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THE ROLE OF THE FERAL PIG (*SUS SCROFA*) AS A DISTURBANCE AGENT AND SEED
DISPERSER IN CENTRAL FLORIDA'S NATURAL LANDS

by

CAMILLE ROSE BRESCACIN
B.S. University of Central Florida, 2006

A thesis submitted in partial fulfillment of the requirements
for the degree of Master of Science
in the Department of Biology
in the College of Sciences
at the University of Central Florida
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ABSTRACT

Feral pigs (*Sus scrofa*) are considered to be among the world's worst invasive species due to their successful invasion and ecological and economic impact to native and agricultural plants and animals around the world. Feral pigs are significant disturbance agents that destroy plant communities, change soil characteristics, alter nutrient cycling, and create open sites for colonization of both native and non-native plant species through their foraging behavior called rooting. In contrast to native animal disturbances, rooting is a striking feature in the landscape that varies in space, seasonal timing, frequency (number of times rooted), and intensity (depth of rooting). During this study, feral pigs rooted 7.7% of the search area, which increased to 12% when abandoned patches (baseline patches that were not rooted during this study) were included. Overall, feral pigs rooted and re-rooted habitats along roads and trails significantly more than wetlands. Rooting also varied temporally with the most rooting occurring during July-November, which also corresponds to the peak in rooting intensity. Implications to land managers include avoiding the installation of roads and trails near wet to mesic habitats or other habitats that contain species of concern in order to conserve habitat quality and recreational value. Despite less rooting activity, feral pigs still pose a significant threat to wetlands as evidenced by the large amount of abandoned patches documented. In order to conserve natural areas, effective management and development of efficient control methods is needed to keep feral pig populations in check.

As a large opportunistic omnivore, feral pigs have the potential to be important vectors for endozoochorous seed dispersal of a variety of plant species. Feral pigs can travel long

distances and have a gut retention time up to 49 hours, therefore seeds can be deposited throughout the landscape far from the parent plant. Over the course of this study, feral pigs dispersed 50 plant species from a wide range of ecological and morphological characteristics, though the majority were native, small seeded, wetland species. For most plant species, location of deposition matched their habitat preference and suggests a high probability of survival. Feral pigs disperse mainly wetland plant species, which has important implications for wetland conservation. However, feral pigs also deposited unwanted species into wetlands and predated the seeds of important wetland canopy tree species.

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CHAPTER ONE:INTRODUCTION

Animals play an important role in the creation, modification, and maintenance of habitats (Jones et al. 1994). As disturbance agents, they create vacant sites for plant colonization, alter resources, ecological succession, and patch dynamics (Sousa 1984, Pickett and White 1985, Johnston 1995). As seed dispersers, they influence plant community dynamics and diversity by providing the demographic link between the reproductive cycle of an adult plant and the recruitment of offspring (Jordano and Godoy 2002, Wang and Smith 2002). Through differences in foraging strategies and physical alterations, each animal species uniquely impacts their environment, and it is important to understand the ecological roles that they play (Naiman 1988). Of particular interest are the roles of non-native animal species in their novel environments because they often introduce new forms of disturbance or alter existing disturbance regimes (Naiman 1988, Dantonio and Vitousek 1992, Mack and D'Antonio 1998).

The non-native feral pig, *Sus scrofa*, is among the world's worst invasive species due to its successful invasion and destruction of a variety of ecosystems around the world (Hone 1988, Kotanen 1995, Mitchell and Mayer 1997, Cushman et al. 2004, Adkins and Harveson 2007). In this thesis, I examined the role the feral pig as a disturbance agent and seed disperser in a Floridian ecosystem to assess the ecological impact of this non-native species. In my second chapter, I begin by presenting a literature review on the ecological as well as economic impacts of the feral pig across the United States. Specifically, I focused on their impacts on native and agricultural plants and animals as well as the effect of their diseases. The role of the feral pig as a disturbance agent is evaluated in the third chapter through the documentation of the spatial,

temporal, and intensity patterns of rooting over an 11 month period. Lastly in my fourth chapter, the role of the feral pig as an effective seed disperser is evaluated through the collection of fecal samples for germination trials. In addition, the location of deposition was documented to assess survival of the dispersed plant species. Overall, knowledge of the dual roles of the feral pig is lacking in the United States, though this animal continues to spread and is extremely difficult to eradicate. Information acquired from this study has implications for regeneration, succession, and conservation of natural areas.

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CHAPTER TWO: THE ECOLOGICAL AND ECONOMIC IMPACTS OF FERAL PIGS (*SUS SCROFA*) IN NORTH AMERICA

Introduction

Throughout history, humans have introduced plants and animals outside of their natural ranges intentionally for food, recreation, and environmental enhancement, as well as unintentionally on or within imported items (Bergman et al. 2000). These two transportation vectors have facilitated the introduction of approximately 50,000 non-native species to the United States resulting in both beneficial and detrimental ecological and economic impacts (Pimentel et al. 2005). Of the approximately 30 non-native mammal species established in the United States, the feral pig (*Sus scrofa*) is the most abundant free-ranging ungulate (McKnight 1964, Decker 1978). This animal is often referred to as the single greatest vertebrate modifier of natural plant communities due to its extremely destructive nature and life history characteristics that make it a successful invader (Wood and Barrett 1979).

The feral pig is an opportunistic omnivore that consumes a variety of plant material, including grass, roots, tubers, woody plant stems, seeds, and fruits. Their opportunistic behavior leads them into agricultural lands and forest plantations to forage on crops, livestock feed, and livestock animals when natural food sources are scarce (Taylor and Hellgren 1997, Schmidt et al. 2004). While these generalist qualities allow the pig to successfully invade various habitat types around the world, it is their high reproductive potential and year round breeding that enables them to spread quickly. In fact, feral pigs become sexually mature at 6 to 8 months of age and litter size can range from 3 to 8 piglets (Wood and Barrett 1979, Sweeney et al. 2003, Bieber and Ruf 2005). During the first six months of life, feral pigs experience their highest mortality rates

due to predation, accidents, and starvation. Afterwards, most adults live 4-5 years with the occasional pig living 8+ years depending on hunting pressure by humans and the occurrence of large predators (Giuliano and Tanner 2005).

Sus scrofa is native to Europe and Asia (Ickes et al. 2001), but has been introduced globally where it disrupts plant communities in a variety of ecosystems including grasslands (Kotanen 1995, Cushman et al. 2004), deserts (Adkins and Harveson 2007), forests (Bratton 1974, 1975, Hone 1988, 2002), wetlands (Mitchell and Mayer 1997, Engeman et al. 2007, Zengel and Conner 2008, Doupe et al. 2010), and even reclaimed surface mines (Mersinger and Silvy 2007). It is believed that feral pigs were first introduced in the United States by European settlers in Florida in 1539 (Towne and Wentworth 1950). Subsequent introductions to other states, translocations for food and hunting within the U.S. and, escapees establishing feral populations have all led to the occurrence of the feral pig in at least 39 US states (Wood and Barrett 1979, Taylor and Hellgren 1997, Gibson et al. 1998, Fogerty 2007).

Feral pigs are pests in many ecosystems, so it is important to assemble available information in order to highlight knowledge gaps and research needs. For example, the feral pig exhibits a unique foraging behavior in which it uses its snout to turn over soil and expose food sources. This destructive behavior potentially affects many different components of the ecosystem including water, soil, plants, and animals (Taylor and Hellgren 1997, Ickes et al. 2003). However, there is no general consensus on the extent to which feral pigs impact plants and animals. The purpose of this review is to compile available information in order to assess the ecological and economic impacts of the feral pig across the United States. My objectives are to

evaluate the documented impacts of feral pigs on native and agricultural plants and animals as well as the effect of their diseases.

Plant Community Impacts

Native Plants

The disturbance created by feral pig rooting is quite different from most native animal disturbances of the United States. With the exception of the grizzly bear, native animals produce small-scale soil disturbances through burrowing and excavation that bury the surface vegetation (Kotanen 1995, Tardiff and Stanford 1998). In contrast, feral pig rooting has been reported to disrupt vegetation and soil 5-70 cm in depth and the extent of damage can range from many small 1 m² patches to a hectare or more (Imeson 1977, Vallentine 1990, Kotanen 1997, Welander 2000, Chavarria et al. 2007). Due to the large extent of this disturbance by feral pigs, different abiotic and biotic components of native plant communities can be altered. Feral pigs accelerated the mineral loss but increased nitrogen concentrations in terrestrial and stream soils and stream water in the northern hardwood forest type of the Great Smoky Mountains National Park. Increased soil erosion, and an 88% increase in bare ground cover were also documented (Singer et al. 1984). Another study conducted in the high elevation Beech forest of the Great Smoky Mountains National Park also reported increased nutrient mobilization, which was attributed to the mixing of the superficial organic layers with soil horizons (Lacki and Lancia 1986).

Many studies report that feral pigs set back succession by revisiting previously rooted areas, damage plant roots and structures, and alter community composition (Wood and Barrett

1979, Kotanen 1995, Taylor and Hellgren 1997, Tardiff and Stanford 1998, Cushman et al. 2004). However, the effects of feral pig rooting may depend on the system, and it remains unclear whether or not feral pigs facilitate invasion of non-native species through their disturbance. Both an experimental exclosure and simulation of feral pig rooting in California coastal prairie meadows was found to increase plant species richness (Kotanen 1995, 1997). Similar results were obtained in an impounded floodplain marsh of central Florida (Arrington et al. 1999) and an experimental tilling study in South Carolina wetlands (Kirkman and Sharitz 1994). In contrast, feral pig rooting caused a significant decrease in plant species richness in a Gray Beech forest in Smokey Mountains National Park (Bratton 1975) and in Namadgi National Park in Australia (Hone 2002). Effects of pig rooting are especially devastating in habitats that are sensitive to disturbance, like some Florida wetlands and the Hawaiian Islands. In fact, USDA (2002) reported that feral pig activities at Eglin Air Force Base have affected 22 rare, threatened, and endangered plant species that are found in their wetlands.

Because feral pig rooting decreases native plant density and exposes soils, it may facilitate invasion by non-native plants into native communities. Again, a link between feral pig rooting and invasive plants may be context dependent. For example, Kotanen (1995) reported that neither native nor non-native species were exclusively benefited, while Cushman (2004) reported that feral pigs promoted non-native plant species. Simberloff and Von Holle (1999) suggested that feral pigs can act as dispersal agents that facilitate the spread of nonnative plant species like *Myrica faya* in Hawaii Volcanoes National Park (Stone and Taylor 1984). Although more studies are needed before a consensus can be reached, the effects of feral pigs will most

likely depend on the habitat type (i.e. composition and structure of the vegetation) and the frequency and intensity of rooting.

Agricultural Plants

Feral pigs damage pastures, timber and agricultural crops by consuming plants as well as rooting and trampling of soils (Wood and Barrett 1979, Beach 1993). Agricultural crops that are commonly consumed are corn, milo, rice, watermelon, peanuts, hay, turf, wheat and other grains (Rollins 1993). Crop predation is heaviest near the end of the growing season when most crops are mature (Beach 1993). Approximately \$800 million in agricultural crops each year are estimated to be damaged by feral pigs, which is a conservative estimate and equates to \$200 in damages per year per pig if one assumes 4 million feral pigs inhabit the United States (Pimentel et al. 2005). Damages can be extensive for any one agricultural operation; one incident of feral pig damage to a peanut crop resulted in a loss of \$39,600 (Beach 1993). In addition, feral pigs damage ranch structures and facilities like fences, irrigation, and water supply (Rollins 1993).

Animal Impacts

Wildlife

Feral pigs may indirectly impact wildlife by modifying the abiotic and biotic components of the ecosystem, but they also impact wildlife directly through predation and competition for food (Wood and Barrett 1979, Beach 1993). Analyses of feral pig stomach contents report very little consumption of animal material, consisting mainly of invertebrates and small vertebrates (Wood and Roark 1980, Howe et al. 1981, Taylor and Hellgren 1997). However, feral pigs are considered to be a significant predator of five different endangered and threatened marine sea

turtle species because the feral pig destroys up to 80% of nests in some parts of Florida (USDA 2002). Feral pigs are also implicated as predators of ground nesting animals like the bobwhite quail (*Colinus virginianus*) (Rollins and Carroll 2001), though the significance of that predation has been debated. In a study that simulated 192 quail nests in Texas, pigs predated 28% of the nests in one site, but only 8% in another, suggesting that predation is affected by densities of both bobwhite quails and feral pigs plus other factors, such as food availability (Tolleson et al. 1993). Though bones and feathers of birds were found in some stomach samples, it is unknown whether they were scavenged or preyed upon (Henry and Conley 1972, Taylor and Hellgren 1997).

Food habit studies are also used to infer competitive interactions between feral pigs and wildlife due to lack of research in this area (Henry and Conley 1972, Wood and Roark 1980, Howe et al. 1981, Taylor and Hellgren 1997). Because feral pigs are omnivores, they have the potential to compete with a wide range of wildlife. For example, potential competition between feral pigs and white-tailed deer has been a concern due to high dietary overlap, which may be greatest during low mast crop years for acorns (*Quercus* spp.) and Hickory (*Carya* spp.) (Henry and Conley 1972, Taylor and Hellgren 1997). Other wildlife like wild turkey (*Meleagris gallopavo*), squirrels (*Sciuridae* sp.), and black bear (*Ursus americanus*) may also be affected due to their dependence on mast crops as well (Wood and Barrett 1979, Taylor and Hellgren 1997). In most cases it is impossible to disentangle the primary mechanism (habitat modification by rooting, predation, or competition) by which feral pigs impact wildlife without experimental testing (e.g., exclosures). Such experiments must be carefully designed and conducted over large

spatial scales and multiple years if results are to be considered conclusive. In the meantime, the feral pig is linked to the declining numbers of invertebrates (Howe et al. 1981), amphibians (USDA 2002), and small mammals (Singer et al. 1984) but without definitive evidence of the severity or distribution of this link.

Livestock

Livestock are also impacted by feral pigs through predation, though competition is less likely. Feral pigs are underestimated as significant predators of large animals for several reasons (Wade and Browns 1985, Beach 1993). Even though a small percentage of animal material is consumed in their diet, economic loss of even one livestock animal is costly (Seward et al. 2004). In Texas alone, the loss of approximately 1,243 sheep and goats were attributed to feral pig depredation with an estimated value of \$63,000 (Rollins 1993). These numbers are probably underestimated because feral pigs consume the whole carcass and don't leave animal parts as evidence of predation. In the cases where newborn livestock are targeted, predation is often mistaken as low productivity of the herd. However, even when scat or stomach analyses reveal livestock remains, there is still the possibility that these remains were scavenged (Wade and Browns 1985, Beach 1993). In Australia, it is estimated that livestock predation costs over \$80 million annually due to the 4 to 20 million feral pigs present (Emmerson and McCulloch 1994). Unfortunately, the number of livestock depredated by feral pigs and the associated economic loss is unknown in the United States (Seward et al. 2004).

Diseases

Feral pigs act as disease reservoirs that can threaten the health of native wildlife, livestock and even humans, especially because pigs can travel substantial distances through natural and agricultural areas. In Florida, feral pigs have been documented to carry 45 different parasites and infectious diseases, which include 37 parasite, 7 bacteria, and 1 virus species. For most of these diseases, very little is known about disease transmission and how pig populations are affected (Forrester 1991). Due to ongoing Federal Eradication Programs, brucellosis and pseudorabies are two diseases that have been fairly well documented because of economic losses through transmission to other mammals (Frankenberger and Nicoletti 1993) . Brucellosis is caused by *Brucella suis*, a bacterium transmitted through contact with infected tissues and fluids (Wood et al. 1976). Forrester (1991) reported 3% to 37% infection prevalence in feral pigs of Florida with a majority of older animals being infected. Pseudorabies is a herpesvirus that is transmitted through inhalation of nasal discharges, mating, and ingestion of milk (Trainer 1981). Although primarily a concern for the swine industry, this disease is fatal when contracted by other mammals especially those that prey on feral pigs. For example, a Florida panther (*Puma concolor coryi*) died after consumption of an infected feral pig (Glass et al. 1994). Beyond brucellosis and pseudorabies, little further research has been conducted on feral pigs as disease reservoirs or transmitters; this research topic would appear to be relevant for wildlife and livestock safety in regions with feral pigs, and may be of concern for hunters of feral pigs.

Concluding Remarks

The feral pig causes significant ecological and economic impacts across the United States through destruction and predation of native and agricultural plants and animals and disturbance

of soils in natural and agricultural lands. Despite these negative impacts, feral pigs continue to persist across the landscape due to the economic and recreational value placed on them by humans. The profits generated from pork sales and hunting, however, cannot be compared to the massive economic loss of agricultural crops, livestock, natural resources, and biodiversity in which the value is unknown or underestimated (Engeman et al. 2004, Seward et al. 2004). It is even more difficult to assign a monetary value to the loss of a species, especially if endangered or threatened, such as the depredation of sea turtle eggs (Engeman et al. 2002, USDA 2002).

Additional significant costs are incurred to control feral pig populations, which will continue to increase as feral pigs expand their ranges. Presently, feral pig management and control in the United States occurs through the use of fencing, snares, cage traps, aerial and night shooting, and hunting with dogs (Seward et al. 2004, West et al. 2009). Controlling feral pig populations is labor intensive, and the most successful campaigns usually involve a combination of methods in order to outsmart the pigs. One approach may be to learn from Australia's success with chemical toxicants, which are economically inexpensive and easily disseminated to feral pig populations. However, Australia has no native generalists like raccoons and bears that occur in the U.S. and elsewhere, so development of a chemical toxicant that targets only feral pigs will be required and will surely be a challenge (West et al. 2009).

The information currently available has not only provided insight into the detrimental effects of feral pigs, but has also highlighted research gaps. More studies on feral pigs are needed to determine (1) the frequency and intensity of feral pig rooting among different ecosystems and regions (2) the potential for facilitation of non-native plant species, (3) the predation rate on

native and livestock animals and the associated ecological and economic loss, (4) the degree of competitive interactions with native wildlife, (5) the risk of disease transmission to native and livestock animals, and (6) if chemical toxicants can be safely used in the US. A considerable amount of money and time is spent each year in the United States to control non-native species (Pimentel et al. 2005). Though feral pigs themselves constitute a significant economic loss, their potential to facilitate other non-natives by rooting (Cushman et al. 2004) and acting as dispersal agents (Simberloff and Von Holle 1999) only adds to their direct costs. Thus, feral pig control may be another important avenue in the management of non-native plant species. Accurate knowledge of feral pig predation rates on livestock can help ranchers and farmers take proper actions to protect livestock and improve yields (Seward et al. 2004). As for land managers, significant predation rates and competition with wildlife, especially those that are threatened and endangered, can provide grounds for stricter management or even eradication of feral pig populations. Risk assessment of the probability of disease transmission to other animals provides vital information that can aid in predicting and planning disease outbreaks. In the end, more science-based information about the impacts of feral pigs in the research areas highlighted here can help guide land managers and government agencies to develop sound conservation strategies and a strict management policy towards the control of feral pigs.

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CHAPTER THREE: THE FERAL PIG (*SUS SCROFA*) AS A DISTURBANCE AGENT: EVALUATING SPATIAL, TEMPORAL, AND INTENSITY PATTERNS OF ROOTING

Introduction

Natural disturbance is integral in the maintenance of diversity and structuring of ecological systems (Grime 1973, Connell 1978, Sousa 1984, Pickett and White 1985). The key features of disturbance are the creation of vacant sites and alteration of resources and succession that allows for the recruitment of new individuals to these disturbed areas (Sousa 1984, Pickett and White 1985). Unfortunately, non-native species also take advantage of these vacant sites, and thus the dual role of disturbance can actually threaten ecological systems (Elton 1958, Mooney and Drake 1986, Dantonio and Vitousek 1992, Hobbs and Huenneke 1992, Cushman et al. 2004). This complex interaction poses a significant challenge to conservation biologists and land managers who integrate disturbance into management plans in order to preserve native species, but by doing so may also unintentionally promote exotic invasion. The role of disturbance in maintaining native diversity vs. promoting invasion by exotic species will depend greatly on the spatial (extent and distribution), temporal (frequency and timing), and intensity patterns of the disturbance (Sousa 1984, Pickett and White 1985, Lockwood et al. 2007).

