation (Noe et al. 2013, Stagg et al. 2017). Maximum fluxes in tidal swamps occur between 1.2 and 2.0 ppt salinity, which is at the threshold of conversion to marsh (Liu et al. 2017b).

Salinity

Seasonal low flow periods in late summer and fall typically coincide with increases in salinity in tidal swamps (Krauss et al. 2009b, Anderson and Lockaby 2012). Soil salinity is known to influence marsh plant community composition (Hackney and Avery 2015) and tree community composition (Allen et al. 1996). Typically there is a conversion of tidal swamp to oligohaline marsh as salinity increases to chronic soil salinities of about 1.75 ppt (Day et al. 2007, Hackney and Avery 2015). Increased soil salinity changes forest growth, productivity, and stand height, which reduces canopy cover and promotes understory growth (Krauss et al. 2009b, Liu et al. 2017a). Tidal swamps with salinity concentrations of 1.3 ppt or greater typically support a basal area of less than 40 m^2/ha, whereas swamps with salinity less than 0.7 ppt have basal areas as high as 87 m^2/ha (Krauss et al. 2009b). Wetland transition is caused by both salinity

stress and the conversion of soil bacteria to sulfate reducing species, which increases hydrogen sulfide (Hackney and Avery 2015). Freshwater species are not adapted to this change in soil biogeochemistry (Hackney and Avery 2015). Plant community changes caused by salinity fluctuations may also affect the amount and distribution of some types of microtopography, for example hummocks (which may be built upon ‘nurse log’ trees).

Microtopography

Microtopography in tidal swamps is influenced by tidal ranges, with more soil erosion and scouring occurring with larger tidal ranges (Pasternack 2009). These differences in microtopography are affected differently respective to the groundwater table and the height of surface flooding, which can, in turn, affect plant growth and survival (Pasternack 2009). Hummocks are a microtopographic feature that have been found to influence tidal swamp plant communities (Duberstein and Conner 2009). Hummocks were hypothesized to provide a physiological advantage to tree growth, but an investigation by Duberstein and Conner (2013) did not find any evidence of this with respect to baldcypress trees. Hummocks exhibit greater nitrification fluxes than hollows, suggesting an effect of microtopography (Noe et al. 2013). Events that cause changes in salinity, such as droughts and saltwater intrusion, are likely to impact microtopography by altering vegetation structure (and hence the terrain where plants are present) and reducing the influence of tidal hydrology (e.g., scouring). Hummocks likely provide favorable terrestrial habitats for the fauna that inhabit tidal swamps, but this is undocumented. Our study was initiated, in part, to investigate this hypothesis.

Drought and Saltwater Intrusion

Droughts reduce freshwater flows and contribute to saltwater intrusion in the coastal portions of rivers (Doyle et al. 2007). Drought and saltwater intrusion additively reduce dissolved carbon transfer, which has ramifications for wetland accretion (Ardon et al. 2016). Wetland soils in Australia acidified during droughts, when pyrite converted to sulfuric acid in dry soils (Mosley et al. 2014). When water returned, pH values dropped and metals were leached from soil (Mosley et al. 2014). Nitrogen differences in tidal swamps may be indirectly affected by saltwater intrusion (Cormier et al. 2013). Saltwater intrusion reduced litterfall and nitrogen loading in tidal swamps of the Savannah and Waccamaw Rivers (Cormier et al. 2013). Trees in all study areas were fairly inefficient at resorbing nitrogen, possibly exacerbating a nitrogen limitation on growth (Cormier et al. 2013).

Several droughts occurred on the Savannah River during the last two decades (USACE 2012b). Field measurements at the Interstate 95 Savannah River crossing recorded salinity intrusion (i.e., floodwater above historical salinity levels) during about 42 percent of a 10 year drought period, and the number of low flow occurrences doubled (USACE 2012a). The lunar cycle also affects saltwater intrusion, with larger intrusions occurring during new moon phases (USACE 2012a). A drought management plan was created to ameliorate the negative impacts of drought on the Savannah River estuary (USACE 2012b). The plan consists of four drought levels, with each higher level resulting in less water released through the four dams (USACE 2012b). The most recent

plan proposed higher water levels be maintained in reservoirs upstream (McCord 2017). However, this plan would reduce freshwater flows in lower portion of the river and increase the risk of saltwater intrusion in the Savannah River estuary if lower flows were implemented during times when salinity intrusion is more likely, such as during the new moon lunar phase. Anthropogenic water uses may further exacerbate this risk as river water is managed to include natural and human use, particularly during drought.

Dams

The Corps of Engineers manages the Hartwell, Richard B. Russell, and J. Strom Thurmond reservoirs, plus the New Savannah Bluff Lock and Dam, as a system of multipurpose dam projects on the Savannah River (USACE 2012a). Managed dam releases for these projects require many considerations (engineering, social, economic, environmental), and results may be mixed if goals of releases are not compatible with current uses (McCartney and Acreman 2001). Water released from the dams are different temperatures than downstream waters, and they are usually hypoxic and nutrient rich since they are extracted from the reservoir bottoms (Zakova et al. 1993, Smock et al. 2005). Managed dam releases on the Savannah River were made in 2005 and 2006 in an attempt to improve downstream floodplains, and the releases elicited some positive biotic responses (Richter et al. 2006, USACE 2012a). The Corps of Engineers also considered a water release plan from the J. Strom Thurmond Dam to mitigate the effects of proposed dredging (USACE 2012a). However, analyses indicated that large releases would be

required, and the plan was dropped due to the impacts it would have on upstream water users (USACE 2012a).

Dams fragment rivers and alter the flow of sediments, nutrients, energy, and biota (Ligon et al. 1995). One assessment considered the Savannah River as “strongly” fragmented by dams, suggesting that only 25 to 49 percent of the river is not impacted (Dynesius and Nilsson 1994). This un-impacted stretch of the river is primarily in the lower river and the estuary (Smock et al. 2005). The effects of dams can be felt hundreds of kilometers downstream. Worldwide, dams have been deemed as causal to disruption of river continuums and flood pulses by changing the timing and magnitude of flood events (Ward and Stanford 1995, Junk et al. 1989, Acreman et al. 2000, McCartney et al. 2001). Flood events on rivers with dams may occur on variable, unpredictable schedules; however, a more common issue is that they make systems more stable and reduce “flashy” changes in water levels (Bunn and Arthington 2002, Meile et al. 2011). Dams may also increase the risk of saltwater intrusion in tidal swamps by reducing freshwater flows and impeding sediment accretion (Acreman et al. 2000, McCartney et al. 2001, Hupp et al. 2009). Other forms of anthropogenic flow alterations, such as channelization and water control structures, compound these issues.

Flow Alterations

Channelization has shortened the lower Savannah River by 13 percent (Schmitt and Hornsby 1985), which may make the estuary more vulnerable to saltwater intrusion and storm surges. Flow regulation and channelization together have reduced the

frequency and magnitude of downstream flooding, allowing development in the floodplain (Smock et al. 2005). In addition, there has been a decrease in the size and inundation period of the floodplain (Smock et al. 2005). Despite this, past flow alterations have not seemed to significantly alter floodplain forest structure on the Savannah River when compared to the Altamaha River, which is unaltered (Lee 2008).

There are many irrigation canals, dikes, and levees present in the tidal wetlands of the Savannah River, which are a legacy of rice agriculture (Doar 1936, Doyle et al. 2007). Rice agriculture peaked from the 1840s to the 1850s during the antebellum era of the 19th century and quickly declined after the Civil War (Doar 1936). Canals can reduce groundwater tables, increase soil salinity, and prevent sediment transport, all of which influence wetland plant communities (Franklin et al. 2009, Xie et al. 2011, Wilson et al. 2015, Liu et al. 2017c). However, these effects may be offset by the frequent periodicity of tidal flooding, which has not been assessed. Levees can increase flood and drawdown speeds in tidal areas, and they minimize flooding outside of the levees (Lockaby 2009). Levees far enough from river channels do not greatly impact the presence of floodplain forest species, but levees too close to river channels may have large impacts (Gergel et al. 2002).

Dredging has been proposed as part of a Savannah Harbor expansion project (USACE 2012a). Impacts from high sedimentation rates associated with active dredging may be mitigated in tidal wetlands because tidal currents quickly move sediments out of an area, as was seen in a dredging project on the Edisto River in South Carolina (Van Dolah et al. 1984, 1992). Dredging in tidal creeks in Virginia did not lead to noticeable

differences in fish species abundances, and only subtle differences in species biomass (Bilkovic 2011). However, one study evaluating the impacts of dredge spoils from previous Savannah River dredging projects found that heavy metals were leached from the spoil material (Winger et al. 2000). The study found that these heavy metals had the potential to be bio-accumulated in vertebrates, specifically birds and mammals (Winger et al. 2000). Dredging for shipping lanes increased tidal amplitude by 1 meter in the Delaware River (DiLorenzo et al. 1993). In the long-term, dredging may reduce the level of flood tides, increase tidal ranges, and cause changes in freshwater flows (Zhu et al. 2014, Yuan and Zhu 2015). These problems may be amplified if there are ongoing or future anthropogenic water diversions in rivers where flow alterations are present.

Water Diversions

The city of Savannah, Georgia, as well as several industrial water users, divert up to 55 million gallons/day of water from an intake from Abercorn Creek, located at or near the current limit of tidal influence on the Savannah River (USACE 2012a). This creek is just upriver from our most upstream study site above the Interstate 95 river crossing. Weyerhaeuser also operates another intake on-site near the Highway 170 river crossing that draws 12-15 million gallons/day of estuary water into their wood pulp and paper plant (USACE 2012a). The City of Savannah is under directive from the State of Georgia to decrease groundwater usage, which may increase demand for surface water from the Abercorn Creek intake (USACE 2012a). Water diversions for urban areas put more strain on rivers and their aquatic resources and can lead to conflicts over water levels, uses, and

distribution (Fitzhugh and Richter 2004). Simulated water diversion scenarios for a Louisiana estuary indicated that diversions back into coastal wetlands (or lack thereof) could change salinity by about 10 ppt (Das et al. 2012). When wetland freshwater flows dropped to less than 10 to 15 percent of the average river discharge in coastal Louisiana, saltwater intrusion and wetland retreat occurred (Das et al. 2012). The impacts of water diversions will likely be greater in the future, since long-term stressors such as climate change and sea level rise may put more pressure on freshwater inputs for coastal and estuarine wetlands.

Climate Change and Sea Level Rise

Climate change will increase temperatures, alter rainfall patterns, increase storm frequency and intensity, and cause sea level rise (SLR; Osland et al. 2014, Gabler et al. 2017). These impacts will, in turn, cause changes in freshwater inputs and increase rates of saltwater intrusion in coastal rivers (Titus 1989, Nicholls and Cazenave 2010, Osland et al. 2014, Gabler et al. 2017). Rates of SLR in the 21st century are projected to be higher than rates of the 20th century, and thermal expansion of seawater will continue for several decades, even in the best-case climate change scenarios (Michener et al. 1997). Coastal wetland vegetation will likely shift in response to changing precipitation and temperature patterns (Osland et al. 2014, Gabler et al. 2017). Coastal wetlands are expected to retreat and migrate inland in response to increased tidal inundation and saltwater intrusion from SLR (Titus 1989, Nicholls and Cazenave 2010). This is expected to cause large changes in plant and animal communities, with possibly catastrophic results for biodiversity and

community structure (Galbraith et al. 2002, Day et al. 2007). For example, natural and artificial barriers may prevent tidal wetlands from being able to shift inland, a situation referred to as 'coastal squeeze' (*c.f.* Torio and Chmura 2013).

There are uncertainties in predicting climate change impacts to coastal and estuarine ecosystems due to interacting environmental, biological, and anthropogenic feedbacks (Titus 1989, Baustian et al. 2012, Kirwan and Megonigal 2013, Torio and Chmura 2013). Documented and simulated effects of climate change on coastal wetlands reveal large-scale impacts. Over the span of 120 years, 82 km^2 of tidal swamps converted to marsh and 66 km^2 of tidal swamps converted to forest-marsh transitional habitat in the Big Bend region of Florida (Raabe and Stumpf 2016). SLR simulations for the Gulf of Mexico indicate that there will be larger losses of tidal swamps in the western Gulf than the eastern Gulf (Doyle et al. 2010). Effects of SLR, storms, and drought were compounded on a hardwood hydric hammock community in west-central Florida, resulting in vegetation shifts and eventual hammock loss (Williams et al. 2003). Current rates of SLR seem to be overtaking tidal wetlands in areas such as the Chesapeake Bay (Kirwan and Megonigal 2013, Beckett et al. 2016). By some estimates, a one meter rise in sea level could drown between 25 and 80 percent of U.S. coastal wetlands (Titus 1989).

Herpetofauna in Tidal Swamps

Published accounts of wildlife studies for tidal swamps are lacking in general. As such, there are relatively few studies involving herpetofauna in estuaries or estuarine

floodplains (Dunson and Seidel 1986, Rubbo and Kiviat 1999, Kinneary 1993). Swarth and Kiviat (2009) gave two reasons for this lack of research: tidal wetlands occur in a relatively small extent of coastal rivers, and the soft sediments in tidal wetlands make field work difficult. No research or studies have specifically assessed the ecology of herpetofauna that occur in tidal swamps. In all of the existing reviews, authors have noted that there are no herpetofauna known to exclusively occur in tidal swamps.

Odum and others' (1984) foundational review of tidal freshwater wetlands listed 102 possible species of herpetofauna. They based their list on known geographic distributions and the fact that herpetofauna occurring in non-tidal wetlands can also occur in tidal wetlands. The *Nerodia* genus of snakes, and lizards as a whole, were the only herpetofauna Odum et al. (1984) specifically mentioned to use tidal swamps. However, their review was primarily focused on tidal freshwater marsh habitats. Another review by Odum (1988) comparing freshwater and salt marshes further identified species using tidal marshes. It is assumed that these species use both tidal marsh and swamps because of their proximity and connectivity, but this assumption is untested. Odum noted in both reviews that herpetofauna species richness declined from freshwater marsh to salt marsh. Marsh and tidal creek surveys in a New York estuary detected low densities of herpetofauna, with few turtle and snake species and only one frog species (Rubbo and Kiviat 1999). No salamanders were detected below the mean water level, though some species were found on elevated terrain (Rubbo and Kiviat 1999).

Swarth and Kiviat (2009) pointed out the lack of information about the occurrence and ecology of herpetofauna in tidal freshwater wetlands. Several hypotheses were

generated by Swarth and Kiviat (2009) to explain why wildlife may be excluded from tidal freshwater wetlands. Although the ebb and flow of tides can redistribute nutrients and plant material for wildlife and increase ease of access, they can also subject animals to increased predation or anoxic water conditions (Swarth and Kiviat 2009). Aquatic animals can be trapped in small water bodies during low tide, or terrestrial animals can be left exposed during high tides (Swarth and Kiviat 2009). For amphibians, the increased salinity, dynamic flow regime, and high abundances of fish predators are thought to limit populations (Swarth and Kiviat 2009). Terrestrial salamanders (e.g. *Ambystoma*—the 'mole salamander' genus) may not be present due to the consistent tidal submergence of the wetlands (Swarth and Kiviat 2009).

Dodd and Barichivich (2017) conducted herpetofauna surveys within the Savannah National Wildlife Refuge from 2004 to 2006. Their surveys detected a higher number of amphibian species than expected, given the annual fluctuations in water levels and salinity. However, they only sampled within the managed moist soil impoundments, ponds, and non-tidal wetlands of the refuge. Despite this, their species inventory for the impoundments may reflect some of the species that can occur within tidal wetlands. This is because the impoundments are close to the Back River and its associated tidal swamps and marshes, just upstream of the impoundments. The Back River is a distributary of the Savannah River, and it is the water source that is used to flood the impoundments. Therefore, any wildlife using the Back River, or its associated wetlands, could easily immigrate into the impoundments.

Factors Influencing Herpetofauna

Factors currently argued to influence reptile and amphibian populations worldwide are land use change, invasive species, pollution, disease, exploitation, and climate change (Gibbons et al. 2000, Collins and Storfer 2003). Interactions of these factors are suspected to drive most recently observed population levels. It is possible that observed changes in population levels are the result of long-term, natural fluctuations that are becoming better appreciated as long-term data are collected (Gibbons et al. 2000). These factors can take years or decades to manifest in populations, but we were not equipped to assess the influences of every factor in our study system. We will only address some of the global factors, since not all of these factors are within the scope of our study. In addition to the aforementioned global factors, herpetofauna in tidal swamps are further influenced by disturbances such as hurricanes, salinity, and anthropogenic alterations to coastal rivers.

Land Use Change

Historical land use change has had a noticeable impact on the lower Savannah River, yet these impacts either have been or are being mitigated. Currently, about 66 percent of the Savannah River basin is forested, about 25 percent is agricultural or urbanized, and another 9 percent of the area is in other land uses (Smock et al. 2005). Since there is potential for further human development in the Savannah River basin, it is possible that this may become a more prominent influence on herpetofauna in the future via habitat loss. Our study sites in the Savannah National Wildlife Refuge were in close

proximity to two of the largest cities in the surrounding counties, and these cities have both experienced recent population growth (United States Census Bureau 2018). Land use change could exacerbate the previously mentioned threats to herpetofauna in tidal wetlands by reducing habitat connectivity and constraining future tidal wetland migration pathways (Leonard et al. 2017) if SLR or salinization displace their current habitat. Examples of wetland migration barriers include bulkheads, levees, impoundments, dams, and transportation infrastructure (Titus 1989, Nicholls and Cazenave 2010, Leonard et al. 2017). It will be up to the stakeholders within these regions (citizens, government agencies, and non-profit organizations) to decide the best options for mitigating these issues going forward, if they decide to mitigate them at all. Land use changes may bring unforeseen problems for natural ecosystems, one of which is the introduction of invasive species.

Invasive Species

Mosquitofish (*Gambusia affinis*; Baird and Girard 1853) were captured in multiple sample plots during our study. They were often captured in low numbers, but they were widespread throughout our study area. Mosquitofish negatively impact amphibian populations by eating eggs and larvae (Pyke 2008). As their name implies, this fish eats mosquitos and hence has been introduced in many areas as a biocontrol species for mosquito populations (Pyke 2008). This invasive species may be expected to exert an impact on the amphibians in tidal swamps where they co-occur because fish depredation of eggs and larvae reduces recruitment of new individuals into amphibian populations

(Pyke 2008). This, when compounded with adult herpetofauna mortality, stochastic population fluctuations, and other population stressors, can lead to population declines.

Chinese tallow (*Triadica sebifera*; Small) is a tree that can grow and spread rapidly, and it is cultivated as an ornamental in the United States (Radford et al. 1964, Scheld and Cowles 1981). We observed this species at one sample plot in our most downstream study site over the past two years. An experiment by Conner (1994) gave evidence that tallow trees can tolerate higher salinity levels (up to 10 ppt) than native trees, though extended flooding increased tree mortality. Chinese tallow reduces anuran growth and survival in autumn-breeding species because the leaves cause mortality to various anuran larvae via phenolic toxins and increased oxygen demands (Leonard 2008, Cotten et al. 2012).

We observed feral hogs (*Sus scrofa*; Linnaeus 1758) at several of our study sites. Feral hogs disturb soil, which changes decomposition rates and nutrient cycling, and destroys or degrades habitat (Lacki and Lanci 1986, Taylor and Hellgren 1997). We observed hog soil disturbance in multiple swamp and marsh areas; plants at impacted sites were usually quick to recover from disturbance (Godfrey, personal observations). Annual plants typically recolonized the sites instead of the pre-disturbance perennial plants, which may offer an indirect benefit to herpetofauna by creating habitat heterogeneity. Feral hogs are also known to depredate herpetofauna (Jolley et al. 2010). Herpetofauna were present in about 20 percent of stomach samples from feral hogs in Fort Benning, Georgia, and they were estimated to eat 3.16 million herpetofauna per year on the 736 km^2 military installation (Jolley et al. 2010). Feral hog depredation can have a

larger impact during low temperatures, during breeding events, and in situations where species are already under environmental stress (e.g., tidal swamps; Jolley et al. 2010).

Common reed (*Phragmites australis*; Trin. ex Steud) invasions have become widespread, and they been observed in a variety of coastal wetlands (Chambers et al. 1999, Chambers et al. 2003). We observed *Phragmites* at one of our most downstream study sites. *Phragmites* is constrained by salinity, sulfide, and flooding duration in tidal wetlands (Chambers et al. 2003). The invasion risk for this species is higher in low-salinity or hydrologically altered marshes (Chamber et al. 2003). Water quality and sediment retention are not substantially impacted in areas where *Phragmites* has replaced native plants (Chambers et al. 1999). *Phragmites* presence increased the risk of wetland desiccation at sites in Canada, but there were no observed effects on amphibian populations (Mazerolle et al. 2014). *Phragmites* had a positive effect on bullfrog larvae performance due to increased leaf litter production (Rogalski and Skelly 2012).

Although the Cuban Treefrog (*Osteopilus septentrionalis*; Dumeril and Bibron 1841) has not been detected in our study area, it occurs in Georgia and South Carolina (Elliot et al. 2009). This large frog directly impacts native ecosystems by eating native herpetofauna (Glorioso et al. 2012). This species has been demonstrated to cause declines in native tree frog occupancy (Waddle et al. 2010). Cuban Treefrog larvae withstood higher salinity treatments than six U.S. native frog species in a laboratory study (Brown and Walls 2013). The Cuban Treefrogs displayed survival up to 12 ppt salinity, whereas no native species survived past 10 ppt (Brown and Walls 2013). This difference in tolerances may have major implications for invasion potential and faunal community

changes (Brown and Walls 2013). Cuban Treefrog invasions in areas of increased salinity may have a higher probability of success and establishment due to reduced presence and competition from native species. For these reasons, it is possible that tidal freshwater wetlands could serve as favorable introduction sites for Cuban Treefrogs in the future.

Substantial numbers of invasive aquatic species have the potential to be introduced through ports via ballast discharges, ship exteriors, and ballast sediments (Ruiz et al. 2000, Drake and Lodge 2007, Briski et al. 2010). Nematodes are the most common species found in ballast sediments, and copepods are the most common in ballast water (Duggan et al. 2005). The Corps of Engineers has found three invasive clam and crab species introduced from the port of Savannah (USACE 2012a). Invasive species can also enter the port as insect larvae in pallets or in soil containing seeds or plants, which are associated with the number of shipping containers arriving at the port (USACE 2012a). The potential for invasive species introduction through the port of Savannah exists with or without a proposed harbor expansion, so the expansion is not expected to significantly increase risk of plant or insect species introductions (USACE 2012a). Long-term stressors such as climate change and sea level rise may be a more pertinent problem, since they can create unstable environmental conditions that impede specialist and native species while favoring generalist and invasive species

Climate Change and Sea Level Rise

Climate change is predicted to exert negative impacts on both reptiles and amphibians (Gibbons et al. 2000, Collins and Storfer 2003). Climate change will increase

the frequency and occurrence of droughts, which negatively impact aquatic herpetofauna by reducing aquatic habitats (Walls et al. 2013a). Wetlands with shorter hydroperiods are predicted to decline in number and extent with the impacts of climate change (Walls et al. 2013b). Salamander occupancy declined in areas of the southeastern U.S. impacted by drought, and the reduction of wetlands with favorable hydroperiods was suspected as the primary cause (Walls et al. 2013b). Climate change may increase disease risks by lowering animals' defenses to infections (Rohr and Rafflel 2010). Many reptile and amphibian species could lose the microhabitat conditions that they need to survive (Sinervo et al. 2010). Changes in nest success and sex ratios have occurred in reptiles with temperature dependent sex determination (e.g., turtles, crocodilians; Janzen 1994, Jensen et al. 2018). Sex reversals have also been documented in lizards (Whiteley et al. 2017). One study assessing lizard responses to climate change revealed that the lizards adopted a 'live fast, die young' survival strategy, which the authors determined would lead to population extinctions in the next 20 years (Bestion et al. 2015). Sea level rise will create many of the same impacts on herpetofauna as they do on coastal wetlands. The most direct impact from SLR will be the direct loss and conversion of wetland habitats due to salinization and tidal inundation. SLR may also reduce the availability of habitat crucial to survival and reproduction, such as nesting habitat. In addition, climate change has been forecast to increase the frequency of extreme weather events, such as hurricanes, which have the capability to rapidly restructure plant and animal communities.

Hurricanes

Hurricane impacts on wildlife are usually short-term, and animals may respond by relocating or altering behavior (e.g., Switzer et al. 2006, Langtimm et al. 2006). Hurricanes can negatively affect aquatic wildlife in the short-term by creating hypoxic conditions, siltation, and saltwater intrusion (Conner et al. 1989). However, some impacts can lead to long-term, community-level shifts. Three hurricanes in coastal Louisiana reduced herpetofauna species richness but increased species evenness in coastal wetlands (Schriever et al. 2009). Amphibian abundance drastically decreased, but changes in reptile abundance were species-specific (Schriever et al. 2009). The authors of the study hypothesized that increased species evenness could lead to community restructuring by 'resetting the board' on competitive interactions (Schriever et al. 2009). Storm surge inundation of isolated wetlands on the coast of Florida only temporarily reduced the number of amphibian species, though some observed changes in community composition were longer lasting (Gunzburger et al. 2010). Salinity changes associated with storm surges in coastal wetlands are likely to have a significant impact on freshwater and salt-sensitive plant and animal species (e.g., amphibians), though new evidence suggests that some groups may be more resilient to salinity changes than previously thought.

Salinity

Salt-tolerance is more widespread in amphibians than has been previously thought, with a recent review finding evidence of surprisingly high salt-tolerance in 144 species of amphibians worldwide (Hopkins and Brodie 2015). Southern Leopard Frogs

(*Lithobates sphenocephalus*; Cope 1886) and Green Treefrogs (*Hyla cinerea*; Schneider 1799) seem to be more abundant in salt-intruded coastal wetlands, even if average salinities are above lethal doses for eggs and larvae (Albecker and McCoy 2017). Despite this, salinity increases during early life-stages of most amphibians can increase development times and greatly reduce survival (Kearney et al. 2014). Exposure of three Texas frog species' tadpoles to salinity revealed that a sublethal exposure to salinity did not increase tolerance to later exposures and instead made them more vulnerable to mortality (Hua and Pierce 2013). Salinity experiments show older larvae handle salt increases best, which suggests ontogenetic impacts of salinity (Kearney et al. 2014). Adults may offset egg vulnerability by selecting oviposition sites (Wilder and Welch 2014).

Reptilian salt-tolerances are generally higher than amphibian tolerances due to reduced permeability of their skin and adaptive behavioral responses (Dunson and Seidel 1986, Dunson and Mazotti 1989). However, freshwater-associated reptiles are also limited by salinity. Adult freshwater turtles in a Florida estuary were unable to maintain mass or grow when salinity exceeded 14 ppt, and Snapping Turtles (*Chelydra serpentina*; Linnaeus 1758) were unable to osmoregulate above a salinity of ~13 ppt (Dunson and Seidel 1986). *Nerodia* watersnakes showed mixed reactions to increased salinities in a study evaluating the overlap of freshwater and saltmarsh *Nerodia* (Dunson 1980). Most individuals died because of accidental swallowing of saltwater, but others were able to avoid this behavior and survive in brackish marshes (Dunson 1980, Dunson and Mazotti

1989). River alterations will likely increase the impacts of salinity on estuarine herpetofauna by reducing freshwater flows and increasing the risk of saltwater intrusion.

River Alterations

Many aquatic organisms have life histories built around specific flow regimes (Lytle and Poff 2004, Rolls et al. 2012). Flow alterations change flooding regimes and water depths, which may isolate populations and increase predation and/or competition (Rolls et al. 2012). Flow alterations also impact water chemistry, which can have large impacts on aquatic organisms (Bunn and Arthington 2002). For example, waters released from dams are usually different temperatures than the water downstream, which can disrupt environmental cues for breeding (Bunn and Arthington 2002). Reduced flows can also decrease dissolved oxygen, which affects all salamander life stages and can greatly reduce survival (Mills and Barnhart 1999, Sheafor et al. 2000, Bunn and Arithington 2002, Stevens et al. 2006, Woods et al. 2010). Similar impacts may be expected for frogs.

Flow alterations can differentially impact aquatic plant germination, which can alter habitat structure and lead to subsequent changes in water quality (Suren and Riis 2010). Dams and channelization may have impacts on herpetofauna by reducing overbank flooding to wetlands and reducing channel migration in rivers (Reich et al. 2010, Mims and Olden 2013). However, channelized stretches of river in Louisiana and Texas did not have lower counts of turtles than natural stretches (Hartson et al. 2014). This implies that, for some herpetofauna, effects of channelization may not impart detrimental impacts. Erratic flows from dams are known to impact fish and

macroinvertebrates (Bishop and Bell 1978), which could be expected to similarly impact aquatic herpetofauna, particularly their eggs and larvae.

Justification and Objectives:

The ongoing Savannah Harbor Expansion Project may result in altered hydrology and increased saltwater intrusion in the Savannah River estuary (USACE 2012a). Tidal swamps are likely to be strongly impacted unless mitigation procedures are properly planned and successfully implemented. There could be additional impacts on tidal swamp microhabitat availability via the loss of soil stabilization and the foundational substrate provided by trees. Wildlife species in tidal swamps could be negatively affected if they are sensitive to these changes or other changes in habitat. However, due to the lack of studies for wildlife in tidal swamps, we do not know to what extent they will be affected by these alterations.

We sought to address the lack of information for wildlife in tidal swamps by studying reptile and amphibian species in tidal swamps that exist along a gradient of increasing soil and water salinity within the Savannah National Wildlife Refuge near Hardeeville, South Carolina, USA. We specifically focused on reptiles and amphibians in tidal swamps because: (a) reptiles and amphibians are important components of most trophic webs (Deutschman and Peterka 1988, Regester et al. 2006); and (b) most amphibians display a biphasic life cycle with an aquatic larval stage that is sensitive to environmental changes (Rowe et al. 2003). This last trait could be a useful proxy for assessing impacts on other aquatic freshwater wildlife.

We compiled a herpetofauna inventory, assessed possible microhabitat associations, and tested for salinity's impacts on herpetofauna occupancy and community composition in tidal swamps. Our hypotheses were: 1) Herpetofauna species richness and diversity will decrease with increasing salinity; 2) Herpetofauna occurrence will decrease with increasing salinity; 3) Herpetofauna richness and diversity will be greater in areas with more hummock microtopography; and 4) There are distinct communities of herpetofauna associated with changes in salinity.

CHAPTER TWO

METHODS AND RESULTS

Study Site

The Savannah River acts as the state line between Georgia and South Carolina along its 476 kilometer length, and its watershed is approximately 27,414 $kilometers^2$ (Smock et al. 2005). The river is currently used for recreation, hydroelectric power generation, thermoelectric cooling, as a drinking water source, and for commercial shipping and navigation (Smock et al. 2005, USACE 2012a). The lower portion of the Savannah River undergoes a regular tidal flooding regime twice a day and is a salt-wedge type estuary (Hansen and Rattray 1966). The tidal range of this river is greater than 3 meters, and tidal influences persist up to 45 kilometers upstream of the river mouth (Duberstein and Kitchens 2007). Tidal ranges in some areas may be lower, averaging 1.5 to 2 meters (Duberstein and Kitchens 2007). The range and consistency of the tides keep most tidal swamp soils constantly saturated, even during the extended droughts (Duberstein and Kitchens 2007). Tidal flooding can occur in areas closer to the river, but the more remote areas are probably influenced by tidal forcing of the groundwater table, which best explains their persistently saturated soil conditions (Duberstein and Kitchens 2007).

The Savannah National Wildlife Refuge is located in the tidal zone of the Savannah River and has 11,736 hectares of freshwater marshes, tidal rivers and creeks, and bottomland hardwoods (USACE 2012a). Historically, the lands of this refuge have been impacted by land clearing for rice agriculture (Doar 1936). Rice cultivation in the

tidal marshes failed after the Civil War, and much of the land was abandoned (McKenzie et al. 1980). Wetlands in this area are also likely to have been logged prior to acquisition by the U.S. Fish and Wildlife Service (Duberstein and Kitchens 2007). The presence of some remaining stumps in tidal marsh areas suggests that the tidal forest once extended at least 8 km further downstream than their current extent (Duberstein and Kitchens 2007), and regional maps from 1825 suggest that tidal swamps at that time may have extended further to the existing port of Savannah, Georgia (Mills 1825). Several anthropogenic river alterations have impacted the Savannah National Wildlife Refuge in the recent past. A tide gate became operational in May 1977, but it was taken out of service in October 1990 due to unanticipated environmental impacts (Figure 2.1; Wetzel and Kitchens 2007, USACE 2012a). Canal systems were constructed, and channel alterations were made to increase freshwater supply in response to salt wedge migration from harbor deepening in the 1970s (USACE 2012a). This canal system was rehabilitated in 2010 to ensure that freshwater supplies at the Savannah National Wildlife Refuge would not be compromised (USACE 2012a). The New Cut Canal was also closed to increase downstream freshwater flows (Figure 2.1; USACE 2012a).

Krauss et al. (in preparation) have determined that there are about 7,900 hectares of tidal swamps within the Savannah National Wildlife Refuge; approximately 400 hectares of these swamps are considered to be salt-stressed. Previous work by Duberstein and Kitchens (2007) established four distinct forest communities in the tidal swamps of the Savannah River. The predominant tree species at the Savannah River study sites are flood-tolerant species such as water tupelo (*Nyssa aquatica*), swamp tupelo (*Nyssa*

biflora), water oak (*Quercus nigra*), and baldcypress (*Taxodium distichum*). The predominant shrub species are hazel alder (*Alnus serrulata*) and dwarf palmetto (*Sabal minor*).

Field Methods

Two 140 hectare study areas were chosen within the floodplain of the Savannah National Wildlife Refuge, each approximately 42 river kilometers (26 river miles) from the mouth of the river (Table 1; Figure 1). These study areas were chosen to capture the current extent of an existing tidal swamp salinity gradient and measure observed differences in species between the Savannah River and the Back River, one of its distributaries. The streamside study area is next to the main channel of the Savannah River and contains several tidal streams. The backswamp study area is located off of the Little Back River, a distributary of the Savannah River. Four study sites were created within the streamside study area along the salinity gradient to assess the impact of increasing salinity on herpetofauna occupancy and community composition (Table 2.1; Figures 2.2, 2.3). These study sites are concurrently being monitored for soil salinity and plant community changes. Only one study site was created in the backswamp study area to expand the spatial scope of our study into more remote areas of the estuary and assess differences in herpetofaunal community composition and occupancy related to hydrology and salinity (Figure 2.2).

Stratified random sample plots (N = 82; Table 1; Figure 2.2) were sampled in the streamside and backswamp study sites over the course of two field seasons. The sample

plots were stratified based on representative habitat types along the salinity gradient. Plots were sampled from March 1st – June 1st 2016 and 2017. During 2016, sample plots (N = 52) were sampled one day per month for a total of three visits per plot. In 2017, the sample plots (N = 30) were sampled three days per month for a total of nine visits per plot. All sample plots were placed at least 100 meters from the nearest river or tidal creek to minimize edge effects and avoid areas that might have drastic differences in soil composition and hydrology (e.g., high flow rates during ebb conditions).

Study Area	Study Sites	2016 Sample Plots	2017 Season Sample Plots	Total Number of Plots
Streamside	4	36	24	60
Backswamp	1	16	6	22
Total - 2 areas	Total - 5 sites	Total - 52 plots	Total - 30 plots	Total - 82 plots

Table 2.1: Study areas with number of study sites and sample plots surveyed for reptiles and amphibians in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

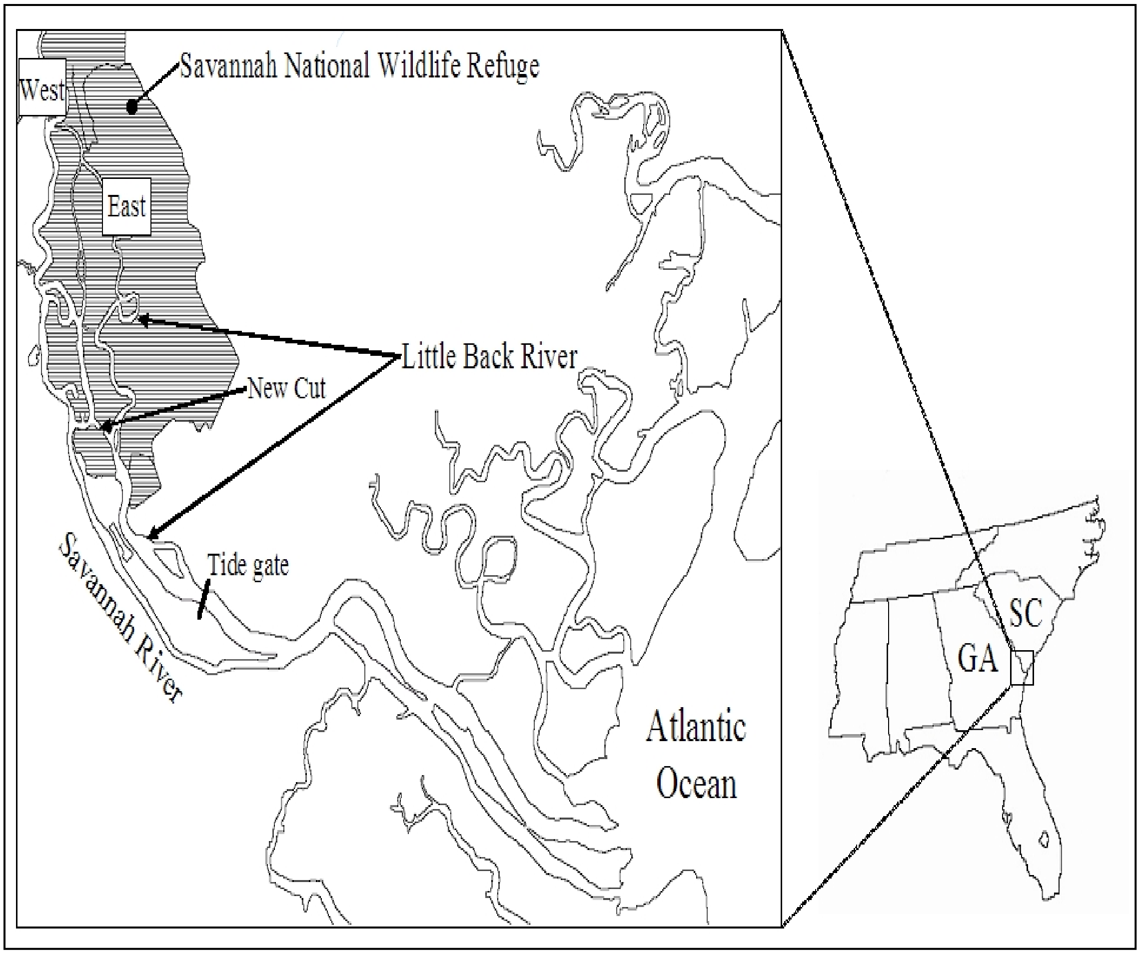


Figure 2.1: Map of Savannah River and the Savannah National Wildlife Refuge, Georgia and South Carolina (used with permission from Duberstein and Kitchens, 2007). West and East zones in this image align with the streamside and backswamp study areas, respectively.

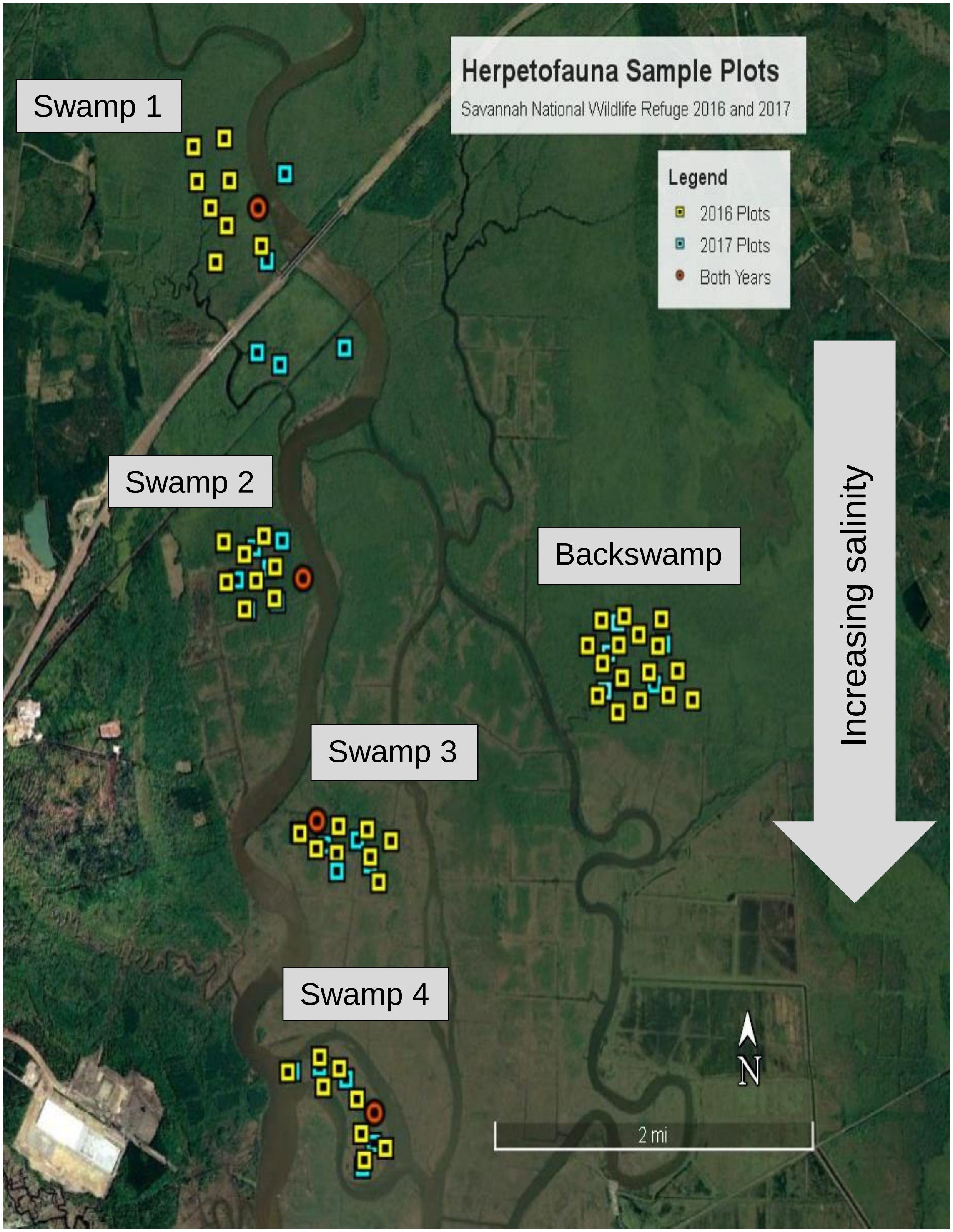


Figure 2.2: Map of the herpetofauna study sites and sample plots surveyed in tidal swamps of the Savannah River National Wildlife Refuge during March to June 2016 and 2017.

Study plots were sampled for herpetofauna using multiple methods outlined by Heyer et al. (1994) and Graeter et al. (2013). These methods were: area-constrained visual surveys, anuran vocalization surveys, aquatic traps (pyramid crawfish traps, Gee minnow traps, turtle hoop nets, and trash can traps), and cover boards. We used dip nets and 'frogloggers' (see below) to collect supplementary information on amphibian reproduction. We chose to use multiple methods with the hopes that it would maximize our detections and create a complementary survey effort that abated each method's separate biases and limitations (Ribeiro-Junior et al. 2008, Hutchens and DePerno 2009, Sung et al. 2011, McKnight et al. 2015).

We conducted area-constrained visual encounter surveys within pre-established 10 x 10 meter (100 meter^2) grids at each of the sampling plots. We standardized survey efforts at each plot by instituting a minimum survey time of 10 minutes. This mitigated issues arising from variation in habitat structure between study sites (i.e., plots with little to no habitat structure did not take as long to survey as plots that had more structure). All animals were field identified to species level, measured for snout-vent length and tail length (if applicable), and released. Data for environmental variables was recorded prior to the start of each visual encounter and anuran vocalization survey. The environmental variables and their measurement units are listed below in Table 2.2. Two additional variables, dissolved oxygen and conductivity, were measured during the 2017 field season.

Variable	Measurement Unit	Abbreviation
water and soil salinity	practical salinity units	psu
air and water temperature	degrees Celsius	°C
relative humidity	percentage value	not applicable
wind speed	miles per hour	mph
pH level	moles per liter	mol/L
maximum water depth	centimeters	cm
dissolved oxygen	milligrams per liter	mg/L
conductivity	micro-Siemens per centimeter	μS/cm
soil compaction	kilograms per square centimeter	kg/cm^2
tree canopy cover	percentage value	not applicable
hummock/hollow cover	percentage value	not applicable
basal area	square meters per hectare	m^2/ha

Table 2.2: Environmental variables collected during reptile and amphibian surveys and their measurement units.

We estimated hummock and hollow habitat microhabitat cover within the same 10 x 10 meter grids used for the area-constrained visual surveys (Table 2.1). The grids were subdivided into sixteen 2.5 x 2.5 meter quadrats, and we visually estimated percent cover of hummocks and hollows within each quadrat. Hummocks were delineated by:

raised soil topography, at least 10 centimeters in height; at least 1 meter^2 in total area; and that area was not covered by any trees with a diameter at breast height ≤ 10.0 centimeters. The average height of most hummocks is 15-20 centimeters, so this minimum height should have included any below-average height hummocks (Duberstein and Conner 2009). Hollows were delineated as: lower elevation areas, less than or equal to the base elevation of the floodplain (Duberstein and Conner 2009).

Anuran vocalization surveys were conducted at the same time as the visual encounter surveys at each plot. The anuran vocalization surveys lasted for a period of five minutes. We used the anuran call index outlined by Weir and Mossman (2005) to assess anuran species abundance and supplement visual encounter survey detections. Individual anurans were counted as 'in' if they were within 25 meters of the plot and counted as 'out' if they were over 25 meters from the plot. Consideration was only given to calls that were counted as 'in'. This system prevented large groups of chorusing frogs from being counted 'in' repeatedly, for example if the same chorus could possibly be heard at multiple plots.

Aquatic traps were placed in suitable areas that reduced the risk of desiccation when the tides receded and conversely reduced the risk of drowning when the tides advanced. One pyramid crayfish trap and one minnow trap were set at each plot. Hoop nets and trash can traps were set in locations that had sufficient depth and/or were located along movement corridors (e.g., tidal creeks and rivulets). The traps were checked daily, in accordance with Clemson University Institutional Animal Care and Use Committee protocols. Four 0.91 x 0.61 meter cover boards were arrayed in a grid pattern at each plot

and were checked during the visual surveys. We conducted dip netting as outlined by Shaffer et al. (1994) to capture larval amphibians for supplementary occupancy and abundance data.

A total of six automated recording devices ('frogloggers'; Song Meter Model SM1, Wildlife Acoustics, Maynard, Massachusetts, USA) were randomly placed in the streamside and backswamp study sites for supplementary anuran vocalization data. Five recording devices were deployed within the four salinity gradient study sites (two recorders were placed in the Swamp 1 study site due to its larger size), and the sixth recording device was deployed in the backswamp study site. The recording devices were spaced at a sufficient minimum distance to ensure sampling independence (≥800 meters). All recorders were programmed to record daily for three minutes at the start of each hour from 8:00 P.M. to 1:00 A.M. Eastern standard time. The automated recorders were deployed for a minimum of ten days each month.

Data Analyses

We transcribed the detection/non-detection, site covariate, and observation covariate data into a digital format. Detections/non-detections were entered as a categorical variable, with a '1' indicating a detection and a '0' indicating a non-detection. Site covariates included all of the environmental covariates listed in Table 2.2. Observation covariates included: Julian calendar date, starting time, air temperature, wind speed, and the weather condition during sampling. When necessary, the site and

observation covariate data were standardized to have a mean of 0 and a standard deviation of 1 to account for the variation in measurement units.

The backswamp study site was not being monitored for soil salinity changes, in contrast to the streamside sites. To remedy this lack of sample coverage, we averaged the soil salinity values for the streamside sites and extrapolated the average value to the backswamp plots. The averaged soil salinities were within the expected range, given its position and compared to other sites along the salinity gradient. We hypothesized that some of the observation covariates may have had quadratic relationships with the occupancy and detection probabilities. That is, there was likely a set of peak values for these observation covariates that had the largest effect on the occupancy and detection probabilities. So, we modeled the air temperature, date, and start time covariates with both a linear and a quadratic effect to test this assumption.

We ran single-season occupancy models using the functions within the 'unmarked' package of the 'R' statistics software (R Core Team 2013, MacKenzie et al. 2002). We modeled occupancy as a function of seven site covariates and five observation covariates, using a logit link function. The observation covariates were evaluated separately, after which the top selected observation covariate model was combined with the site covariates to create multi-covariate candidate models. This resulted in a set of approximately 20 candidate models per species for AIC model selection. Models that failed to converge were discarded from the model selection and subsequent interpretation. Occupancy models were assessed via their Aikake Information Criterion (AIC; Akaike 1973, Burnham and Anderson 2002) scores, with the lowest scores indicating the model

that had the highest likelihood of being selected among the candidate models. The metrics used to assess the models included the AIC scores, the ΔAIC values, and the AIC weights. Next, we back-transformed the occupancy and detection probability estimates from the top models and calculated their 95 percent confidence intervals. We calculated the effect sizes of the site and observation covariates for each of the top models and determined the significance and predictive power of the models by comparing their associated standard error and p-values. Lastly, we calculated the estimated proportion of sites occupied for each of the species along with 90 percent confidence intervals.

We used PC-ORD Version 6 (McCune and Mefford 2011) software as well as the 'vegan' package in the 'R' statistics software to conduct the community analyses. These analyses included: species richness and diversity calculations, indicator species analysis, non-metric multidimensional scaling, redundancy analysis, and cluster analysis. Sample plot by species matrices and sample plot by environmental variable matrices were created as the bases for analysis. Thirteen of the 82 plots (~16%) were removed due to zero detections for all species. Site differences were evaluated by averaging the total species richness and Shannon diversity values for both survey years, then using a one-way Analysis of Variance (ANOVA) to test for overall differences followed by a post-hoc Tukey test for pairwise comparisons.

Finally, we conducted standard least squares regressions with environmental covariates as the explanatory variables and species detection/non-detection data as the response variables. We tested for hierarchical effects of sample groupings by creating various combinations of samples. This created four different regression analyses. One

regression analysis did not average any of the samples and ran the raw data (156 values for the 2016 season, 90 values for the 2017 season), whereas the other regression analyses used the mean values of the explanatory and response variables. The next regression analysis focused on the variations in years and study sites by averaging monthly samples and plot-level samples to create one value per site (5 site-level values per year). Another regression analysis focused on the variations in years, sites, and months by averaging plot-level samples (15 site-level values per year). The final regression analysis focused on the variations in years, sites, and plots by averaging monthly samples (52 plot-level values for the 2016 season and 30 plot-level values for the 2017 season). We then evaluated the statistical significance of the relationships between species occupancy and the environmental covariates for each regression.

Results

Occupancy Analyses

The single-season occupancy analyses selected models for five species which had sufficient data (Table 2.3). Occupancy and detection probabilities of the top models varied considerably (Table 2.4). Soil salinity, basal area, pH, water depth, average percent hummock cover, soil compaction, and even the null model were selected as top site covariates (Table 2.5). Soil salinity was consistently selected as one of the top site covariates for most of the species across both years. The top observation covariates included date, the quadratic effect of date, air temperature, weather condition, and wind speed (Table 2.6). The confidence intervals of some of the estimates overlapped 0 and 1

(Table 2.4), and these estimates should be interpreted with caution since they indicate a large amount of uncertainty. The observation and site covariate effect sizes also varied and were largely species specific (Tables 2.5, 2.6). The proportions of sites occupied by each species were consistently below 50 percent across both years for all species (Table 2.7).

Species		Candidate Models[a]	AIC	ΔAIC	AIC weight
Two-lined salamander (*Eurycea cirrigera*)					
		(psi)Soil Salinity + pH + Basal Area, (p)Wind Speed	87.31	0.00	0.36
	2016	(psi)Soil Salinity, (p)Wind Speed	87.56	0.25	0.32
		(psi)Soil Salinity + Basal Area, (p)Wind Speed	89.22	1.91	0.14
		(psi)Water Depth + Hummock Cover, (p)Wind Speed	44.30	0.00	0.46
	2017	(psi)Water Depth, (p)Wind Speed	44.58	0.27	0.40
		(psi)Null, (p)Wind Speed	48.20	3.89	0.07
Green treefrog (*Hyla cinerea*)					
		(psi)Null, (p)Weather Condition	160.40	0.00	0.19
	2016	(psi)Basal Area, (p)Weather Condition	160.67	0.27	0.17
		(psi)Soil Salinity, (p)Weather Condition	161.32	0.91	0.12
		(psi)Soil Compaction, (p)Date^2	79.58	0.00	0.27
	2017	(psi)Soil Salinity + Basal Area, (p)Date^2	80.15	0.57	0.21
		(psi)Basal Area, (p)Date^2	81.42	1.84	0.11
Green anole (*Anolis carolinensis*)					
		(psi)Soil Salinity, (p)Date^2	77.67	0.00	0.30
	2016	(psi)Soil Salinity + Basal Area, (p)Date^2	77.80	0.14	0.28
		(psi)Soil Salinity + pH + Basal Area, (p)Date^2	78.63	0.96	0.19
		(psi)Soil Salinity + Basal Area, (p)Date	106.30	0.00	0.39
	2017	(psi)pH + Soil Salinity, (p)Date	108.33	2.03	0.14
		(psi)pH, (p)Date	109.05	2.75	0.10
Gray Treefrog (*Hyla chrysoscelis*)					
		(psi)Null , (p)Date	47.71	0.00	0.36
	2016	(psi)pH , (p)Date	49.13	1.42	0.18
		(psi)Soil Compaction , (p)Date	49.27	1.56	0.17
		(psi)Hummock Cover, (p)Air Temperature	39.91	0.00	0.44
	2017	(psi)Water Depth + Hummock Cover, (p)Air Temperature	40.97	1.06	0.26
		(psi)Basal Area, (p)Air Temperature	43.19	3.28	0.09
Green Frog (*Lithobates clamitans*)					
		(psi)Soil Salinity + Basal Area, (p)Date	140.29	0.00	0.35
	2016	(psi)Soil Salinity, (p)Date	140.29	0.008	0.35
		(psi)pH + Soil Salinity, (p)Date	142.24	1.95	0.13
		(psi)Soil Salinity, (p)Date^2	42.80	0.00	0.31
	2017	(psi)Null, (p)Date^2	44.31	1.50	0.14
		(psi)Soil Salinity + Basal Area, (p)Date^2	44.79	1.99	0.11

Table 2.3: Top three occupancy models selected via AIC model selection and their associated model selection information for several reptile and amphibians species surveyed in tidal swamps of the Savannah National Wildlife Refuge during March-June 2016 and 2017. (psi) = Occupancy probability, (p) = Detection probability

Species	Top Model[a]	Occupancy Prob	95% CI	Detection Prob	95% CI
Two-lined salamander					
(*Eurycea cirrigera*)					
2016	(psi)Soil Salinity + pH + Basal Area, (p)Wind	0.14	(0.03, 0.49)	0.26	(0.12, 0.46)
2017	(psi)Water Depth + Hummock Cover, (p)Wind	0.09	(0.002, 0.87)	0.11	(0.01, 0.58)
Green treefrog					
(*Hyla cinerea*)					
2016	(psi)Null, (p)Weather	0.59	(0.34, 0.82)	0.35	(0.22, 0.52)
2017	(psi)Soil Compaction, (p)Date^2	0.40	(0.18, 0.67)	0.72	(0.39, 0.91)
Green anole					
(*Anolis carolinensis*)					
2016	(psi)Soil Salinity, (p)Date^2	0.39	(0.09, 0.80)	0.07	(0.02, 0.22)
2017	(psi)Soil Salinity + Basal Area, (p) Date	1.00	(2.61 e -77, 1.00)	0.33	(0.23, 0.44)
Gray Treefrog					
(*Hyla chrysoscelis*)					
2016	(psi)Null, (p)Date	0.99	(3.40 e -20, 1.00)	0.02	(0.007, 0.08)
2017	(psi)Hummock Cover, (p)Air Temperature	0.38	(0.11, 0.77)	0.05	(0.004, 0.39)
Green Frog					
(*Lithobates clamitans*)					
2016	(psi)Soil Salinity + Basal Area, (p)Date	1.00	(2.66 e -06, 1.00)	0.22	(0.14, 0.31)
2017	(psi)Soil Salinity, (p)Date^2	0.43	(0.02, 0.97)	0.29	(0.08, 0.66)

Table 2.4: The top occupancy models and their estimated occupancy and detection probabilities for several reptile and amphibian species surveyed in tidal swamps of the Savannah National Wildlife Refuge during March-June 2016 and 2017. (psi) = Occupancy probability, (p) = Detection probability, 95% CI = 95 percent confidence intervals

Species		Site Covariates[a]	Effect Size	Standard Error	p-value
Two-lined salamander (*Eurycea cirrigera*)					
		Soil Salinity	-1.60	0.86	0.06
	2016	pH	-1.29	0.71	0.07
		Basal Area	1.57	0.86	0.07
		Water Depth	7.57	7.80	0.33
	2017	Hummock Cover	-3.93	4.00	0.33
		Null	-3.91	1.36	0.004
Green treefrog (*Hyla cinerea*)					
		Null	-0.62	0.34	0.07
	2016	Basal Area	0.56	0.47	0.23
		Soil Salinity	-0.02	0.44	0.96
		Soil Compaction	-1.44	0.91	0.11
	2017	Soil Salinity	-1.02	0.60	0.09
		Basal Area	-1.28	0.62	0.04
Green anole (*Anolis carolinensis*)					
		Soil Salinity	1.83	0.82	0.02
	2016	pH	0.49	0.75	0.52
		Basal Area	-1.13	0.94	0.23
		Soil Salinity	-6.33	28.50	0.82
	2017	Basal Area	38.02	79.50	0.63
		pH	10.4	21.00	0.62
Gray Treefrog (*Hyla chrysoscelis*)					
		Null	-3.68	0.62	2.42 e -09
	2016	pH	1.74	3.42	0.61
		Soil Compaction	1.36	2.78	0.63
		Hummock Cover	2.51	1.23	0.04
	2017	Water Depth	-1.46	2.45	0.55
		Basal Area	1.19	1.05	0.26
Green Frog (*Lithobates clamitans*)					
		Soil Salinity	8.54	9.06	0.35
	2016	Basal Area	-2.48	3.34	0.46
		pH	-0.24	0.99	0.81
		Soil Salinity	-4.61	7.72	0.55
	2017	Null	-1.58	0.57	0.005
		Basal Area	0.30	2.58	0.91

Table 2.5: Top three selected site covariates and their associated effect sizes along with the standard error and p-value estimates for several reptile and amphibian species surveyed in tidal swamps of the Savannah National Wildlife Refuge during March-June 2016 and 2017.

Species	Observation Covariates[a]	Effect Size	Standard Error	p-value
Two-lined salamander (*Eurycea cirrigera*)				
2016	Wind	-0.70	0.47	0.14
2017	Wind	-3.20	1.29	0.01
Green treefrog (*Hyla cinerea*)				
2016	Weather	-0.46	0.24	0.06
2017	$Date^2$	-1.51	0.61	0.01
Green anole (Anolis carolinensis)				
2016	$Date^2$	0.85	0.35	0.01
2017	Date	0.69	0.26	0.007
Gray Treefrog (*Hyla chrysoscelis*)				
2016	Date	0.81	0.56	0.15
2017	Air Temperature	2.80	1.64	0.09
Green Frog (*Lithobates clamitans*)				
2016	Date	0.70	0.25	0.004
2017	$Date^2$	-3.1	1.93	0.11

Table 2.6: Top selected observation covariates and their associated effect sizes along with the standard error and p-value estimates for several reptile and amphibian species surveyed in tidal swamps of the Savannah National Wildlife Refuge during March-June 2016 and 2017.

Species	PSO	90% CI
Two-lined salamander		
(*Eurycea cirrigera*)		
2016	0.11	(0.09, 0.23)
2017	0.06	(0.05, 0.12)
Green treefrog		
(*Hyla cinerea*)		
2016	0.18	(0.18, 0.40)
2017	0.09	(0.09, 0.18)
Green anole		
(*Anolis carolinensis*)		
2016	0.15	(0.08, 0.30)
2017	0.21	(0.21, 0.21)
Gray Treefrog		
(*Hyla chrysoscelis*)		
2016	0.40	(0.40, 0.40)
2017	0.08	(0.06, 0.13)
Green Frog		
(*Lithobates clamitans*)		
2016	0.31	(0.28, 0.36)
2017	0.15	(0.08, 0.18)

Table 2.7: Estimated proportion of sites occupied (PSO) calculated via the top selected occupancy models for several reptile and amphibian species surveyed in tidal swamps of the Savannah National Wildlife Refuge during March-June 2016 and 2017. 90% CI = 90 percent confidence intervals

Community Analyses

The indicator species analysis, non-metric multidimensional scaling, redundancy analysis, and cluster analysis also failed to detect any trends between species assemblages and environmental covariates. The cluster and indicator species analyses found

significant groupings, but post-hoc fitting of environmental variables did not result in any clear patterns of species groupings and environmental variables. However, species richness/diversity analyses yielded interpretable results.

Herpetofaunal Richness

We detected a total of 232 individuals comprising 20 amphibian and reptile species during 3 survey events in 2016 and 9 survey events in 2017. We detected 8 amphibian (6 frog, 2 salamander) and 12 reptile (7 snake, 3 lizard, and 2 turtle) species. Individual detections for each species ranged from 1 to 62 (Mean = 11.60, SD = 16.05), and detections at each site ranged from 18 to 81 (Mean = 46.4, SD = 26.74). Two amphibian (1 frog, 1 salamander) and four reptile (3 snake, 1 turtle) species were detected only once. Of the 20 herpetofauna we detected, one reptile species [Black Swamp Snake (*Liodytes pygaea*; Cope 1871)] was listed under the South Carolina Wildlife Action Plan as a species of greatest conservation need. This species was only detected during sampling at the Swamp 2 study site, but we had dozens of incidental detections southeast of the study areas in moist soil impoundments managed by the U.S. Fish and Wildlife Service. The Green Anole (*Anolis carolinensis*; Voigt, in Cuvier and Voigt 1832) and Banded Watersnake (*Nerodia fasciata*; Linnaeus 1766) were the most common reptile species, occurring in 39% and 16% of plots, respectively. Green Treefrog and the Southern Two-lined Salamander (*Eurycea cirrigera*; Green 1831) were the most common amphibian species, occurring in 29% and 22% of plots, respectively.