Human activities have greatly altered the size, frequency, and intensity of natural disturbance regimes (Hobbs and Huenneke 1992, Mack and D'Antonio 1998). For example, urbanization fragments natural lands and decreases natural disturbance regimes such as the frequency and intensity of fires and flooding of rivers and floodplains (Hobbs and Huenneke 1992). In addition, human activities have also intentionally and unintentionally introduced non-

native species, which themselves are responsible for altering natural disturbance regimes or even introducing new forms of disturbance to the area (Naiman 1988, Dantonio and Vitousek 1992, Mack and D'Antonio 1998, Bergman et al. 2000). A non-native species of particular interest is the feral pig (*Sus scrofa*), which is an extremely successful invader worldwide. Feral pigs destroy plant communities and seedbanks, set back succession, change soil characteristics, and alter nutrient cycling through their foraging behavior called rooting (Wood and Barrett 1979, Singer et al. 1984, Lacki and Lancia 1986, Kotanen 1995, Giuliano and Tanner 2005, Engeman et al. 2007, West et al. 2009).

The feral pig is an opportunistic omnivore that turns over soil much like a plow to expose below-ground food sources like roots, tubers and invertebrates (Howe and Bratton 1976, Kotanen 1995, Taylor and Hellgren 1997). With the exception of the grizzly bear, native North American animals that commonly disturb the soil do so by burrowing underground and subsequently burying nearby vegetation (Kotanen 1995, Tardiff and Stanford 1998, Cushman et al. 2004). In contrast, feral pigs create patches of disturbed soil ranging in size from many small 1 m² patches to a hectare or more (Vallentine 1990, Welander 2000). Though feral pigs prefer to root in mesic to hydric soil or areas near roads and trails, rooting still occurs throughout the landscape and varies temporally depending on available food resources (Bratton 1975, Bratton et al. 1982, Laurance and Harrington 1997, Mitchell and Mayer 1997, Welander 2000, Hone 2002, Chavarria et al. 2007, Mitchell et al. 2007). In addition, previously rooted patches are often revisited, which can keep habitat patches in a chronically disturbed state (Vallentine 1990, Kotanen 1995). The subsequent mounds and depressions created within a rooted patch vary

anywhere from 3-70 cm deep, and can remove or smother the vegetation and seedbank (Imeson 1977, Vallentine 1990, Kotanen 1995, 1997, Chavarria et al. 2007). Compared to undisturbed areas, rooted patches have distinct environmental conditions due to accelerated leaching of nutrients and increased decomposition rates (Singer et al. 1984, Lacki and Lancia 1986). Rooting also exposes soil that permits new plant growth of native and non-native plant species (Kotanen 1995, Cushman et al. 2004). Overall, feral pig rooting is a major disturbance that occurs at the landscape scale and varies in space, seasonal timing, frequency (number of times rooted), and intensity (depth of rooting).

Though knowledge about these disturbance components is important to assess the ecological impact of rooting by this introduced species, most studies have focused on the spatial and/or temporal patterns of feral pig rooting. Previous studies have typically documented the percentage of rooted ground in randomly-placed plots in a variety of habitat types (Bratton et al. 1982, Bowman and McDonough 1991, Laurance and Harrington 1997, Engeman et al. 2007, Zengel and Conner 2008). Only one study has quantified rooting intensity across different habitats (Chavarria et al. 2007), while none have quantified rooting frequency. Therefore, the objectives of this study were to (1) identify habitats where feral pig rooting occurs in the landscape, (2) evaluate spatial and temporal patterns of rooting, (3) evaluate intensity of rooting in space and time through a one year period, and (4) assess the potential impact of uncontrolled rooting by feral pigs in the study area. This study presents an account of feral pig rooting patterns in Florida and evaluates multiple components of disturbance (spatial extent and distribution, temporal timing and frequency, and intensity) of feral pig rooting simultaneously.

Methods

Study Area

This study was conducted at the Little Big Econ State Forest (LBESF) in Geneva, Florida on the main property that is north of the Econlockhatchee River (Figure 3-1). No feral pig hunting or trapping occurred in LBESF before or during this study. This study area is approximately 702 hectares and consists of 6 main community types based on Florida Natural Areas Inventory community classification for natural and altered landscapes (FNAI 2010). The natural community types include terrestrial (31%), palustrine wetlands (17%), and riverine (4%) habitats. The last habitat was excluded from this study since feral pigs are unable to root in this habitat. The rest of the landscape consists of altered landcover types such as pine plantation (27%), pasture (20%), and unpaved road/trails (1%). Terrestrial natural communities are characterized by xeric or mesic soils with upland plant species that are not adapted to inundation for more than 10% of the growing season. Palustrine wetland communities are typically small, shallow bodies of water with plant species that are adapted to longer seasonal inundation (FNAI 2010).

Site selection

Feral pig rooting is described by a negative exponential frequency distribution in which most sites have little or no rooting activity and few sites have concentrated rooting (Howe and Bratton 1976, Hone 1988, Mitchell and Mayer 1997). Therefore, it is important to first identify sites where feral pig rooting occurred in the landscape, so that they can be monitored in the final study of the spatial, temporal, and intensity patterns of rooting. In this preliminary study, 60

stratified random transects were sampled from December 2008 to January 2009 for the occurrence of pig rooted patches (Figure 3-2). Transects consisted of four main categories: road/trail (Road), parallel to an ecotone (Ecotone), perpendicular to an ecotone (Across), and within the habitat interior (Within). Except for Roads, these categories were then stratified by the following subcategories: terrestrial, palustrine wetland, pine plantation, and pasture community types. Within transects consisted of the 4 subcategories only, but Ecotone and Across transects consisted of 5 subcategories. This occurred because Ecotone and Across transects span two subcategories (i.e., terrestrial – palustrine wetland, terrestrial – pasture, etc), and all possible combinations between the subcategories were created. Locations of transects were randomly determined in ArcGIS.

Each random transect was located with a Trimble Nomad GPS and was 50 meters long and 15 meters wide. If multiple pig rooted patches occurred within the search width, only one was chosen to represent the transect, with preference given to newly rooted patches. Then, the patch was recorded by walking the perimeter with the GPS to form a polygon. In addition, rooted patches discovered while driving along the road/trail system or hiking to random points were also recorded using the same method.

Rooted patches were present on 11 out of 60 (18%) random transects. Approximately 73% of the rooted transects occurred either parallel to (55%) or across (18%) an ecotone with 87.5% of ecotone patches being at palustrine wetland ecotones. Only 18% occurred along roads/trails or within (9%) habitat transects. However, 17 rooted patches were discovered near roads/trails while en route to randomly-selected transects. Thus a total of 28 sites across the

landscape were found rooted by feral pigs, with 50% at palustrine wetland ecotones and 40% along roads/trails. The majority (93%) of the rooted patches mapped occurred within 20 meters of a road, trail, or wetland edge. Out of the 8 different palustrine wetland habitats found at the LBESF, only depression marshes, basin swamps, and hydric hammocks were rooted by feral pigs.

Data collection of rooted patches

After identifying sites where feral pig rooting occurred, 7 wetlands were randomly selected; 4 depression marshes, 3 basin swamps, and 1 hydric hammock. In addition, the south central portion of the road/trail system where rooting was most prevalent was divided into four segments of approximately 0.5 kilometers each (Figure 3-1). Beginning in March 2009, each selected site was thoroughly searched within a 20 meter radius of the wetland or road edge for both old and new rooted patches. Large (greater than 2 m²) rooted patches that fell within the search radius were recorded by walking the perimeter with a Trimble Nomad GPS to form a polygon, while a GPS point was recorded for small patches (less than 2 m²) along with the measured length and width. In addition to new patches, old patches were only recorded in March 2009 to serve as the baseline for new patches observed at the next sample date. Thereafter each selected site was monitored bi-monthly for newly rooted patches through January 2010. New patches can be distinguished from old because they contain freshly turned, moist soil in which there is no leaf litter or seedlings emerging. Because fresh rooting could vary in age from a day to a month (after which rootings are more clearly old), sampling occurred bi-monthly to ensure that rootings had sufficient time to age to better distinguish old from new. It is important to note

that the search area shifted for some wetlands because the flooded interior of most wetlands could not be searched during the wet season. Approximately 2-6 weeks were needed to document all patches during a given sampling month, depending on the amount of rooting activity.

GPS-obtained polygons representing rooted patches were edited in ArcGIS 9.3.1 (ESRI 2009) to remove errors caused by momentary loss of GPS signal or to untangle false vertices that crossed in thin polygon corners. Small patches, initially recorded as points, were converted to polygons using the size recorded in the field and overlaid onto large patches. The search area for each site was defined in GIS by buffering the edges of the roads, trails, and wetland margins by 22 meters (20 m plus an extra 2 m for GPS inaccuracy). Any part of a patch that extended beyond the search boundary was clipped since it was not searched at each sampling period.

Spatial-temporal pattern analyses

The total area rooted over the entire study was calculated by summing the areas of the rooted patches. This represents the net rooted area during the study (i.e., spatial extent, regardless of the number of re-rooting events). In addition, the proportion of site rooted over the entire study period was calculated by dividing total area rooted by the defined search area for roads and average search area for wetlands, since wetland areas changed seasonally.

The patch polygons from all sampling months were merged and the number of times rooted was recorded for each polygon. The subsequent polygons were used to create a rooting frequency map. Patches recorded in March 2009 (baseline data) that were not rooted during this study period were considered abandoned, while any patches rooted adjacent or outside of this

baseline data were considered to be expanded. The total area re-rooted, defined as the sum of areas for patches rooted multiple times, was calculated over the entire study period. In addition, the proportion of site re-rooted was also calculated by dividing total area re-rooted by the defined search area for roads and average search area for wetlands. Lastly, to investigate temporal changes, the proportion of site rooted and proportion of site re-rooted was calculated for each month. Though the search area remains the same for roads, the defined search area for wetlands changed with water levels each month.

Rooting intensity

Rooting intensity was quantified for patches greater than 2 m² using the chain-and-tape method for surface roughness or rugosity (Luckhurst & Luckhurst 1978). A 2-meter chain was placed in a straight line across the rooting allowing it to conform to the mounds and depressions of soil and vegetation. The straight-line (tape measure) length between the chain's end-points was then measured to determine distance lost to surface roughness. For example, the ends of a 2-meter chain on a rough surface may be 1.7 meters apart, thus 0.3 meters were taken up due to surface roughness (Figure 3-3) and the intensity score is 1.7.

The number of intensity scores per patch was geometrically related to patch size, which was estimated by the greatest length and width of the patch. The greatest length through the patch was used as a transect line, and the chain-and-tape was placed perpendicular to the transect line at 2-12 randomly selected transect positions, depending on transect length. In addition, control intensity scores were also taken adjacent to the rooted patch in undisturbed ground, with the number of control transects also geometrically related to patch size.

Based on the above information, rooting intensity for each patch was calculated as:

$$\text{Patch Intensity} = \frac{\text{average control score} - \text{average intensity score}}{2} \times 100 \quad (\text{Equation 1})$$

This calculation converted patch intensity into a percentage score per meter that increased with greater surface roughness and that had a minimum possible value of 0% (flat or no rooting) and a maximum possible value of 100% (a vertical wall) lost to surface roughness. If a site was rooted, its mean patch intensity was calculated for each month.

Data analyses

Spatial patterns

A one-way ANOVA using R 2.11.1 (R Statistical Program) was used to test for differences in proportion of sites rooted across 3 habitats: roads and trails (RT), open canopy wetland (OW), and closed canopy wetland (CW). A one-way ANOVA was also used to compare proportion of site re-rooted across 3 habitats. Several transformations were performed (i.e., square root, \log_{10} , natural log, and arcsine) in order to select the best transformation that met the assumption of normality and homogeneity of variance. Log transformations met both assumptions and were performed on both datasets. In addition, a Tukey's HSD test for unplanned comparisons was performed if significant results were obtained. One of the road/trail sites (RT 2) was noticeably different in feral pig rooting patterns than other road/trail sites and contributed to greater variance in results. The habitat along this segment was an open pasture, which was very different from the rest of the closed canopy roads. In addition, it was disked and burned in December prior to the start of sampling in January. Therefore, analyses were performed with and without RT2 to evaluate its effect on the results.

Temporal patterns of rooting and intensity

I do not have enough replication to statistically evaluate differences between habitats in proportion of site rooted or patch intensity over time. Therefore, temporal results of this natural experiment were graphed and interpreted directly. However, curve estimation was used to identify the curve that best described patch intensity trends over time.

Results

Spatial patterns

During the 11-month study, feral pigs rooted 2,476 new patches that resulted in an annual disturbance of 1.95 ha of total area rooted in the 25.2 ha search area (7.7% of the search area). In addition, another 1.05 ha consisted of abandoned patches, which increased the total area rooted to 3 ha or 11.9% of the search area. The size of rooted patches ranged from .04 m² to 1964.24 m², but the size distribution was strongly skewed toward smaller patches (Figure 3-4). A total of 2,033 small (less than 2 m²) and 443 large (greater than 2 m²) patches were mapped.

Roads and trails were more commonly rooted by feral pigs than were wetlands, but rooting was variable among surveyed sites. Roads and trails contained 1.44 ha of total area rooted in 10.07 ha searched, while wetlands only contained .51 hectares in 15.13 ha searched with the majority (.41 ha) in closed canopy wetlands. There was a large amount of variability in proportion of site rooted, especially for roads and trails (Figure 3-5). For instance, the proportion of site rooted in roads and trails during the study period ranged from 0.006 to 0.246. When abandoned area is added, the range increased to 0.032 to 0.37 of habitat along the road/trail being rooted. Because road/trail 2 included significantly fewer rooted patches than the other road/trails,

data were analyzed with and without this site. When RT 2 was omitted, the average proportion of site rooted on an annual basis changed from 0.133 ± 0.122 SD to 0.175 ± 0.108 SD. Overall, the range was much lower in wetlands with the proportion of site rooted ranging from 0.006 to 0.097, and increasing to 0.009 to 0.132 when abandoned area is added. The average proportion of site rooted for closed canopy wetlands was 0.057 ± 0.035 SD and 0.012 ± 0.023 for open canopy wetlands. There was no evidence of differences in proportion of site rooted between habitats when RT 2 was included ($F=2.12$, $df=2$, $p=.182$; Table 3-1). However, when RT 2 was excluded from analysis, the proportion of sites rooted was significantly different among habitats ($F=7.30$, $df=2$, $p=.02$; Table 3-2) with open canopy wetlands (OW) rooted significantly less than roads and trails (RT) (Tukey's HSD, $p=.02$, Table 3-3; Figure 3-6).

Roads and trails were not only rooted more extensively overall, but they also were re-rooted significantly more than wetlands. Using all data the proportion of site re-rooted was significantly different between habitats ($F=5.03$, $df=2$, $p=.04$; Table 3-4). A Tukey's HSD test further revealed that roads and trails (RT) had significantly more total area re-rooted than open canopy wetlands (OW) ($p=.04$; Table 3-5). Results were consistent when RT 2 was excluded from analysis because the proportion of site re-rooted remained significantly different between habitats ($F= 9.47$, $df=2$, $p=.01$; Table 3-6). Tukey's HSD again revealed that roads and trails (RT) had significantly more proportion of site re-rooted than open canopy wetlands (OW) ($p=.01$, Table 3-7; Figure 3-6). The average proportion of site re-rooted along roads and trails was 0.068 ± 0.073 SD and increased to 0.090 ± 0.071 SD with RT 2 removed. As for wetlands,

the average proportion of total re-rooted area was 0.013 ± 0.001 SD in closed canopy and 0.001 ± 0.002 SD in open canopy wetlands.

Out of the 1.44 ha of total area rooted along roads and trails, 29.8% of the patches were abandoned, 33.8% expanded, and 36.4% were rooted anywhere from 2-4 times (Figure 3-7 and 3-8). In contrast, the majority of patches in wetlands were either abandoned (46.7%) or expanded (43.6%), with a small percentage of the patches (9.7%) rooted up to 2 for open canopy wetlands and 3 times for closed canopy wetlands.

Temporal patterns

The proportion of site rooted by feral pigs changed over time for both roads/trails and wetlands (Figure 3-9). Rooting along road/trail sites did not begin until May but increased thereafter to a peak in July at 0.062 of sampled area, followed by another peak in November at 0.048. In contrast, feral pigs were rooting wetlands in March, slightly decreased activity in May, and gradually increased rooting until its peak in November at 0.014. Overall, temporal patterns of rooting appear to lag behind the 2009 rainfall data. Differences among habitats for rooting trends were not apparent because large variation existed within habitats for a given month (Figure 3-11, Figure 3-12, Figure 3-13). In March, feral pigs were only rooting in wetlands, especially the closed canopy wetland BS 2. However, by May, rooting in wetlands shifted to the open depression marsh DM 1 and RT 3. Proportion of rooting in all roads (except RT 2) was higher than all wetlands in July. Afterwards rooting shifted to closed canopy wetlands, but still mostly in RT 3 in September and RT 4 in November. All rooting substantially dropped off by January, with feral pigs primarily rooting in RT 4.

Re-rooting was first recorded in May and occurred in the road and trail segments, where it made up at least half of the rooting activity thereafter until a dramatic decrease in January. In wetlands, a very small proportion of re-rooting (0.001) was first documented in July, but September and November had the most re-rooting activity (each at 0.003), which occurred only in closed canopy wetlands.

Intensity

Patch intensity scores over the entire study period ranged from -0.25% to 21.5% and were normally distributed. Therefore, the majority of patches were intermediately disturbed while few were disturbed either very intensely or minimally. Regardless of habitat, patch intensity gradually increased each month until a peak in July through September, and then began to gradually decrease in intensity through January (Figure 3-10). This trend is best described by a quadratic function which explains 46.6% of the variation in the data. Habitats do not appear to differ because patch intensities are intermixed within each month. In addition, wetlands or roads/trails are each best described by quadratic functions, which are slightly shifted because roads/trails were not rooted in March. Overall, patch intensity appears to closely follow the temporal pattern of rooting activity, with the most intense rooted patches occurring during the months with the most rooting activity.

Discussion

Feral pigs are a significant biotic disturbance agent responsible for disturbing 7.7% of the search area and creating a mosaic of patches varying in size, age, frequency, and intensity throughout the landscape. Studies from around the world have shown that feral pigs prefer mesic

to hydric habitats as well as areas near roads and trails (Bratton 1975, Bratton et al. 1982, Hone 1988, Laurance and Harrington 1997, Mitchell and Mayer 1997, Welander 2000, Hone 2002, Chavarria et al. 2007, Mitchell et al. 2007). Therefore, it is no surprise that feral pigs also preferred these habitat types at the LBESF. More specifically, feral pigs rooted and re-rooted along roads/trails significantly more than the open canopy depression marsh wetlands, with closed canopy basin swamps and hydric hammock wetlands rooted at intermediate levels. Because feral pigs pose a significant threat to these habitats in particular, delving deeper into the spatial, temporal, frequency, and intensity patterns of rooting at these sites will help in the assessment of their ecological impact and how they are altering existing disturbance regimes.

Basic biology and differences in habitat quality and food availability may explain why feral pigs rooted more along forested roads and trails than open canopy wetlands. Though feral pigs are highly adaptable and opportunistic feeders, they are limited by their need to thermo-regulate since they lack sweat glands. Therefore, they wallow in mesic to wet areas and forage more in shady closed canopy habitats to keep cool in Florida's subtropical climate (Giuliano and Tanner 2005, Heinken et al. 2006, West et al. 2009). The habitats along the selected roads and trails at the LBESF (except road/trail 2) were closed canopy with mostly mesic soils. Though the closed canopy wetlands also provide moisture and relief from the heat, they were utilized much less by feral pigs. This is most likely due to differences in food availability between these habitats especially because the canopy of the roads and trails at the LBESF consists of large Oak trees (*Quercus sp.*). Acorn mast is not only a preferred food item of feral pigs, but has also been linked to successful reproduction in some areas (Zimmerman et al. 1960, Matschke 1964, Henry

1966). Lastly, these habitats may have been rooted more extensively simply because they are more accessible since feral pigs use roads and trails as travel corridors and forage as they travel (Bratton 1975, Mitchell and Mayer 1997).