Detections of species varied among methods (Table 2.8). We detected 5 amphibian (4 frog and 1 salamander) and 6 reptile (4 snake, 1 lizard, and 1 turtle) species primarily via visual encounter surveys. Two reptile (1 snake, 1 turtle) species were only detected a single time during visual encounter surveys. Cover boards detected 2 amphibian (1 frog, 1 salamander) and 5 reptile (3 snake, 2 lizard) species, with 2 reptile (both snake) species that were not detected via visual surveys. Two reptile (1 snake, 1 lizard) species were only detected a single time using this method. We detected herpetofauna during approximately 6% of all cover board checks. Aquatic traps yielded 3 amphibian (2 frog, 1 salamander) and 3 reptile (4 snake, 1 turtle) species. One amphibian (1 salamander) and 2 reptile (1 snake, 1 turtle) species that were detected with the aquatic traps were not detected via visual encounter surveys. One amphibian (salamander) and one reptile (snake) species were detected only once using aquatic traps. Traps were surprisingly inefficient; we only captured herpetofauna during about 3% of all trap attempts. Anuran vocalization surveys detected 6 frog species, 2 of which were not detected via visual encounter surveys.

Taxon	Common Name	Swamp 1	Swamp 2	Swamp 3	Swamp 4	Backswamp	VES	CB	AVS	TRAP
Frogs										
Hyla cinerea	Green treefrog		X	X	X	X	X		X	
Hyla chrysoscelis	Gray treefrog	X	X						X	
Hyla squirrela	Squirrel treefrog[a]		X			X			X	
Lithobates clamitans	Green frog	X	X	X		X	X	X	X	
Lithobates sphenocephalus	Southern leopard frog		X	X		X	X		X	X
Lithobates hecksherii	River frog	X	X			X	X			X
Salamanders										
Eurycea cirrigera	Southern two-lined salamander	X		X		X	X	X		
Siren intermedia	Lesser siren[a]					X				X
Snakes										
Nerodia fasciata	Banded watersnake	X	X	X	X	X	X	X		X
Nerodia taxispilota	Brown watersnake		X			X	X			
Agkistrodon piscivorus	Eastern Cottonmouth	X	X				X			
Liodytes pygaea	Black swamp snake[a]		X							X
Opheodrys aestivus	Rough green snake[a]						X			
Diadophis punctatus	Ring-necked snake	X	X			X		X		
Thamnophis sauritus	Eastern ribbonsnake[a]		X					X		
Lizards										
Anolis carolinensis	Green anole	X	X	X	X	X	X			
Plestiodon laticeps	Broad-headed skink		X				X	X		
Plestiodon fasciatus	Common five-lined skink	X	X		X	X	X	X		
Turtles										
Kinosternon subrubrum	Eastern mud turtle[a]	X					X			
Sternotherus odoratus	Common musk turtle			X		X				X

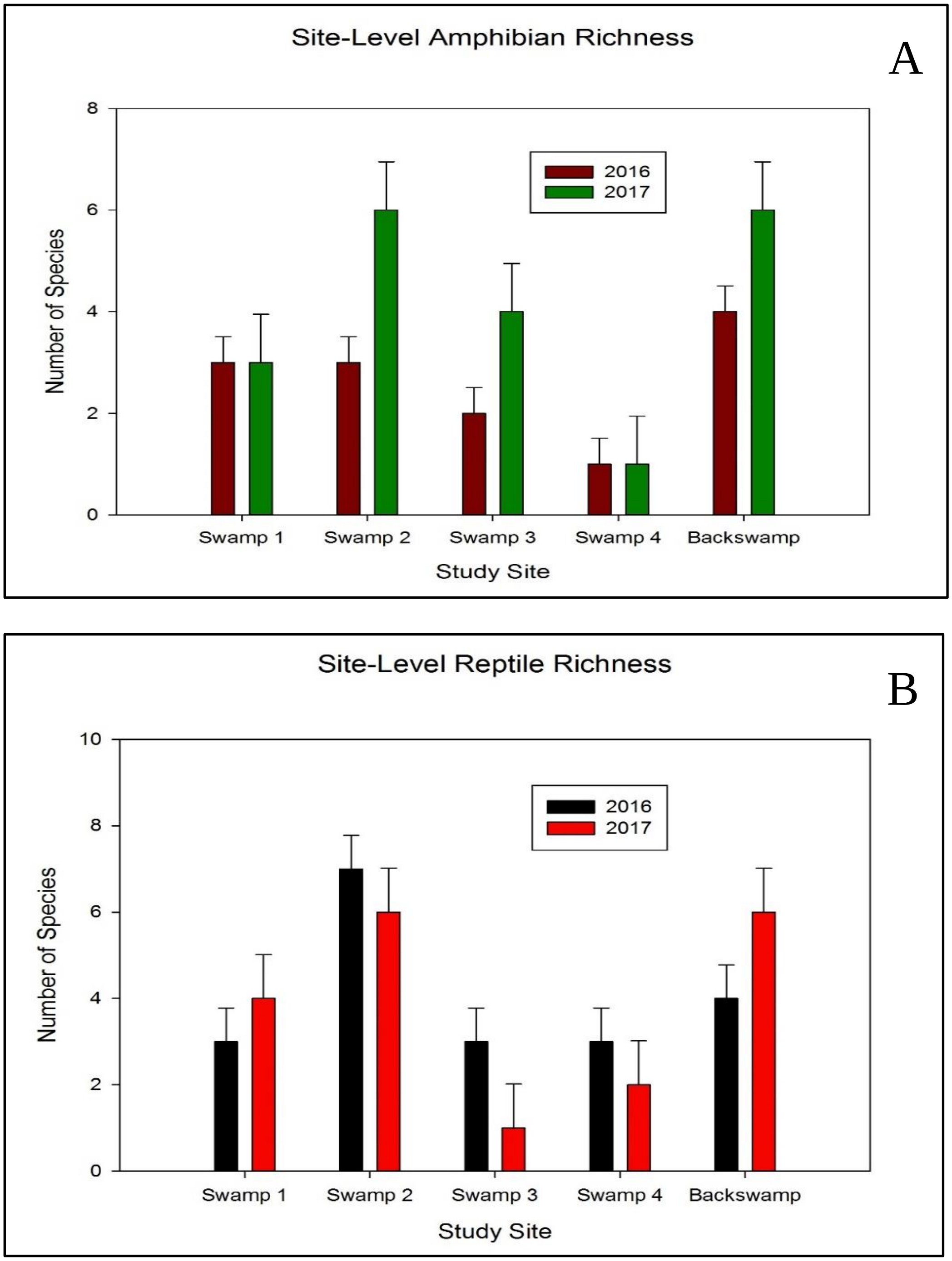
[a] Species only detected once

Table 2.8: List of all species encountered during herpetofauna surveys in 2016 and 2017. Sampling codes: VES = Visual Encounter Survey, CB = Cover board, AVS = Anuran vocalization survey, TRAP = aquatic traps.

Dip netting was not an efficient method, as we did not detect any amphibian eggs, larvae, or adults using this method despite the fact that at least some larvae and adults were present. We only detected one ranid tadpole (*Lithobates* spp.) and one frog egg mass (also *Lithobates*) during the 2016 and 2017 field seasons. The tadpole was found in a pyramid crayfish trap in the Backswamp site during May 2016. It was small enough to move through the netting and escaped before a proper field identification to the species level could be made. The frog egg mass was found in a tidal rivulet in the Swamp 1 site during April 2017. The rivulet dried completely several days later and killed all of the developing embryos. This also prevented proper field identification to the species level. However, we are confident that the egg mass and tadpole both displayed all the characteristic features belonging to eggs and larvae of the *Lithobates* genus.

Observed amphibian richness varied from 1 to 6 species per site (SD = 1.77) and was greatest in the Swamp 2 and Backswamp sites (Figure 2.3A). One-way analysis of variance (ANOVA) failed to reject the hypothesis that there were no differences in amphibian richness among sites. Observed reptile richness varied from 1 to 7 species per site (SD = 1.91) and also was greatest in the Swamp 2 and Backswamp sites (Figure 2.3B). One-way ANOVA and post-hoc Tukey tests indicated that the Swamp 3 site had significantly lower observed reptile richness than the Swamp 2 site ($p = 0.04$). Total observed species richness varied from 4 to 12 species per site (SD = 3.31), with the greatest richness again observed in the Swamp 2 and Backswamp sites (Figure 2.3C). A one-way ANOVA and post-hoc Tukey test indicated that the observed species richness in the Swamp 3 and Swamp 4 sites were significantly lower than the observed richness in

the Swamp 2 and Backswamp sites (p = 0.01). Shannon diversity values ranged from 2.14 to 7.36 (SD = 2.02), with the same trend among sites (Figure 2.3D).



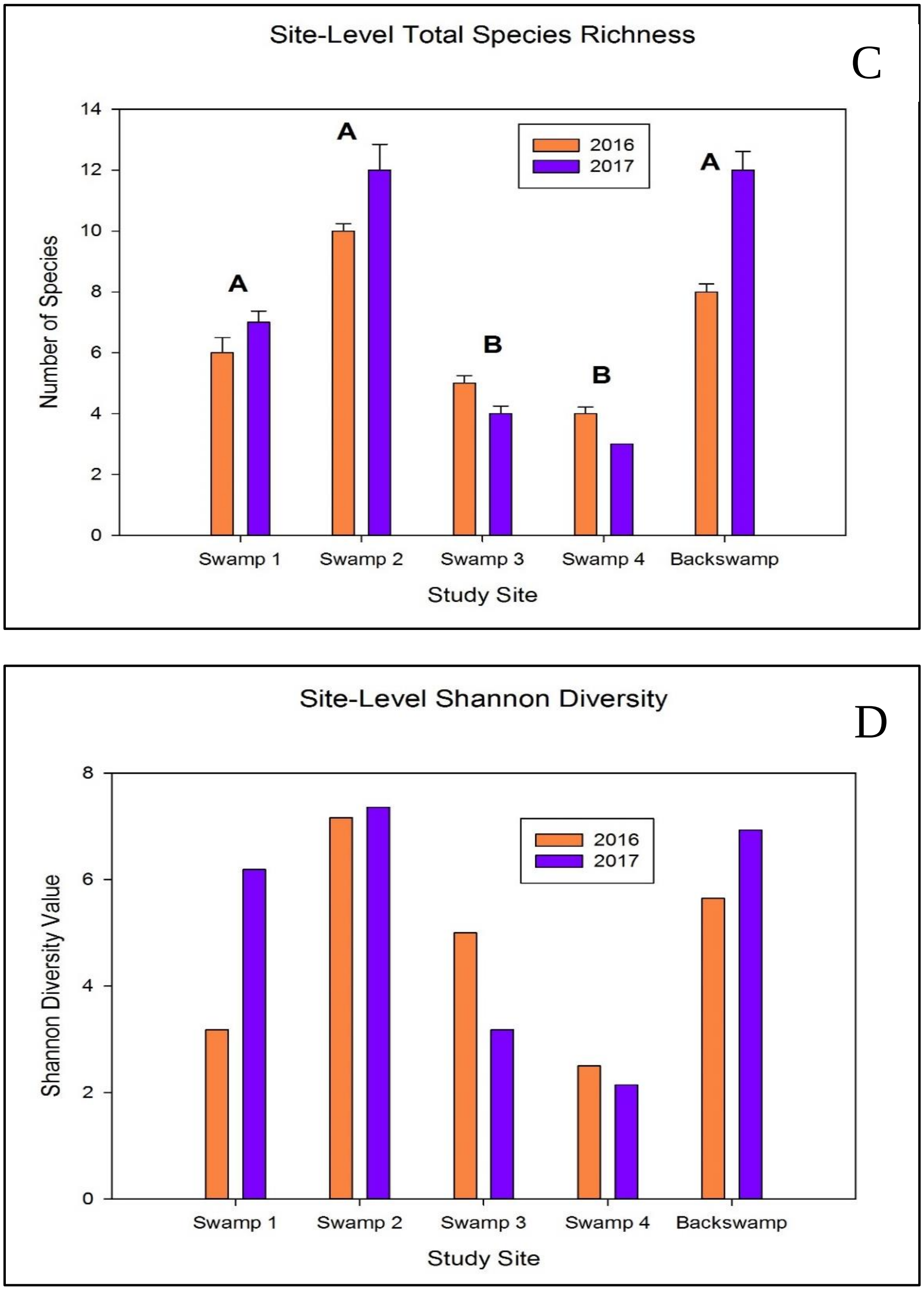


Figure 2.3: Observed amphibian richness (A), reptile richness (B), total species richness (C), and Shannon diversity values (D) among study sites sampled during the spring of 2016 and 2017 in the tidal swamps of the Savannah National Wildlife Refuge.

Herpetofaunal Species Turnover and Richness Estimates

We calculated the mean estimated dissimilarity between plots using the Bray-Curtis dissimilarity statistic. Values close to zero suggest that sites share the same species, whereas values close to one suggest that sites do not share any species. The mean Bray-Curtis dissimilarity between plots was 0.85. We also estimated Whittaker's species turnover by dividing the gamma diversity (20 total species) by the mean alpha diversity among sample plots (~4.65) and subtracting one from the quotient. This yielded a species turnover estimate of 3.30 species between sites. We estimated the total species richness for the areas we sampled by using the Chao, first order jackknife, second order jackknife, and bootstrap estimators. These estimators yielded the following estimates (with standard error, SE) of total species richness, respectively: 24.39 (SE = 4.70), 25.85 (SE = 2.39), 27.85 (SE = 2.39), and 22.89 (SE = 1.60). The highest estimate of approximately 28 species loosely aligns with the total of 34 species that we incidentally observed (Appendix A).

Standard Least Squares Regression

The results of the standard least squares regressions were dependent on which hierarchical groupings were tested (Tables 2.9-2.13, Figures 2.4-2.16). The relationships between the environmental covariates and species detections were strongest in the analysis that focused on variations in years and study sites. The other analyses had significant relationships between species detections and the covariates, but their relationships were weak. In total, there were 10 species (1 salamander, 4 frogs, 1 lizard,

and 4 snakes) that had significant relationships with the environmental covariates (Table 2.9). There were 9 species (1 salamander, 4 frogs, and 4 snakes) with significant relationships to environmental covariates for regressions with no groupings and no averaged covariates (Table 2.10, Figures 2.4-2.8). Monthly soil salinity levels were the most common significant environmental covariate, and it was significant for 7 species (1 salamander, 2 frogs, 1 lizard, and 3 snakes). In this analysis, water depth and pH were only significant for amphibians (1 salamander, 3 frogs).

Taxon	Common Name	pH	Soil Salinity	Water Salinity	Water Depth	Air Temperature	Water Temperature	Weather	Wind Speed
Frogs									
Hyla cinerea	Green Treefrog		+	−	−	+			
Hyla chrysoscelis	Gray Treefrog	−	−	−	−	+			
Lithobates clamitans	Green Frog	+	+	−		+	+	+	−
Lithobates sphenocephalus	Southern leopard Frog	+	+						
Salamanders									
Eurycea cirrigera	Southern Two-lined Salamander	−	−		+				−
Snakes									
Nerodia fasciata	Banded Watersnake		+	+			+		
Nerodia taxispilota	Brown Watersnake					+	+		
Agkistrodon piscivorus	Eastern Cottonmouth	−	−						
Diadophis punctatus	Ring-necked Snake		+					+	
Lizards									
Anolis carolinensis	Green Anole		+		−	+	+		

Table 2.9: All statistically significant ($p < 0.05$) standard least squares regression results (all combinations of hierarchical groupings) for species with sufficient presence data. A ‘+’ denotes a positive statistically significant relationship between a species’ presence data and the environmental covariate, and a ‘-’ denotes a negative relationship.

Species	Environmental Covariate	Effect Size	p-value
Southern Two-lined Salamander	pH	-0.15	0.0175
(*Eurycea cirrigera*)	Soil Salinity	-3.89	0.0003
	Wind Speed	-0.15	0.0029
	Water Depth	0.02	<0.0001
Green Treefrog	Water Depth	-0.007	0.0156
(*Hyla cinerea*)	Air Temperature	0.02	0.0531
Gray Treefrog	pH	-0.08	0.0323
(*Hyla chrysoscelis*)	Air Temperature	0.01	0.0265
	Soil Salinity	-0.34	0.0359
Green Anole	Soil Salinity	3.47	0.0010
(*Anolis carolinensis*)	Air Temperature	0.02	0.0218
	Water Temperature	0.03	0.0443
Green Frog	Air Temperature	0.02	0.0339
(*Lithobates clamitans*)	Wind Speed	-0.15	0.0010
	Soil Salinity	3.30	0.0274
	Water Temperature	0.02	0.0419
Southern Leopard Frog	pH	0.08	0.0061
(*Lithobates sphenocephalus)*			
Ring-necked Snake	Soil Salinity	1.53	0.0036
(*Diadophis punctatus*)			
Eastern Cottonmouth	Soil Salinity	-0.24	0.0591
(*Agkistrodon piscivorus*)			
Banded Watersnake			
(*Nerodia fasciata*)	Soil Salinity	1.41	0.0360

Table 2.10: Statistically significant ($p < 0.05$) standard least squares regression results for the analysis in which no sample groupings were averaged.

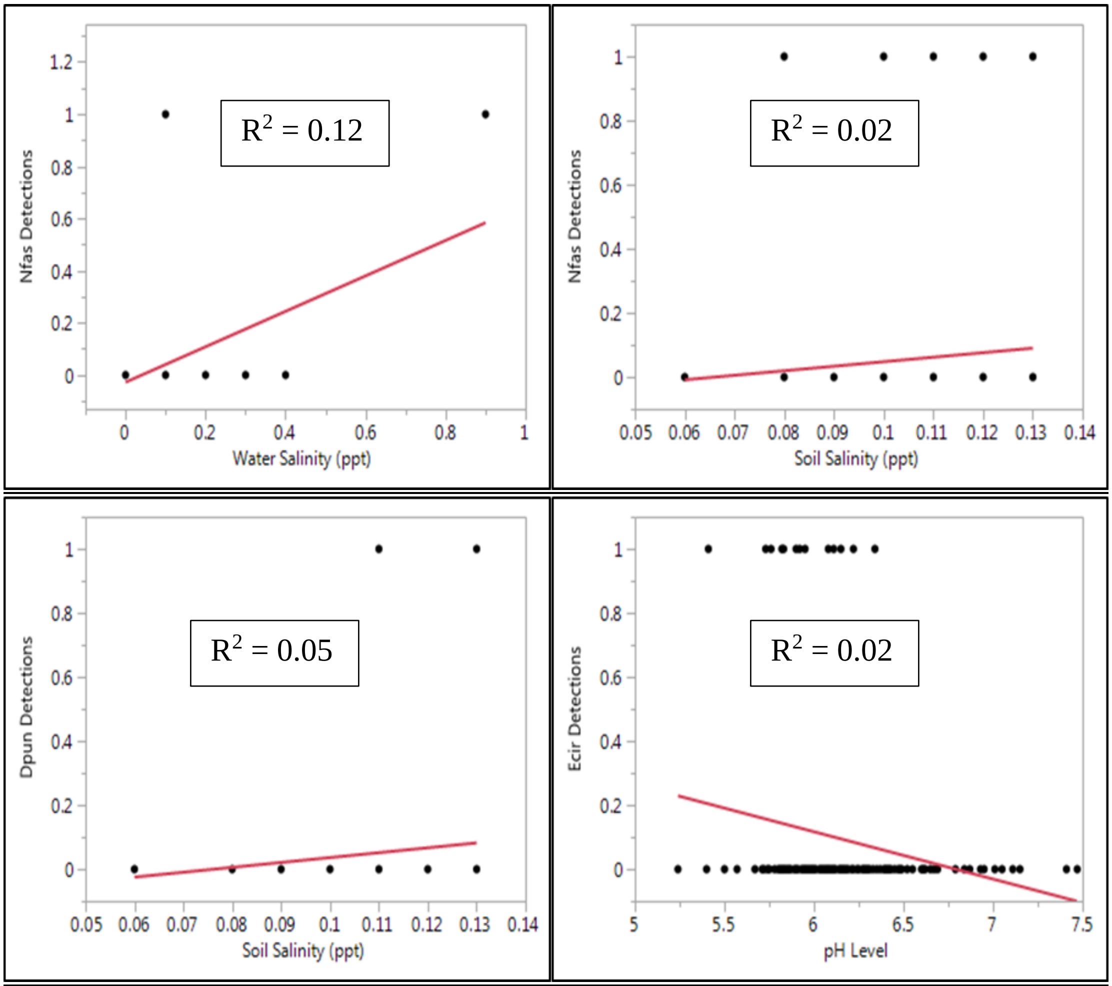


Figure 2.4: Regression analysis results with statistical fit values for the analysis in which there were no sample groupings or averaging of variables. Graphs show standard least squares regression residuals for environmental covariate (explanatory variable) and species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Nfas = Banded Watersnake, Dpun = Ring-necked Snake, Ecir = Southern Two-lined Salamander

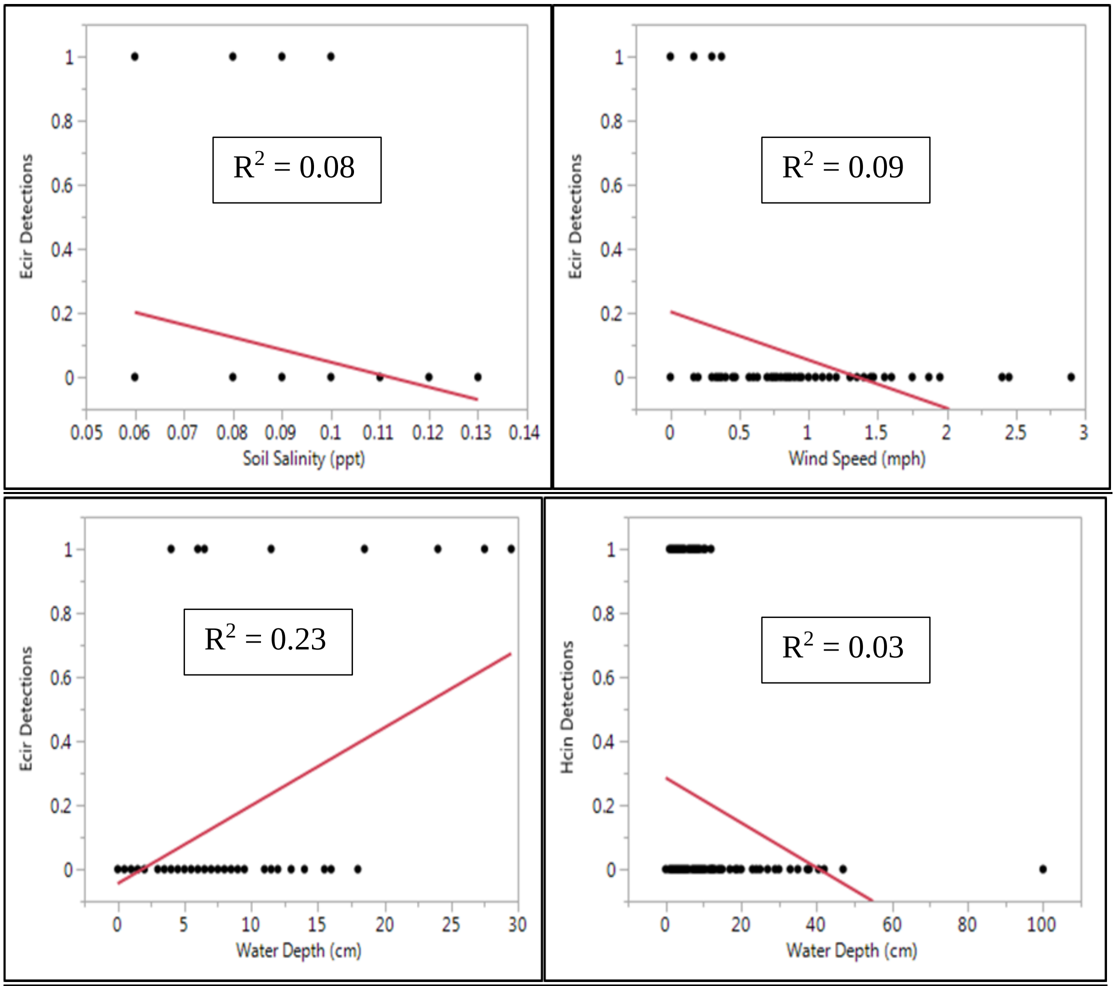


Figure 2.5: Regression analysis results with statistical fit values for the analysis in which there were no sample groupings or averaging of variables. Graphs show standard least squares regression residuals for environmental covariate (explanatory variable) and species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Ecir = Southern Two-lined Salamander, Hcin = Green Treefrog

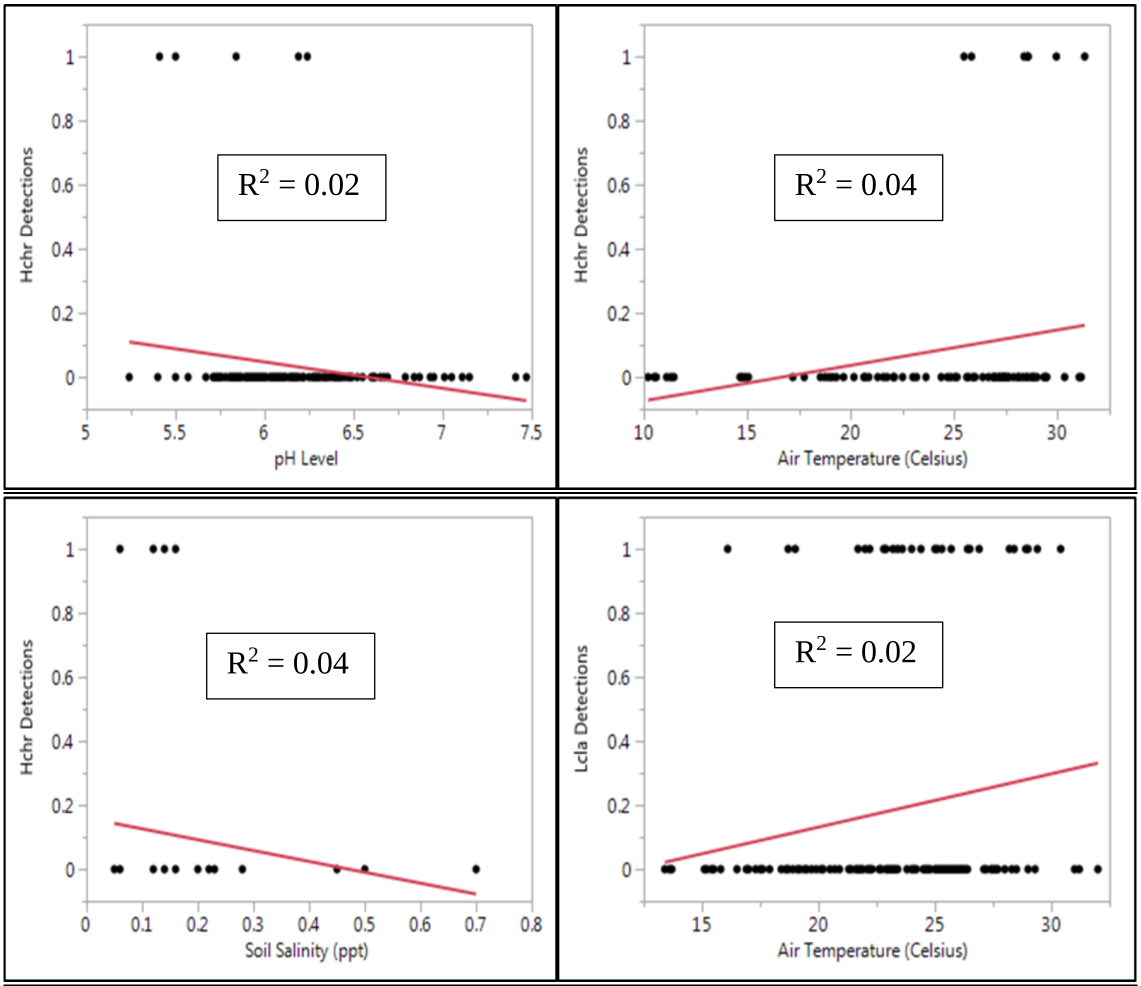


Figure 2.6: Regression analysis results with statistical fit values for the analysis in which there were no sample groupings or averaging of variables. Graphs show standard least squares regression residuals for environmental covariate (explanatory variable) and species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Hchr = Gray Treefrog, Lcla = Green Frog

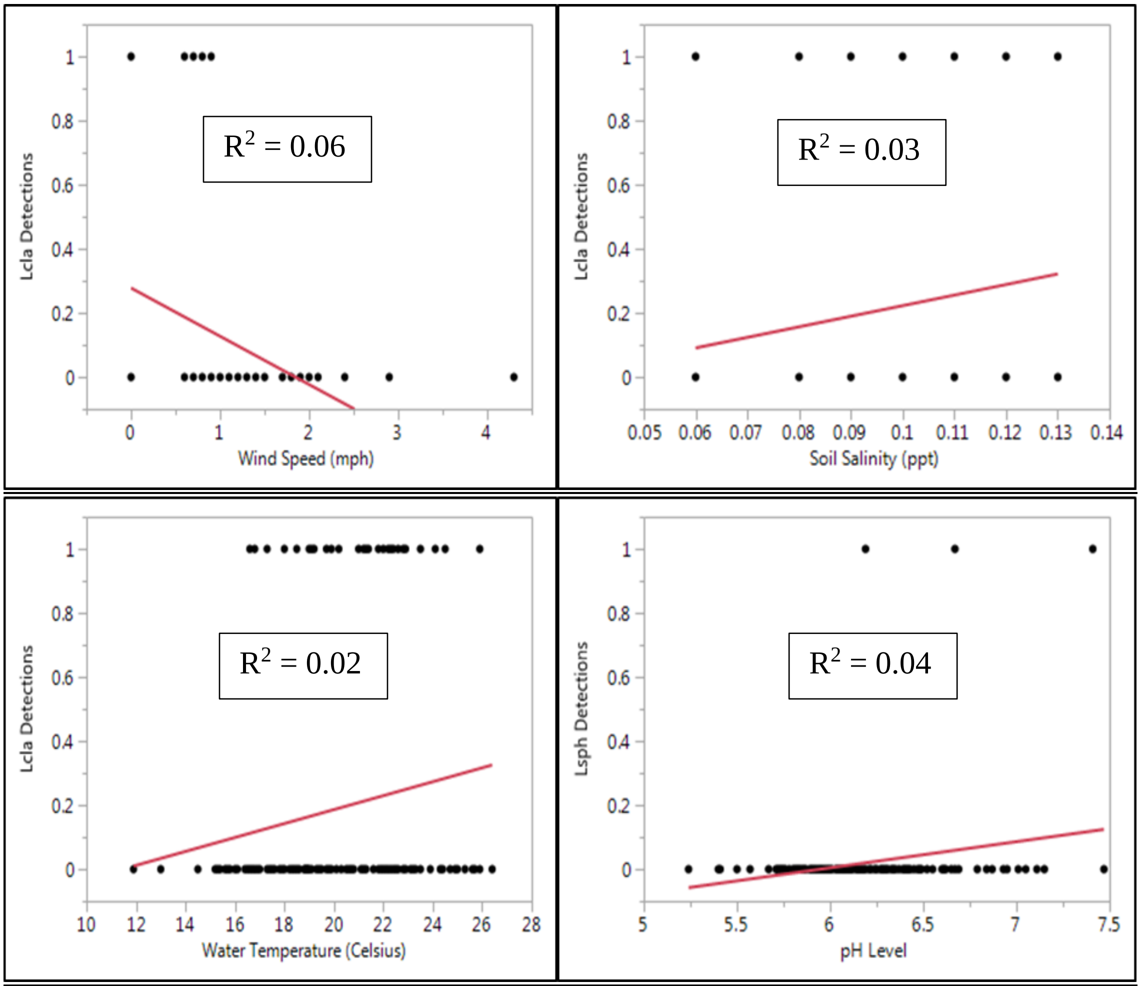


Figure 2.7: Regression analysis results with statistical fit values for the analysis in which there were no sample groupings or averaging of variables. Graphs show standard least squares regression residuals for environmental covariate (explanatory variable) and species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Lcla = Green Frog, Lsph = Southern Leopard Frog

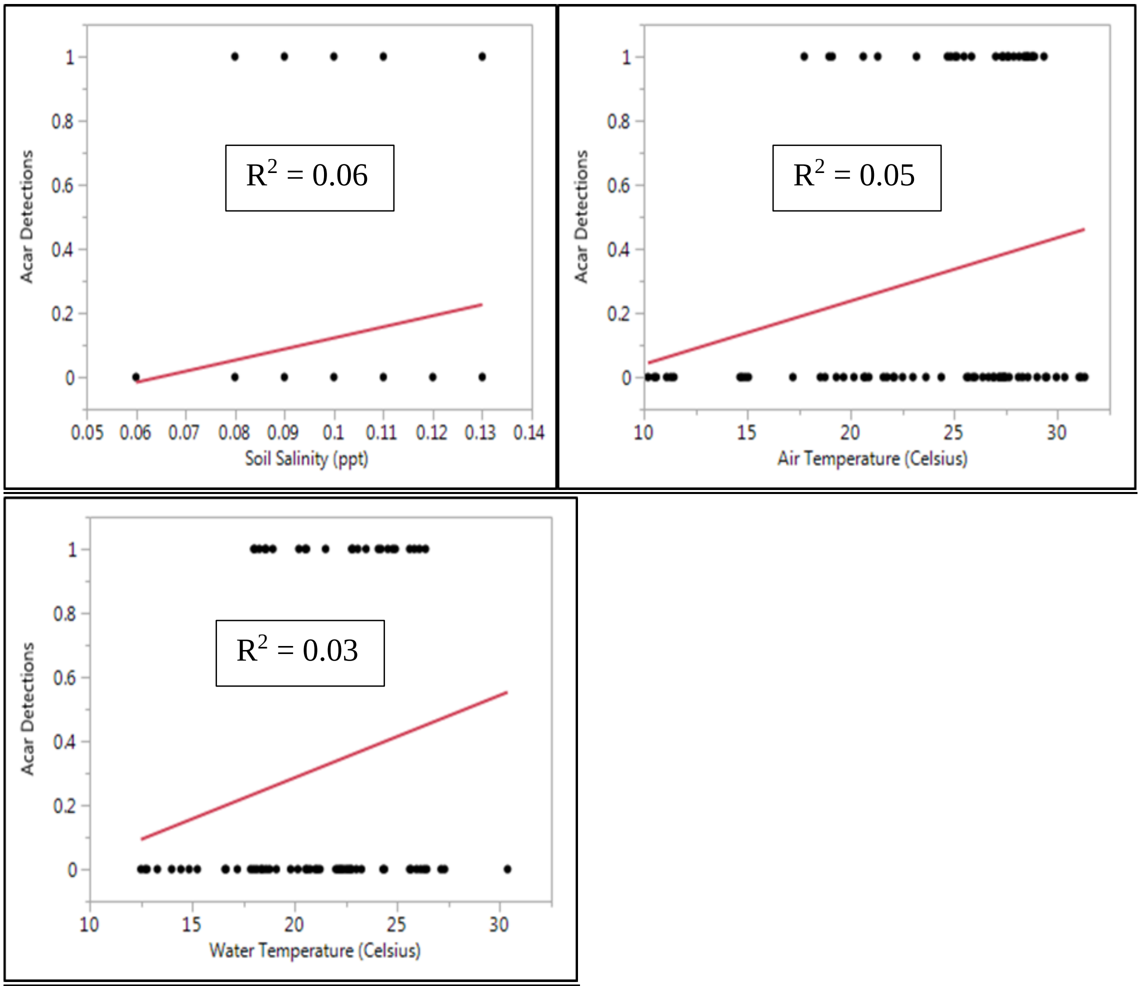


Figure 2.8: Regression analysis results with statistical fit values for the analysis in which there were no sample groupings or averaging of variables. Graphs show standard least squares regression residuals for environmental covariate (explanatory variable) and species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Acar = Green Anole

The three analyses that focused on hierarchical effects of sample groupings each had 7 species with significant relationships to environmental covariates. However, the number of significant species per taxa and the number of significant environmental variables per species changed with each grouping. Regressions evaluating year and site

variations by averaging monthly and plot-level samples had 1 salamander, 3 frogs, and 3 snakes with significant relationships to environmental covariates (Table 2.11, Figures 2.12-2.13). Soil and water salinity were both the most common environmental covariate, and it was also significant for 4 species (3 frogs, 1 snake). Water depth and weather condition were only significant for amphibians (1 salamander, 1 frog).

Species	Environmental Covariate	Effect Size	p-value
Southern Two-lined Salamander	Water Depth	0.06	0.0105
(*Eurycea cirrigera*)			
Gray Treefrog	pH	-0.23	0.0092
(*Hyla chrysoscelis*)	Water Depth	-0.01	0.048
	Water Salinity	-0.73	0.0503
Green Frog	Soil Salinity	-0.24	0.0131
(*Lithobates clamitans*)	Water Salinity	-0.31	0.0326
Southern Leopard Frog	Soil Salinity	0.82	0.0651
(*Lithobates sphenocephalus)*			
Eastern Cottonmouth	pH	-0.11	0.0460
(*Agkistrodon piscivorus*)			
Brown Watersnake	Air Temperature	0.03	0.0593
(*Nerodia taxispilota*)			
Banded watersnake	Water Salinity	-0.39	<0.0001
(*Nerodia fasciata*)	Soil Salinity	-0.25	0.0360

Table 2.11: Statistically significant ($p < 0.05$) standard least squares regression results for the analysis evaluating year and site variations by averaging monthly and plot-level samples of data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

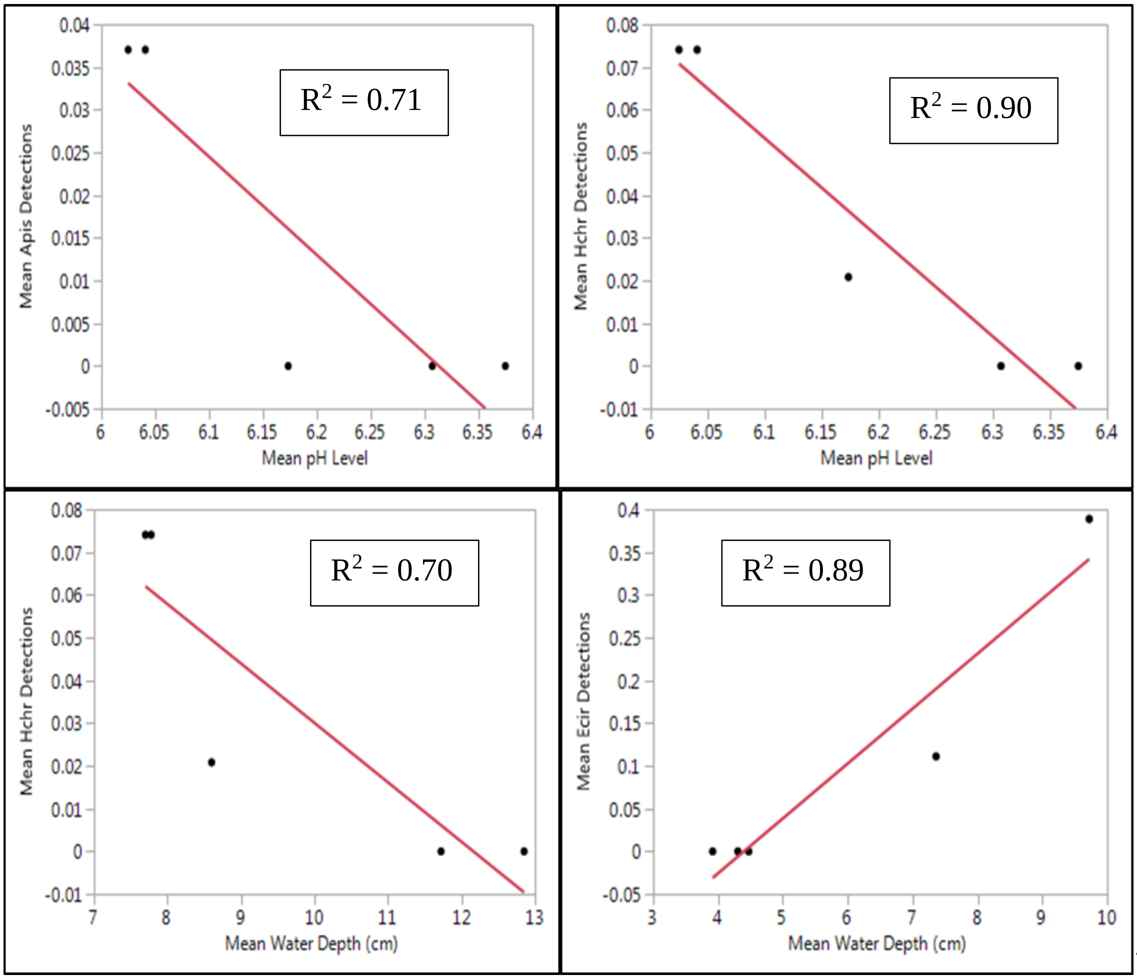


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Figure 2.9: Regression analysis results with statistical fit values for the analysis which focused on variation in years and sites by averaging monthly and plot-level samples. Graphs show standard least squares regression residuals for mean environmental covariate (explanatory variable) and mean species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Apis = Eastern Cottonmouth, Hchr = Gray Treefrog, Ecir = Southern Two-lined Salamander

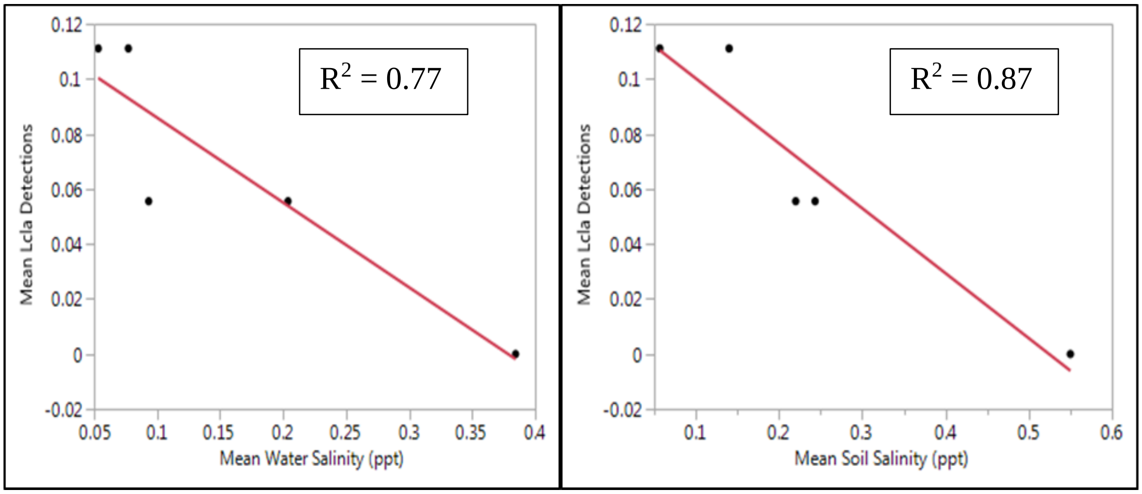


Figure 2.10: Regression analysis results with statistical fit values for the analysis which focused on variation in years and sites by averaging monthly and plot-level samples. Graphs show standard least squares regression residuals for mean environmental covariate (explanatory variable) and mean species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Lcla = Green Frog

Regressions evaluating variations in years, sites, and months by averaging plot-level samples had 1 salamander, 3 frogs, 1 lizard, and 2 snakes with significant relationships to environmental covariates (Table 2.12, Figures 2.14-2.16). Soil salinity was again with the most common environmental covariate, and again it was significant for 4 species (1 salamander, 1 lizard, and 2 snakes). The pH level was only significant for amphibians (3 frogs).

Species	Environmental Covariate	Effect Size	p-value
Southern Two-lined Salamander	Soil Salinity	-3.88	0.0345
(*Eurycea cirrigera*)	Water Depth	0.05	0.0011
Gray Treefrog	pH	-0.12	0.0052
(*Hyla chrysoscelis*)			
Green Anole	Soil Salinity	3.66	0.0406
(*Anolis carolinensis*)	Water Depth	0.02	0.0655
Green Frog	pH	0.11	0.0340
(*Lithobates clamitans*)	Wind Speed	-0.21	0.0375
Southern Leopard Frog	pH	0.09	0.0130
(*Lithobates sphenocephalus*)			
Ring-necked Snake	Soil Salinity	1.57	0.0247
(*Diadophis punctatus*)			
Banded Watersnake	Water Salinity	0.40	0.0454
(*Nerodia fasciata*)	Water Temperature	0.01	0.0698
	Soil Salinity	1.48	0.0020

Table 2.12: Statistically significant ($p < 0.05$) standard least squares regression results for the analysis evaluating year, site, and month by averaging plot-level samples of data collected from tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

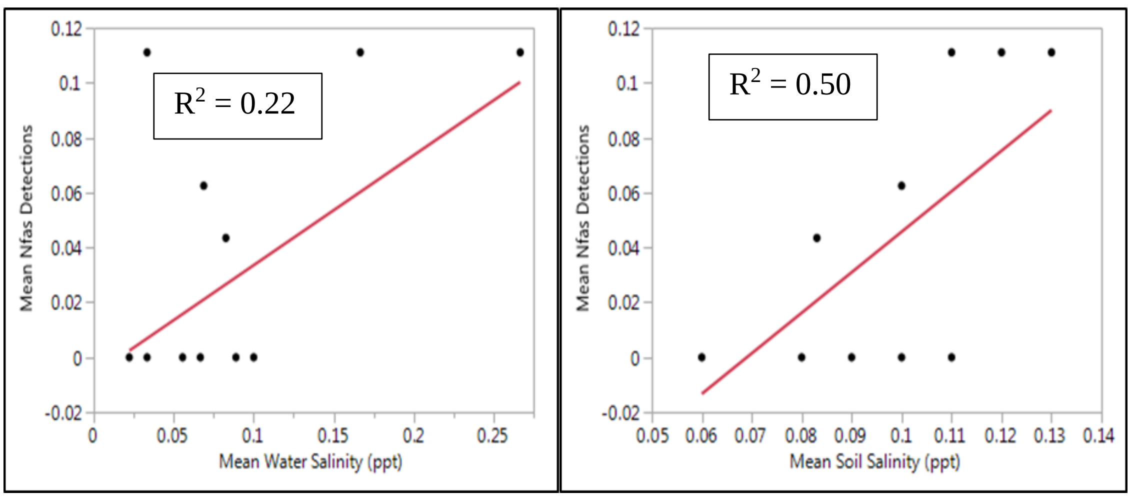


Figure 2.11: Regression analysis results with statistical fit values for the analysis which focused on variation in years, sites, and months by averaging plot-level samples. Graphs show standard least squares regression residuals for mean environmental covariate (explanatory variable) and mean species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Nfas = Banded Watersnake

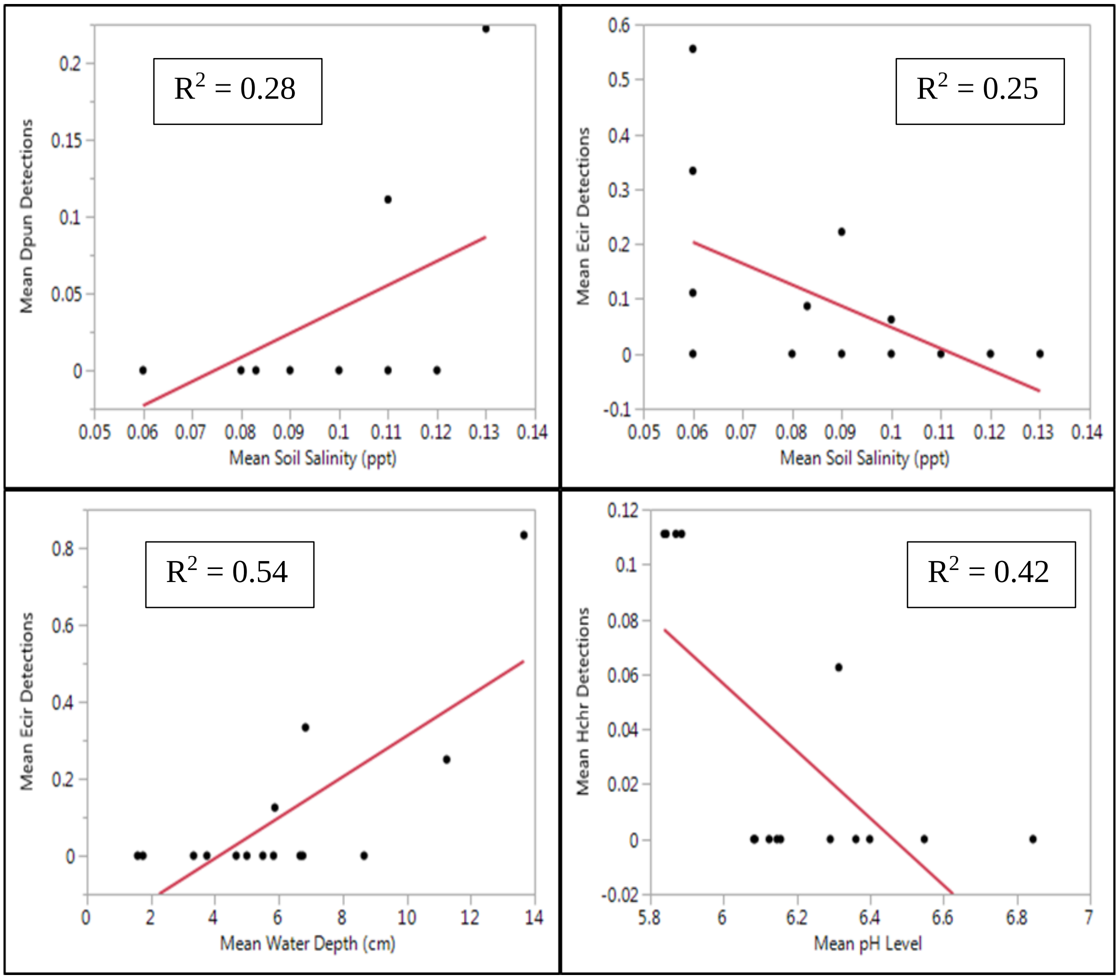


Figure 2.12: Regression analysis results with statistical fit values for the analysis which focused on variation in years, sites, and months by averaging plot-level samples. Graphs show standard least squares regression residuals for mean environmental covariate (explanatory variable) and mean species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Dpun = Ring-necked Snake, Ecir = Southern Two-lined Salamander, Hchr = Gray Treefrog

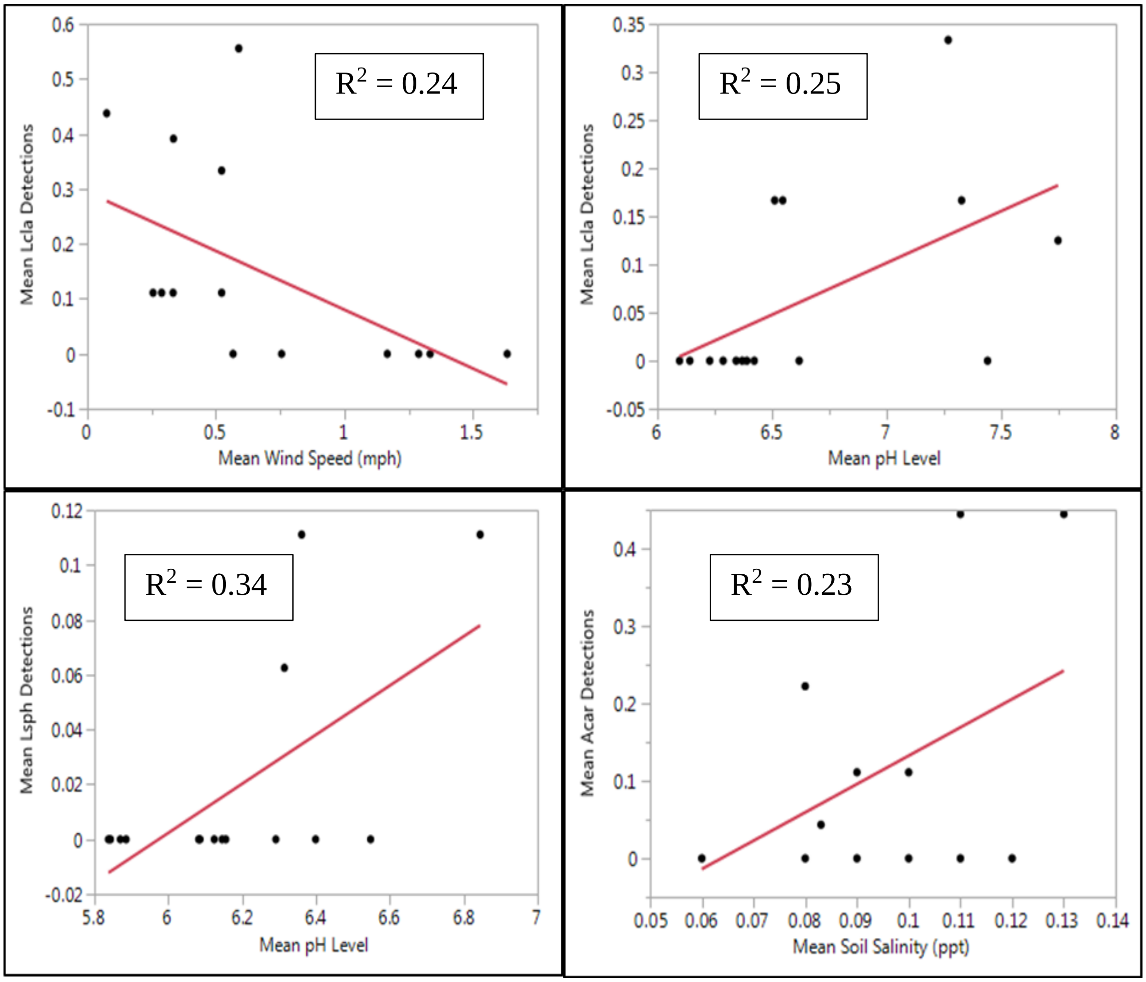


Figure 2.13: Regression analysis results with statistical fit values for the analysis which focused on variation in years, sites, and months by averaging plot-level samples. Graphs show standard least squares regression residuals for mean environmental covariate (explanatory variable) and mean species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Lcla = Green Frog, Lsph = Southern Leopard Frog, Acar = Green Anole

Standard least squares regressions evaluating year, site, and plot variations with averaged monthly samples had 1 salamander, 2 frogs, and 4 snakes with significant relationships (Table 2.13, Figures 2.9-2.11). Soil salinity was again the most common environmental

covariate, and it was significant for 4 species (1 salamander, 1 frog, and 2 snakes). Wind speed and water depth were only significant for amphibians (1 salamander, 1 frog).

Species	Environmental Covariate	Effect Size	p-value
Southern Two-lined Salamander	pH	-0.21	0.0693
(*Eurycea cirrigera*)	Soil Salinity	-6.16	<0.0001
	Wind speed	-0.27	0.0013
	Water Depth	0.03	<0.0001
Gray Treefrog	pH	-0.13	0.0492
(*Hyla chrysoscelis*)			
Green Frog	Wind Speed	-0.19	0.0023
(*Lithobates clamitans*)	Soil Salinity	4.78	0.0132
Ring-necked Snake	Soil Salinity	1.78	0.0064
(*Diadophis punctatus*)	Weather	0.05	0.0192
Eastern Cottonmouth	Soil Salinity	-0.26	0.0354
(*Agkistrodon piscivorus*)	pH	-0.11	0.0126
Brown Watersnake	Water Temperature	0.01	0.0535
(*Nerodia taxispilota*)			
Banded Watersnake	Air Temperature	0.007	0.0598
(*Nerodia fasciata*)			

Table 2.13: Statistically significant ($p < 0.05$) standard least squares regression for the analysis evaluating year, site, and plot by averaging monthly samples of data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

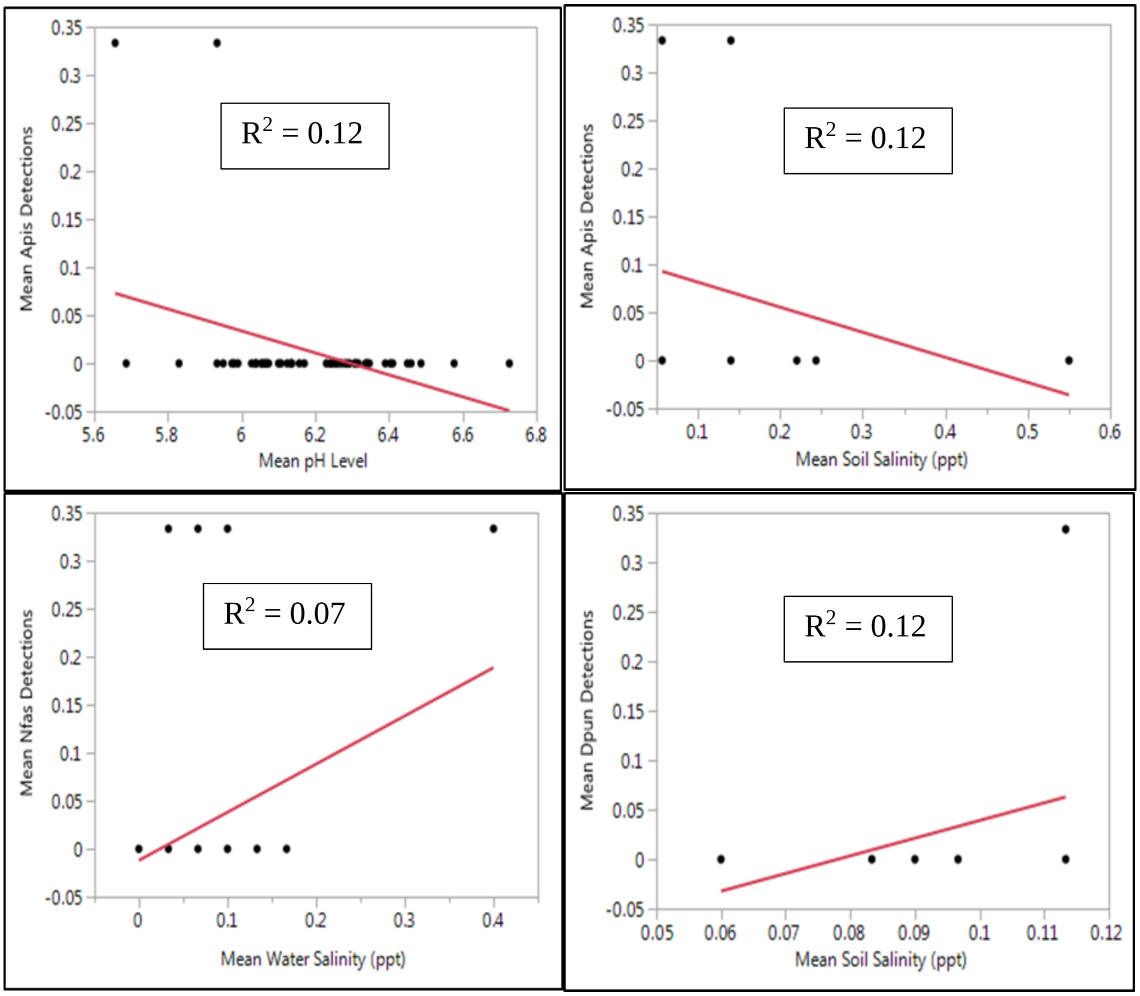


Figure 2.14: Regression analysis results with statistical fit values for the analysis which focused on variation in years, sites, and plots by averaging monthly samples. Graphs show standard least squares regression residuals for mean environmental covariate (explanatory variable) and mean species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Apis = Eastern Cottonmouth, Nfas = Banded Watersnake, Dpun = Ring-necked Snake

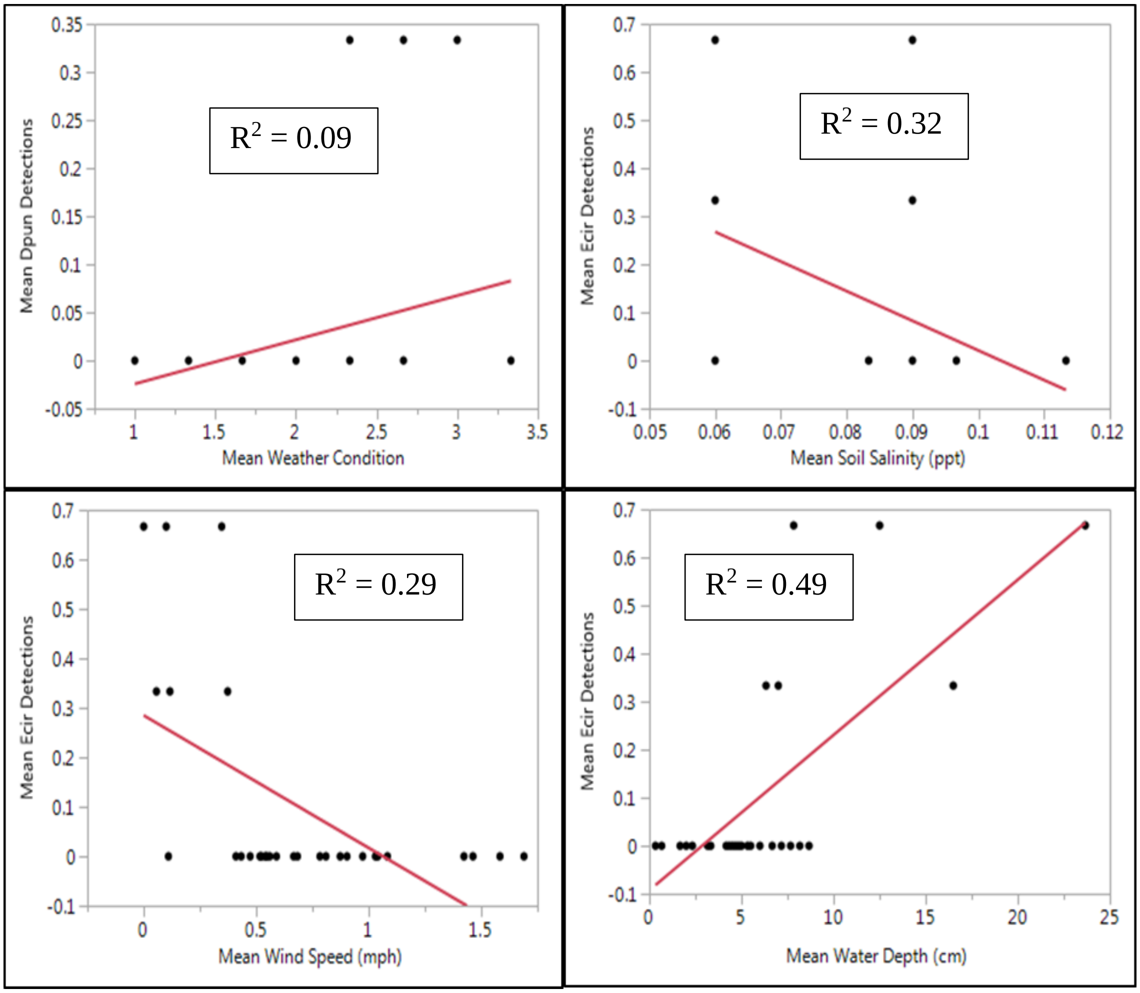


Figure 2.15: Regression analysis results with statistical fit values for the analysis which focused on variation in years, sites, and plots by averaging monthly samples. Graphs show standard least squares regression residuals for mean environmental covariate (explanatory variable) and mean species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Dpun = Ring-necked Snake, Ecir = Southern Two-lined Salamander