Most patches were small ($<1 \text{ m}^2$) consistent with results of a study performed in the forests and grasslands of Sweden (Welander 2000). Rooted patch size may be related to food distribution, where small patches may contain isolated resources (e.g., roots) while large patches may contain larger amounts of food resources (Welander 2000). Alternatively, these patterns may also be a product of feral pigs searching for food in small patches and actually finding food in large patches (Hone 1988). Although both scenarios are likely to be at work, it could also be a product of group sizes with individuals like lone males creating small patches and sounders (females and their piglets) creating the large patches as they forage together. Small patches contributed very little to the proportion of site rooted but were quite numerous and created considerable heterogeneity in the landscape.

Temporal rooting patterns by feral pigs should also be driven by food availability and thermo-regulation needs, which differ between roads/trails and wetlands. In March when LBESF was at its driest, feral pig rooting was only found in wetlands, with the most rooting found in Basin Swamp 2 which is connected to the Econlockhatchee River. By May, the beginning of the wet season, feral pigs began to move back into roads as the soils moistened and plants began their growing season. Several stomach content analyses have revealed that feral pigs will mainly graze on herbage and foliage, especially new shoots during this time, and secondarily forage for roots (Wood and Roark 1980, Howe et al. 1981, Belden et al. 1985, Taylor and Hellgren 1997).

Above average rainfall in May that inundated soils, coupled with high summer temperatures, most likely led to the first peak in rooting for roads in July as pigs searched for both available food sources above water line and a place to cool off. Not only were these soils now easier to forage in, but invertebrates such as earthworms and insects may have been closer to the surface (McIlroy 1993). In addition, piglets were also observed foraging with their mothers at this time, which could mean that population size may be correlated with rooting (Belden and Pelton 1975, Ralph and Maxwell 1984, Anderson and Stone 1993, Hone 2002). Because feral pigs have been documented to forage at the margin of wetlands for grasses, sedges, tubers, and roots (Wood and Brenneman 1980, Bowman and McDonough 1991, Giuliano and Tanner 2005, Doupe et al. 2010), rooting peaked in November soon after wetlands had dried down due to below average rainfall. In addition, cooler temperatures enabled feral pigs to move into open depression marshes as well. During this time, the habitats along roads and trails also experienced their second peak in rooting most likely due to the availability of acorns, which is the primary food eaten by pigs during Fall and Winter (Henry and Conley 1972, Wood and Roark 1980, Howe et al. 1981, Belden et al. 1985, Taylor and Hellgren 1997). In fact, during years of good mast production feral pigs will stay in these oak stands until spring (Henry and Conley 1972).

Overall, the peak rooting period from July-November at the LBESF was in contrast with other studies that report a peak in mid-autumn to early spring (Kotanen 1995, Welander 2000, Cushman et al. 2004). Two of these studies focused on a coastal prairie (Kotanen 1995) and grassland (Cushman et al. 2004) in California, which experience cool wet winters due to their Mediterranean pattern of rainfall. The last rooting study occurred in Sweden, and Welander

(2000) attributes peak rooting to the availability of acorns. In Florida's subtropical climate, it makes sense that the peak in rooting would shift towards the wet summers. Habitats along roads and trails can be utilized almost year-around by feral pigs if food is available, while wetlands, and especially open canopy depression marshes, are restricted to fall and winter usage in central Florida.

Shifting feral pig rooting patterns resulted in the abandonment of previously rooted patches, expansion into adjacent or new area, and re-rooting of patches up to 4 times in the study year, depending on habitat. No comparable data exist for feral pigs, but grizzly bears returned to previously-disturbed patches in a California meadow to forage on glacier lily bulbs (*Erythronium grandiflorum*) that were more nutritious and productive than bulbs in the adjacent undisturbed meadows (Tardiff and Stanford 1998). The physical disturbance of soils by grizzly bears increased ammonium-N and nitrate-N levels available for absorption, while the consumption of lily bulbs minimizes competition for nutrients and space between surviving plants (Tardiff and Stanford 1998). Feral pig rooting also increases ammonium and nitrate levels in the soil (Singer et al. 1984, Kotanen 1997), which could lead to more nutritious roots, bulbs, and stems. The balance of recovery time for plants, greater nutrient content, and easier rooting conditions may explain why feral pigs re-root patches after some time and may explain why so many patches were only rooted twice. However, the surplus of one food source (acorns) or the availability of many different food sources over time probably led to the high frequency of disturbance along the roads and trails. Wetlands may require more time to recover from rooting and thus did not provide sufficient food sources to attract frequent re-rooting, as evidenced by the majority of

patches being abandoned or expanded. Ultimately, feral pigs are not only responsible for creating a mosaic of patches in different stages of succession and recovery, but can also chronically disturb some patches to the point where nothing can grow back.

The intensity of feral pig rooting is an important component of disturbance that has received very little attention, though it directly impacts the recovery of the vegetation and soil characteristics of the patch. Unlike the spatial and frequency dynamics, intensity does not appear to be significantly different between habitats in this study. In contrast, Chavarria et al. (2007) reported that wet to mesic habitats in southeastern Texas were rooted more intensely than upland and slope habitats, with the exception of pine savannahs, though they only evaluated 2-4 soil depths per patch visually. In addition, the highest intensity scores were usually found in seasonal floodplains, drainage areas, and ephemeral ponds (Chavarria et al. 2007). Intensity scores recorded here may be exceeded in other regions and may have been truncated in this study by the relatively little rooting that occurred in open canopy depression marshes. Instead of varying clearly among habitats in this study, rooting intensity changed through time and closely followed the temporal pattern of rooting, with patches being rooted more intensely during the peak of rooting activity from July-November. Regardless, even light surface rooting can profoundly impact the recovery of vegetation and soil characteristics of the patch because the vast majority of the active seed bank is located less than 5 cm from surface and is consequently smothered by overturned soil (Leck 1989, Kotanen 1997). This also results in the mixture of leaf litter and woody debris into the soil, which accelerates decomposition (Singer et al. 1984). As rooting intensity increases, it takes even longer for erosion to re-level soil and roots are left exposed,

which has the potential to decrease plant growth and increase mortality (Bratton 1975, Singer et al. 1984, Chavarria et al. 2007). Just like the when Indian crested porcupine (*Hystrix indica*) digs in the deserts of Israel, the soil pockets created by feral pigs during rooting may actually act as a pitfall trap for seeds to provide a refuge from heat and drought that is free of vegetation (Boeken et al. 1995, Kotanen 1997, Alkon 1999). Thus more intense rooting should inhibit re-growth of existing vegetation and enhance the chance of colonization by other plants arriving as seeds.

Evaluation of spatial, temporal, frequency, and intensity patterns of rooting indicate that feral pigs negatively impact habitats along roads, trails, and wetlands at the LBESF and their populations need to be controlled. During this study, feral pig rooting and re-rooting altered a substantial portion of the habitat by removing vegetation and mixing soil horizons and organic material, which presumably increased decomposition rates, smothered the seedbank, exposed plant roots, and continually set back succession. This was especially the case along roads and trails and near forested wetlands.

Because feral pigs use travel corridors, land managers should avoid installing roads and trails near wet to mesic habitats or other habitats that contain species of concern in order to conserve habitat quality and recreational value of these areas. Though relatively little rooting and re-rooting occurred in open depression marshes during this study, this outcome may be specific to LBESF; feral pigs are clearly documented as a significant threat to these wetlands and rooting patterns can change annually (Bratton et al. 1982, Kotanen 1995, Welander 2000, Hone 2002, Cushman et al. 2004). In this case, below average rainfall most likely spared most of the depression marshes by allowing them to dry out by the time feral pigs were ready to move back

into them in November. In addition, an abundance of acorns along roads and trails probably helped satisfy feral pigs through the winter of this year. Because feral pigs did attempt to root in all depression marshes by producing many small patches, there is always the chance that wetland vegetation is still recovering and that abandoned patches of this study will be rooted in the following fall to winter. Either way, feral pig rooting negatively impacts wetlands in the same way as roads and trails, especially through decreased water quality and destruction of the seedbank, an integral part of wetland vegetation establishment (Leck 1989, Zengel and Conner 2008, Doupe et al. 2010).

In conclusion, feral pigs were a strong biotic disturbance agent at the LBESF, responsible for disturbing 7.7% of the search area at LBESF and altering natural disturbance regimes. Their unique disturbance can only be compared to the tilling of land by humans or digging by grizzly bears (Kotanen 1995, Tardiff and Stanford 1998), neither of which occurs naturally in Florida. In fact, natural soil disturbance by animals in Florida is limited to burrowing by gopher tortoises and rodents, scratching by turkeys, and diggings by armadillos that result in very small patches of buried vegetation. In contrast, feral pigs dominate the non-human disturbance regime as they disrupt the soil and vegetation in patches ranging from many small $<2 \text{ m}^2$ patches to extremely large patches of the habitat. In addition, feral pig disturbance occurs more frequently than other natural biotic and abiotic disturbances like fire, hurricanes, and drought. Their disturbance keeps substantial portions of habitat in a chronically disturbed state of exposed soil with distinct environmental conditions compared to surrounding undisturbed areas (Singer et al. 1984, Lacki and Lancia 1986, Kotanen 1997). In those patches that are able to recover, understanding the

source of propagules will be an important determinant to whether feral pig disturbance maintains native biodiversity or promotes exotic invasion. Until feral pig populations are effectively managed at LBESF, it is likely that very few patches will be abandoned long enough for vegetation to fully recover. Identifying and mapping areas of pig rooting activity is a useful tool for land managers to direct trapping efforts and evaluate the recovery of patches once populations are reduced.

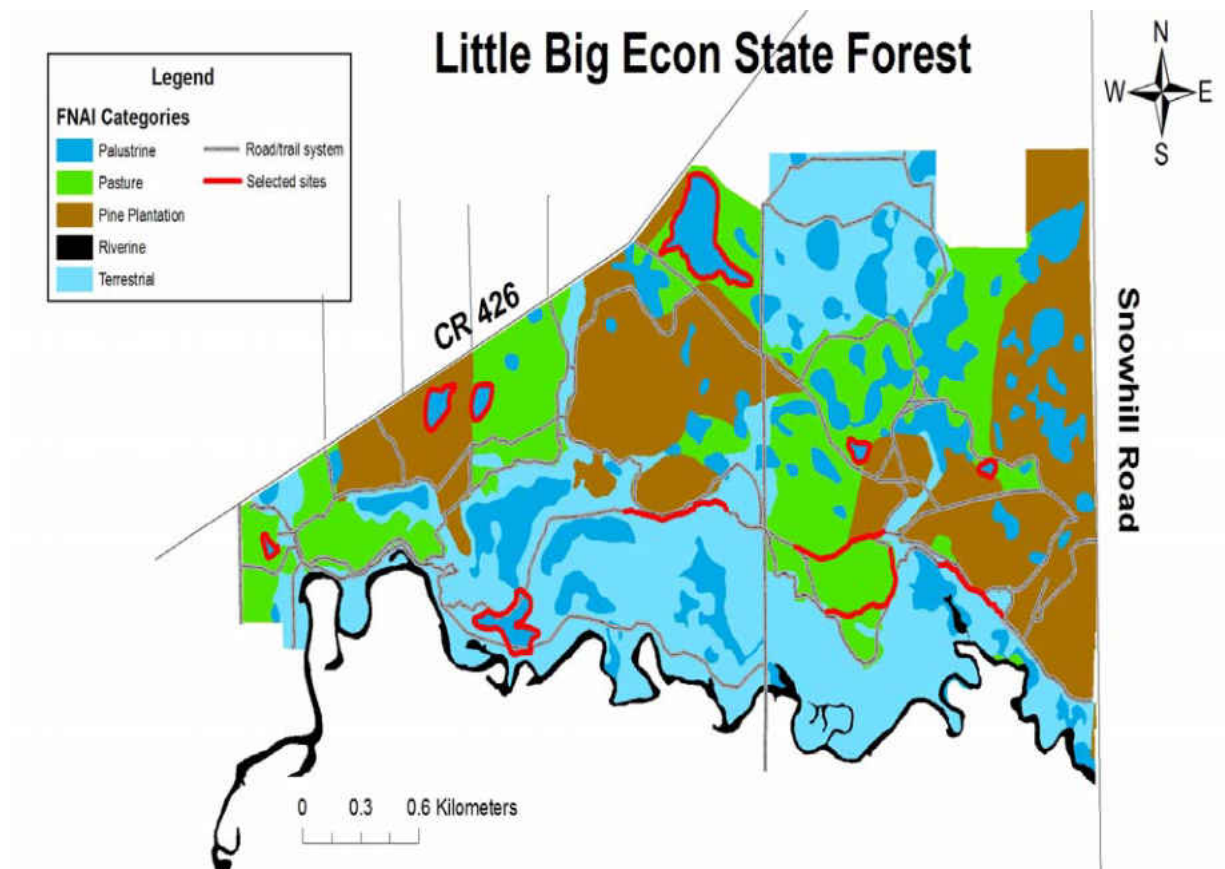


Figure 3-1: Map of Little Big Econ State Forest study site showing FNAI categories, selected sites (see site selection), and road/trail system.

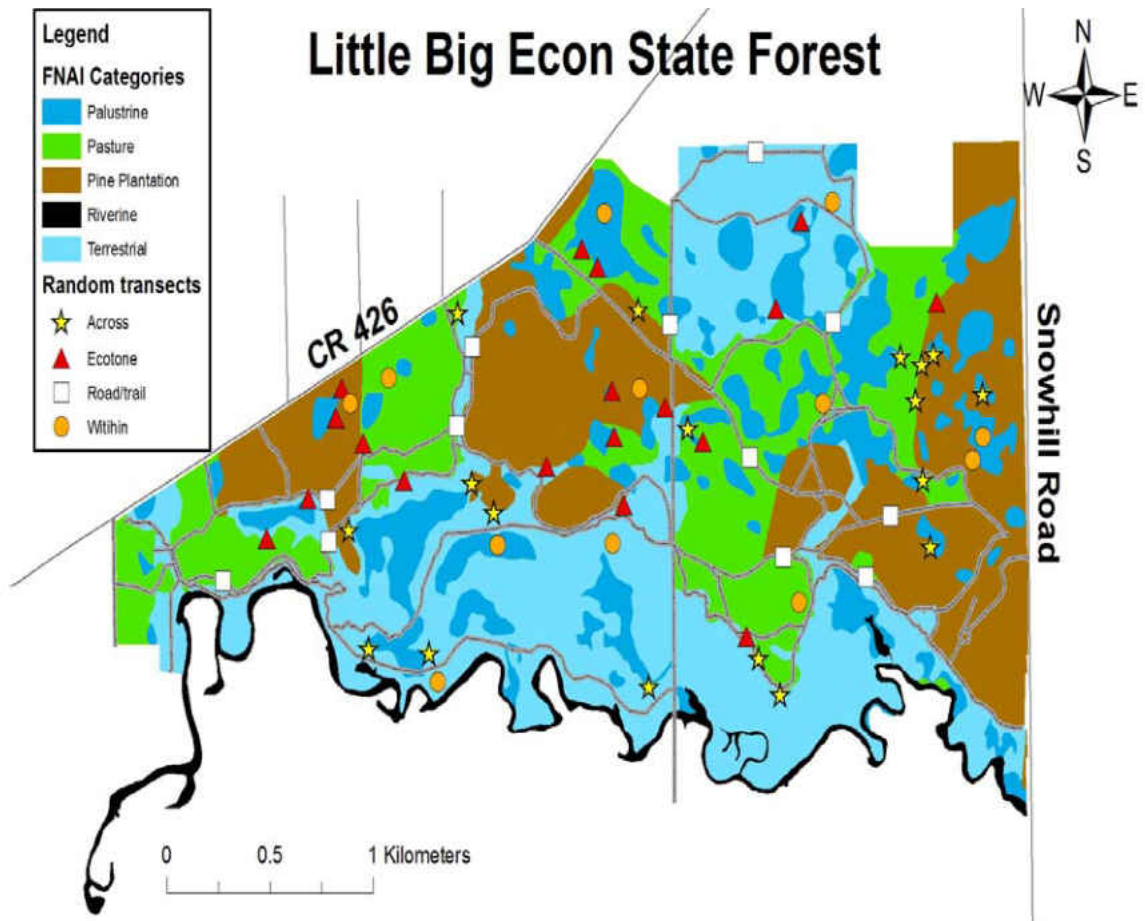


Figure 3-2: Map of LBESF showing location of the 60 stratified random transects used to select sites where pig rooting occurred.

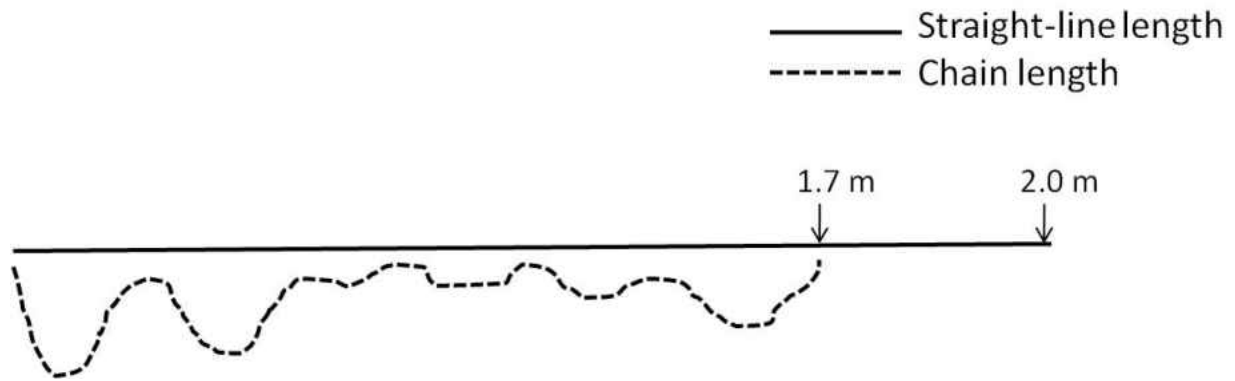


Figure 3-3: The cross section of a rooted patch depicting a 2-meter chain conforming to the surface of the ground. Due to the roughness created by feral pigs, the chain only reaches 1.7 meters.

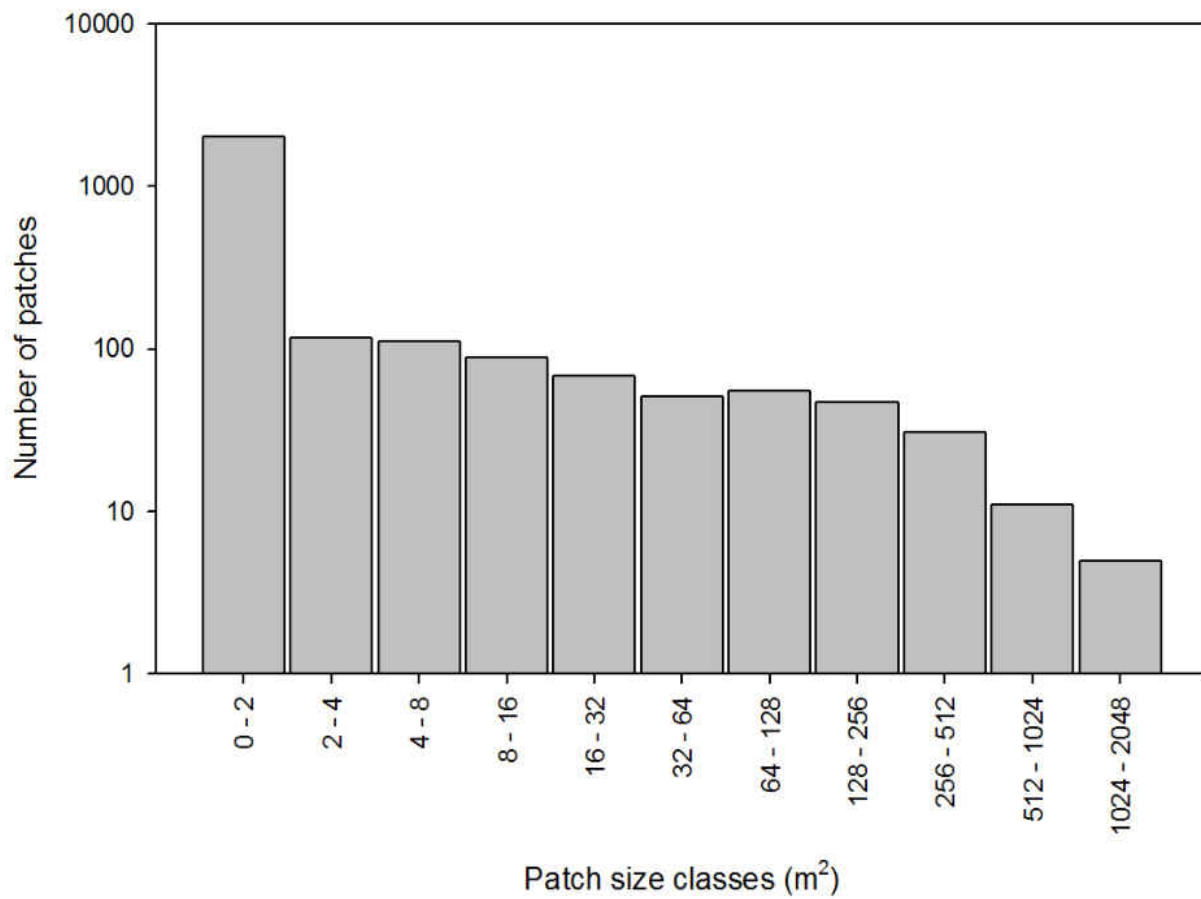


Figure 3-4: Histogram of patch size classes ranging from small (less than 2 m²) to large patches expressed on a log scale.