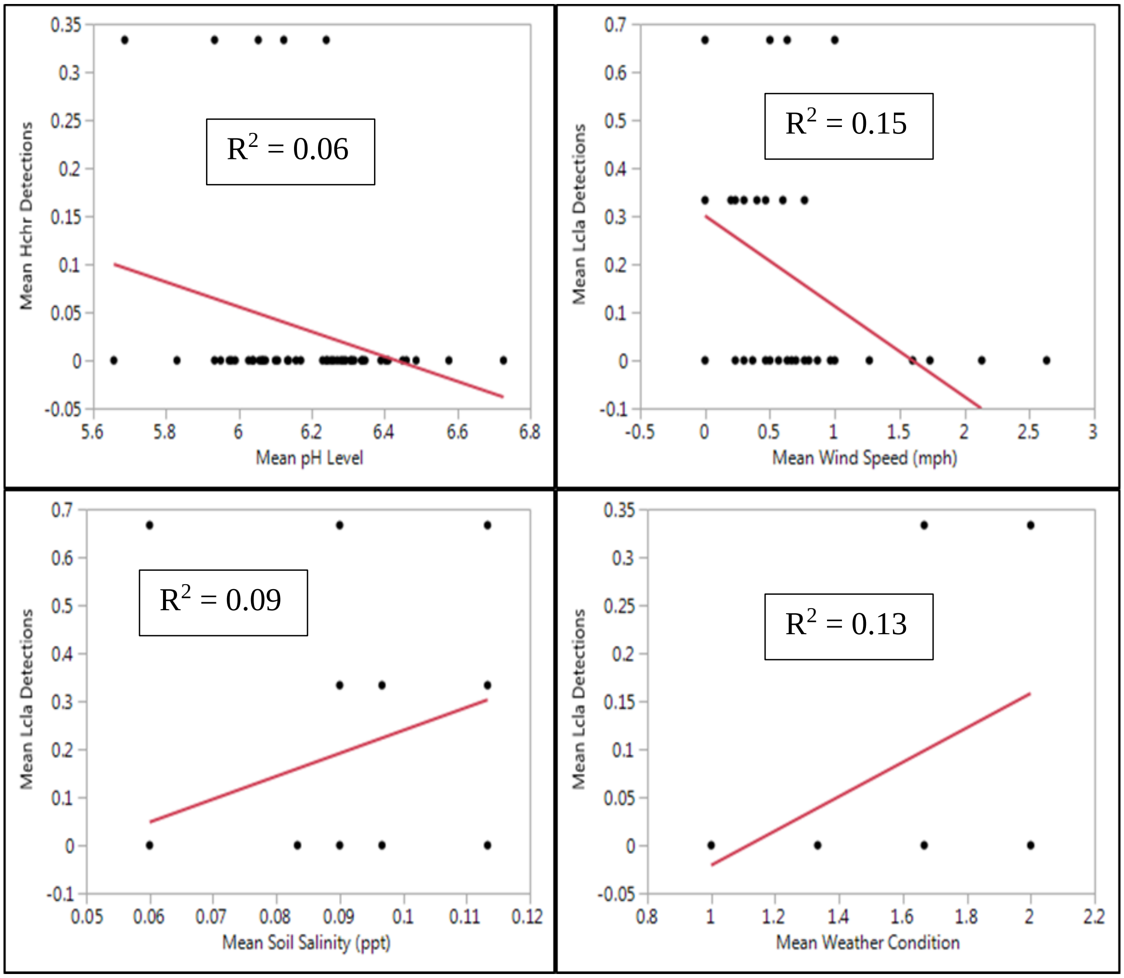


Figure 2.16: Regression analysis results with statistical fit values for the analysis which focused on variation in years, sites, and plots by averaging monthly samples. Graphs show standard least squares regression residuals for mean environmental covariate (explanatory variable) and mean species detection (response variable) data collected from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. Hchr = Gray Treefrog, Lcla = Green Frog

CHAPTER THREE

DISCUSSION

Herpetofauna Occupancy:

The Swamp 2 study site exhibited the highest total species richness and diversity levels along the salinity gradient (Figure 2.3). Increased salinity, feral hog rooting activity, and edge effects created by two canals produced a mosaic of marsh and forest habitats at this site. This site had the some of the highest hummock microhabitat cover in our study area (Appendix B). The increase in hummocks was accompanied by higher numbers of shrubs, and may have been influenced by a relatively large amount of dead and wind-thrown trees that may have acted as substrates for hummock formation. The increased amount of terrestrial habitat, in addition to the mosaic of marsh and forested habitat types, likely provided favorable conditions for herpetofauna. We suspect that this is why the species richness and diversity were highest at this site. In the Backswamp site, which had the second highest richness/diversity, there was much heterogeneity in water depths and hydrology due to a tidal creek and the transition into backswamp areas. The habitat heterogeneity at these sites could explain why species richness and diversity did not exhibit a linear decrease along the salinity gradient as we had originally predicted (Figure 2.3). A landscape mosaic (see Angelstam 1992, Debinski et al. 2001) of marsh and forest habitats, as well as water depths and hydrology, may be factors driving herpetofauna richness and diversity in tidal swamps.

If hummock cover had an influence on herpetofauna occurrence, we would have expected hummock microhabitat cover to be a significant covariate for a majority of species, yet this was only the case for two species (Table 2.3). The Ring-necked Snake (*Diadophis punctatus*; Linnaeus 1766) was primarily found in Swamp 2 (which had the highest amount of hummocks), and all detections of this species were on hummocks. However, hummock cover was not selected as a top site covariate for this species in either the occupancy analyses or the standard least squares regressions. It is possible that a statistical relationship between hummock cover and individual species data are not detectable. Yet, the lack of a significant relationship between this species' occurrence and hummock cover is perplexing. The lack of a statistical relationship between hummock cover and species diversity/richness data suggests that this covariate is not directly influencing herpetofauna in tidal swamps.

With these ideas in mind, we tested the statistical relationship between increased hummock cover and species richness and diversity. We ran a correlation analysis of site-level species richness/diversity and the average percent hummock cover per site. The 2016 data had a moderate level of correlation ($R = 0.66$), but an F-test failed to detect a statistically significant relationship ($p = 0.11$). The 2017 data had a weaker relationship ($R = 0.37$), and an F-test again failed to detect a significant relationship ($p = 0.27$). A landscape-level effect such of habitat mosaics may instead be the driver of observed species richness and diversity patterns. However, we did not collect the data necessary to test for statistical relationships of landscape-level habitat arrangements.

Our occupancy analysis and standard least squares regression results suggest that soil salinity has a large influence on the occurrence of herpetofauna in the tidal swamps that we surveyed. However, the relationships with soil salinity varied substantially between species. Most species detections exhibited a negative relationship with increasing soil and water salinity. Yet the Southern Leopard Frog, Banded Watersnake, and Ring-necked Snake detections appeared to increase in response to increased soil salinities. Banded Watersnake detections also increased in response to increased water salinities. Soil salinity is directly increased by increases in water salinity via diffusion into soil pore spaces, though it can also be elevated via changes in groundwater levels and additions of contaminants (Odum et al. 1984, Krauss et al. 2009b). Soil salinity has a longer residence time and therefore a larger influence on wetland vegetation, which is probably why it was the most common significant covariate in our analyses.

In one instance, the interpretation of the Green Frog's (*Lithobates clamitans*; Latreille, in Sonnini de Manoncourt and Latreille 1801) relationship between species detections and soil salinity changed depending upon the specific analysis. Green Frogs exhibited both a positive and negative relationship with soil salinity in the occupancy analyses, depending on which sample season was analyzed (Table 2.5). Green Frogs exhibited a positive relationship with increasing soil salinity in the standard least squares regression in which no values were altered and regression which focused on the variation in years, sites, and plots by averaging monthly samples. However, in the regression which only focused on variations in years and sites by averaging plot-level and monthly values, Green Frogs exhibited a negative relationship with increasing soil salinity (Figure

2.10). The regression which focused on variations in year, sites, and months by averaging plot-level values failed to detect a significant relationship. The directional change in the Green Frog's relationship with salinity was likely an effect of sample grouping. The only analysis which exhibited a negative relationship with soil salinity had larger variation in detection values due to a greatly reduced sample size (N = 5).

Salinity levels and water pH are interrelated and exert influences on each other (Robinson 1929). As salinity increases, pH tends to move toward neutral (Robinson 1929). However, depending on the initial chemistry, the pH may increase with salinity (Robinson 1929) This is because natural salts present in water act as bases which react with hydrogen and increase pH values (Robinson 1929, Millero 1986). Thus, increases in pH usually result from a corresponding increase in salinity. Large temporal spikes in salinity corresponded with spikes in pH values in our measured environmental data, supporting this trend (Appendix B). This explains the somewhat counterintuitive pattern of decreasing amphibian detections in response to increasing pH values, and vice versa. The pH values are also influenced by increasing temperature, exhibiting a negative relationship (Ashton and Geary 2011, Appendix B). This is why our measured environmental data display a stable or decreasing trend in pH values over the course of both seasons despite increasing salinity levels (Appendix B). Based on the positive relationship between Green Frog's detections and increasing pH values in the other analyses, which had larger sample sizes, the data seem to support a positive relationship with increasing salinity levels.

As previously mentioned, increasing salinity has been known to convert plant communities from forest to marsh. This transition allows more sunlight penetration and favors shrubs and herbaceous vegetation, providing more variation in habitat structure than primarily forested areas. Both basal area and canopy cover had high negative correlations with soil salinity, so increasing soil salinity could be considered as a proxy for reduced forest cover. This is one probable reason why several species exhibited an increase in detections in response to increasing salinity. On the other hand, species that require salt-sensitive vegetation structure, such as tree canopy cover, would be expected to exhibit a negative relationship with increasing salinity. For example, Southern Two-Lined Salamanders were only detected in forested plots, and they exhibit a negative relationship with increasing salinity. The fact that canopy cover was not a significant variable in the analyses can be attributed to the general lack of variation in the data (Appendix B). That is, the majority of our plots were forested or open marsh, with very few transitional plots.

Another possible explanation of the relationship between salinity and herpetofauna occurrence is that the changes in vegetation structure along the salinity gradient affected our detections. That is, the transition from forest to marsh habitat affected visibility and therefore affected detections. This is unlikely, since the standard least squares regression analyses found similar trends regardless of which sample groupings were analyzed (i.e., no unique plot-level trends). In addition, the occupancy modeling suggested that the sample date, weather conditions, or air temperature were most likely to affect detections (Table 2.3). All of the species exhibiting a positive

relationship with increasing salinity were habitat generalists, which implies that no specific habitat structure influenced detections. Changes in habitat structure could also be assumed to increase abundances of some herpetofauna prey species. Increasing detections also could have occurred as a response to increased prey abundance along the salinity gradient. It is possible that increases in Banded Watersnake detections may have been driven by increases in fish prey abundance along the gradient (Appendix D). This species occurred in all of our study sites, so differences in habitat structure do not adequately explain the increase in detections for this species. Increases in prey species abundances better explain the increases in this species' detections with increasing salinity.

Several species were influenced by water depth. In particular, the Southern Two-Lined Salamander exhibited an increase in occupancy probability with increasing depths (Tables 2.5, 2.9). The trend in the salamanders is likely a result of tidal flooding that led them to crowd on whatever terrestrial habitat remained during the time of our surveys, which increased detections. Salamander detections continued to increase up to the maximum mean depth recorded (~25 centimeters), by which point almost all terrestrial habitats were submerged (Appendix D). Another possibility is that lower elevation areas retain more water than shallower areas after tides recede, so the Two-lined Salamander may have greater detectability in areas with lower elevations (i.e., more "permanent" pools). Conversely, Green and Gray Treefrogs exhibited decreasing detections with increasing depths (Tables 2.5, 2.9; Appendix D). Green and Gray Treefrogs were usually detected in shallow habitats further away from flooding, which may negate tidal fluxes. The data indicate that Green Treefrogs were not detected past water depths of 20

centimeters, and Gray Treefrogs (*Hyla chrysoscelis*; Cope 1880) were not detected past water depths of 8 centimeters. Another consideration is that increasing water depths may increase the presence of Green and Gray Treefrog larval predators (e.g., fish), which would negatively affect their occurrence.

Lastly, several reptiles and amphibians exhibited relationships with increasing meteorological variables. Increasing wind speeds negatively influenced several amphibian species' detections, which is to be expected given amphibians' sensitivity to desiccation (Tables 2.5, 2.9). Weather conditions also influenced some reptile detections. Green Frogs and Ring-necked Snakes both exhibited a positive relationship with overcast weather conditions. Increased air humidity and reduced temperatures during overcast weather may provide favorable conditions for amphibians and smaller-bodied reptiles that are vulnerable to desiccation. In the case of the Ring-necked Snake, increased detections on overcast days may have been an indirect result of increased prey (e.g., salamander, earthworm) activity. Green Frogs and Green Anoles both exhibited a positive relationship with increasing temperature (Tables 2.5, 2.9). Increased detections in response to air and water temperatures are also to be expected since these species are ectotherms and respond favorably to higher temperatures near their thermal optima. The Green Frog's relationship with water temperature was expected given their aquatic lifestyle, but Green Anole's relationship with water temperature was interesting and slightly unexpected.

We have three possible explanations for this relationship. The first is that increased water temperatures facilitate swimming, which may be a necessary form of

locomotion for this species in tidal swamps, by reducing heat exchange between the lizards and the water. This would be important because the relatively small size of these lizards increases the surface area-volume ratio and thus heat exchange (Schmidt-Nielsen 1984). Water temperature would not be expected to be significant for the other reptile species in our study because they are either larger-bodied (less surface area for heat exchange) or they do not spend as much time in the water (e.g., skinks, Ring-necked Snakes). The second explanation is that increasing water temperatures increased the abundance of Green Anole prey species (e.g., emerging aquatic insects) and led to an increase in Green Anole foraging activity. Third, air temperature and water temperature are highly correlated. So, water temperature's significant relationship with Green Anole detections may just be an artifact of collinearity in our data. That is, because air temperature and water temperature display follow similar patterns with the detection data (Appendix D), both were found to be significant.

Study Design Limitations:

The field component of our study, like many wildlife studies, was limited by the logistical tradeoff between the maximum number of samples we could obtain and the time and effort required to adequately collect the necessary data. It may seem obvious, but the tidal fluctuations made balancing this tradeoff more difficult. A major limitation to our surveys was the difficulty of walking through the soft, unstable soils in the tidal swamps, which greatly reduced our mobility and increased travel time between plots. This reduced the number of plots we could sample. The soft soils and surface water

transferred vibrations from our movements and may have alerted the animals to our presence before they were detectable. On most occasions, we were able to detect and positively identify herpetofauna, even if we were unable to capture them for additional data collection. However, on a number of occasions we were unable to get close enough to the animals to gain a positive identification. We had hoped to counter these issues with our cover boards and aquatic traps. Yet, these methods performed poorly, which reduced our number of detections and associated data points.

It seems that some conventional sampling methods for herpetofauna are simply ineffective in tidal swamps. Surprisingly, this has been true for the trash can traps, turtle hoop nets, and dip nets in our study. For some species, such as aquatic salamanders and rare aquatic snakes, capture rates may be influenced by sampling intensity, specific sampling locations, or trap types. For example, aquatic salamander surveys at the Okeefenokee Swamp in Georgia had an overall capture rate of about five percent, whereas crawfish traps had a capture rate of about 23 percent, and minnow traps had a capture rate of less than one percent (Sorenson 2002). Cover board grids in southern Georgia found similar numbers of species compared to natural cover, but at lower rates and with more variability in numbers (Houze and Chandler 2002). We regularly checked natural cover objects, when available. However, natural cover objects were usually lacking due to tidal movement of debris, and we did not notice any appreciable differences in detections between the cover boards and natural cover objects.

The poor performance of the aquatic traps was unexpected, given their performance in other studies of wetland herpetofauna. Despite the dynamic tidal fluxes of

water that occurred in our sample plots, we did our best to place traps in depressions or rivulets that would maintain standing water after tides had receded. The constant captures of aquatic bycatch species implied that we had placed our traps in areas that received adequate water levels for aquatic organisms to persist. We placed cover boards on the highest elevation terrain possible, though some sample plots had no appreciable changes in terrain. We made several adjustments to try and rectify perceived issues with our sampling methods. We created a hybrid of area- and time-constrained surveys (by instituting a minimum search time within constrained plots) after it became apparent that some plots may not have been sampled evenly due to variation in vegetation structure. If necessary, we scoured the soil to create water-holding depressions for the aquatic traps.

We also tried baiting the traps with sardines during the last month of the 2016 season in an attempt to improve capture rates. The baiting failed to improve herpetofauna captures, though we did note an increase in bycatch. We used glow stick attractants as bait for our traps during the entirety of the 2017 season in a similar attempt. These attractants increased amphibian captures in other studies (Grayson and Roe 2007, Bennett et al. 2012). Capture rates did not noticeably improve, though we again captured more bycatch. The increased bycatch may have attracted the only aquatic salamander we captured during our study. When we realized that aquatic traps were failing to capture aquatic salamanders and larval amphibians, we made several dedicated dip netting efforts. These efforts did not improve our detections, suggesting that there a natural dearth of aquatic herpetofauna.

The analytical component of our study was limited by the lack of data that resulted from the previously mentioned sampling issues. This limited the number of analyses that we could complete, which in turn limited the amount of information we could produce. The standard least squares regression analyses function similarly to the occupancy analysis by attempting to determine the relationship between species occurrence data and select environmental covariates. However, the regression analyses do not incorporate imperfect detection probabilities and must complete the analyses with apparent occupancy data instead. It should also be noted that the regression analyses were only conducted with univariate models (one species, one environmental covariate), which precludes inferences as to whether an environmental covariate was the primary driver of apparent occupancy or part of a group of environmental covariates driving occupancy.

The standard least squares regression analyses failed to generate accurate occupancy estimates (i.e., adjusted occupancy probabilities). Imperfect detection has been demonstrated to skew abundance estimates by an order or magnitude, and it could likewise be expected to skew occupancy estimates (Royle et al. 2005, O'Donnell and Semlitsch 2015). Accounting for imperfect detection is critical to make accurate population inferences (Royle et al. 2005). Therefore, any estimates generated via the regressions may not be useful in predicting quantitative species responses to changing covariate values. However, we can still assess general occurrence patterns with this approach. One advantage to using the regression analyses was our ability to evaluate hierarchical effects in the data set. This proved useful for the Green Frog regression results, which were contradicting depending on which analysis results were interpreted. It

also proved useful in interpreting whether or not some of the relationships exhibited in the regression results may have been influenced by increases in apparent detections rates. However, we cannot fully rule out this possibility since we were not able to incorporate detection probabilities into our analyses and had to rely on raw detection data.

Future Impacts to Tidal Swamp Herpetofauna:

The Savannah Harbor Expansion Project (SHEP) is an ongoing Corps of Engineers project to deepen the shipping channel of the Savannah Harbor by 1.52 meters to improve container ship access and increase trade (USACE 2012a). Increased salinity and decreased DO levels are predicted to result from the Savannah Harbor expansion (USACE 2012a). Water quality modeling indicated that flow re-routing and an oxygen injection system would be needed to mitigate the predicted project impacts (USACE 2012a), and both mitigation measures are currently being implemented. Project completion is expected during 2018 (USACE 2012a). Even with mitigation, DO is predicted to decrease in the upper reaches of the river near the I-95 bridge crossing and increase in the lower reaches near Tybee Island (USACE 2012a).

Conversion of salt marsh to brackish marsh will occur as a result of mitigation features (USACE 2012a). Without mitigation, ~1,100 acres of tidal freshwater wetlands were expected to be lost, but with mitigation this estimate drops to ~220 acres (USACE 2012a). The Corps of Engineers’ flow alterations are expected to have a positive impact on the herpetofauna of tidal swamps by increasing freshwater flow and closing existing canals (USACE 2012a), which will create new wetland habitat as canals fill with

sediment. The flow re-routing is also expected to restore marsh at Onslow Island (USACE 2012a). However, an initial increase in surface water salinity arising from SHEP will likely increase soil salinity, which has been suggested by our analyses to differentially influence herpetofauna occurrence.

The overall impact of SHEP will be species dependent. Even after increased freshwater flows are established by the Corps of Engineers' mitigation strategy, soil salinities may still be elevated. No conversion of tidal freshwater marsh to tidal swamp is anticipated in the areas targeted for mitigation (USACE 2012a). Therefore, we anticipate a net loss of tidal swamp extent within the upper reaches of the Savannah River estuary. Our results suggest that some species may decline during an initial increase in soil salinity. The largest impacts will be on herpetofauna that are dependent on forest structure or the environmental conditions therein (i.e., Southern Two-Lined Salamanders). Generalist species will likely be able to persist despite an initial salinity increase. If initial salinity changes promote a mosaic of swamp and marsh habitats, there may be positive impacts on herpetofauna richness and diversity. However, if salinity increases are more severe and greatly reduce the extent of tidal swamps, then the impacts for most herpetofauna will be negative. Conditions for herpetofauna will improve after the mitigation strategies go into full effect.

In the long-term, sea level rise will continue to negatively influence conditions in tidal swamps and convert them to marsh and open water unless there is intervention. Most herpetofauna can be expected to disappear from existing tidal swamps unless preemptive measures are taken to ensure tidal swamp persistence. In this regard, there are

some options. Salt resistant strains of baldcypress have been identified and used in several restoration projects associated with post-hurricane restoration efforts (Krauss et al. 2007). Restoration success in tidal forests can be variable and depends on the existing forest structure and the seedling source population (Conner et al. 2012). These type of restoration efforts have been considered as a tool to mitigate the effects of climate change and SLR on tidal swamps. Wastewater effluent additions to wetlands in Louisiana almost matched historical wetland subsidence rates (Rybczyk et al. 2002). The wastewater effluents did not degrade the wetlands (Rybczyk et al. 2002), so this could be another viable option for mitigating SLR. A final alternative is the planning and creation of migration corridors to facilitate tidal swamp migration further inland (Leonard et al. 2017).This option is probably the best long-term strategy for conservation of herpetofauna in tidal swamps, given the trends and available information.

Future Research Topics:

One of the first surprises during our research, which begs further study, was the distinct absence of larval amphibians during our surveys. Despite using multiple larval amphibian sampling methods, we only detected one tadpole and one egg mass during the entirety of our study. We found aquatic salamanders in mucky, unconsolidated soils that are constantly water-saturated instead of the water columns, likely because of tidal constraints. Could larval amphibians be using similar habitats for their development? If so, this could be a novel behavioral adaptation to the fluctuating water levels in tidal swamps.

We found a relatively low number of adult amphibians, which initially was not surprising. Yet given the apparent absence of amphibian larvae, there does not appear to be enough successful amphibian reproduction occurring within tidal swamps to maintain the adult populations that we encountered during our study. It is possible that tidal swamps act as population sinks for some herpetofauna. Could immigration of individuals from outside the tidal swamps or from transitional zones (tidal to non-tidal swamp, wetland to upland) be offsetting amphibian reproductive failure in tidal swamps? If amphibian larvae are inherently difficult to detect in tidal swamps, or if they are using novel habitat features or behaviors that make them unobservable, then this may be a moot point. However, this could be an interesting topic for future research.

The lack of aquatic salamander (i.e. *Siren, Amphiuma*) detections was another surprise, given the amount of area we surveyed and the large number of traps we had running during any given sampling period. We expected to encounter more of these salamanders during our study because the tidal swamps had an abundance of habitats with characteristics that are positively associated with their occurrence (Snodgrass et al. 1999). Siren and amphiuma are only known to regularly burrow during droughts, though they may spend a large amount of time in muck in some regions (Sorenson 2002). Yet, the aquatic salamanders we detected were only found in these muck habitats, and not in the water column. Could aquatic salamanders in tidal swamps be displaying a novel behavioral pattern or a unique microhabitat association in response to the hydrology of tidal swamps?

Finally, while reviewing our data, we hypothesized that the relatively low number of adult frogs, as well as the absence of larval amphibians, could be a byproduct of a predator subsidy (see Ostfeld and Keesing 2000, Wesner 2010 for examples). Since tides subsidize nutrients in tidal swamps, there may be a bottom-up trophic cascade that is elevating fish predator abundances (e.g., mummichogs). The elevated fish populations would likely exert increased predation pressure on amphibian eggs and larvae. The elevated fish abundances may in turn subsidize watersnake populations, which predate adult amphibians. The effect of these predator subsidies, in combination with the pre-existing environmental constraints, could reduce amphibian populations to the low levels that we encountered during our study. If amphibian populations were to drop below the foraging thresholds exhibited by aquatic snakes and/or fish, then they could switch to an alternative prey base (e.g., snakes could switch over to the increased fish predators) until the amphibian populations recovered. An investigation of this topic could help clarify herpetofauna ecology and trophic dynamics in tidal swamps.

Conclusion:

Based on our observations and the results or our analyses, we concur with Swarth and Kiviat's (2009) position that herpetofauna are limited in tidal swamps by their tidal regimes. The tidal regime determines water depths, as well salinity; these changes in salinity in turn influence other factors such as pH. All of these factors appear to influence a number of the herpetofauna species in the tidal swamps of the Savannah National Wildlife Refuge, though soil salinity seems to have a large influence. However, observed

species richness and diversity patterns were less clear and may be related to landscape-level configurations of tidal swamp and marsh habits, as well as hydrology. In the short-term, the Savannah Harbor Expansion Project is expected to create mixed impacts on the herpetofauna in tidal swamps. Changes in habitat will likely exert large impacts on herpetofauna richness and diversity, though these impacts may be difficult to predict. Changes in water conditions resulting from the Corps of Engineers' mitigation strategies are likely to create positive impacts on herpetofauna occurrence, though there may initially be negative impacts. In the long term, sea level rise is likely to negatively impact herpetofauna occurrence in tidal swamps unless they, and their habitats, are able to migrate further inland. All of these impacts will vary spatially and temporally in response to natural feedbacks and future anthropogenic influences on coastal rivers.

APPENDICES

Appendix A

Species Inventory and Detection Data

Total Species Inventory March-June 2016 and 2017
(Common Name, Scientific Name, Four Letter Species Abbreviation)

FROGS:
Green Treefrog (*Hyla cinerea*; Hcin)
Grey Treefrog (*Hyla chrysoscelis*; Hchr)
Spring Peeper
(*Pseudacris crucifer*; Pcru)*
Bronze Frog
(*Lithobates clamitans*; Lcla)
Leopard Frog
(*Lithobates sphenocephalus*; Lsph)
Squirrel Treefrog (*Hyla squirrela*; Hsqu)
River Frog (*Lithobates hecksheri*; Lhec)
American Bullfrog
(*Lithobates catesbeianus*; Lcat)*
Pig Frog (*Lithobates grylio*; Lgry)*

SALAMANDERS:
Southern Two-lined Salamander
(*Eurycea cirrigera*; Ecir)
Lesser Siren (*Siren intermedia*; Sint)
Two-toed Amphiuma
(*Amphiuma means*; Amea)*

TURTLES:
Eastern Mud Turtle
(*Kinosternon subrubrum*; Ksub)
Common Snapping Turtle
(*Chelydra serpentina*; Cser)*
Yellowbelly Slider
(*Trachemys scripta*; Tscr)*
Common Musk Turtle
(*Sternotherus odoratus*; Sodo)
Florida Softshell Turtle
(*Apalone ferox*; Afer)*

LIZARDS:
Green Anole (*Anolis carolinensis*; Acar)
Common Five-lined Skink
(*Plestiodon fasciatus*; Pfas)
Broad-headed Skink
(*Plestiodon laticeps*; Plat)

CROCODILIANS:
American Alligator
(*Alligator mississippiensis*; Amis)*

SNAKES:
Cottonmouth
(*Agkistrodon piscivorous*; Apis)
Brown Watersnake
(*Nerodia taxispilota*; Ntax)
Banded Watersnake
(*Nerodia fasciata*; Nfas)
Plain-bellied Watersnake
(*Nerodia erythrogaster*; Nery)*
Eastern Ribbon Snake
(*Thamnophis sauritus*; Tsau)
Black Racer
(*Coluber constrictor*; Ccon)*
Ring-necked Snake
(*Diadophis punctatus*; Dpun)
Yellow Ratsnake
(*Pantherophis alleghaniensis*; Pall)*
Mud Snake (*Farancia abacura*; Faba)*
Rainbow Snake
(*Farancia erytrogramma*; Fery)*
Glossy Swamp Snake
(*Liodytes rigida*; Lrig)*
Black Swamp Snake
(*Liodytes pygaea*; Lpyg)
Rough Green Snake
(*Opheodrys aestivus*; Oaes)

* = Only detected outside of study plots

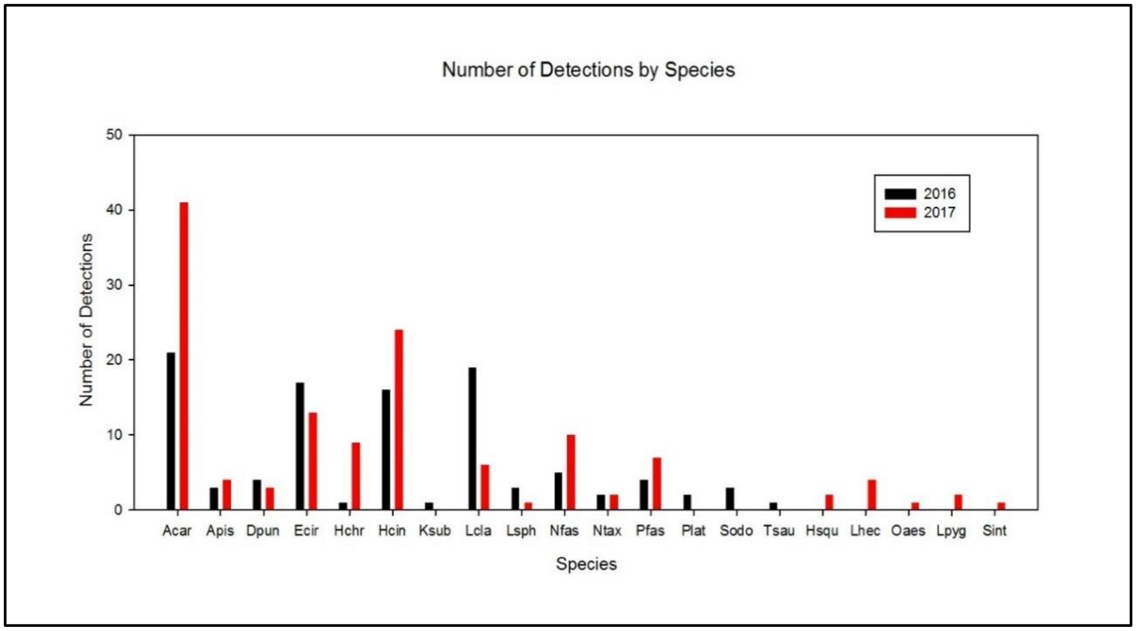


Figure A-1: Number of detections per species for both years of sampling in tidal swamps of the Savannah National Wildlife Refuge. Sampling occurred during March to June 2016 and 2017. See species inventory for listing of species abbreviations.