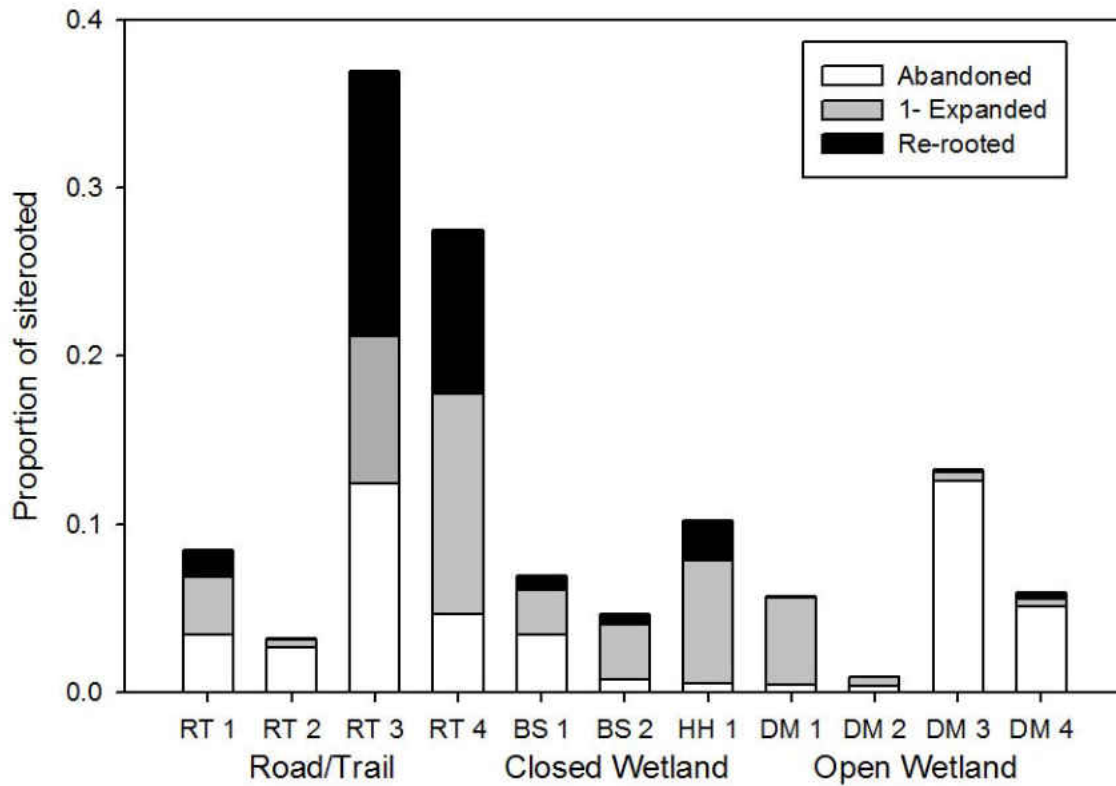


Figure 3-5: Proportion of abandoned, 1 time rooted (expanded), and re-rooted area at the end of the study for each site, indicated by numbers. RT = road/trail, BS = basin swamp, HH = hydric hammock, and DM = depression marsh. Abandoned patches were not rooted during the study period, while expanded patches were rooted in new areas outside of baseline data.

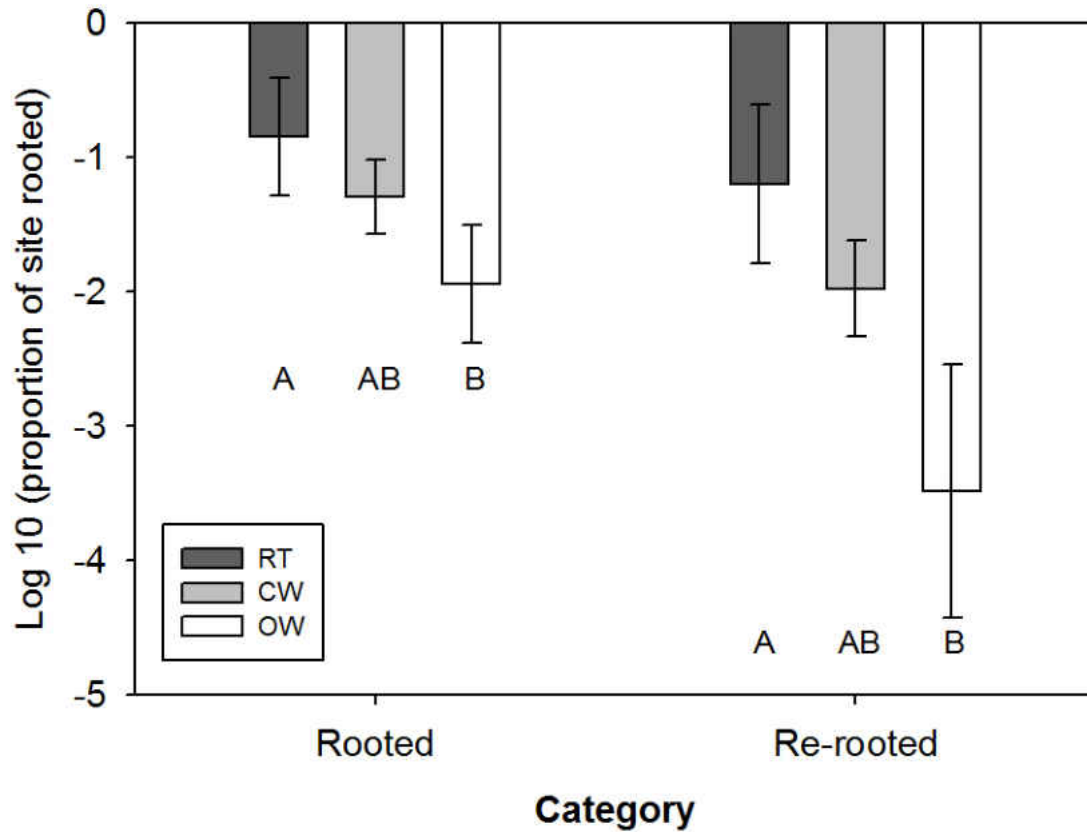


Figure 3-6: Results from the one-way ANOVA's that compared the log of the proportion of site rooted and re-rooted across three levels of habitat: road/trail (RT, n=3), closed canopy wetland (CW, n=3) and open canopy wetland (OW, n=4).

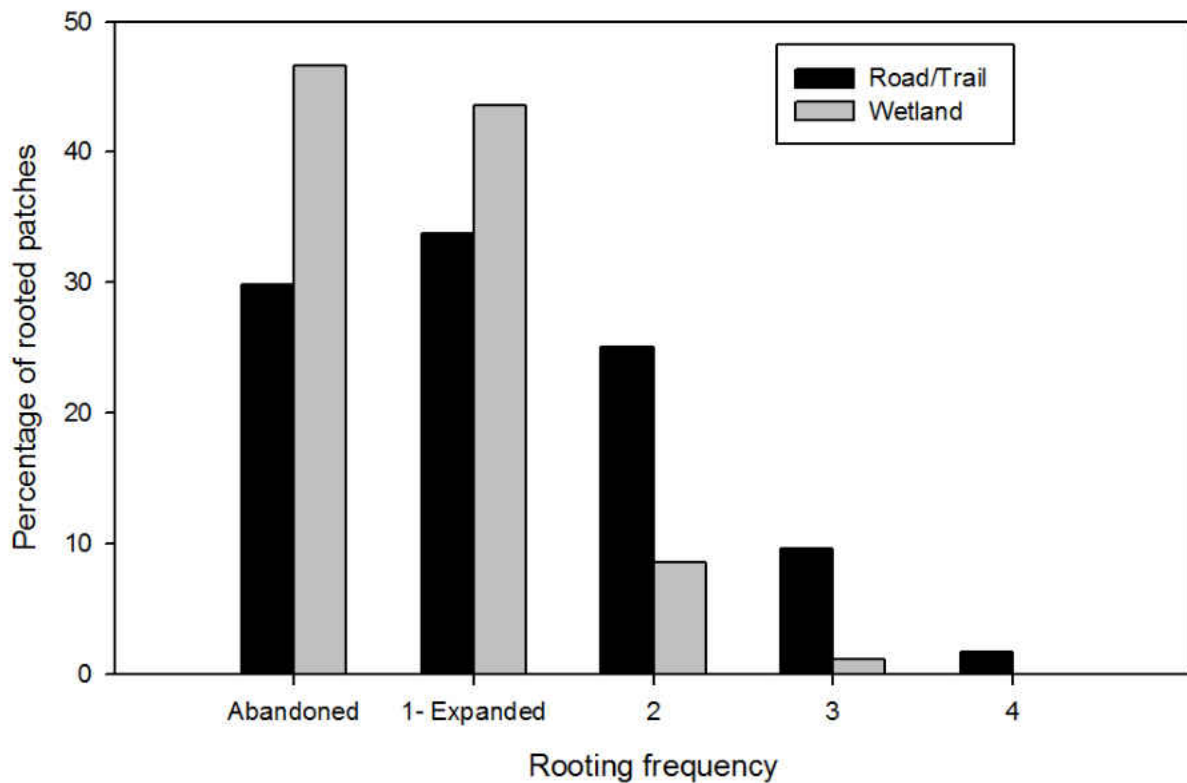


Figure 3-7: The percentage of rooted patches that fall within each rooting frequency category for road/trail and wetlands. Abandoned patches were not rooted during the study period, expanded patches were rooted in new areas outside of baseline data. The rest of the patches were rooted 2-4 times.

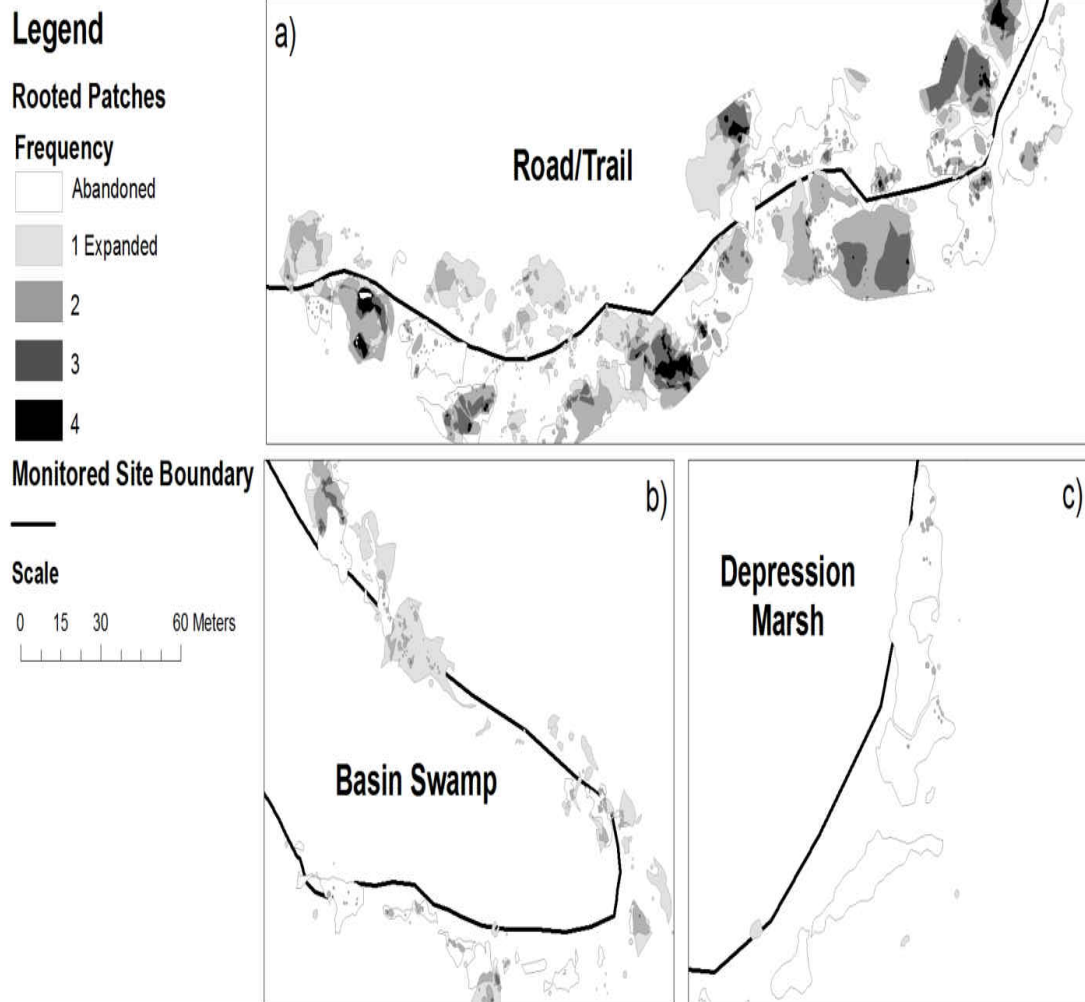


Figure 3-8: Rooting frequency maps magnified on one road segment (a), portion of a basin swamp (b), and a depression marsh (c). Rooted patches ranged in feral pig activity from abandoned (baseline data that was not rooted) to rooted up to 4 times during the study period (March 2009- January 2010).

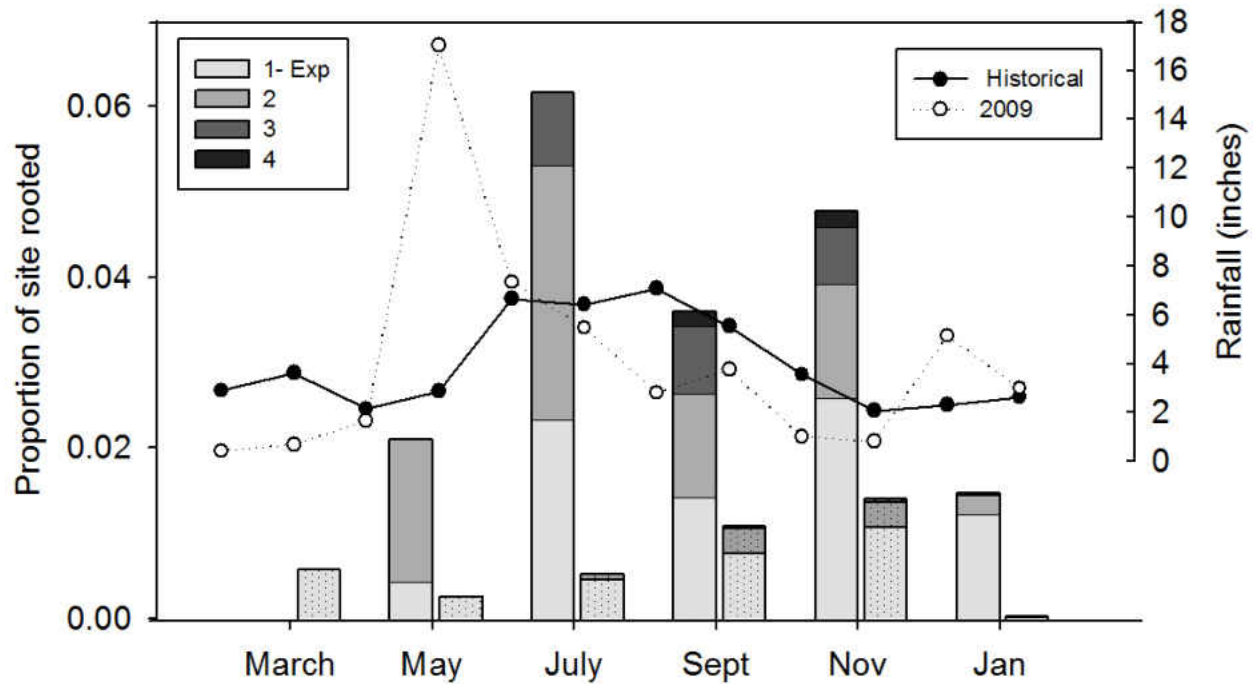


Figure 3-9: Temporal rooting dynamics for roads (plain) and wetlands (patterned) depicting the proportion of site rooted on a monthly basis according to rooting frequency 1 (expanded patches) through 4 times rooted (left axis). In addition, the historical and 2009 rainfall data (EarthInfo 2010) are overlaid (right axis).

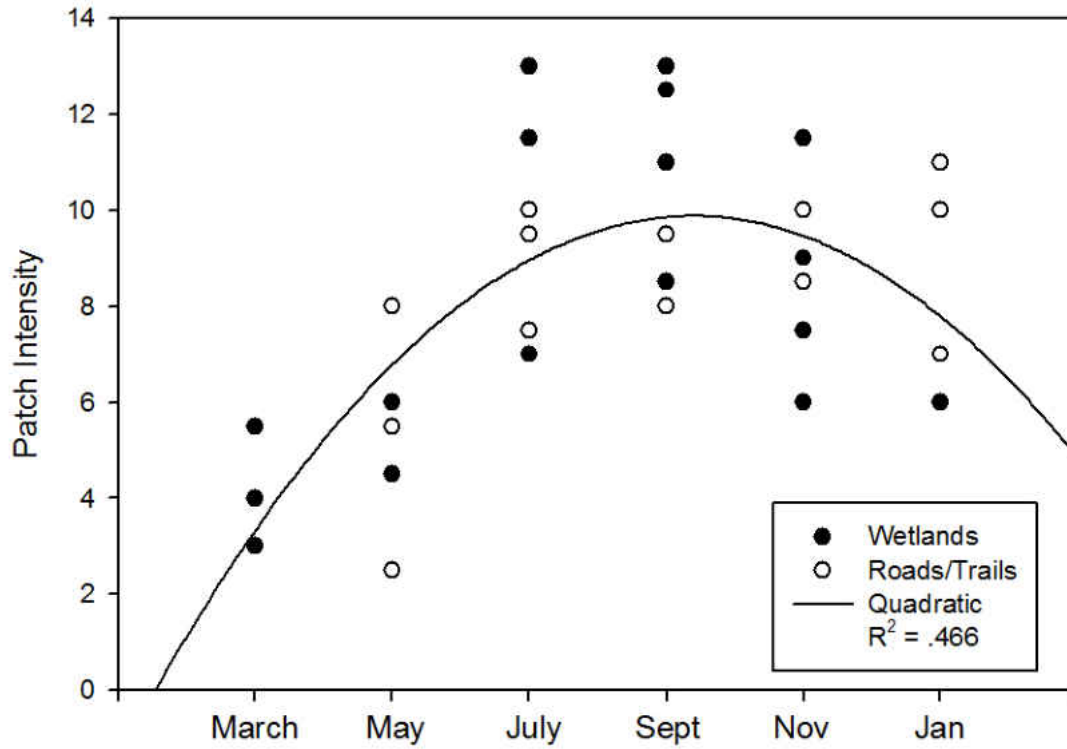


Figure 3-10: Temporal patterns of patch intensity for roads/trails and wetlands with a quadratic function fitted to the data that explains 46.6% of the variation (number of sites = 11, but all sites were not rooted at all sample dates).

Appendix A

Table 3-1: One-way ANOVA comparing proportion of site rooted across habitats.

Source	SS	Df	MS	F-ratio	P-value
Habitat	6.84	2	3.42	2.12	.182
Residuals	12.88	8	1.61		

Table 3-2: One-way ANOVA comparing proportion of site rooted across habitats after removing RT 2.

Source	SS	Df	MS	F-ratio	P-value
Habitat	11.12	2	5.61	7.30	.02 *
Residuals	5.39	7	.77		

Table 3-3: A post-hoc Tukey HSD test to determine which habitats had a significantly different proportion of site rooted.

Comparison	P-value
CW- RT	.38
OW- RT	.02 *
OW-CW	.13

Table 3-4: One-way ANOVA comparing proportion of site re-rooted across habitats.

Source	SS	Df	MS	F-ratio	P-value
Habitat	39.63	2	19.81	5.03	.04 *
Residuals	31.48	8	3.94		

Table 3-5: A post-hoc Tukey HSD test to determine which habitats had a significantly different proportion of site re-rooted.

Comparison	P-value
CW- RT	.87
OW- RT	.04*
OW-CW	.12

Table 3-6: One-way ANOVA comparing proportion of site re-rooted across habitats after removing RT 2.

Source	SS	Df	MS	F-ratio	P-value
Habitat	50.44	2	25.21	9.47	.01*
Residuals	18.63	7	2.66		

Table 3-7: A post-hoc Tukey HSD test to determine which habitats had a significantly different proportion of site re-rooted after removal of RT 2.

Comparison	P-value
CW- RT	.42
OW- RT	.01*
OW-CW	.06

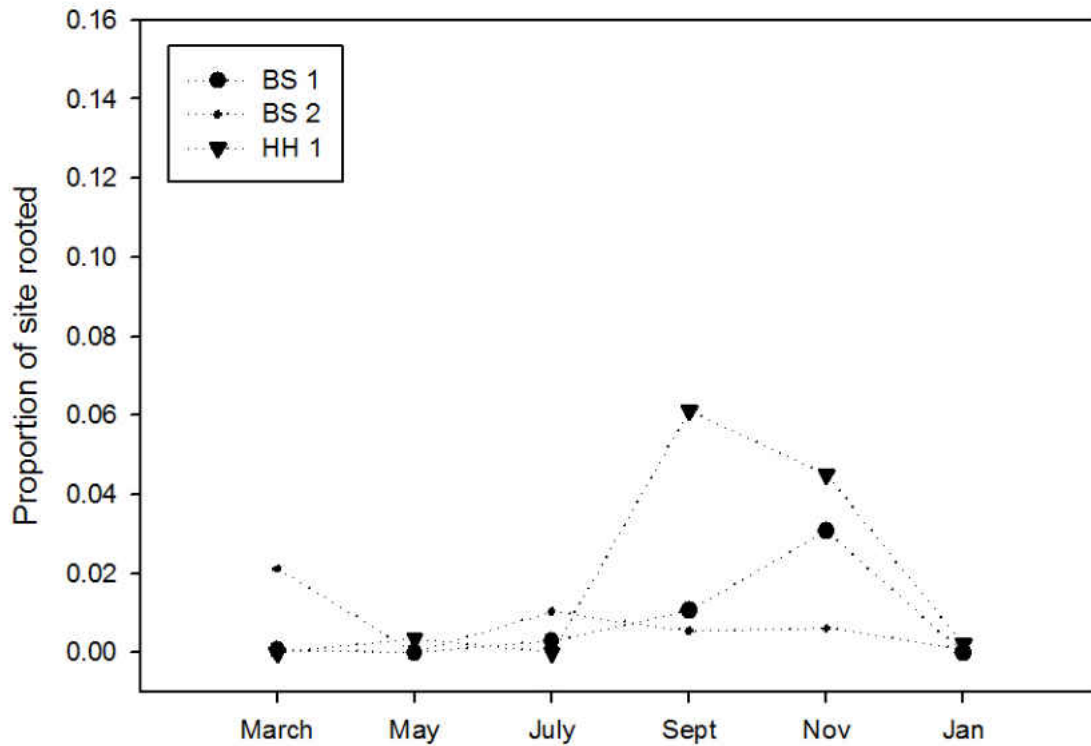


Figure 3-11: Temporal trends in proportion of site rooted for closed canopy wetlands

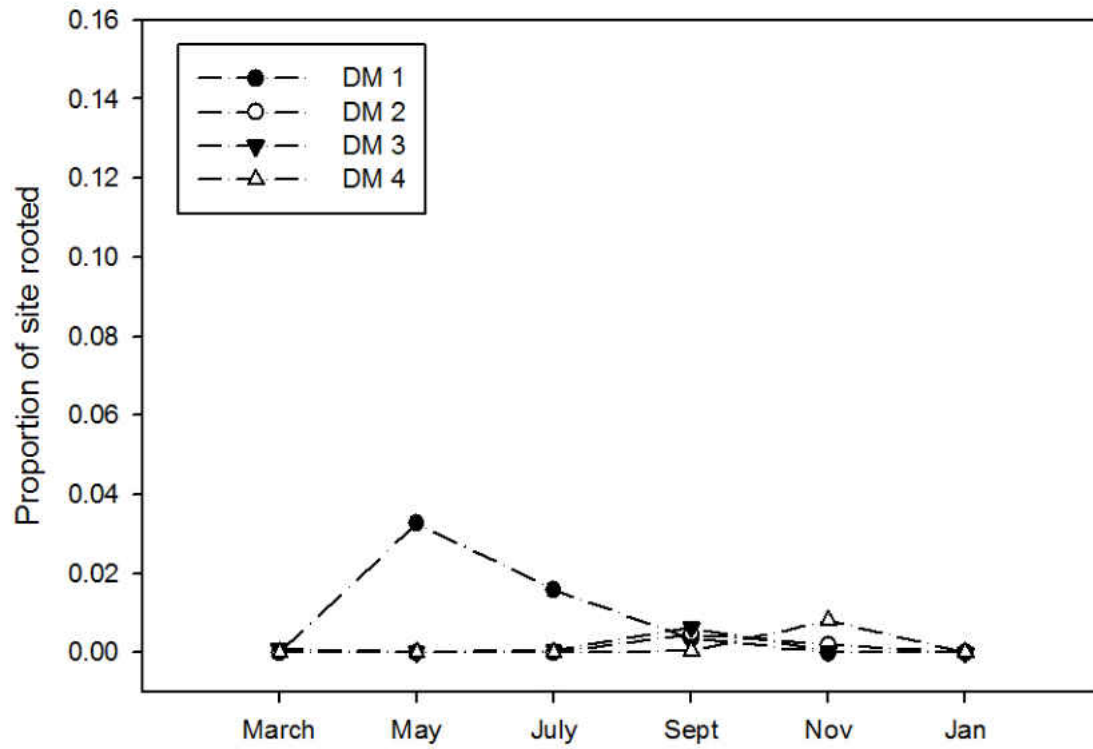


Figure 3-12: Temporal trends in proportion of site rooted for open canopy wetlands

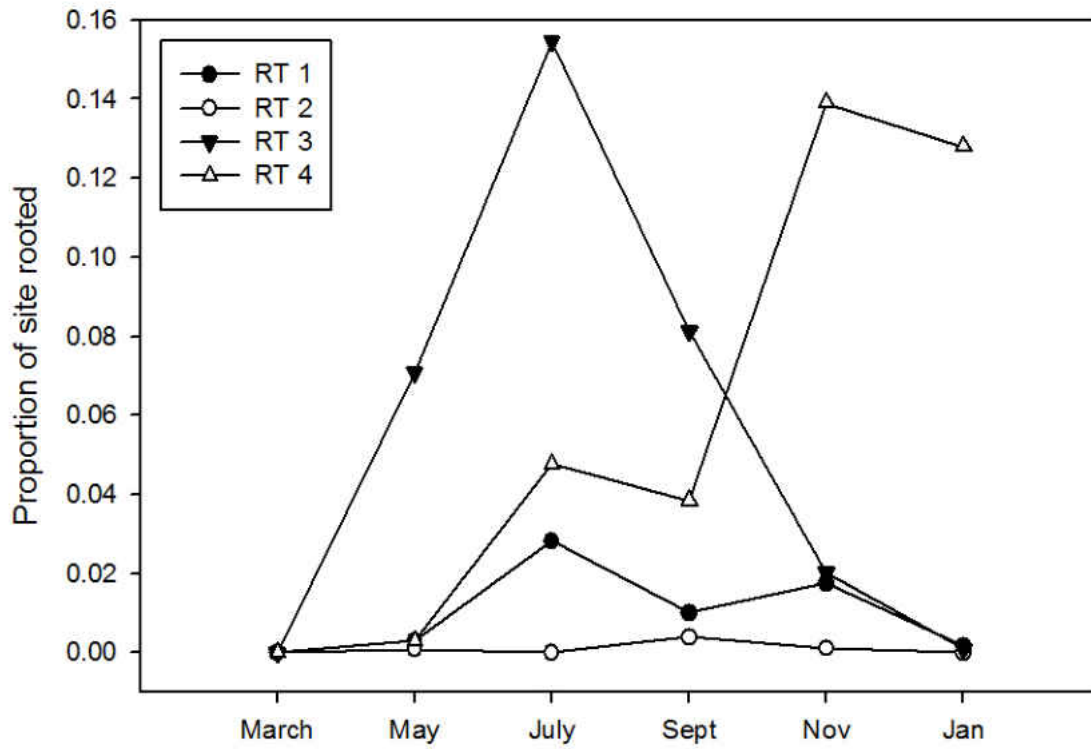


Figure 3-13: Temporal trends in proportion of site rooted for roads and trails. RT 2 was included to further demonstrate how different it behaved compared to the other roads.

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CHAPTER FOUR: THE FERAL PIG (*SUS SCROFA*) AS A DISPERSAL AGENT: EVALUATING THE EFFECTIVENESS OF ENDOZOOCHOROUS SEED DISPERSAL

Introduction

Seed dispersal is crucial to the survival and persistence of native plant communities (Murray 1986). Increasingly as more natural areas become developed, plant communities become isolated in a matrix of roads, housing developments, and agricultural lands. Fragmentation severely limits seed dispersal, resulting in reduced movement of seed vectors that maintain natural habitats as well as colonize previously unsuitable habitats, such as abandoned lands (Bakker et al. 1996, Husband and Barrett 1996, Hanski 1998, Bakker and Berendse 1999, Cain et al. 2000, Bischoff 2002). Though wind (anemochory) and water (hydrochory) are often common dispersal modes, it has become increasingly well documented that animals (zoochory) disperse a large proportion of the plants in a community (Howe and Smallwood 1982, Willson 1986, Willson 1990, 1993, Heinken et al. 2002, Kitamura et al. 2002). Large vertebrate animals often occupy large home ranges and forage in multiple habitats throughout the landscape, so they have the opportunity to disperse a variety of seeds externally by epizoochory or internally by endozoochory, which is the mechanism studied here. Endozoochorous dispersal occurs when animals either feed selectively on fruit and seeds or accidentally ingest seeds while consuming the vegetative portion of plants. Either way, undigested seeds pass through the digestive tract and are deposited in feces (Howe and Smallwood 1982, Janzen 1984, Willson 1990, 1993). Pending their survival through the digestive system, seeds may be deposited far from the parent plant, theoretically having escaped locally detrimental conditions such as seedling competition and

animal predation (Janzen 1970, Connell 1971, Cain et al. 2000, Nathan and Muller-Landau 2000). These long distance dispersal events provide critical connections between habitats that influence biodiversity, evolution, and biological invasions (Harper 1977, Hengeveld 1989, Hanski and Gilpin 1997, Sauer 1998, Hovestadt et al. 1999). Surprisingly, studies that quantify the number and kinds of viable seeds deposited are uncommon in the United States (Willson 1993).

Besides human-based pressures, non-native plant and animal species are also a major threat to natural habitats (Gurevitch and Padilla 2004, Lockwood et al. 2007). Of particular interest is the feral pig (*Sus scrofa*), an extremely successful invader worldwide that inhabits a variety of habitats, consumes large amounts of plant material, and uses its unique foraging behavior (rooting) to severely disturb these areas (Bratton 1974, Hone 1988, Kotanen 1995, Mitchell and Mayer 1997, Welander 2000, Cushman et al. 2004, Adkins and Harveson 2007, Engeman et al. 2007, Mersinger and Silvy 2007). As a large opportunistic omnivore, feral pigs have the potential to either maintain or disturb vegetation depending on the number and kind of plant species dispersed (Wunderle 1997, Heinken et al. 2002, Myers et al. 2004, Schmidt et al. 2004). As a result of consumption of available fruit and seeds while grazing above-ground or rooting below-ground for roots and tubers, feral pigs have the potential to be a significant vector for a variety of native plant species and are therefore able to boost diversity within and between habitats (Henry and Conley 1972, Wood and Roark 1980, Howe et al. 1981, Baron 1982, Belden et al. 1985, Taylor and Hellgren 1997). Because they do forage throughout the landscape where non-natives may be prevalent, feral pigs may also be important vectors for non-native species as

well. In addition, the relationship between feral pigs and plants they feed on may also be more simply a predator-prey relationship if seeds do not survive the crushing teeth and digestive enzymes possessed by this animal (Herrera 1984, Campos and Ojeda 1997, Mandujano et al. 1997).

Feral pigs have already been implicated as important vectors for species that inhabit open landscapes and fringes of forests in Europe. In these studies, plant species from a wide range of growth habits and seed morphologies were dispersed, though the majority were small seeded species with no special features to further dispersal (Middleton and Mason 1992, Heinken et al. 2002, Schmidt et al. 2004). This finding has become increasingly common in the literature for large vertebrates, which were traditionally expected to disperse mainly seeds covered with fleshy pulp endozoochorously based on seed morphology (Janzen 1984, Pakeman et al. 2002, Myers et al. 2004, Mouissie et al. 2005b). In the United States, feral pigs may be important vectors for wetland seed dispersal in particular since they prefer to root in mesic to wet habitats and there is a large amount of small seeded wetland plant species (Bratton 1975, Bratton et al. 1982, Hone 1988, Laurance and Harrington 1997, Mitchell and Mayer 1997, Welander 2000, Hone 2002, Soons 2006, Chavarria et al. 2007, Mitchell et al. 2007). Wetlands are a prominent and unique feature of the landscape that are decreasing in quantity and quality in the United States due to rapid development (Jansson et al. 2000, Hooftman et al. 2003, Soons et al. 2005). Hydrochory (i.e., dispersal by water flow) is thought to be the primary dispersal vector for plants that inhabit riparian wetlands, but many terrestrial wetlands are more vulnerable to land use changes and are hydrologically isolated (Soons 2006). Therefore, the potential for endozoochorous seed dispersal

needs to be explored as terrestrial vertebrate animals like the feral pigs may be extremely important to wetland plant diversity in these fragmented habitats. Up until now, studies that exist for wetlands have concentrated on migratory waterfowl (Mueller and Van der Valk 2002, Neff and Baldwin 2005, Green et al. 2008, Soons et al. 2008).

Though the number and kind of seeds dispersed is important knowledge, whether or not the feral pig is an effective seed disperser will depend greatly on the location of deposition and probability of survival in the landscape (Schupp 1993). Surprisingly, this ultimate outcome of dispersal is not often evaluated because most seed dispersal studies only consider habitat preference of the plant species to suggest where seeds came from (Middleton and Mason 1992, Schmidt et al. 2004). This study instead focuses on the location of deposition within wetlands and road/trail segments, and compares those locations to the habitat preferences of the dispersed plant species to determine survival. Therefore, the purpose of this study is to assess the role of the non-native feral pig as an effective vector for seed dispersal. The following research questions are addressed: (1) Which plant species are being dispersed as viable seeds by feral pigs, and in what quantities? (2) Are there seasonal variations in seed dispersal? (3) Will plant species survive based on the habitat preference of the plant species and location of deposition?

Methods

Study Area

This seed dispersal study was conducted at the Little Big Econ State Forest (LBESF) in Geneva, Florida on the main property north of the Econlockhatchee River that is 702.73 hectares (Figure 3-1; see chapter 3). After identifying sites where feral pig rooting occurred throughout

this landscape (See Chapter 3: site selection), 11 sites were randomly selected to ensure that fecal samples could be found in the future. This is based on the rationale that rooting sites indicated extended feral pig presence. These sites included 4 road/trails segments and 7 wetlands (4 depression marshes, 2 basin swamps, and 1 hydric hammock). A large percentage of the landscape consists of longleaf pine plantation (27%) and pasture (20%) that borders the roads/trails or surrounds most wetlands.

Three out of four of the road/trail segments were located alongside mesic hammocks, which are terrestrial habitats with sand substrate that experience occasional or rare fire. These habitats consist mainly of live oak (*Quercus virginiana*), cabbage palm (*Sabal palmetto*), and saw palmetto (*Serenoa repens*). The fourth road/trail segment is located through longleaf pine (*Pinus palustris*) plantation and pasture only. Depression marsh wetlands are open, small round depressions that experience frequent to occasional fires. These wetlands are mainly characterized by herbaceous vegetation like maidencane (*Panicum hemitomon*), fire flag (*Thalia geniculata*), pickerelweed (*Pontedaria* spp.), and mixed emergents. During times of drought dog fennel (*Eupatorium* spp.) can colonize, while shrubs like willow (*Salix caroliniana*), common buttonbush (*Cephalanthus occidentalis*), and wax myrtle (*Myrica cerifera*) begin to invade when fire is suppressed. Basin swamps are forested wetlands with peat substrate that rarely experience fire and therefore allow for the growth of mixed hardwoods such as cypress (*Taxodium* spp.), blackgum (*Nyssa biflora*), tupelo (*Nyssa aquatica*), swamp bay (*Persea palustris*), gordonia (*Gordonia lasianthus*), and sweetbay (*Magnolia virginiana*). Hydric hammocks are forested wetlands that rarely experience fire and are characterized by sand, clay, or organic soil substrate

that is often formed over limestone. Associated vegetation includes: water oak (*Quercus nigra*), cabbage palm (*Sabal palmetto*), red cedar (*Juniperus silicicola*), red maple (*Acer rubrum*), hackberry (*Celtis laevigata*), hornbeam (*Carpinus caroliniana*), blackgum (*Nyssa biflora*), need palm (*Rhapidophyllum hystrix*), swamp bay (*Persea palustris*), gordonia (*Gordonia lasianthus*), sweetbay (*Magnolia virginiana*), and other mixed hardwoods (Myers and Ewel 1990, FNAI 2010).

Non-native plant species threat

Approximately, 4 hectares of the main property of the LBESF are infested with 15 non-native Category I and II plant species. According to the Florida Exotic Pest Plant Council, 14 of these species are considered Category I invaders meaning that they have been documented to cause ecological damage. This can occur in several ways such as displacing native species, altering ecosystem functions, and hybridizing with natives. The remaining species are considered Category II invaders, defined as increasing in abundance, but not demonstrated to cause ecological damage (FLEPPC 2007). Non-native species have been documented in 6 out of 11 of the selected sites.

Sample collection

Bi-monthly between March 2009 and January 2010, fresh feral pig feces were collected when available from the 11 selected sites. By collecting only fresh samples, I reduced the chances of contamination by wind-dispersed species and removal of seeds by animals. In addition, the bottom of each fecal sample that had contact with the ground was cut off to avoid contamination of seeds from the soil. Feces were found by searching a 20 meter radius from the road, trail, or wetland perimeter, but extended beyond that when established latrines were found

near the site. The location of all fresh feces was marked with a Trimble GPS unit, and samples were randomly collected using a random number generator. The goal was to collect 18 samples each sampling month due to limited space in the enclosure in which the samples were housed.