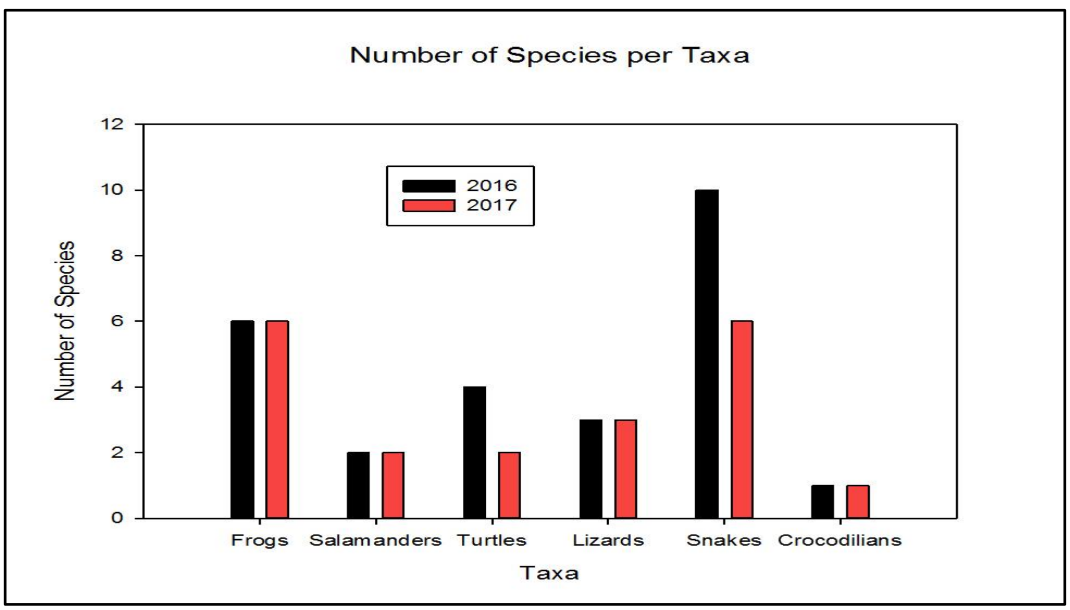


Figure A-2: Number of species in each reptile and amphibian taxa encountered in the tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

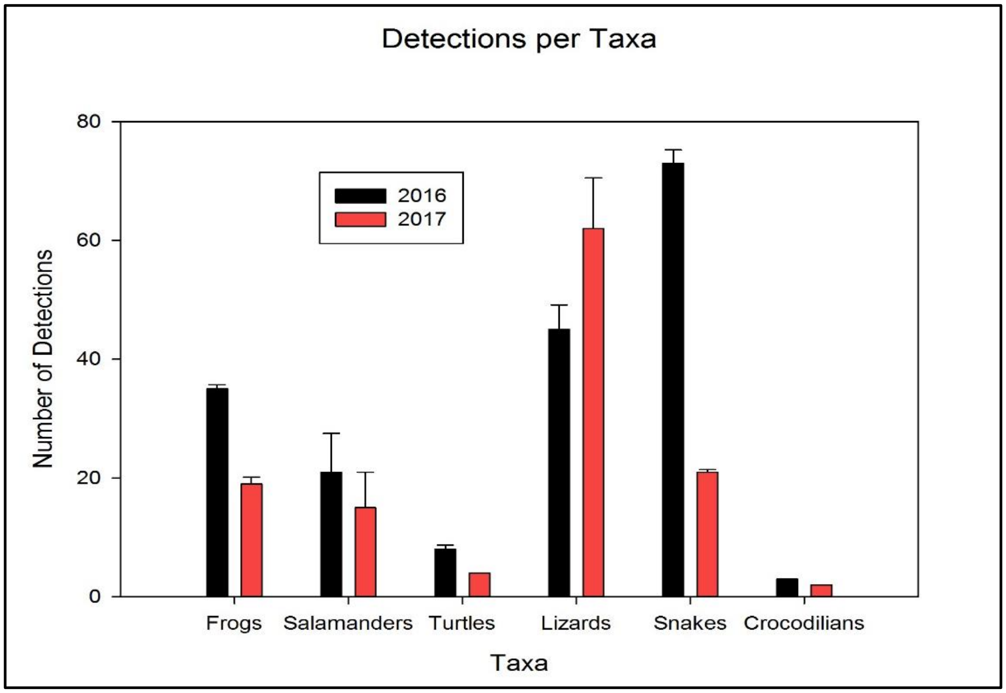


Figure A-3: Number of individual animals detected in each reptile and amphibian taxa Encountered in the tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

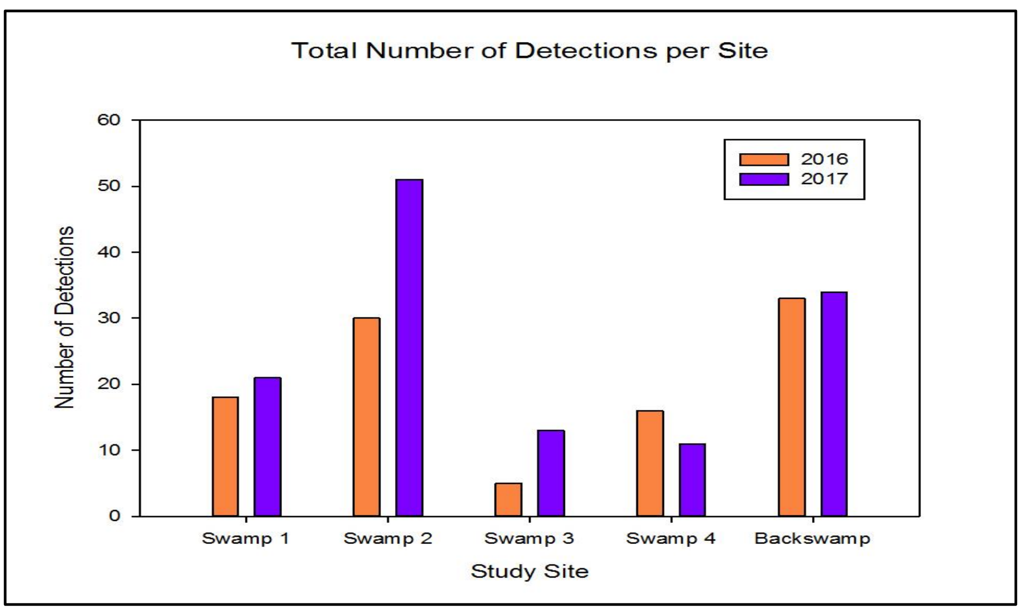


Figure A-4: Number of individual detections per study site in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

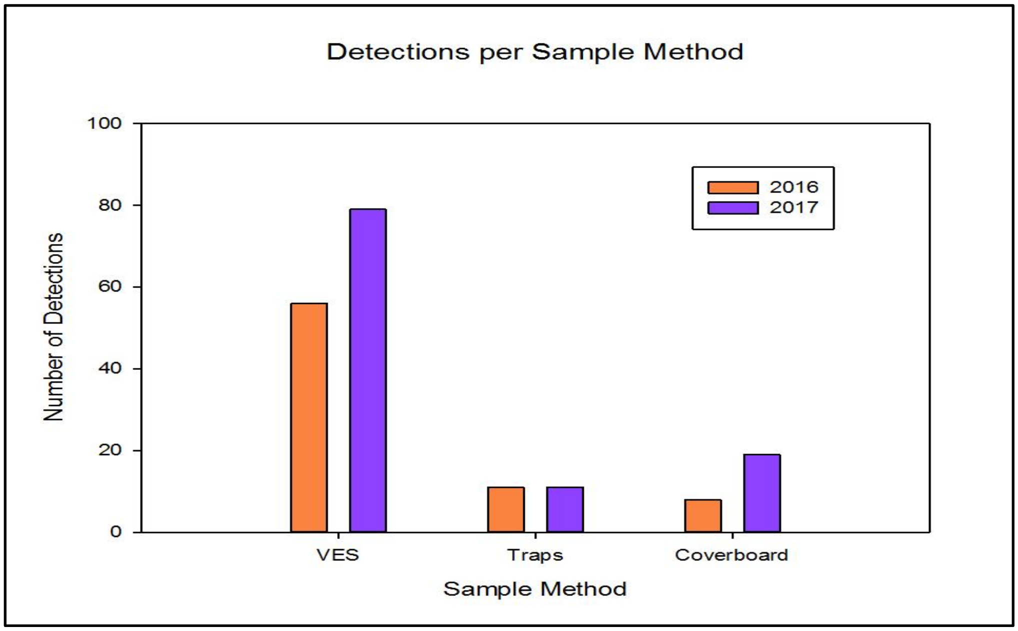


Figure A-5: Number of detections per each of the primary sample methods used at sample plots in the tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. VES = Visual encounter survey, Traps = Aquatic traps

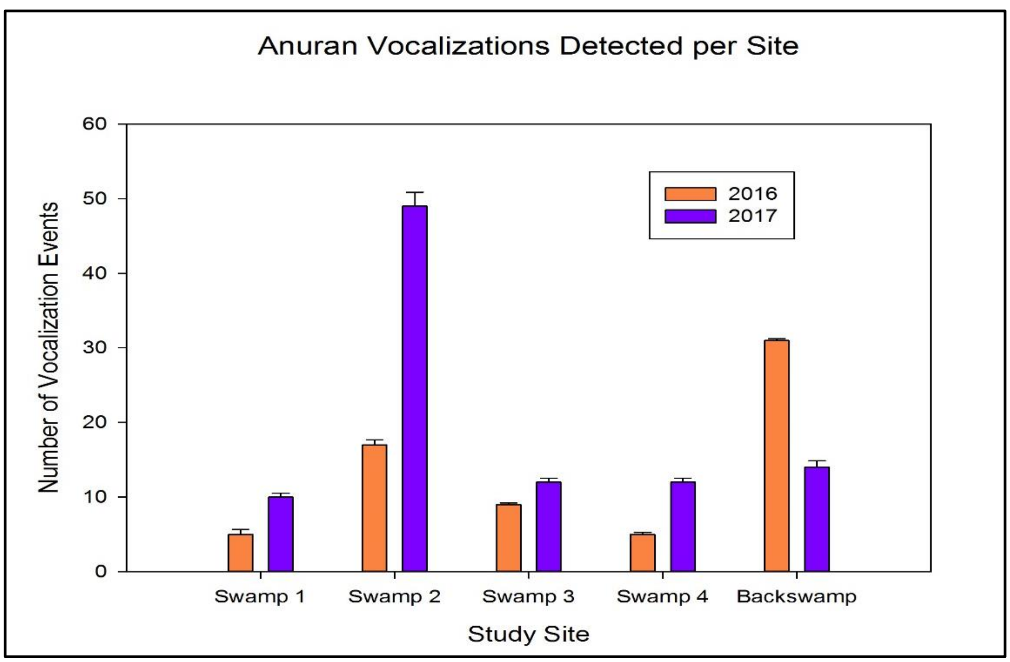


Figure A-6: Number of anuran (frog) vocalizations detected at study sites in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

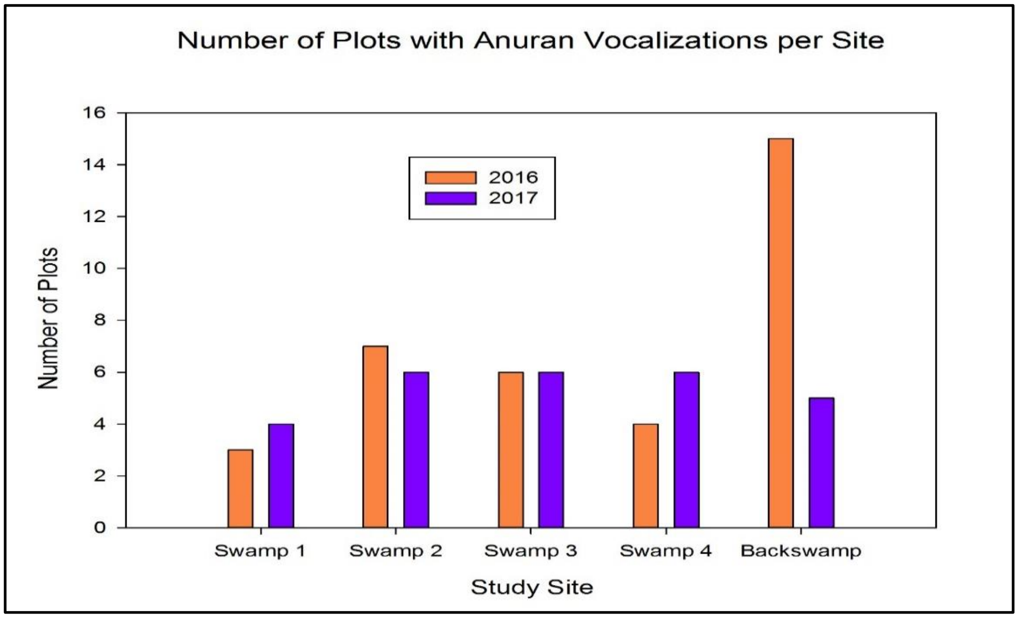


Figure A-7: Number of sample plots where anuran (frog) vocalizations were detected during surveys in tidal swamps of the Savannah National Wildlife Refuge during March to June of 2016 and 2017.

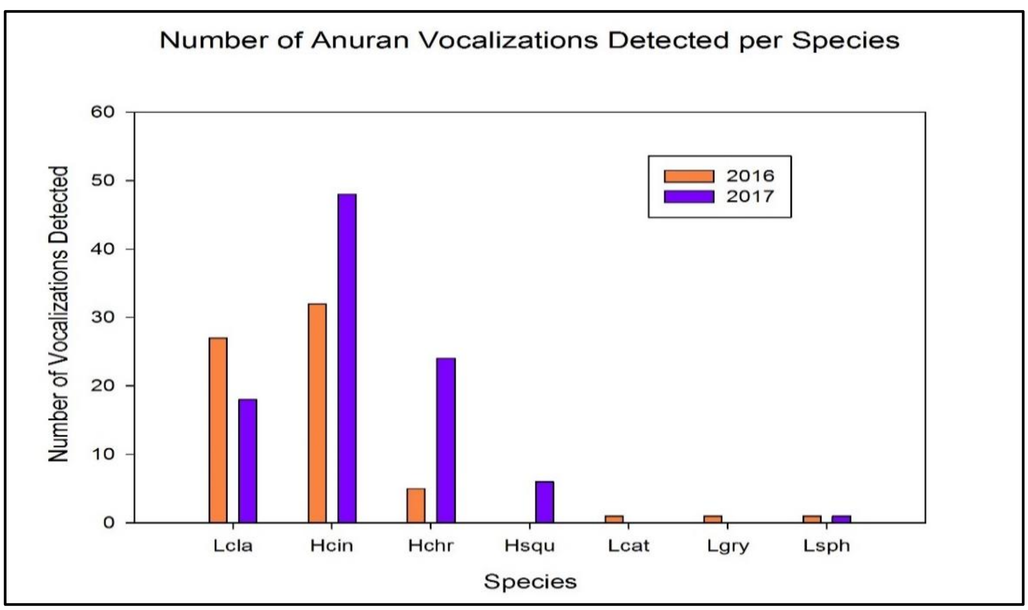


Figure A-8: Number of anuran (frog) vocalizations detected per species in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. See species inventory for listing of species abbreviations.

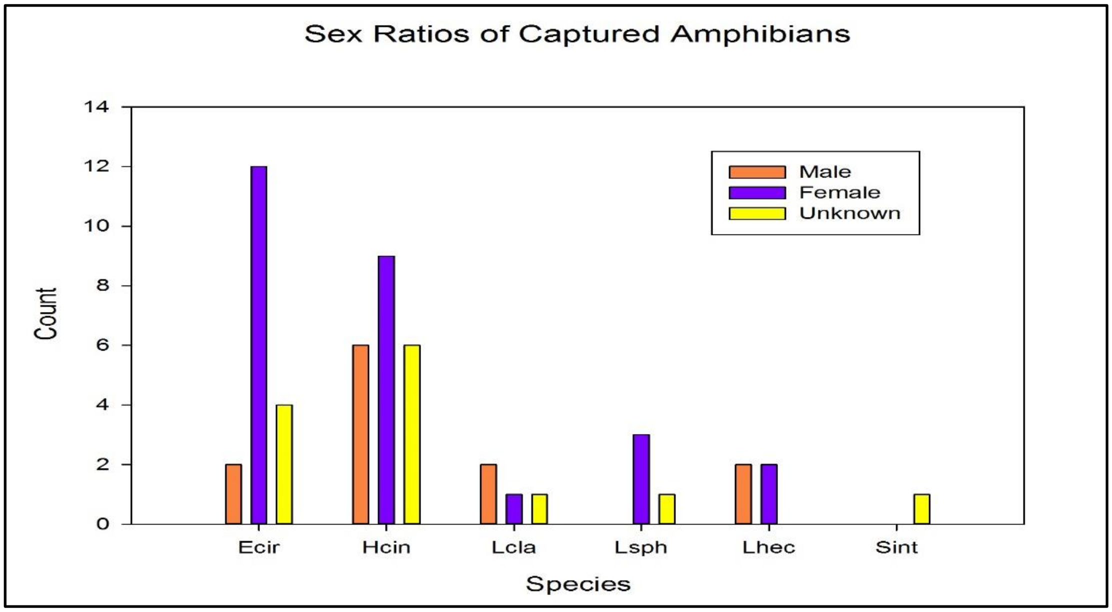


Figure A-9: Ratios of captured individuals per amphibian species that were male, female, or an unknown sex in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. See species inventory for listing of species abbreviations.

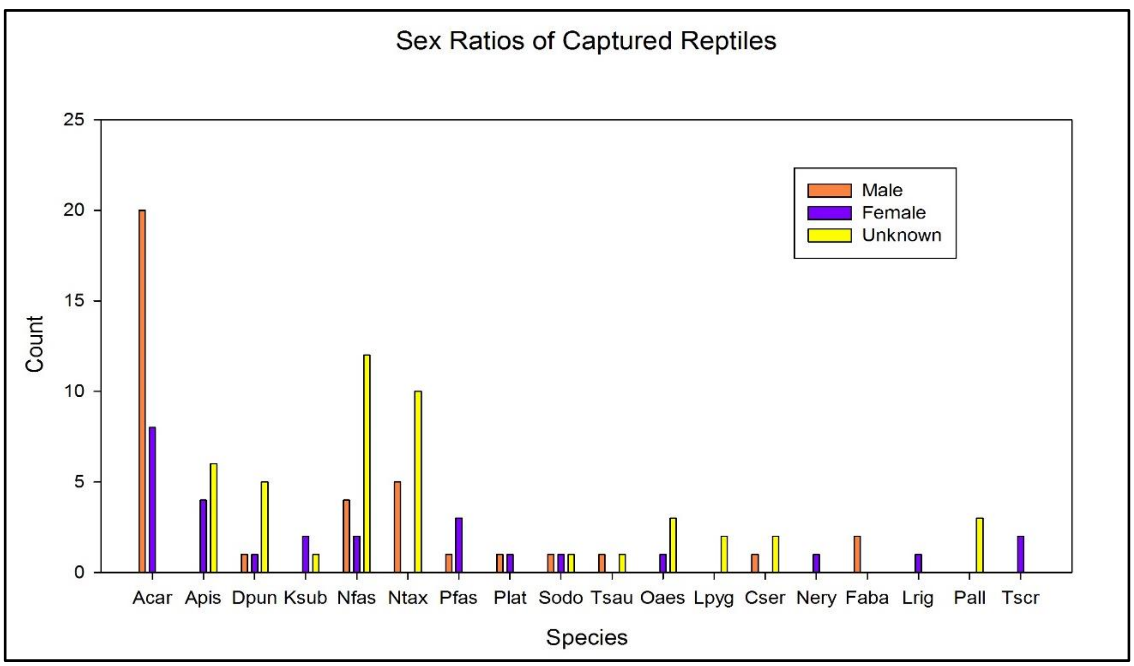


Figure A-10: Ratios of the individuals per reptile species that were male, female, or an unknown sex in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. See species inventory for listing of species abbreviations.

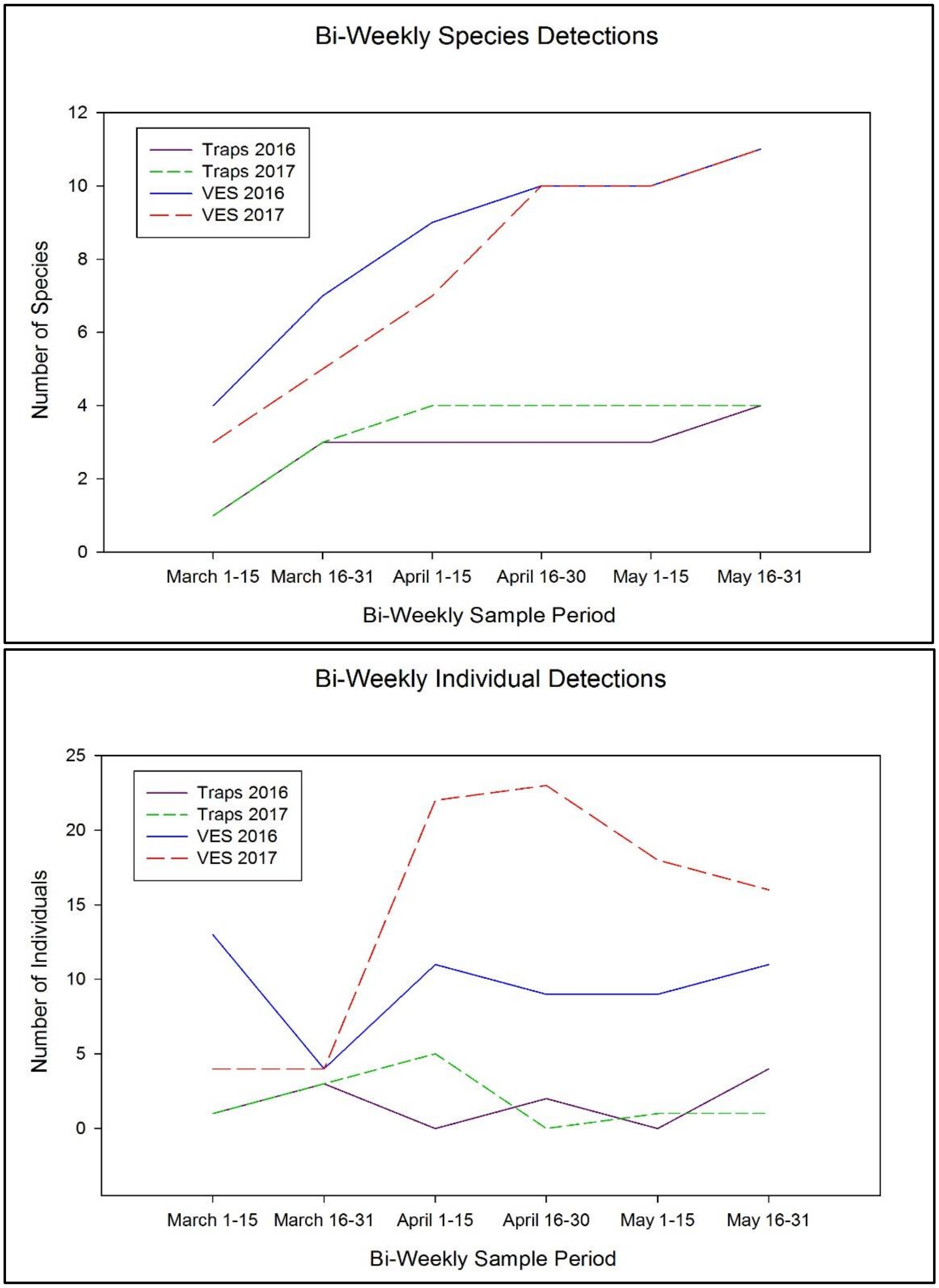
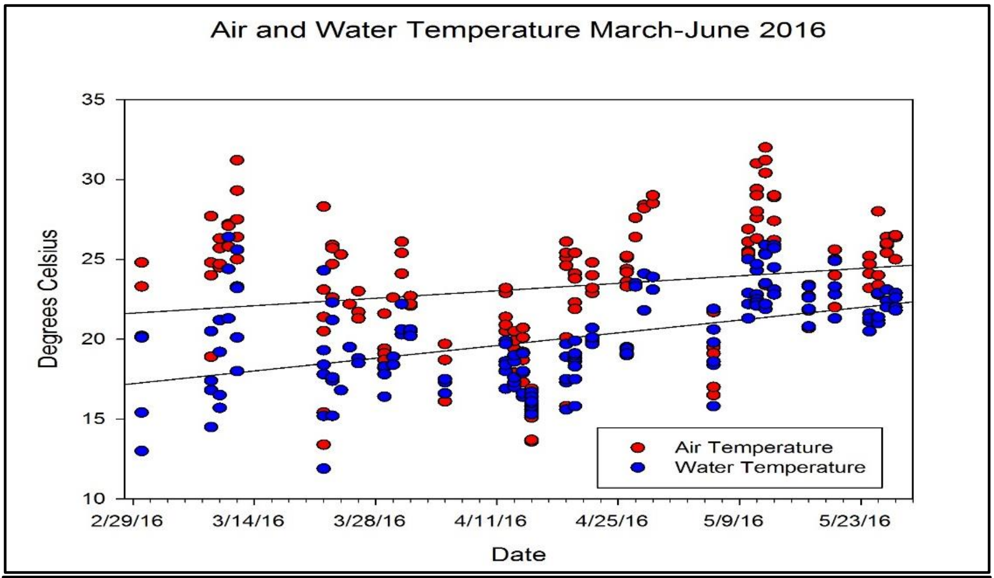


Figure A-11: Bi-weekly species (top) and individual (bottom) accumulation curves for aquatic trapping and visual encounter survey methods in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

Appendix B

Environmental Data



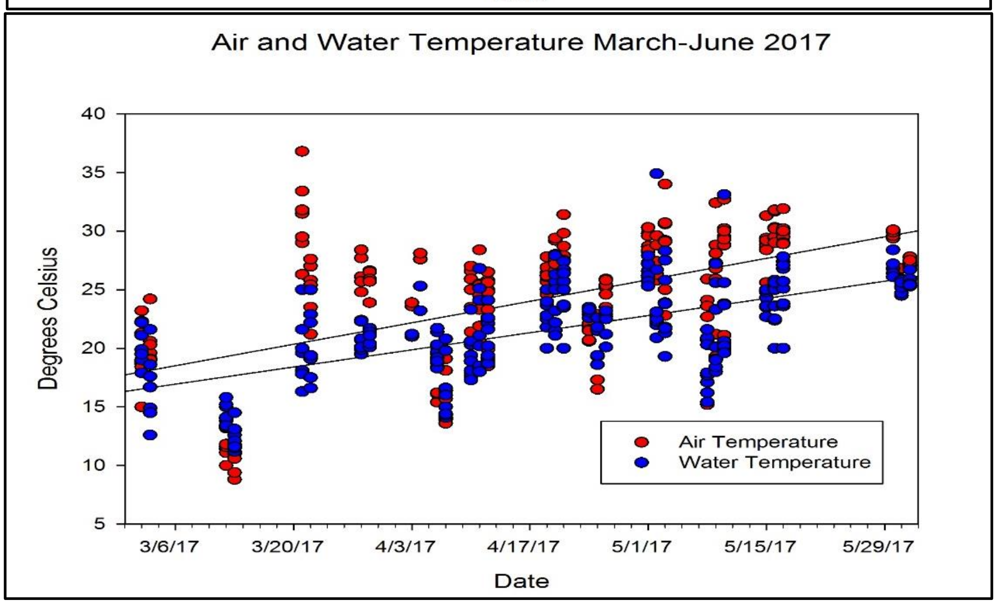


Figure B-1: Air and water temperature readings measured from sample plots in tidal swamps of the Savannah National Wildlife Refuge from March to June 2016 (top) and 2017 (bottom).