Germination trials

The seedling emergence method was used to assess the quantity and identity of viable plant species. Seeds were extracted from the fecal material before planting by gently washing each sample with water through a series of wire mesh sieves (4 mm, 1 mm, and 250 μ m). The left over material was combined, divided in half, and each half was randomly assigned to either a wetland or upland treatment. Because feral pigs have the potential to forage throughout the study site, these treatments were used to promote germination conditions for the greatest number of species possible. The wetland treatment contained a 3:1 soil ratio of Metro-mix 200 series sterilized soil to all purpose sand and the bottom 1/2 of the pot was always submersed in water to keep the soil saturated. The upland treatment contained a 1:1 soil ratio of Metro-mix 200 series sterilized soil to all purpose sand and was kept completely dry. Sieved material from samples was spread thinly on top of soil in each pot.

All samples were housed in an enclosure supported by a PVC frame that was covered in window screen to maintain ambient conditions throughout the year and prevent outside wind-dispersed seeds from contaminating the samples. Control pots of sterile soil in wetland and upland conditions were also maintained throughout the experiment to test for seed contamination. The enclosure contained two benches marked with a grid system onto which the

pots were randomly placed. All samples were watered daily either by natural rainfall or hand watering with dechlorinated tap water.

Plants that germinated from the samples were housed in the screen enclosure until they were able to be identified to species, usually upon flowering. Every 2 weeks, pots were re-randomized and any new emergences were marked with a colored toothpick and photographed. If several plant species were crowding one pot, some were transplanted to avoid seedling competition and ensure growth to an identifiable stage. In this case, sometimes identical plant species were removed all together, but recorded for density estimates. Although individual plants were removed from the pots after identification, the entire pot was not removed from the screen enclosure until all plants in the pot had been identified. In cases where no plants germinated in the sample, the pot was removed after 5 months.

Data Analysis

Simple summary statistics were calculated on a monthly and annual basis to determine the total number of seeds germinated, total number of species germinated, and the percentage of samples with viable seeds. In addition, the mean, median, and maximum seed density (number of seeds germinated per sample) and species density (number of species germinated per sample) was also calculated each month and annually. Lastly, the seed contribution of each species was calculated by dividing total number of seeds germinated for that species by the total number of seeds germinated throughout the study. It is important to note that germination of plant species was used as a proxy for dispersal of viable seeds, therefore there is a chance that feral pigs could actually disperse more seeds and/or species if they did not germinate during this study.

Plant species information was also categorized as follows: Origin (native, non-native), growth habit (forb, graminoid, woody), habitat preference (OBL, FACW, FAC, FACU, NOT), dispersal mode based on seed morphology (anemochory, endozoochory, epizoochory, myrmechory, autochorus, unassisted), seed length (<1 mm, 1 to <2 mm, 2 to <3 mm, 3 to <5mm). Habitat preference is based on the National Wetlands Inventory (NWI) indicator list that ranks plant species according to their probability of occurrence in wetlands. Obligate wetland species almost always occur in wetlands (99% probability), while facultative wetland occur in wetlands 67%-99% of the time. Facultative species are estimated to occur in wetlands 34% to 66% of the time, therefore they are equally likely to occur in wetlands and non-wetlands. Facultative upland species only occur in wetlands occasionally with an estimated probability of 1%-33% of the time (NWI and FWC 1988). I made up the last category (NOT) because several dispersed species were not listed on the NWI list. Seed morphology was used to deduce the dispersal mode for each plant species and is based on six major types of adaptations considered by Wilson et al. 1990. Anemochorus or wind dispersed seeds have wing-like appendages or hairs to enable flight. Seeds adapted to endozoochory are surrounded by a fleshy pulp or aril, while those adapted to epizoochory are hooked, barbed, or sticky to the touch. Seeds that attract ants (myrmechory) in particular contain an appendage called an elaiosome. Autochorus or ballistic dispersal occurs when seeds are ejected from seed-pods of the plant. Lastly, seeds that have no features to suggest a dispersal mode are considered to be unassisted.

Using R.11.1 (R Statistical Program), a chi-square test was used to test the hypothesis that the location of deposition is independent of habitat preference for plant species dispersed.

For each fecal sample the number of species germinated was counted and combined according to habitat preference. Then, the total number of species germinated with the given habitat preference was summed based on the location of deposition inroads/trails and wetlands for use in the Chi-square analysis. Number of species germinated was chosen because I felt it represented independent observations as opposed to number of seeds germinated, which would have been counted multiple times in one sample. Potential survival of the dispersed species into locations was assigned simple binary values (yes or no) based on where seeds were deposited. For instance, obligate and facultative wetland species would most likely survive if deposited back into wetlands and not survive if deposited on the mesic to upland road/trail segments. Lastly, the number of species deposited in suitable habitat based on location of deposition and habitat preference was calculated to determine effectiveness of dispersal by feral pigs.

Non-metric multidimensional scaling

In PC-ORD 5, non-metric multidimensional scaling (NMS) ordination was used to determine if there was a relationship between species composition and time (sampling month). Species abundance data were expressed as presence/absence for each sample month and site in which the sample was deposited. A preliminary NMS ordination using autopilot mode with medium thoroughness and the Sorensen (Bray-Curtis) distance metric was executed using 50 real and 50 randomized runs with random starting points. Because the stress was greater than 10, data were then transformed using Beals smoothing. The final NMS using the slow and thorough autopilot mode and the Sorensen (Bray-Curtis) distance metric was executed. A random starting point was used and 250 real and 250 randomized runs occurred. The number of dimensions in

the final solution was chosen based on recommendations from the program, and the final stress for each dimension. The ordination was graphed in 3-D and the percent of variance explained by each axis was reported. Lastly, multi-response permutation procedure (MRPP) with Sorensen (Bray-Curtis) distance metric was used to test for significant difference between sampling months. The MRPP with Sorensen (Bray-Curtis) distance metric was repeated to investigate if species composition was significantly different among habitats (road/trail and wetland).

Results

A total of 782 seeds germinated from 108 fecal samples collected from roads/trails (64 samples) and wetlands (44 samples) over an 11-month period, which resulted in the dispersal of 50 different species by feral pigs (Table 4-1 and 4-2). Overall, 81% of the fecal samples contained viable seeds, but most (60%) contained only 1-3 seeds that germinated per sample (Figure 4-1a). The annual mean seed density was 7.2 germinations per sample with a median of 2 indicating that a few seed rich samples, especially one that contained 315 seeds, elevated the mean. The same goes for species richness distribution; most fecal samples were species poor with 66% containing only 1-2 species that germinated per sample (Figure 4-1b). Though the maximum number of species germinations found in a sample was 10, the annual species density was only 2 species that germinated per sample with a median of 2.

A wide range of plant species varying in origin, growth habit, and habitat preference were dispersed by feral pigs (Table 4-2). Only 8% of the plant species that germinated (or 2% of the seed contribution) were non-native in origin and these included *Rumex obovatus*, *Trifolium dubium*, *Sacciolepis indica*, and *Ludwigia peruviana*. Of special concern is *Ludwigia peruviana*,

a category I invader (FLEPPC 2007) that germinated in 3 different samples during March and May and made up 71% of the non-native seed contribution. The majority of dispersed plant species were either obligate (32.0%) or facultative wetland (28.0%) graminoids and forbs (Figure 4-2b). Facultative plants made up 26.5% of the species dispersed and was the only category containing woody shrub or tree species. Only 14.3% of the graminoids and forbs dispersed by feral pigs were facultative upland or not associated with wetlands. Although only 3 woody species were dispersed (*Gaylussacia dumosa*, *Sabal palmetto*, and *Myrica cerifera*) compared to 24 graminoid species and 23 forb species, they made up 41.4% of the seed contribution (Figure 4-2a). Therefore, the majority of seeds that germinated were facultative (61.8%), followed by obligate (17.5%), facultative wetland (13.7%), facultative upland (6.3%), and not associated with wetlands (0.8%). Just like with species richness, the number of seeds that germinated was also roughly equal for graminoids and forbs.

Seed characteristics were also represented by a variety of dispersal modes and seed sizes. With four dispersal modes represented, seed contribution was roughly equal between unassisted (45%) and endozoochorous dispersal (42%; Figure 4-3a). Species adapted to anemochory contributed 13%, while those adapted to epizoochory contributed < 1%. However, the majority of species (37) were considered to be “unassisted” (Figure 4-3b). As for seed size, the majority of the seed contribution (75%) and species (51%) came from seeds that were 1 - <2mm, followed by 21.8% of the seed contribution and 32.7% of the species from seeds that were <1mm. Only 8 species produce seeds larger than >2mm with a seed contribution of 2.7%.

Approximately 70% of the annual seed contribution was made up by only 5 plant species: *Gaylussacia dumosa*, *Eupatorium compositifolium*, *Paspalum conjugatum*, *Ludwigia repens*, and *Eleocharis* sp. (Table 1). *Gaylussacia dumosa*, a facultative deciduous shrub producing fleshy-fruited berries, alone contributed 40.6% to the total number of seeds germinated mainly because of one sample in July that contained 312 seeds (40% of seed contribution). Contributing 10% was *Eupatorium compositifolium*, a facultative perennial forb that inhabits disturbed soils and margins of depression marshes followed by *Paspalum conjugatum* (8%), a facultative perennial grass that inhabits similar areas. Lastly, the forb *Ludwigia repens* (6%) and graminoid *Eleocharis* sp. (5%) are both obligate wetland species that inhabit the waters of marshes, swamps, rivers, ponds, and disturbed ditches and canals. Overall, most were uncommon with 38 plant species each contributing less than 1% to the seed contribution over the study period.

Feral pigs dispersed viable seeds throughout the entire year, but species composition changed significantly with each sampling month (MRPP $p=0.002$; Figure 4-4). The NMS ordination of 24 sampling units across 50 plant species was best fit by a 3-dimensional solution (Table 4-3) with a final stress of 8.67 (48 iterations and 0.00 final instability). The first three axes explained 91.4% of variation in the data (axis 1= 38.5%, axis 2 =32.0%, and axis 3 =20.9%). March species composition is clearly set apart from the May, July, and September species composition. November and January are more similar to March in species composition, though some points overlap with May, July, and September sampling points. Overall, 34 species were only dispersed during 1 sampling month, while three plant species were dispersed all year: *Eupatorium compositifolium*, *Cyperus ovatus*, and *Cyperus polystachyos*.

Each sampling month varied in seed number and species richness as well as the percentage of fecal samples that contained viable seeds (Table 4-1, Figure 4-5). In March, 16 species germinated from 52 viable seeds that occurred in 83.3% of the samples, and this results in a mean of 2.9 germinations per sample. Though the number of samples that yielded viable seeds decreased, there was an increase in seed total and mean seed density in May followed by the peak of seed dispersal by feral pigs in July. Though only 12 plant species were dispersed in July, one sample containing 315 seeds elevated the average seed density to 18 seeds per sample. Afterwards, seed dispersal plummeted to its lowest point in November when only 9 species germinated from 34 seeds, resulting in a mean seed density of 2.3 seeds per sample. Seed dispersal greatly increased in January when 95% of the samples contained viable seeds, resulting in the germination of 26 plant species from 204 seeds and a mean seed density of 10.2. In addition, mean and maximum number of species per sample greatly increased in January to 4 and 10, respectively, though it was relatively constant the rest of the study period.

Though species composition changed significantly through time, there was no overall relationship in the NMS between species composition and location of deposition (MRPP $p=0.29$), meaning species were deposited randomly in the landscape. However, a Chi-square test revealed that there was an association between the location and habitat preference of the plant species ($\chi^2 = 10.04$, $df = 4$, $p\text{-value} = 0.038$; Figure 4-6). The mosaic plot (Figure 4-7) shows that less facultative species were deposited in road/trail segments than expected. In addition, fewer facultative upland, facultative wetland, and obligate wetland species were deposited in wetlands than expected. As for survival of these dispersed species, overall 61% of the species would most

likely survive given their habitat preference and location of deposition. As for wetland species alone, only 23% were actually deposited into wetlands.

Discussion

Feral pigs are potentially significant vectors for long distance dispersal of many native plant species from a variety of habitats. I observed 782 germinations from 108 samples during 11 months that resulted in the dispersal of 50 different plant species. From this, 28 were either native obligate or facultative wetland plant species. Though only 233 seeds from these species were dispersed, feral pigs may be important vectors for wetland species in particular. Four plant species were non-native, one (*Ludwigia peruviana*) of which is associated with ecological damage in wetlands (FLEPPC 2007) and comprised the majority of the non-native seed contribution. Most fecal samples were seed poor. This finding is in agreement with all 3 of the studies that examined endozoochory seed dispersal by feral pigs in Europe, among several other mammals. Interestingly, feral pigs still dispersed more species than other mammals despite dispersing less seeds (Middleton and Mason 1992, Heinken et al. 2002, Schmidt et al. 2004). The role of the non-native feral pig as an effective seed disperser of native plant species depends on the quantity and type of seeds dispersed as well the location of deposition in the landscape (Schupp 1993). Both factors are largely due to seasonal behavior patterns of the feral pig, such as the foraging strategy, habitat use and movement of this animal, plus plant and seed attributes that promote dispersal by feral pigs (Howe and Smallwood 1982, Janzen 1984, Willson 1990, Schupp 1993, Hughes et al. 1994, Nathan and Muller-Landau 2000, Cosyns et al. 2005).

Unlike native Floridian mammals, feral pigs are opportunistic omnivores that switch between grazing and rooting strategies, depending on food availability (Taylor and Hellgren 1997). Stomach content analyses reveal that plant material dominates their diet as feral pigs graze primarily during winter and spring on grasses, though forbs and woody foliage are also consumed. When available, fleshy fruit from citrus trees, cactus (*Opuntia* spp.), and grapes (*Vitis* spp.) have also been identified. Rooting below-ground primarily from spring to fall may target a different set of species. Mainly, feral pigs consume roots and tubers from grasses and sedges, but may accidentally intake seeds from the seed bank by swallowing soil (Wood and Roark 1980, Howe et al. 1981, Belden et al. 1985, Taylor and Hellgren 1997). Understanding the diet of feral pigs helps explain the many graminoid species dispersed in this study (11 grasses (Poaceae) and 13 sedges and rushes (Cyperaceae and Juncaceae)) and other endozoochorous seed dispersal studies in Europe (Middleton and Mason 1992, Heinken et al. 2002, Schmidt et al. 2004). In addition, Belden and colleagues (1985) identified plant material in 93 pig stomachs and found several forbs species that were dispersed in this study, including smartweed (*Polygonum* sp.), cabbage palm (*Sabal palmetto*), wax myrtle (*Myrica cerifera*), (*Rumex* spp.), and plants from the Asteraceae family.

Feral pigs forage throughout the landscape in a variety of habitats, as evidenced by the full spectra of upland to wetland plant species that were dispersed. In North America, average yearly home range estimates for feral pigs ranged from 1.8 (Wood and Brenneman 1980) to 35.0 km² (Adkins and Harveson 2007). Because the upper estimate occurred in the Chihuahuan Desert of Texas, feral pigs at LBESF probably use a home range on the lower end of the spectrum.

Wood and Brenneman (1980) radio-collared feral pigs in the Lower coastal plain forest-marsh ecosystems of South Carolina and attributed the small average annual home range size to short distance between food and water. This might also be the case at the LBESF, which has multiple wetlands in a matrix of pine plantations. Individual diel home ranges over a 24-hr period were also recorded and ranged from .02 to .6 km² (Wood and Brenneman 1980). Another study that examined daily movements of feral pigs in California reported that boars often explored their entire home range by traveling 11 km in just 1-2 days, while sows ranged anywhere from .8 km to 4.8 km depending on season (Barrett 1977). Both studies demonstrate that different habitats or even different wetlands could be used on a daily basis at times, and that seeds may be dispersed several kilometers by feral pigs.

The species composition and abundances of seeds dispersed by feral pigs varied through the year. This variation was expected since most plant species set seed during a specific time of year and feral pigs adjust their foraging strategies and movement according to food resources that are available (Wood and Brenneman 1980, Belden et al. 1985, Taylor and Hellgren 1997, Herrera 1998). In March, the LBESF is at its driest and overall seed availability is likely low as it approaches the end of the dry season, which could explain the low number of seeds dispersed. Interestingly, species composition in March was quite different in the NMS ordination. This finding is corroborated by the fact that feral pigs were only rooting in wetlands during this time (see Chapter 3 for temporal rooting pattern). With the onset of the wet season in May, feral pigs most likely take advantage of the growing season by mainly grazing on new shoots and leaves that are available (Wood and Brenneman 1980, Howe et al. 1981, Belden et al. 1985, Taylor and

Hellgren 1997). The number of seeds dispersed increased slightly as wet season species began to produce seed and many are dispersed through September, as evidenced by the overlapping of these months in the NMS ordination. Because of one fecal sample, the number of seeds dispersed peaked in July, which corresponded with the first peak in rooting at the LBESF. In addition, there was a noticeable decrease in species richness. Though rooting activity peaked again in November, the total number of seeds dispersed and species richness dropped to their lowest points in the study. This drop was most likely due to a switch in foraging on oak mast at this time, a highly preferred food item for feral pigs (Henry and Conley 1972, Wood and Brenneman 1980, Howe et al. 1981, Belden et al. 1985, Taylor and Hellgren 1997), and the beginning of the dry season in Florida. By January, the number of seeds dispersed increased dramatically with species richness at its highest in the study. During this time, feral pigs mainly graze on herbage and foliage as rooting decreased significantly at the LBESF (Belden et al. 1985, Taylor and Hellgren 1997). Overall, a negative correlation seems to exist between the amount of rooting activity and the number of species dispersed.

Plant species have strategies to facilitate seed dispersal by animals that can help explain some patterns found in this study. For instance, several plant species were dispersed well after their seed period while others (*Cyperus polystachyos*, *Cyperus ovatus*, and *Eupatorium compositifolium*) were dispersed year round. The palatability of the foliage and the ability to retain seeds on the plant after ripening can help explain both of these patterns found for most species (Janzen 1984). *Gaylussacia dumosa*, a shrub that produces berries contributed to 41% of the observed seeds germinations. Fleshy-fruits are a classic example of seeds adapted to

endozoochory due to reward they offer to their vertebrate seed disperser (Howe and Smallwood 1982, Janzen 1984, Willson 1990). Despite this adaptation, only 4 species that produce fleshy fruit were dispersed by feral pigs. Instead, the vast majority of plant species dispersed were small seeded species that exhibit no features to further dispersal and are therefore considered to be “unassisted” or simply gravity dispersed (Willson 1990, Hughes et al. 1994). This plant strategy has received a lot of attention lately, due its predominance in the feces of large herbivores like cows, horse, sheep, and deer around the world despite not being considered as adapted to endozoochory (Middleton and Mason 1992, Heinken et al. 2002, Pakeman et al. 2002, Myers et al. 2004, Schmidt et al. 2004, Mouissie et al. 2005b). Eight wind dispersed species and 1 species adapted to epizoochory were also dispersed endozoochorously by feral pigs. This finding is not uncommon and further demonstrates that seeds are not always exclusive to one dispersal mode despite morphological indications (Willson 1990, Hughes et al. 1994, Heinken et al. 2002, Pakeman et al. 2002, Myers et al. 2004, Schmidt et al. 2004, Mouissie et al. 2005b).

Though plant strategies may increase the probability, not all seeds consumed by feral pigs will actually be dispersed (Herrera 1984, Campos and Ojeda 1997, Mandujano et al. 1997). This is easily demonstrated by the fact that no *Quercus* spp. acorns germinated from the fecal samples. Whether feral pigs act as a seed disperser or seed predator for a particular plant species depends largely on the size of the seed. In order to be dispersed by feral pigs, seeds must first make it successfully through a powerful bite and chewing with strong teeth adapted for maceration, followed by a digestive system that contains enzymes ready to digest them (Janzen 1984, Sicuro and Oliveira 2002). Feeding trials of various large herbivores have shown that

small, round, and tough seeds have a much higher probability of survival than large, elongated, and soft seeds (Simao Neto et al. 1987, Russi et al. 1992, Gardener et al. 1993, Stallings et al. 1995, Mouissie et al. 2005a). Plant species with seeds >2 mm are relatively rare in feral pig fecal samples, consistent with seed predation of larger seeds. *Sabal palmetto* seeds were the largest dispersed and observed in at least 7 fecal samples, but the majority of the seeds were either crushed or scarified, so that only 4 seedlings germinated in 3 samples. In addition to *Quercus* spp. acorns mentioned, complete predation of saw palmetto (*Serenoa repens*) seeds in September were also observed in fecal samples.