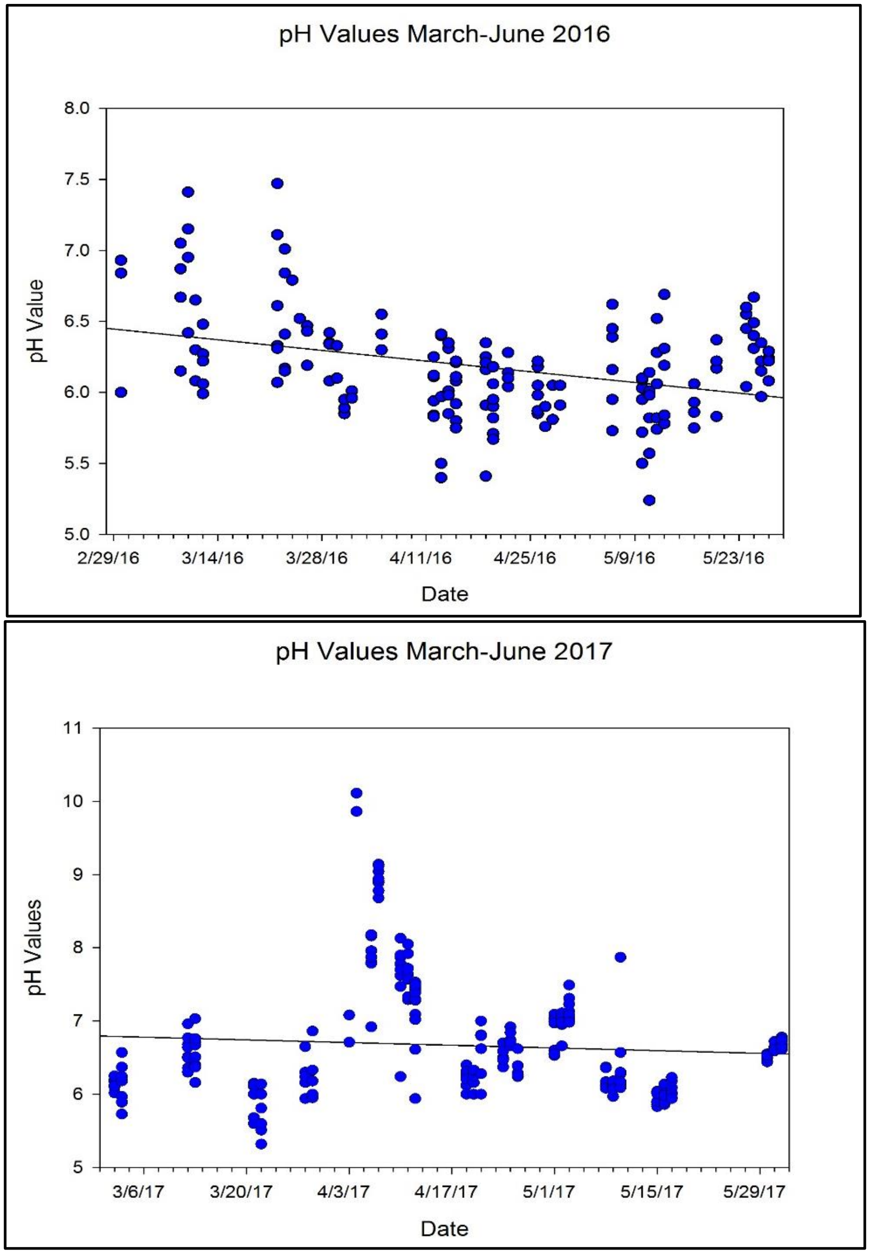


Figure B-2: Measured pH values from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

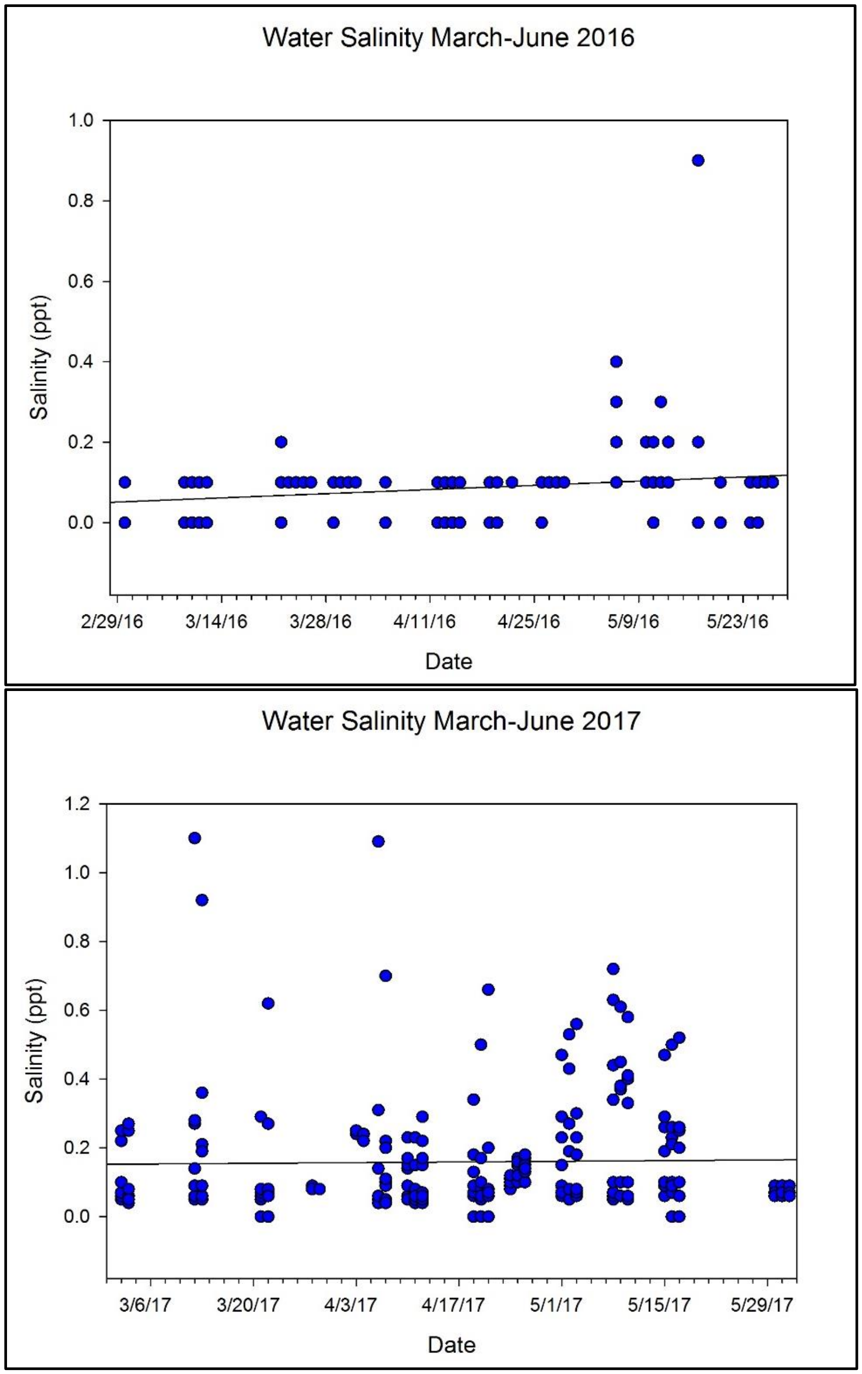


Figure B-3: Water salinity measured from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

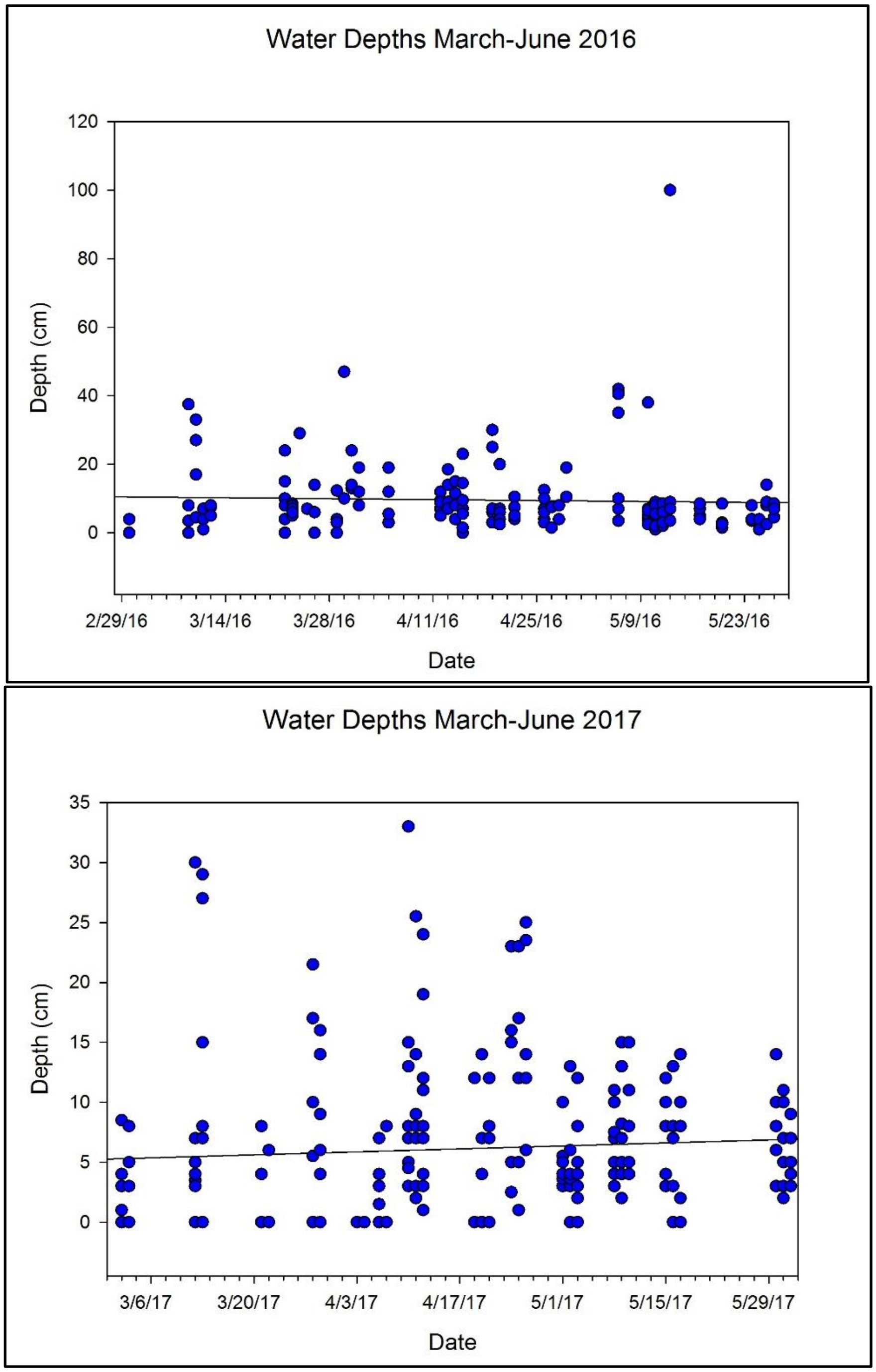


Figure B-4: Water depths measured from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

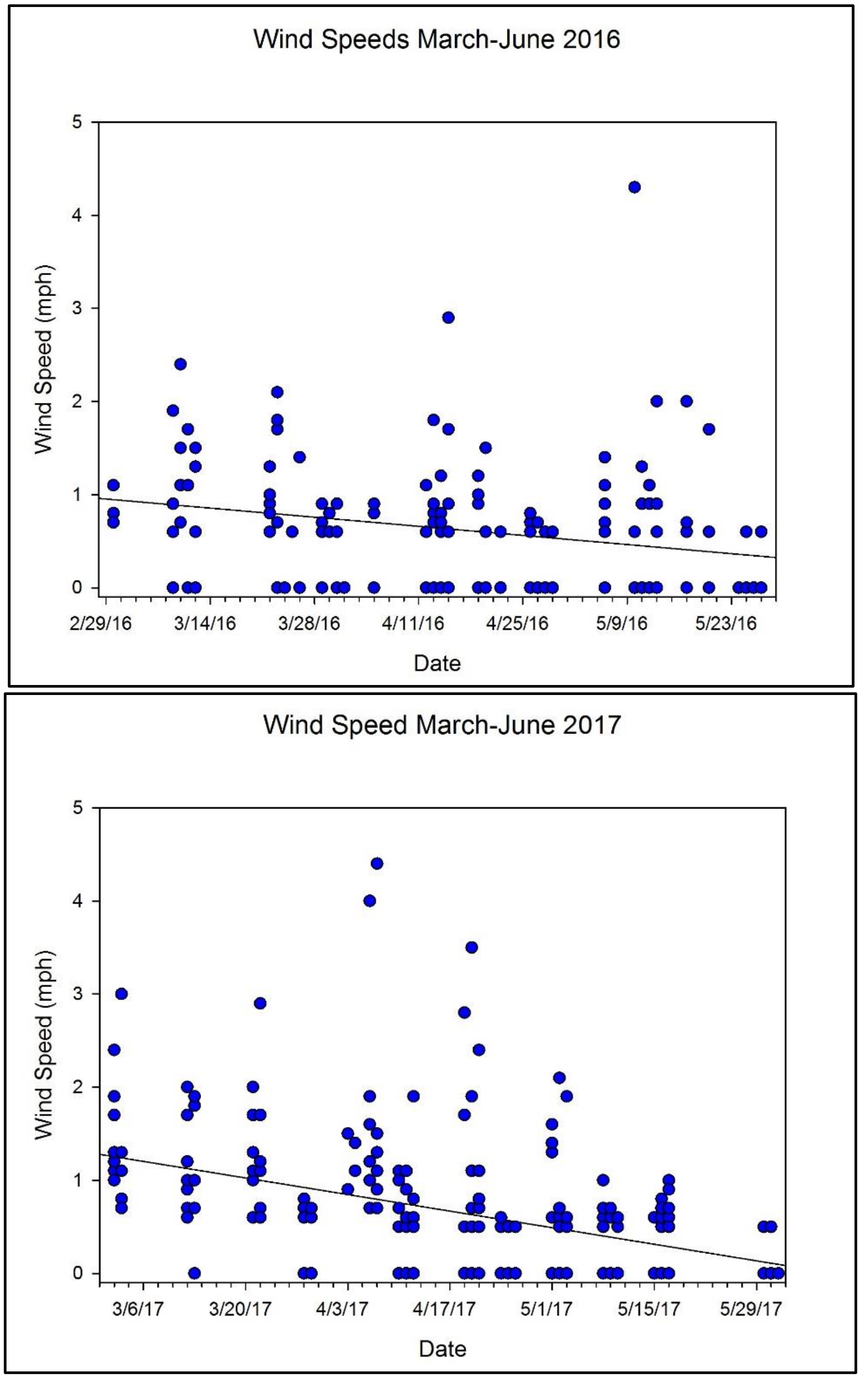


Figure B-5: Wind speeds measured from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

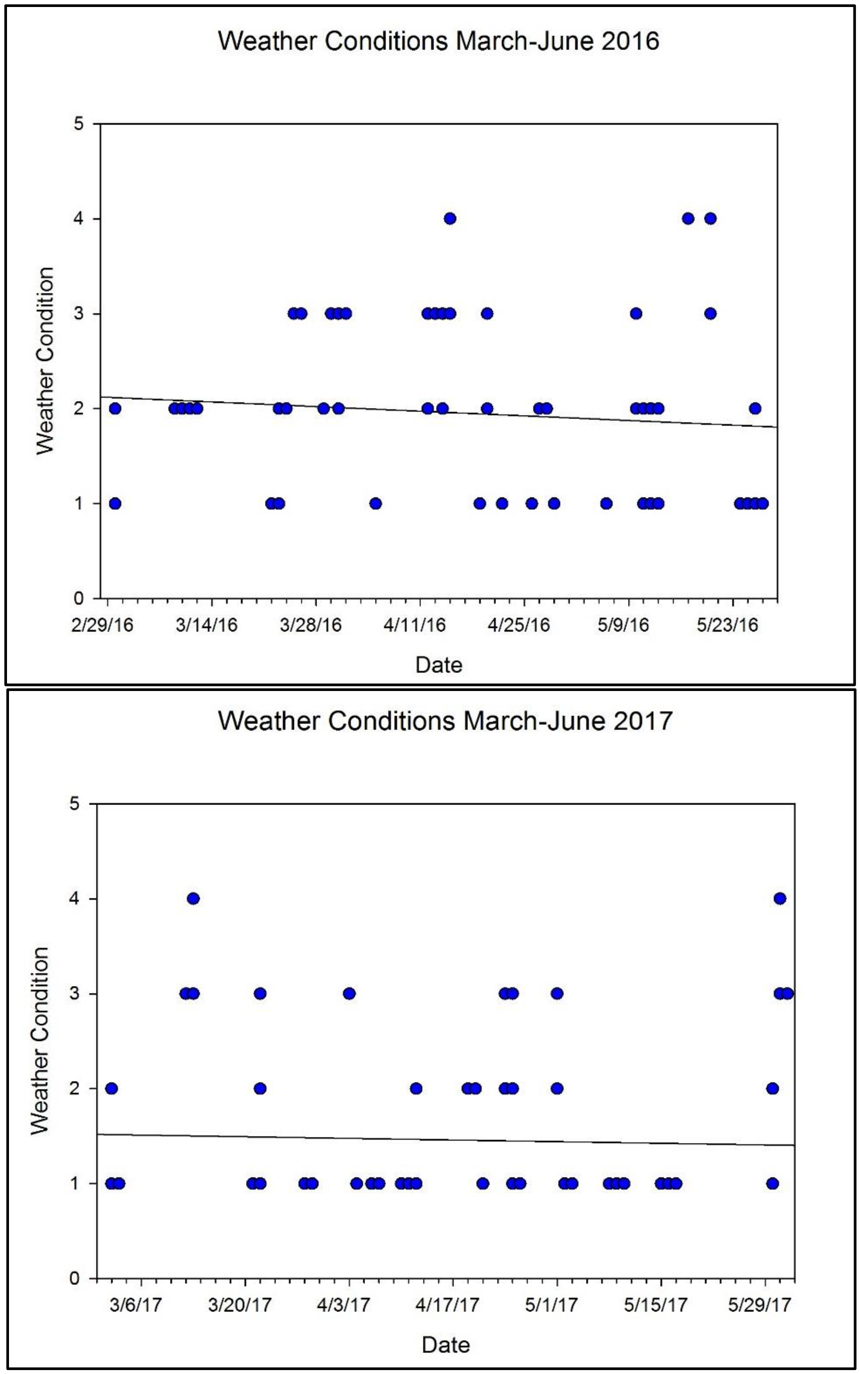


Figure B-6: Weather conditions recorded from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017. The numbers are: 1 = clear, 2 = partly cloudy, 3 = cloudy, and 4 = raining.

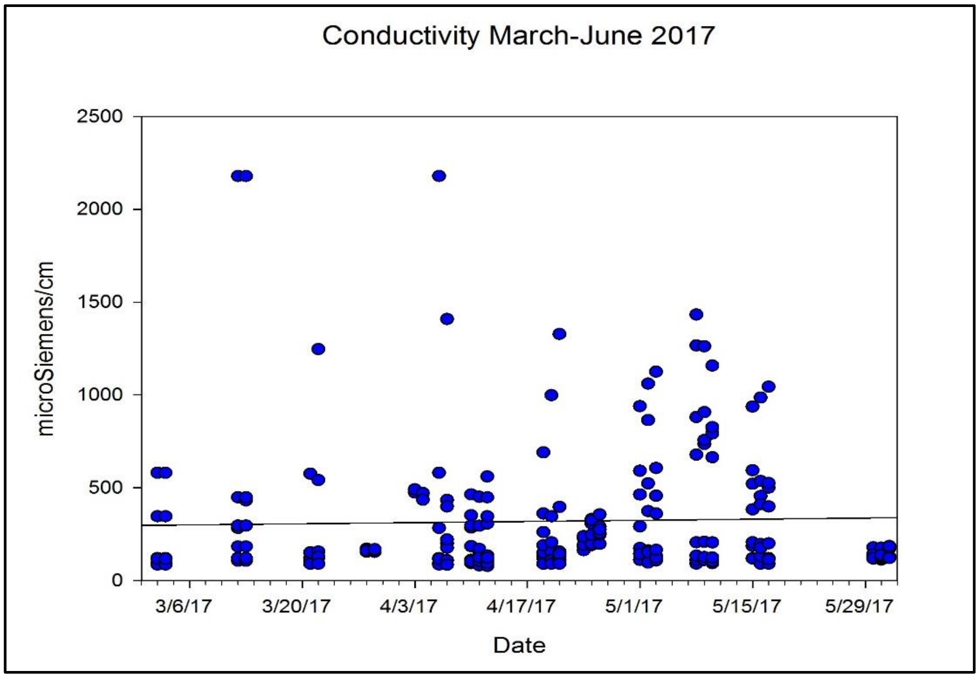


Figure B-7: Conductivity readings measured from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2017.

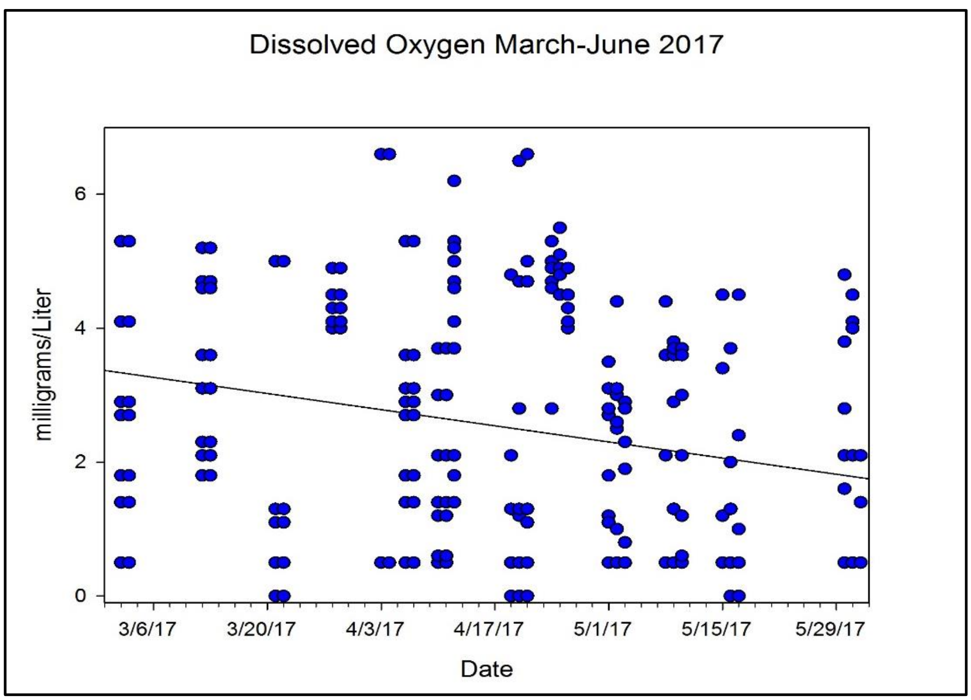


Figure B-8: Dissolved oxygen readings measured from sample plots in tidal swamps of the Savannah National Wildlife Refuge during March to June 2017.

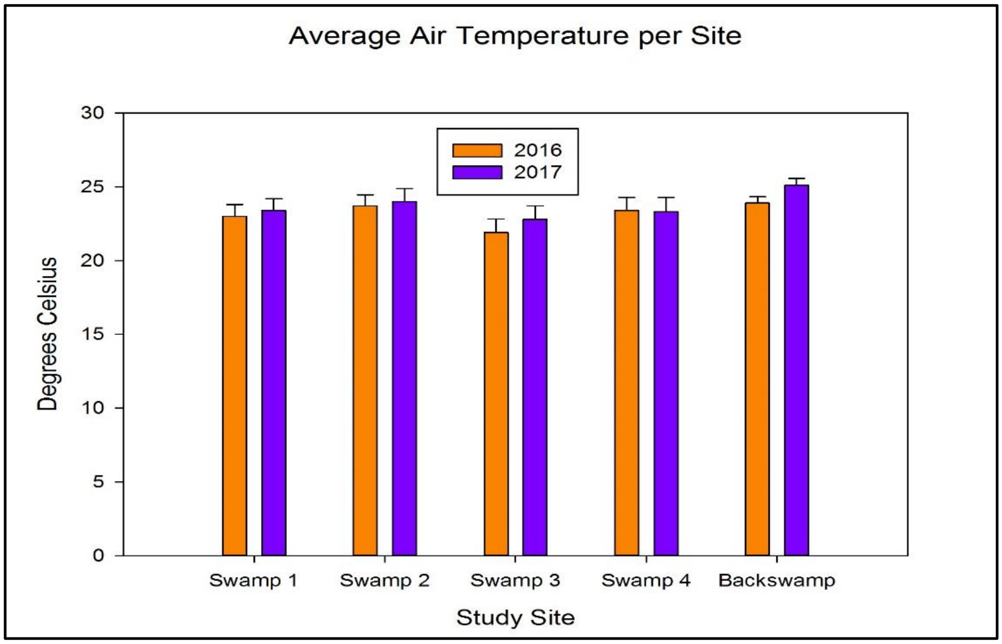
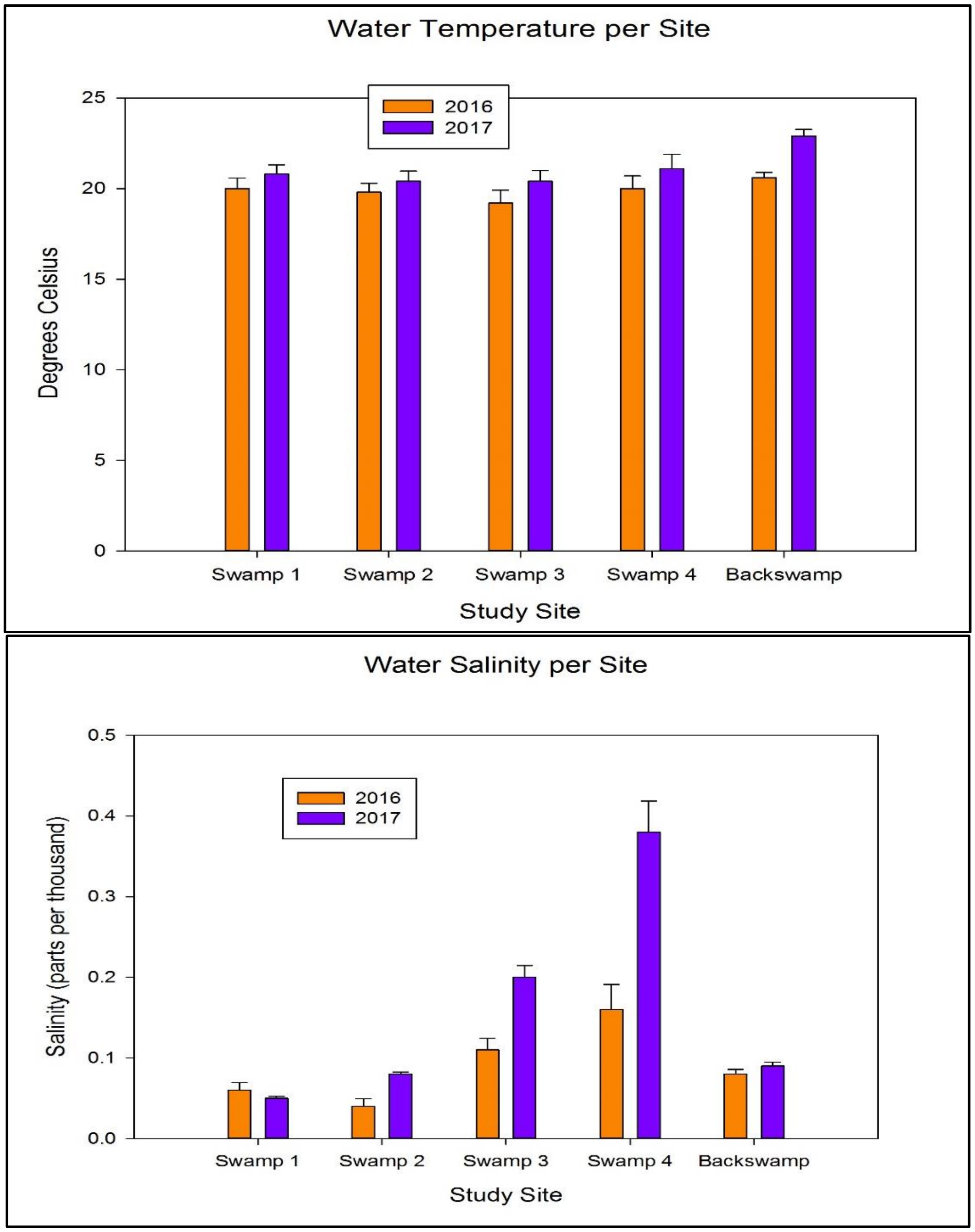
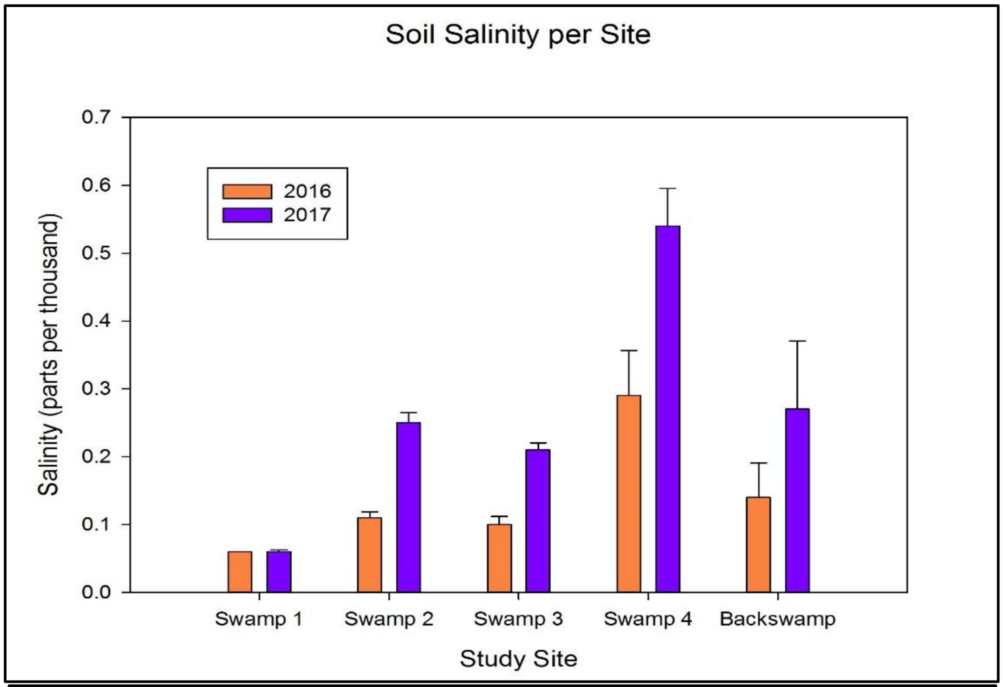
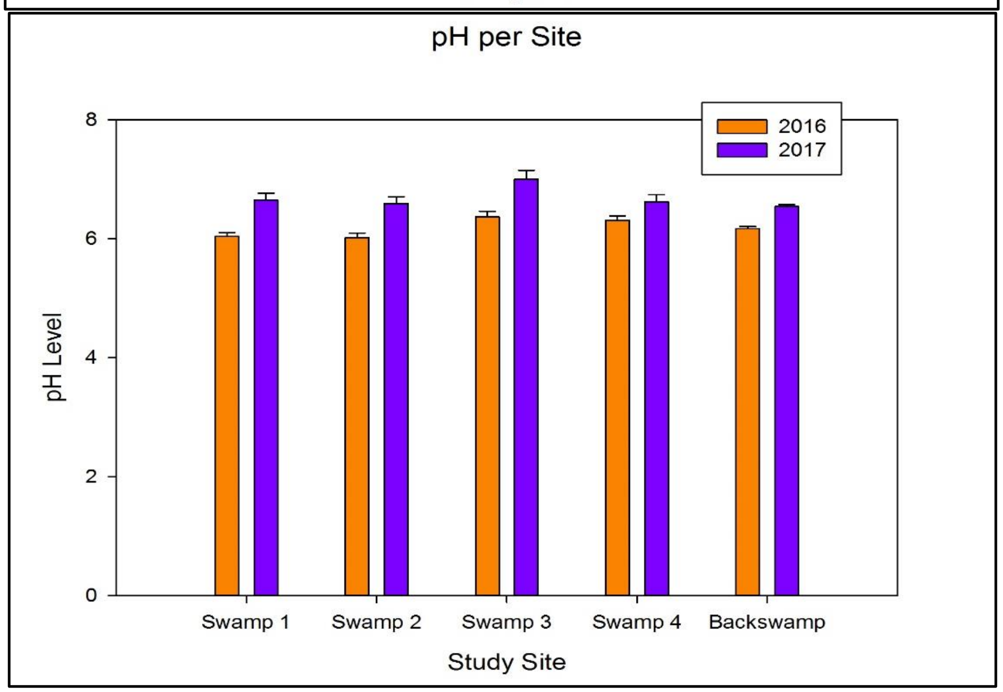


Figure B-9: Average air temperature per study site in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.



B-10: Average water temperature (top) and water salinity per site (bottom) in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.