Upon successful passage through the animal, location of deposition in the landscape depends on animal behavior plus gut retention time (Schupp 1993, Nathan and Muller-Landau 2000). As mentioned previously, feral pigs can occupy a large home range and travel anywhere from 0.02 to 0.6 km² per day (Wood and Brenneman 1980). Those estimates represent the smallest average yearly home range reported in the literature, but coupled with a gut retention time of 37-49 hours, it is clear that feral pigs can deposit seeds far from a parent plant (Wood and Brenneman 1980, Warner 1981). Because most seeds only move short distances of 0 to a few meters (Harper 1977, Howe and Smallwood 1982, Willson 1993, Cain et al. 2000), the long distance dispersal provided by feral pigs allows seeds to escape density-dependent mortality by insect and rodent predation, patpigen attack, or seedling competition near the parent plant (Janzen 1970, Connell 1971). Where feces are actually deposited in the landscape is determined by the movement and habitat use of the feral pigs, which is primarily concentrated in the mesic to wet habitats in this study and other studies conducted around the world (Bratton 1974, Bratton

et al. 1982, Hone 1988, Laurance and Harrington 1997, Mitchell and Mayer 1997, Welander 2000, Hone 2002, Chavarria et al. 2007, Mitchell et al. 2007).

Overall, 61% of the dispersed species were deposited in locations matching their habitat preference, showing that feral pigs are potentially effective dispersal agents for many plant species and is partly consistent with directed dispersal by the feral pig (Howe and Smallwood 1982, Schupp 1993). Classic examples of directed dispersal include ant dispersal of elaiosome-bearing seeds to their nutrient rich nests and birds depositing mistletoe seeds on the stems of host plants, though directed dispersal is increasingly considered common (Howe and Smallwood 1982, Nathan and Muller-Landau 2000, Howe and Miriti 2004). However, this study indicated that this may not be the case for wetland species, as only 23% of the plant species could potentially germinate at the deposition site. Nevertheless, even a small number of successful long distance dispersal events can have profound effects on biodiversity, evolution, and biological invasions of the area (Harper 1977, Hengeveld 1989, Hanski and Gilpin 1997, Sauer 1998, Hovestadt et al. 1999). -Of course, not all seeds will establish once deposited in feces due to possible predation by rodents and ants, decomposition by fungi, and competition (Chambers and Macmahon 1994, Wenny 2000, Wang and Smith 2002).

Implications for wetlands

Traditionally, water has been thought of as the most important vector of dispersal for wetland species. In palustrine wetlands, however, Soons (2006) documented that more species take advantage of wind dispersal via small seed size or appendages that facilitate flight. These same attributes also serve as good candidates for endozoochory seed dispersal by vertebrates.

Some studies have implicated waterfowl as significant vectors for wetland seed dispersal (Mueller and Van der Valk 2002, Neff and Baldwin 2005, Green et al. 2008, Soons et al. 2008), while terrestrial mammals that actually use wetlands year-round go unnoticed .

In particular, feral pigs also appear to be significant vectors for wetland plant species, as the majority of seeds dispersed were from obligate or facultative wetland species. Though not to the extent of roads, feral pigs used wetlands year round as they switched between rooting and grazing strategies to primarily feed on grasses and sedges as well as some forb species. Only 23% of these species were deposited back in wetlands, but the long distance dispersal provided by feral pigs is critically important even if a few species are able to survive. The large home range and long gut retention time coupled with the fact that feral pigs are very numerous and defecate an average of 4.6 times per day (Wood and Brenneman 1980, Warner 1981, Schmidt et al. 2004) suggests that many wetland species may produce seeds that germinate in entirely different wetlands. There is also the potential for substantial gene flow among “isolated” wetlands and active metapopulation and metacommunity interactions among wetlands (Husband and Barrett 1996, Hanski and Gilpin 1997, Hanski 1998). In addition, the species list dispersed by feral pigs would likely increase if epizoochorous dispersal was also examined. Not only does their coarse coat facilitate dispersal of seeds with hooked or barbed appendages, but wallowing at the margin of wetlands traps seeds of various dispersal modes in the mud that adheres to feral pigs (Heinken et al. 2002, Schmidt et al. 2004, Heinken et al. 2006).

Despite dispersal benefits provided to wetland species, feral pigs still pose a significant threat to wetlands mainly through the dispersal of unwanted species into wetlands and predation

of seeds, plus damage by rooting. Though non-natives are present at the LBESF and even overlap with collection sites, the low overall abundance in comparison to native plants most likely led to the lack of dispersal by feral pigs. Regardless, *Ludwigia peruviana* a category I invader was still dispersed several times, and deposited into wetlands where it could establish. The spread of non-native species through endozoochorous seed dispersal should be a primary concern for land managers in places where non-native abundance is much higher. Though not invasive, several unwanted facultative species were also dispersed into wetlands and threaten depression marshes in particular. This includes wax myrtle (*Myrica cerifera*) a facultative shrub that is able to become established and slowly change composition of these herbaceous wetlands in the absence of fires. Secondly is dog fennel (*Eupatorium* spp.), a shrub that encroaches into wetlands during periods of drought. As for closed canopy wetlands, they are threatened by predation of seeds from tree species. For example, feral pigs completely depredated acorns from oak trees, which can have long term effects on canopy composition and regeneration after disturbance events. This is also the case with cabbage palm trees that are typical wetland canopy species, though some were effectively dispersed by feral pigs.

As wetlands decline in number and are increasingly surrounded by human-dominated landscapes, the quality of traditional abiotic vectors such as water and wind also declines. Seeds no longer can travel by water to wetlands that are hydrologically isolated and those dispersed long distances by wind are most likely deposited in the unsuitable matrix that surrounds wetlands (Soons 2006). Endozoochorous seed dispersal by animals is therefore emerging as an important vector for wetland plant species that is potentially able to maintain diversity and gene flow

within and between wetlands. Theoretically, feral pigs can be effective dispersal vectors as shown by 23% of the wetland species being deposited back into wetlands, but *in situ* studies of feces are needed to examine seedling germination and survival in the field. Unfortunately, the benefits do not outweigh the negative impacts caused by these animals as they disperse unwanted species into wetlands, and predate critical wetland tree species. -Most importantly feral pigs are significant disturbance agents that change soil characteristics, destroy wetland vegetation and the seedbank, set back succession, and decrease water quality through their rooting activities (Wood and Barrett 1979, Singer et al. 1984, Lacki and Lancia 1986, Leck 1989, Kotanen 1995, Giuliano and Tanner 2005, Engeman et al. 2007, Zengel and Conner 2008, West et al. 2009, Doupe et al. 2010). In order to conserve wetlands, active management of feral pig populations through a variety of control techniques needs to be undertaken. As feral pigs continue to expand their range across the United States, early detection and eradication before they can establish will also prove to be an important wetland conservation tool.

Table 4-1: Simple summary statistics showing number of samples collected, number of seeds germinated, seed density, species density, and percentage of samples with viable seeds each month and at the end the study.

	March	May	July	Sept	Nov	Jan	Annual
Number of samples collected	18	18	20	17	15	20	108
Total number of seeds germinated	52	74	360	58	34	204	782
Seed density (seeds germinated/sample)							
Mean	2.9	4.1	18.0	3.4	2.3	10.2	7.2
Median	2.5	1.5	1.5	2	1	5	2
Maximum	12	22	315	11	9	48	315
Total number of species germinated	16	17	12	14	9	26	50
Species density (species germinated/sample)							
Mean	1.6	1.6	1.6	1.7	1.3	4.0	2.0
Median	2	1	1	2	1	3	2
Maximum	4	4	5	4	3	10	10
% of samples with viable seeds	83.3%	72.2%	75.0%	70.6%	80.0%	95.0%	81.0%

Table 4-2: List of plant species dispersed by feral pigs over the course of the study including the total number of seeds germinated each month and the annual total.

Genus species	Origin	Habit	NWI	March	May	July	Sept	Nov	Jan	Annual
<i>Spergularia marina</i>	N	F	OBL	12						12
<i>Eupatorium compositifolium</i>	N	F	FAC	9	4	2	1	3	56	75
<i>Ludwigia peruviana</i>	NN	F	OBL	8	2					10
<i>Sesuvium maritimum</i>	N	F	FACW	6	1			15	3	25
<i>Cyperus polystachyos</i>	N	G	FACW	3	2	3	2	3	9	22
<i>Juncus effusus</i>	N	G	FACW	2					22	24
<i>Pluchea odorata</i>	N	F	FACW	2						2
<i>Myrica cerifera</i>	N	W	FAC	2						2
<i>Polyprenum procumbens</i>	N	F	FACU	1	2	17	3			23
<i>Cyperus ovatus</i>	N	G	FACU	1	2	1	8	1	11	24
<i>Cyperus surinamensis</i>	N	G	FACW	1	1		2		13	17
<i>Juncus megacephalus</i>	N	G	OBL	1					2	3
<i>Reimarochloa oligostachya</i>	N	G	OBL	1						1
<i>Panicum anceps</i>	N	G	FAC	1						1
<i>Fimbristylis autumnalis</i>	N	G	OBL	1						1
<i>Drymaria cordata</i>	N	F	FAC	1						1
<i>Eleocharis sp.</i>	N	G	OBL		36		2	1	2	41
<i>Paspalum conjugatum</i>	N	G	FAC		13	11	23	7	11	65
<i>Sabal palmetto</i>	N	W	FAC		3	1				4
<i>Ludwigia repens</i>	N	F	OBL		2	4	6	2	29	43
<i>Carex albolutescens</i>	N	G	FAC		1		2		5	8
<i>Trifolium dubium</i>	NN	F	FACU		1					1
<i>Packera glabella</i>	N	F	FACW		1					1
<i>Fimbristylis puberula</i>	N	G	OBL		1					1
<i>Digitaria filiformis</i>	N	G	NOT		1					1
<i>Dichantherium portoricense</i>	N	G	FACU		1					1
<i>Gaylussacia dumosa</i>	N	W	FAC			316	2			318
<i>Physalis arenicola</i>	N	F	NOT			2				2
<i>Sesuvium portulacastrum</i>	N	F	FACW			1				1
<i>Rhynospora odorata</i>	N	G	OBL			1				1
<i>Echinochloa walteri</i>	N	G	OBL			1				1
<i>Phyla nodiflora</i>	N	F	FACW				3			3
<i>Sacciolepis indica</i>	NN	G	FAC				2			2

<i>Paspalum repens</i>	N	G	OBL				1			1
<i>Dichanthelium laxiflorum</i>	N	G	FAC				1			1
<i>Coreopsis leavenworthii</i>	N	F	FACW					1	1	2
<i>Conoclinium coelestinum</i>	N	F	FAC					1	1	2
<i>Heliotropium curassavicum</i>	N	F	OBL						7	7
<i>Panicum hemitomon</i>	N	G	OBL						6	6
<i>Schoenoplectus etuberculatus</i>	N	G	OBL						4	4
<i>Samolus valerandi</i>	N	F	OBL						4	4
<i>Rhynospora microcarpa</i>	N	G	FACW						3	3
<i>Mikania scandens</i>	N	F	FACW						3	3
<i>Linaria canadensis</i>	N	F	NOT						3	3
<i>Euthamia caroliniana</i>	N	F	FAC						2	2
<i>Dichanthelium dichotomum</i>	N	G	FAC						2	2
<i>Cyperus odoratus</i>	N	G	FACW						2	2
<i>Rumex obovatus</i>	NN	F	OBL						1	1
<i>Polygonum punctatum</i>	N	F	FACW						1	1
<i>Anagallis pumila</i>	N	F	FACW						1	1
				52	74	360	58	34	204	782

Origin: N= Native, NN= Non-native

Growth habit: F= Forb, G= Graminoid, W= Woody

Habitat preference according to the NWI wetland indicator status: OBL= obligate wetland, FACW= facultative wetland, FAC= facultative, FACU= facultative upland, and NOT= not listed

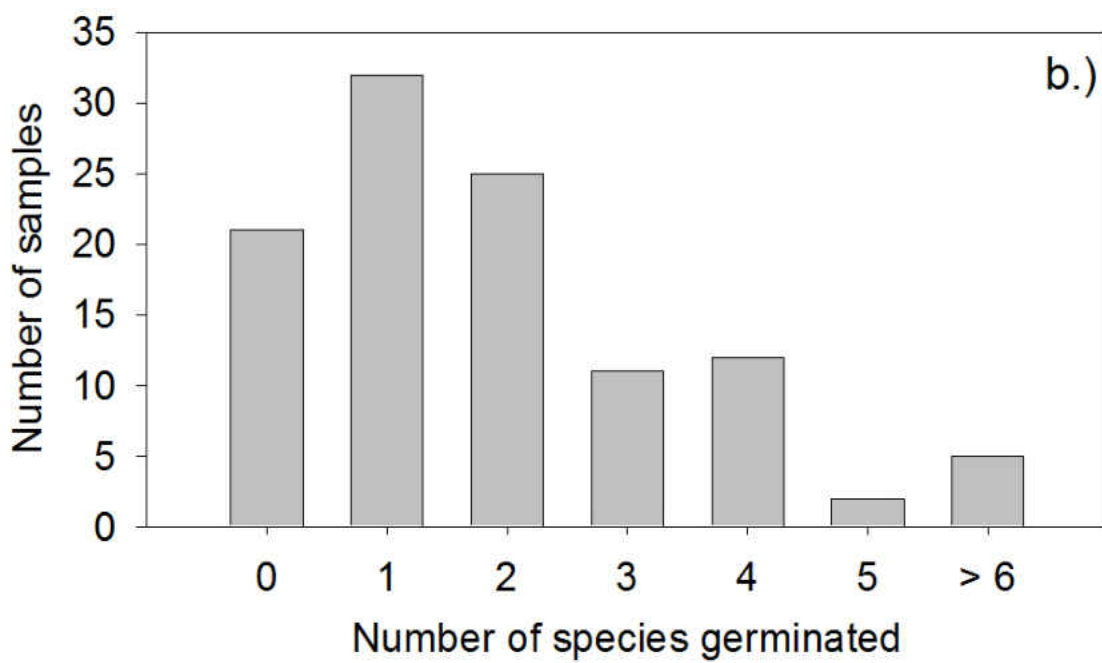
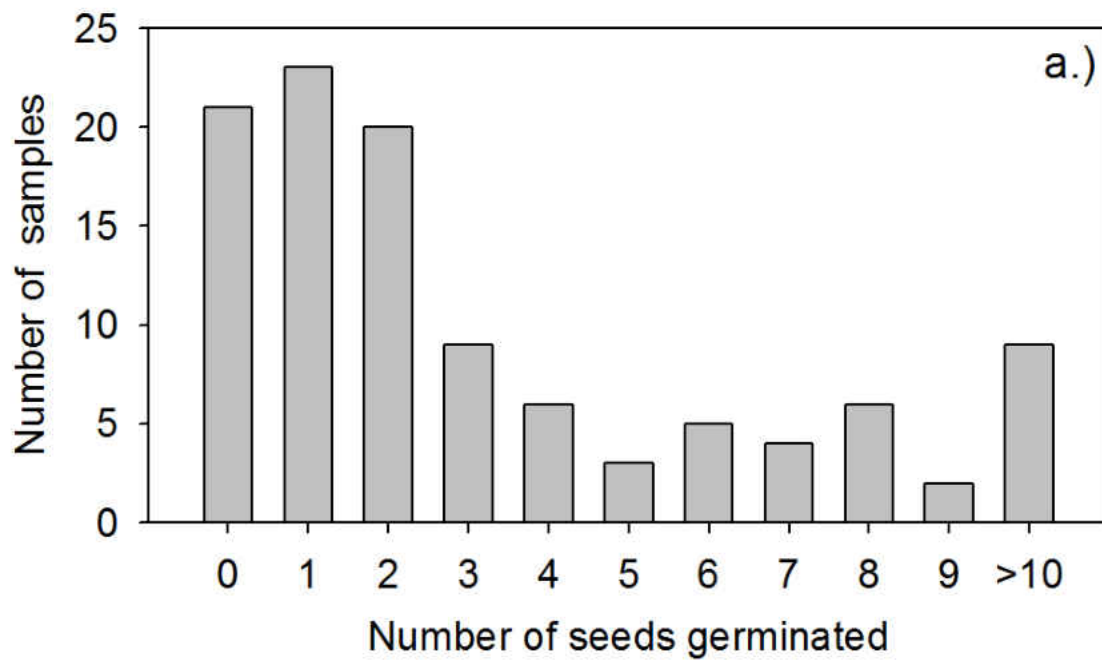


Figure 4-1: Histogram showing the distribution of the number of seeds germinated per sample (a) and number of species germinated per sample (b).

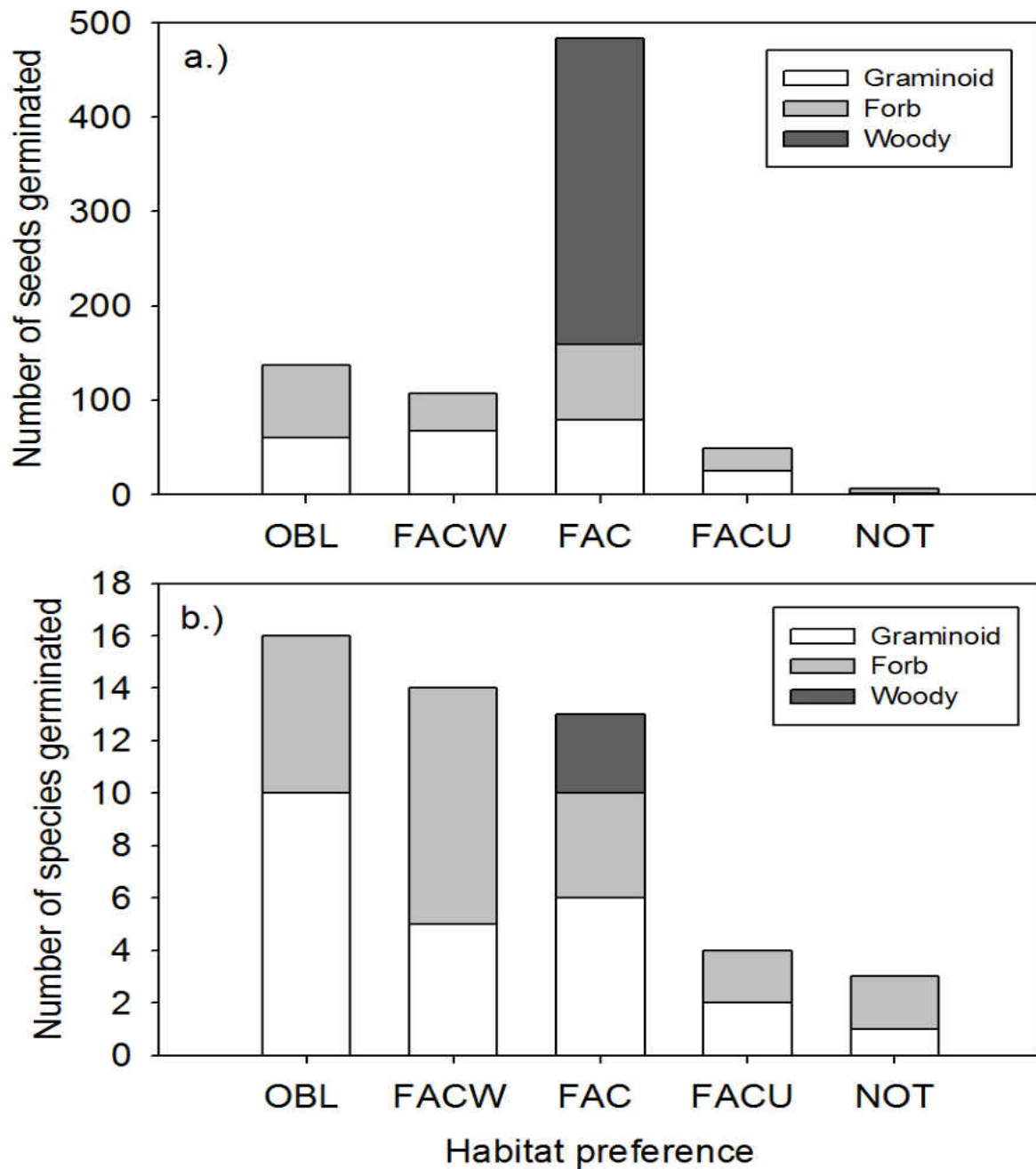


Figure 4-2: The total number of seeds germinated (a) and total number of species germinated (b) based on the growth habit and habitat preference of the plant species.

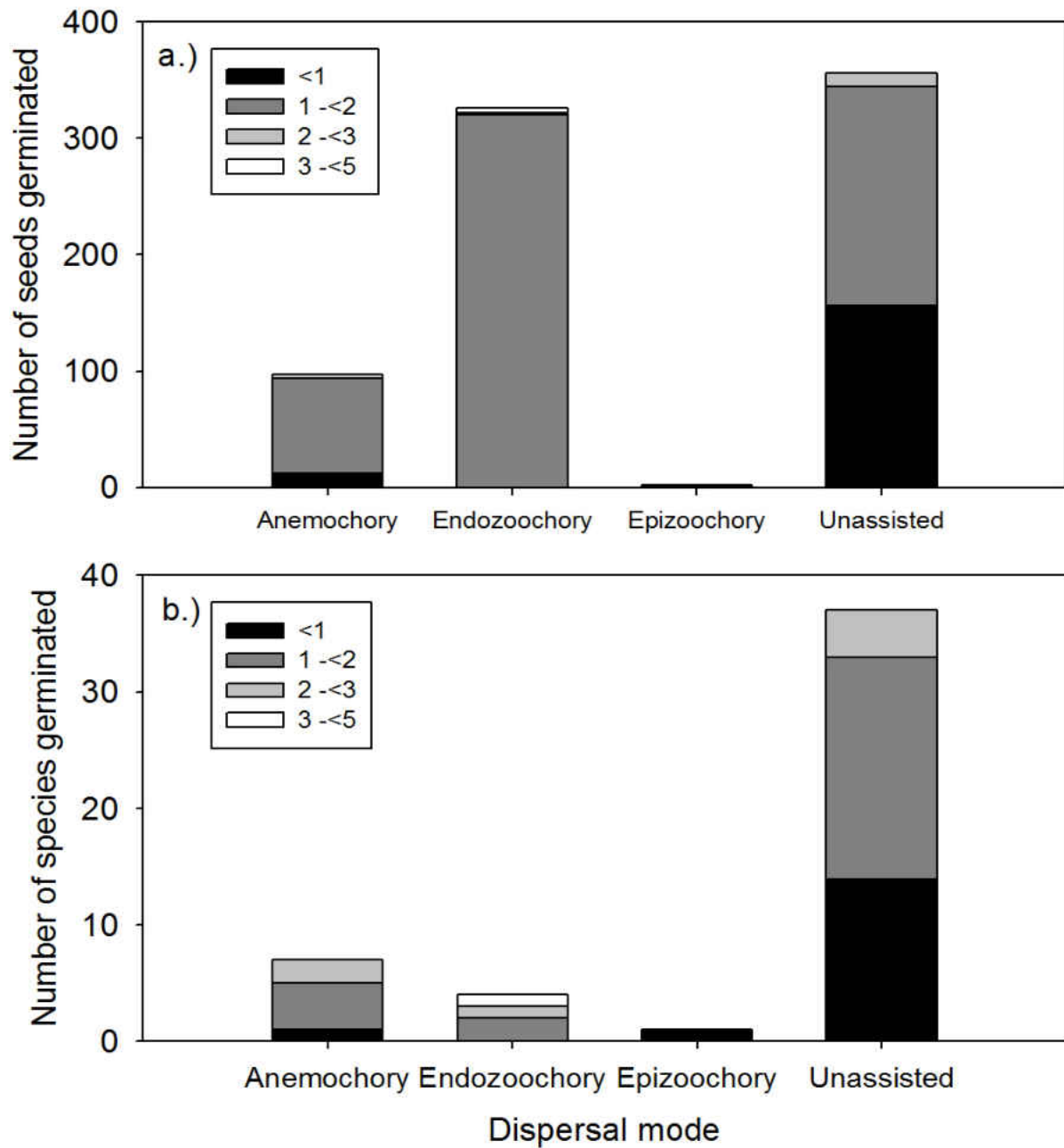


Figure 4-3: The total number of seeds germinated (a) and total number of species germinated (b) based on seed size and dispersal mode deduced from seed morphology of the plant species.

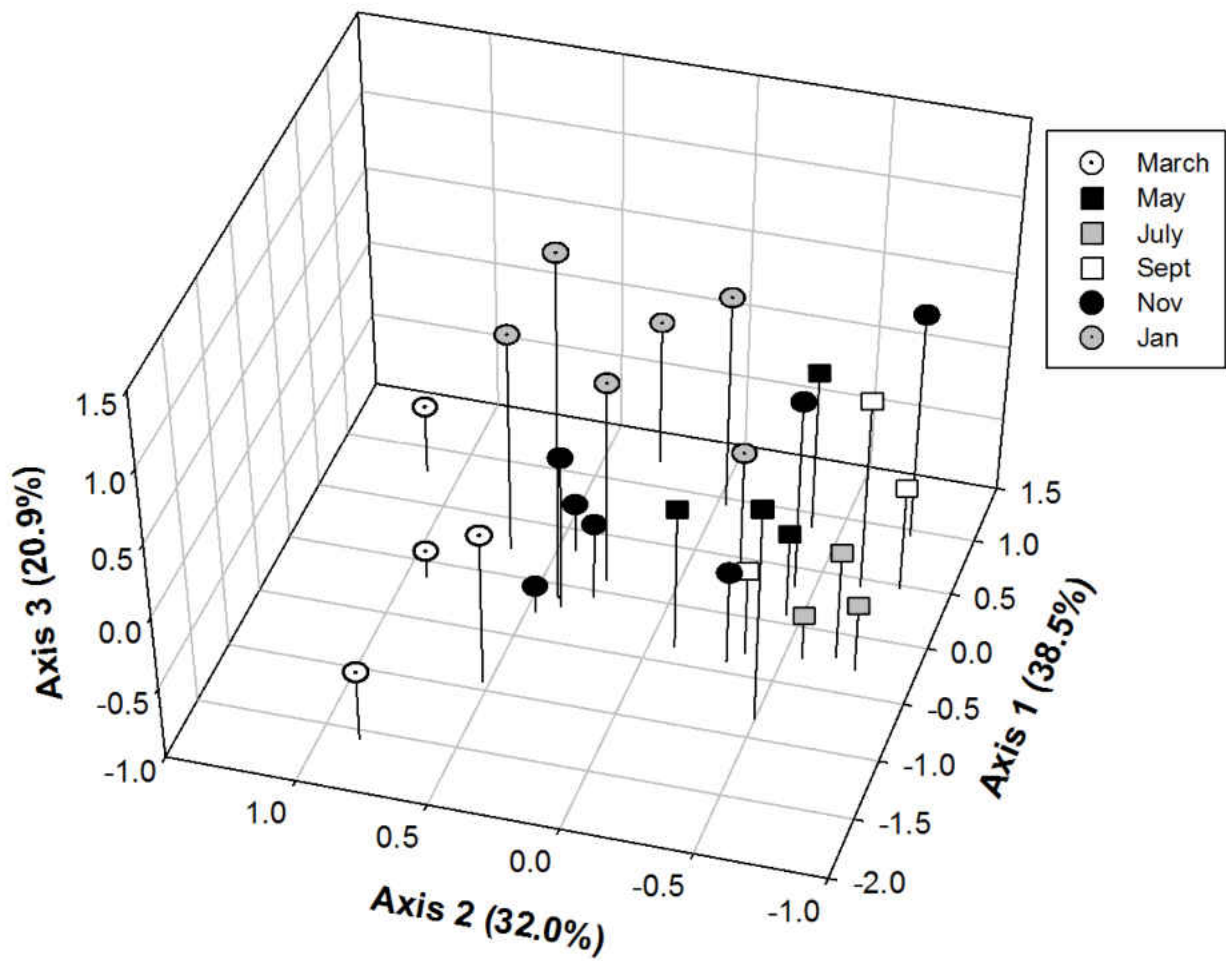


Figure 4-4: A Non-metric multidimensional scaling (NMS) ordination of species composition over time resulted in a 3-D solution. The first three axes explained 91.4% of variation in the data (axis 1= 38.5%, axis 2 =32.0%, and axis 3 =20.9%).

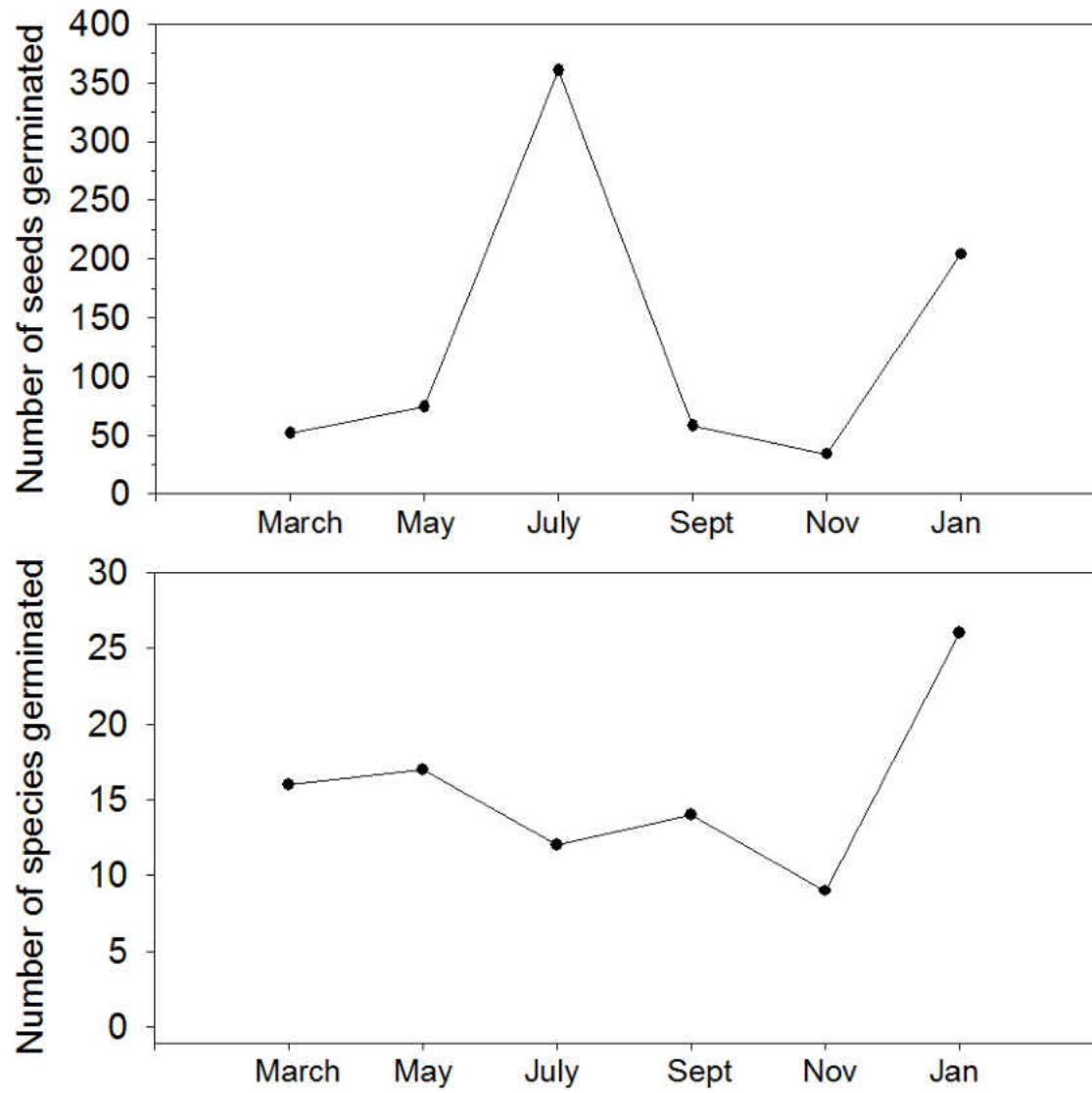


Figure 4-5: Temporal variation in number of seed germinated (a) and number of species germinated (b).

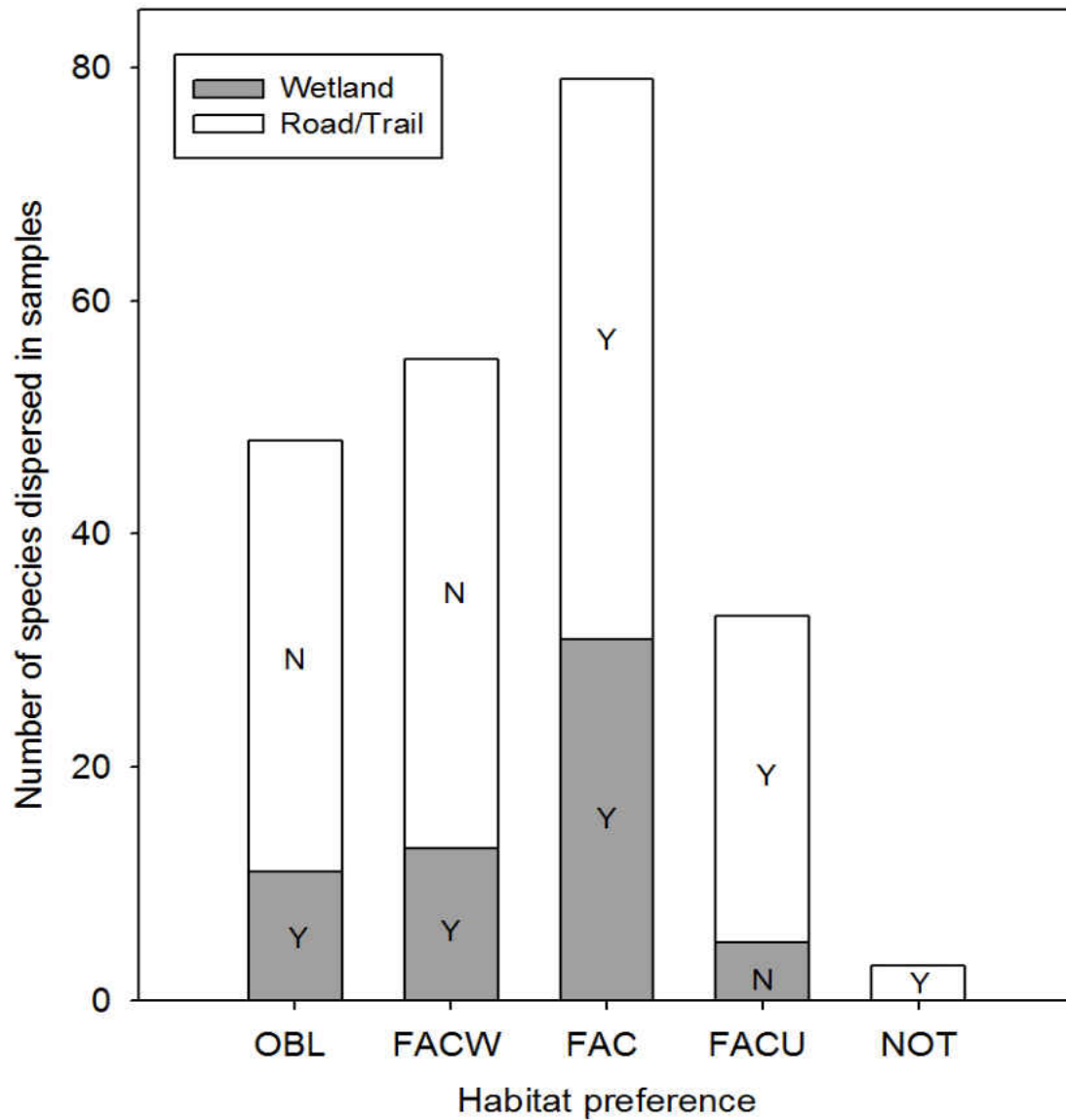


Figure 4-6: The number of species dispersed in samples according to habitat preference and the location of deposition in the landscape. The probability of survival (Y=yes, N= no) is also indicated

Appendix B

Table 4-3: NMS output showing the stress associated with each dimension

STRESS IN RELATION TO DIMENSIONALITY (Number of Axes)							
Stress in real data 250 runs				Stress in randomized data Monte Carlo test, 250 runs			
Axes	Minimum	Mean	Maximum	Minimum	Mean	Maximum	p
1	33.439	45.04	55.278	39.267	49.764	55.278	0.004
2	16.494	18.175	38.124	20.783	26.251	38.136	0.004
3	8.671	9.328	12.708	13.568	16.574	19.976	0.004
4	5.397	5.524	22.143	9.939	11.889	22.21	0.004
5	3.68	3.776	4.481	7.113	8.767	10.666	0.004
6	2.433	2.564	2.775	5.086	6.668	8.334	0.004
p = proportion of randomized runs with stress < or = observed stress							
i.e., $p = (1 + \text{no. permutations} \leq \text{observed}) / (1 + \text{no. permutations})$							

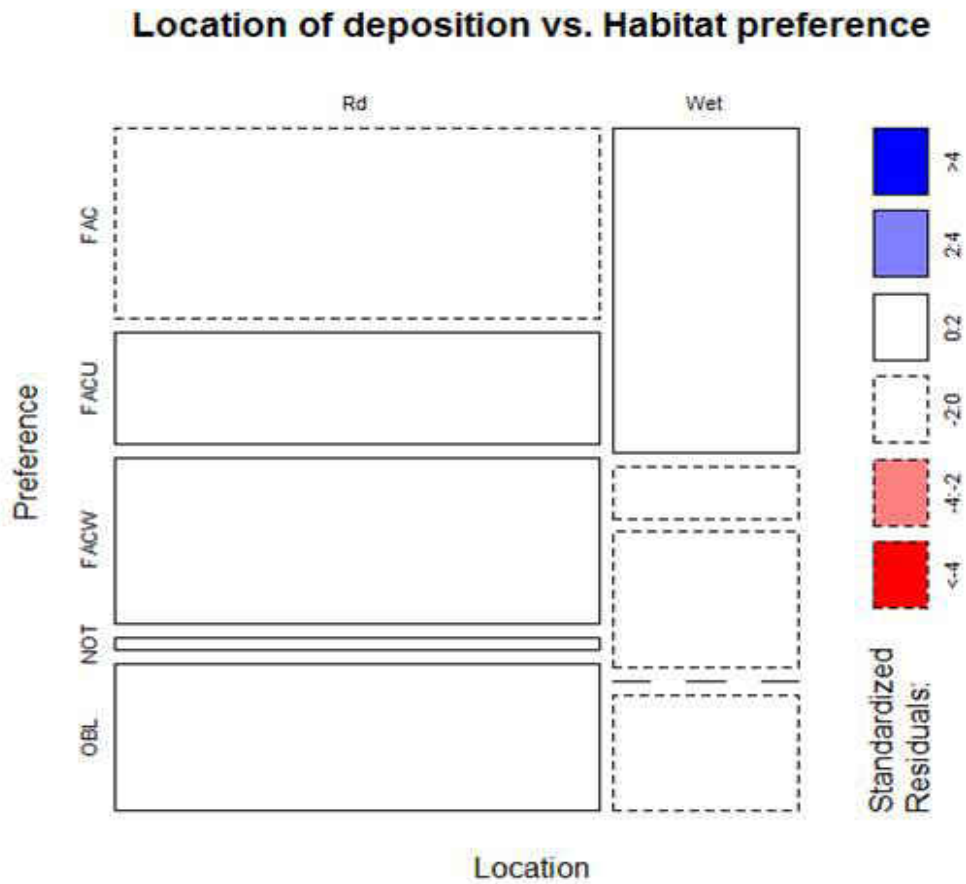


Figure 4-7: Mosaic plot illustrating the relationship between location of deposition and habitat preference of the plant species dispersed by feral pigs. The sizes of the squares are proportional to their frequency in the data set, while the width of the column is proportional to the column total. The standardized residuals indicate whether the observed data is more, equal, or less than expected.

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