B-11: Average soil salinity (top) and pH level (bottom) per study site in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

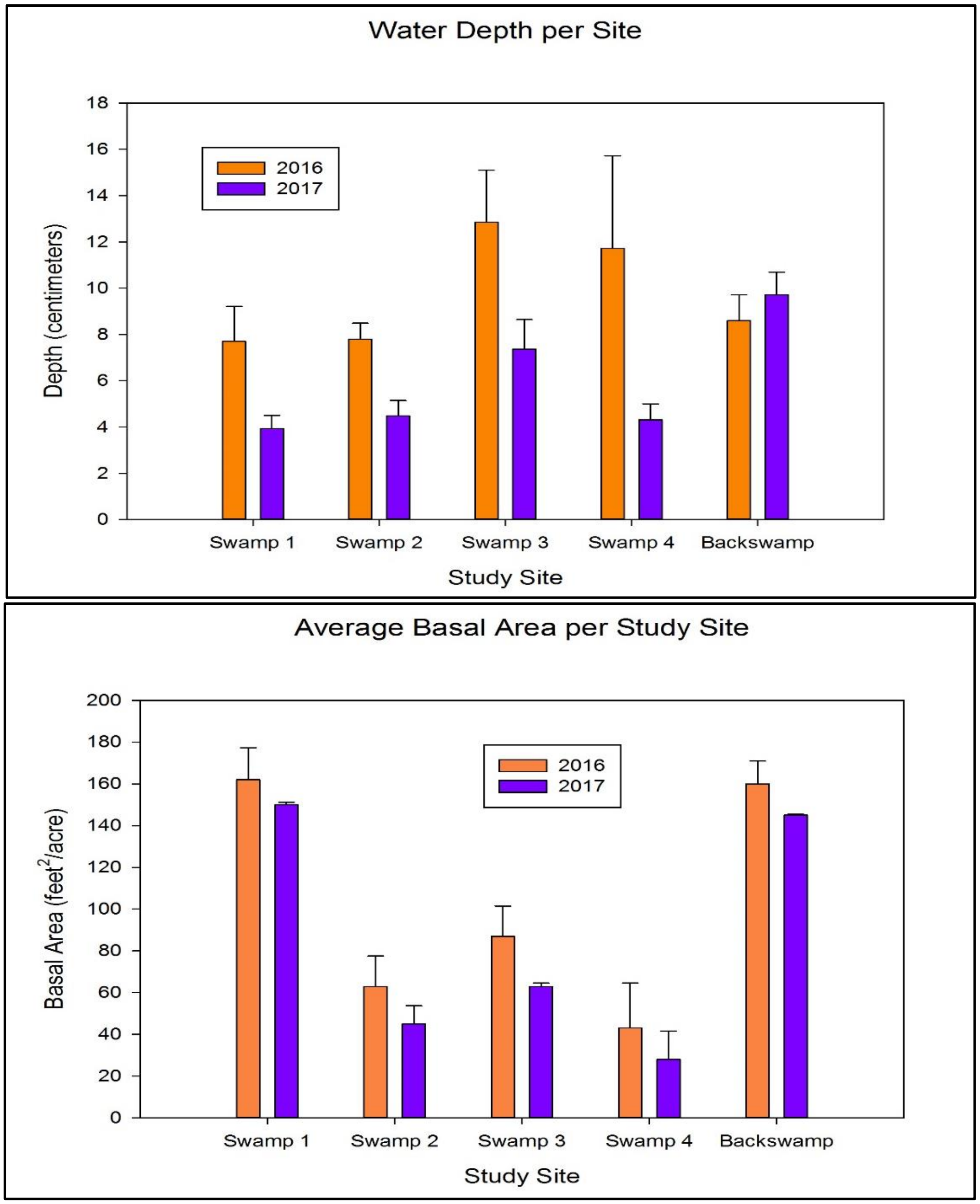


Figure B-12: Average water depth (top) and tree basal area (bottom) per study site in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

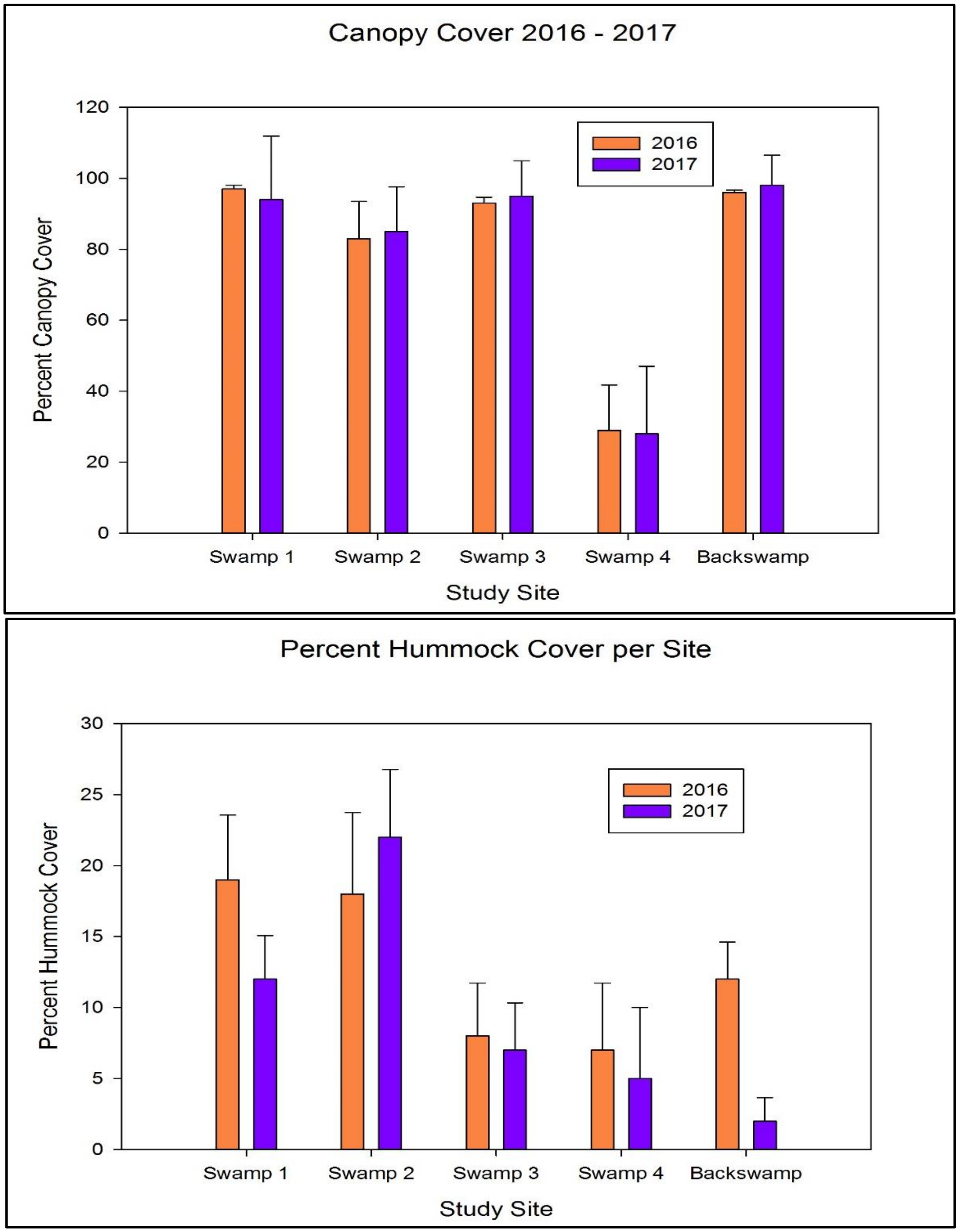


Figure B-13: Average percent tree canopy cover (top) and percent hummock cover (bottom) per study site in tidal swamps of the Savannah River National Wildlife Refuge during April to June 2016 and 2017.

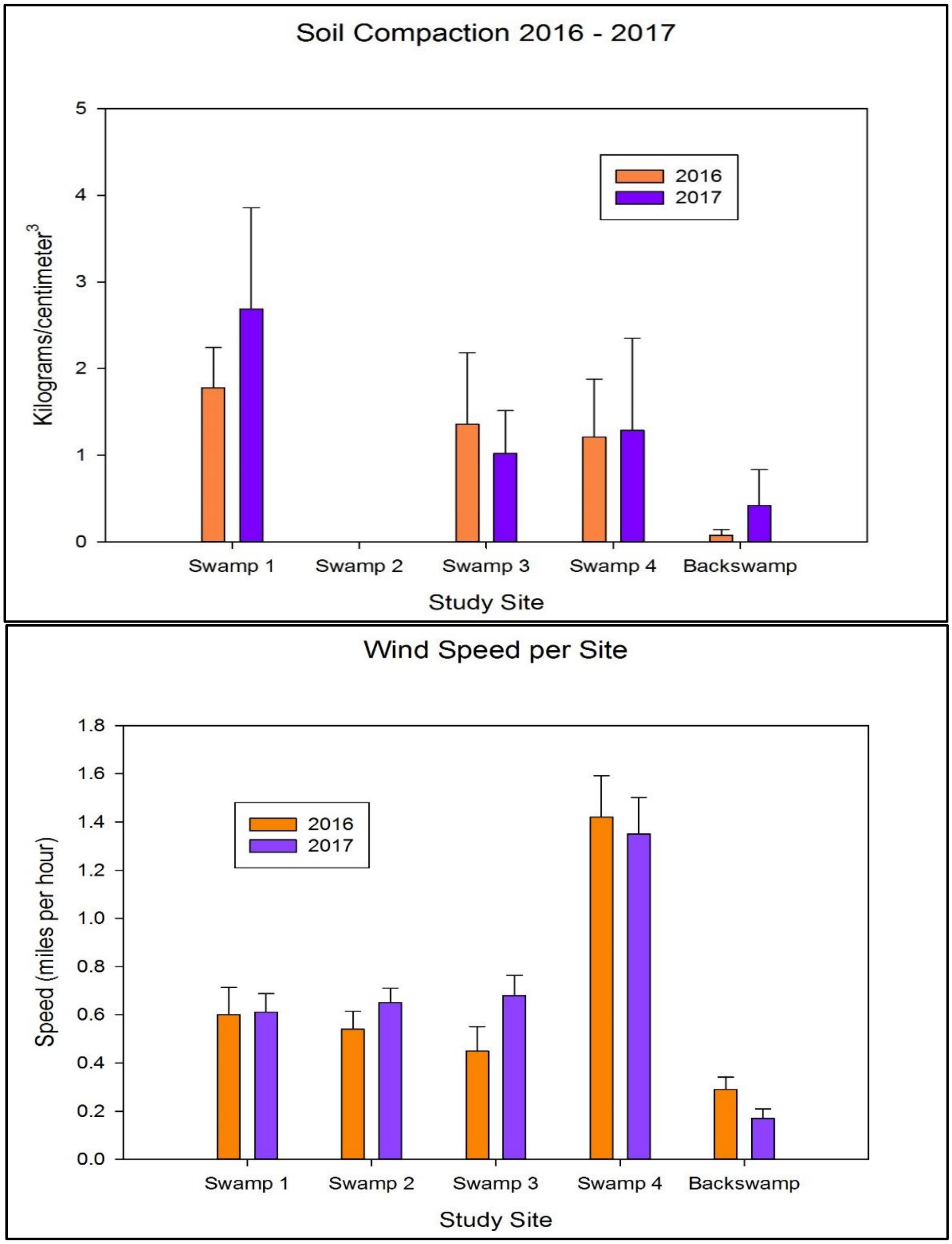


Figure B-14: Average soil compaction (top) and wind speed (bottom) per study site in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

<u>Appendix C</u>

<u>Morphometric Data</u>

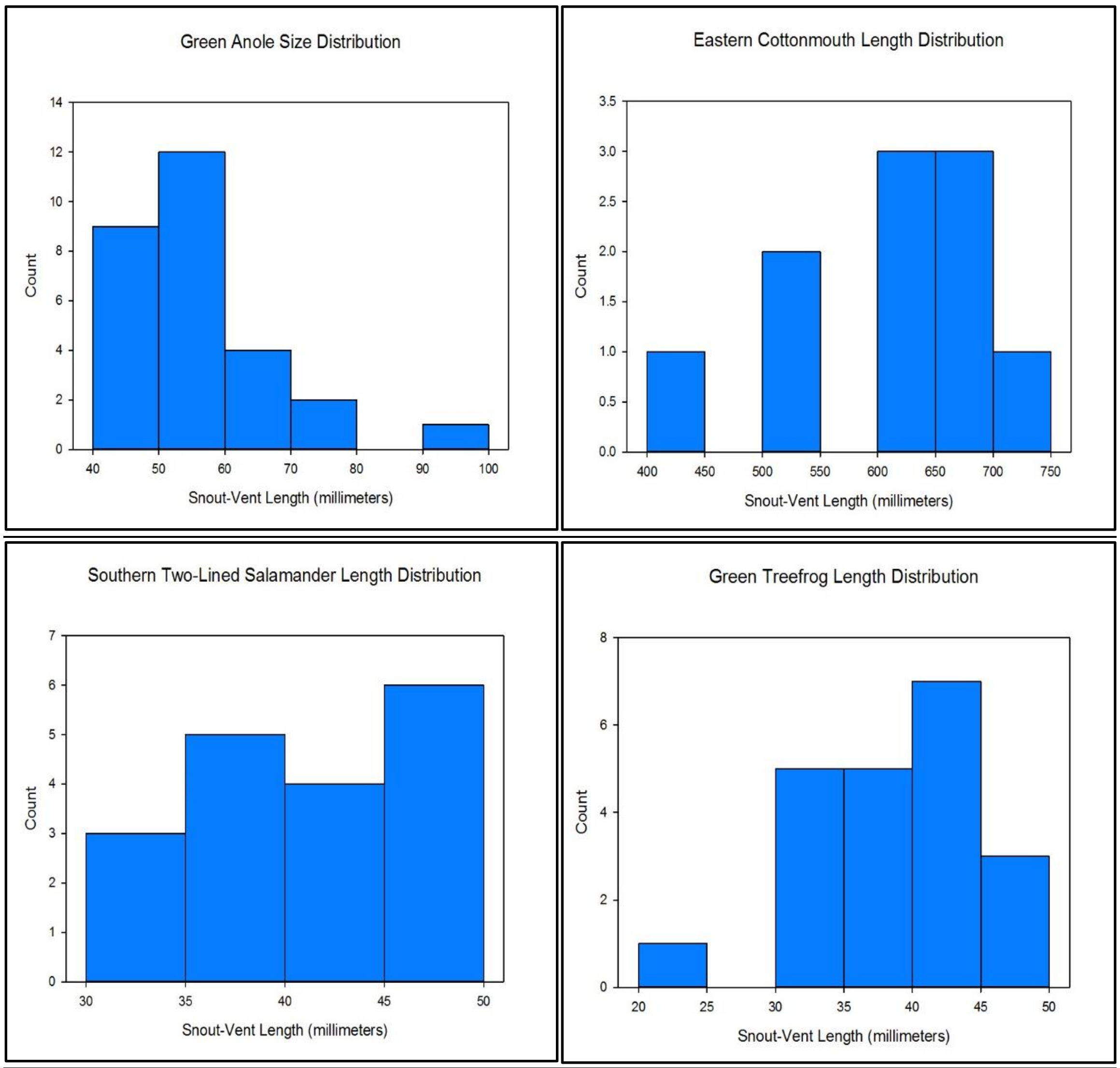


Figure C-1: Length distributions of individual Green Anoles, Eastern Cottonmouths, Southern Two-lined Salamanders, and Green Treefrogs captured from surveys in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

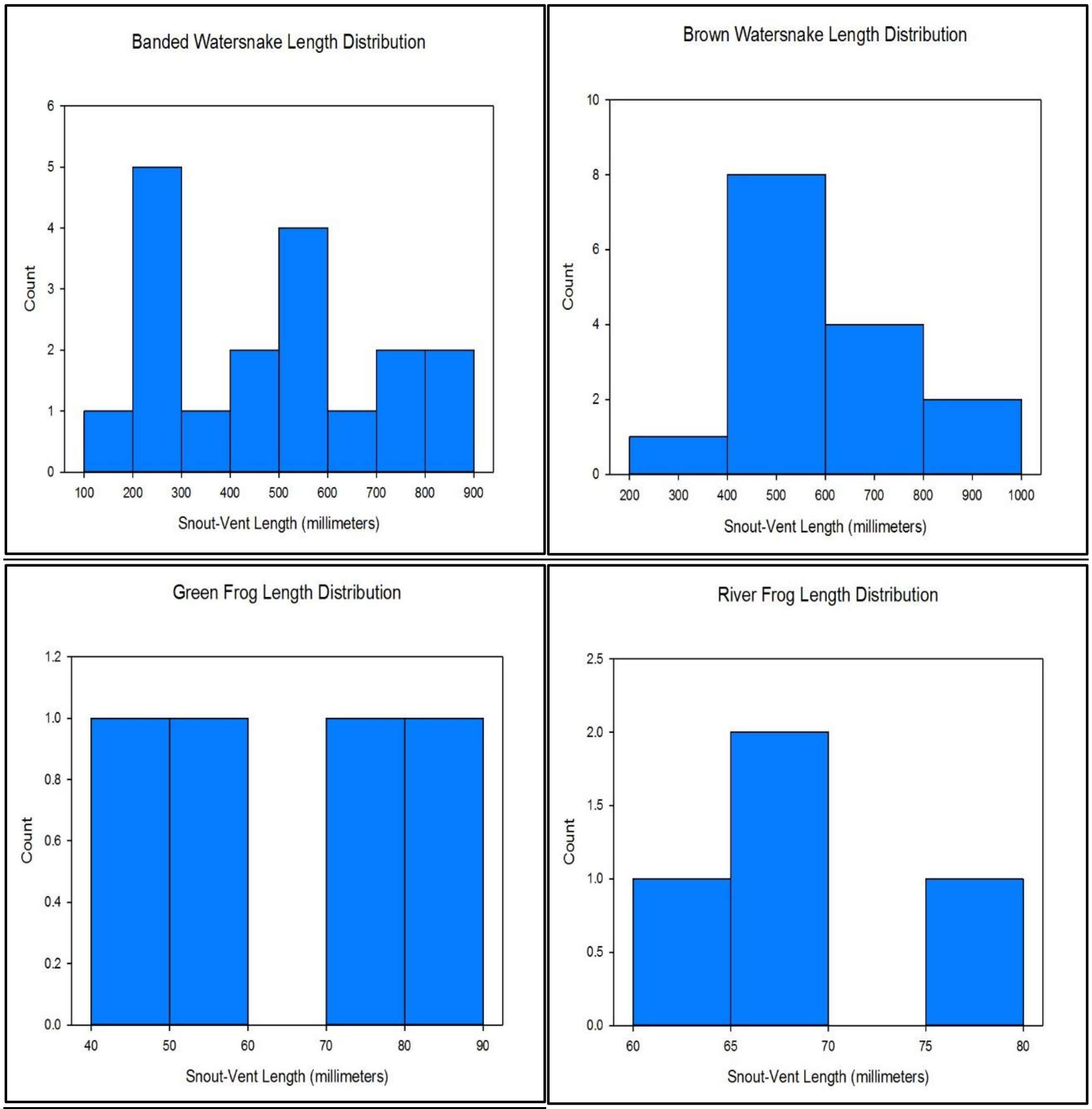


Figure C-2: Length distributions of individual Banded Watersnakes, Brown Watersnakes, Green Frogs, and River Frogs captured from surveys in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

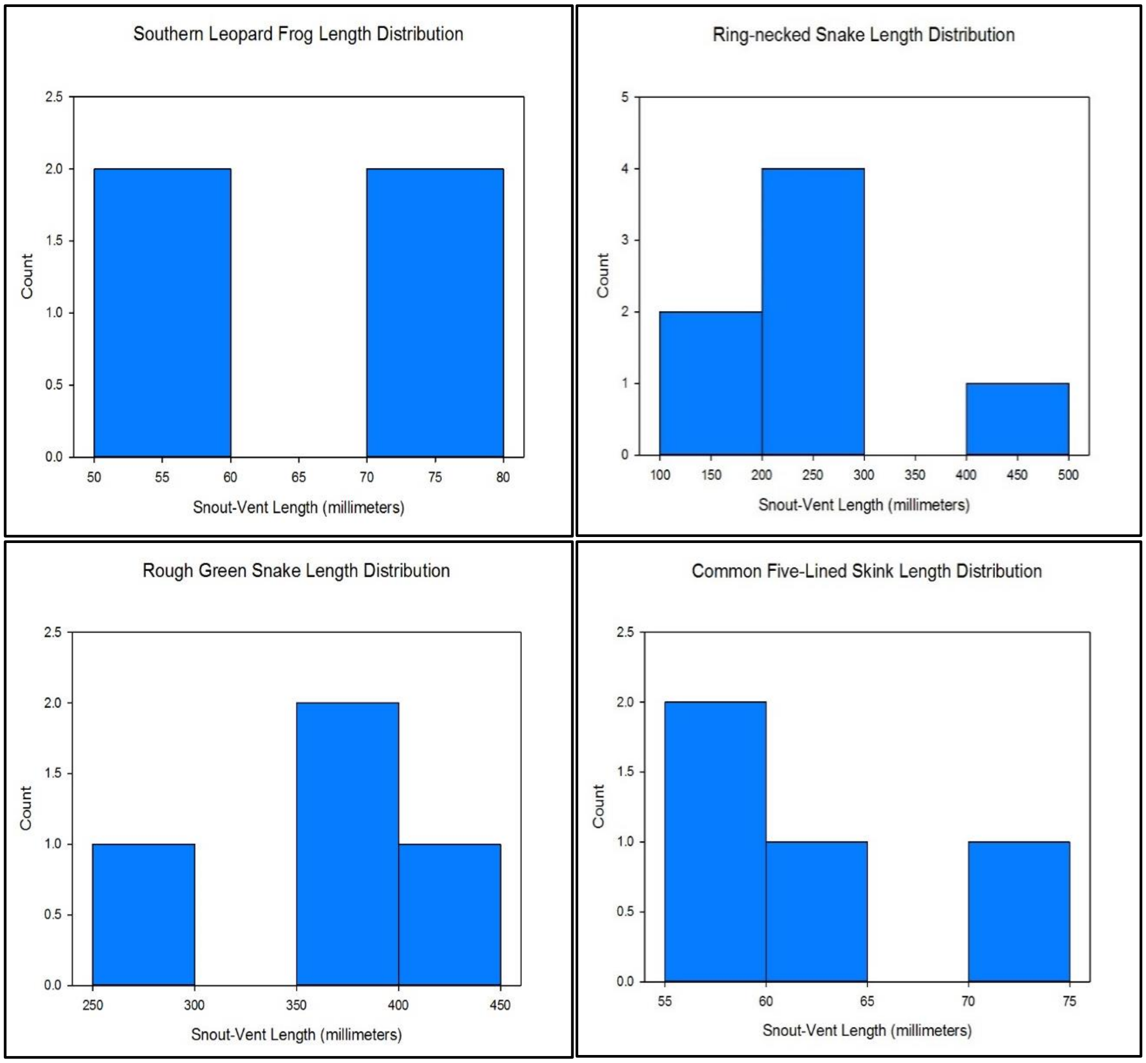


Figure C-3: Length distributions of individual Southern Leopard Frogs, Ring-necked Snakes, Rough Green Snakes, and Common Five-lined Skinks captured from surveys in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

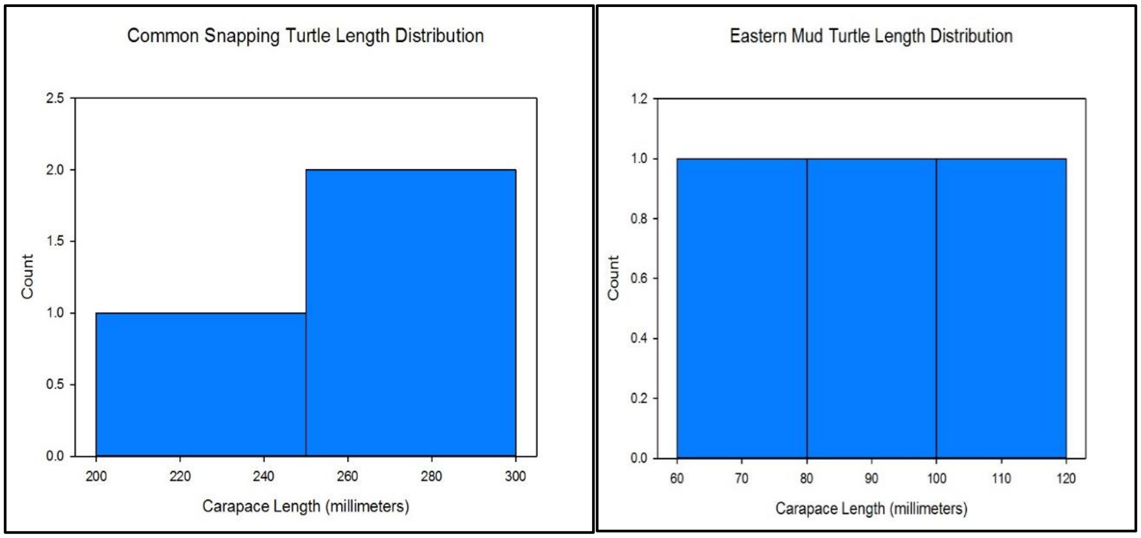


Figure C-4: Length distributions of individual Common Snapping Turtles and Eastern Mud Turtles captured from surveys in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

Appendix D

Bycatch Data

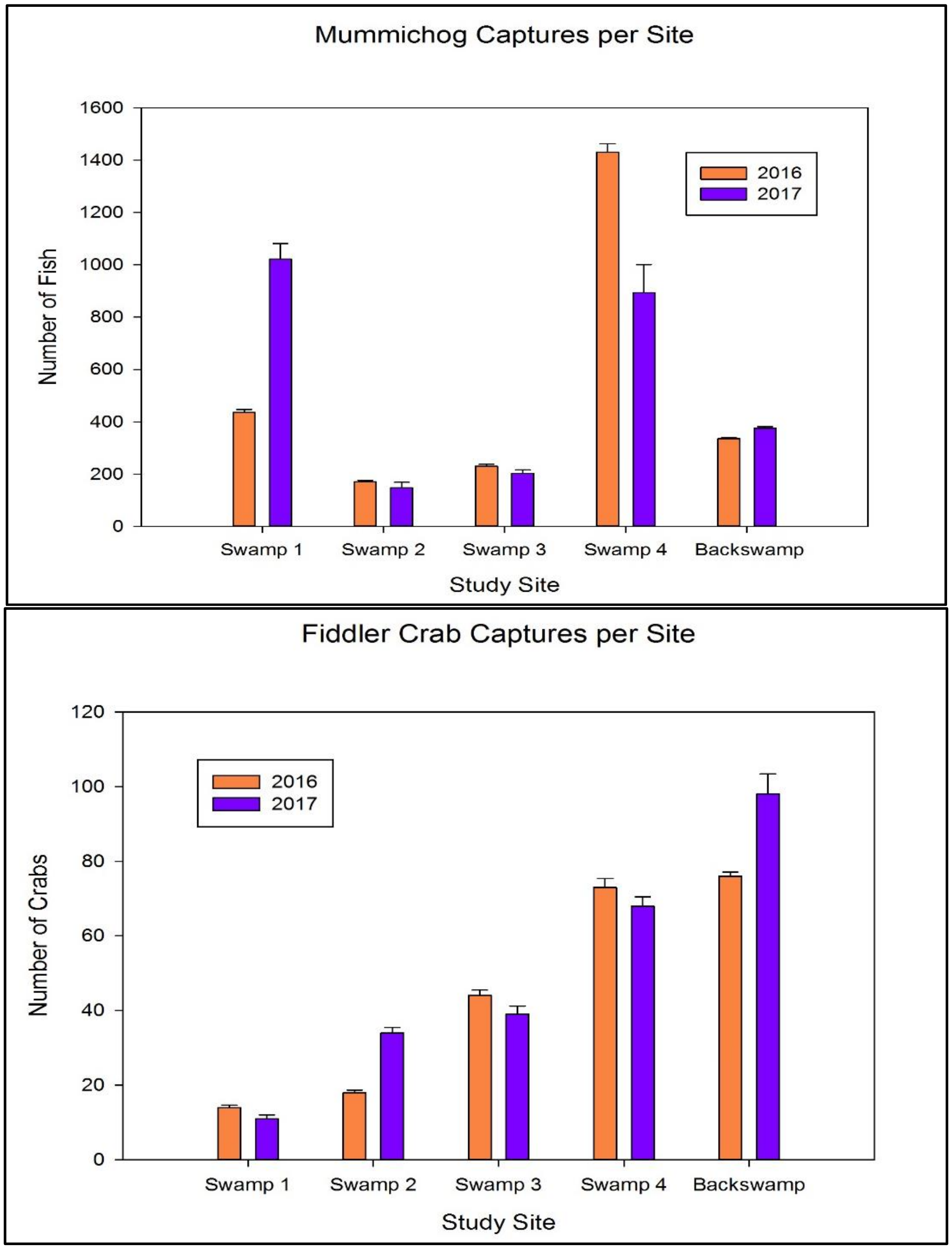


Figure D-1: Total number of mummichog (top) and fiddler crab (bottom) captures per study site in the tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

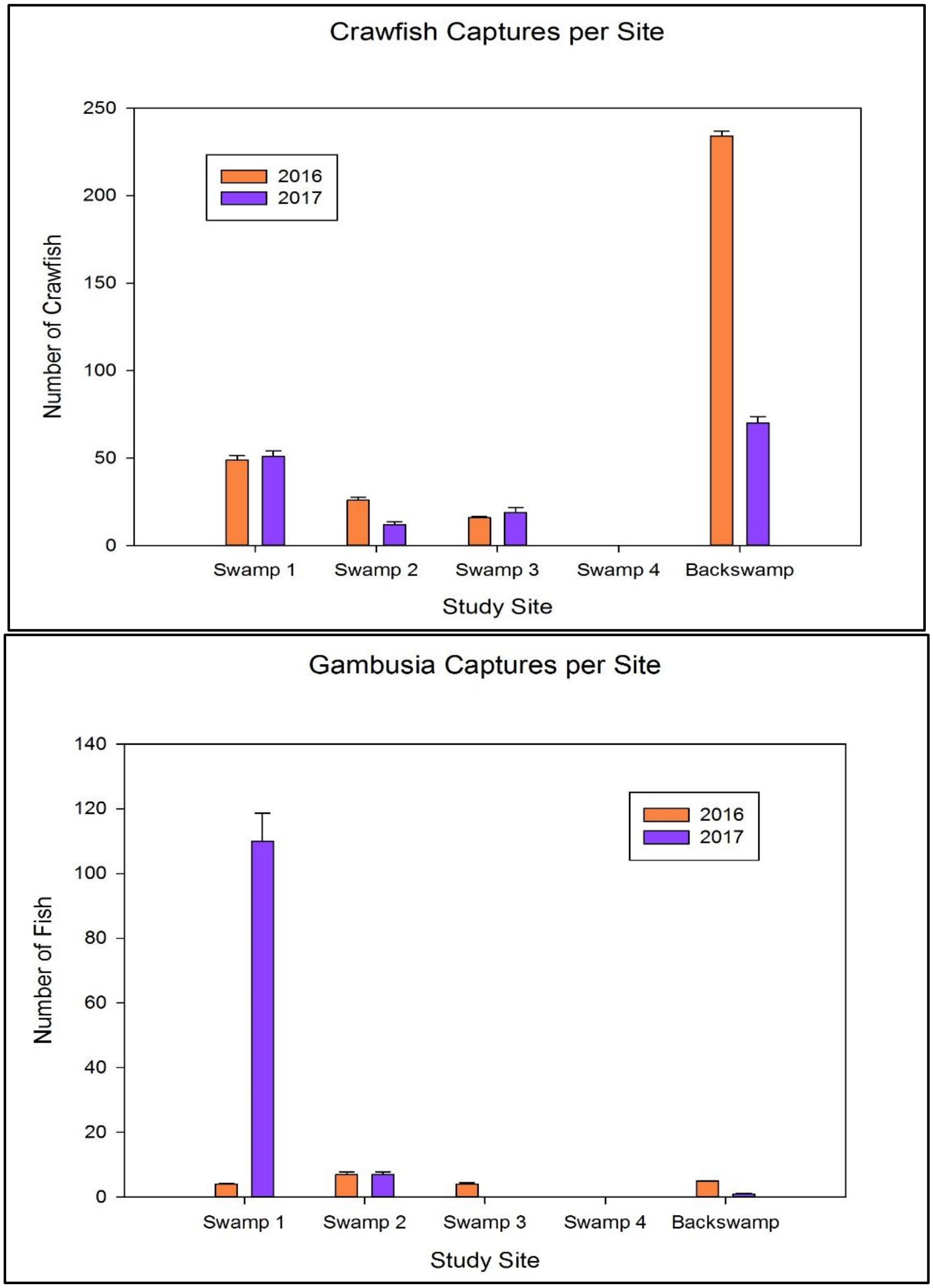


Figure D-2: Total number crawfish (top) and *Gambusia affinis* (bottom) captures per study site in tidal swamps of the Savannah National Wildlife Refuge during March to June 2016 and 2017.

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