THE RELATIONSHIP BETWEEN LAND USE AND THE ECOLOGICAL INTEGRITY OF ISOLATED WETLANDS IN THE DOUGHERTY PLAIN, GEORGIA, USA

by

OUIDA STRIBLING STUBER

(Under the Direction of L. Katherine Kirkman and Jeffrey Hepinstall-Cymerman)

ABSTRACT

Geographically isolated wetlands are common features of the Dougherty Plain physiographic region in southwestern Georgia. Due to a lack of protection at the state and federal levels, these wetlands are threatened by agricultural and silvicultural land use common in the region. To examine relationships between land use and wetland ecological integrity, I quantified historic and current land use within and among isolated wetlands, characterized biotic and environmental variables associated with major land use classes, and described seed bank composition of agricultural wetlands. Intensification of land use over six decades likely resulted in the loss of > 50% of wetlands as suitable habitat for wetland flora and fauna. Wetlands influenced by agriculture were the most degraded, and were associated with high cover of exotic species and elevated nutrient levels. Seed banks in agricultural wetlands are largely dominated by herbaceous species, many of which are native and which are associated with wetlands.

INDEX WORDS: wetland condition, land use, agriculture, silviculture, connectivity, plant community, macrophyte, water quality, seed bank

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DEDICATION

This thesis is dedicated to the ever-shifting community of scientists, naturalists, old-timers, rednecks, hippies, college kids and good ol' boys that make Ichauway the incredibly unusual, incredibly wonderful patch of longleaf pine that it is – a place for thoughtful growth and change, and a place to come home to.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Project Overview

Isolated wetlands occur throughout the United States and are referred to by many different names: vernal pools, Carolina bays, prairie potholes, sinkhole wetlands, rainwater basin meadows, Grady ponds, cypress domes, or wet-weather ponds (Tiner et al. 2002). All of these wetlands are considered “geographically isolated wetlands” because they lack an obvious surficial hydrologic connection to other water bodies (Tiner 2003b). Within the state of Georgia, isolated wetlands are found in abundance in the Coastal Plain region. They are especially numerous in the Dougherty Plain, a physiographic province in the southwestern part of the state (Figure 1.1) characterized by karst topography with commonly featured sinkhole depressions (Beck and Arden 1983). The region is dominated by agricultural and silvicultural land use as well as natural forest, and has experienced significant intensification and fragmentation of land use during the past six decades (Martin et al. 2013).

Geographically isolated wetlands are known to perform ecologically important functions, including habitat provision for a disproportionate amount of biodiversity within the landscape (Kirkman et al. 1999, Battle and Golladay 2002, Smith et al. 2006). However, the absence of a surficial hydrologic connection means that these isolated wetlands are not given the same protected status afforded to other wetlands under the Clean Water Act (*Rapanos v United States* 2006, Leibowitz et al. 2008). Nor are these wetlands protected in most states, including Georgia (Christie and Hausmann 2003). The lack of protection afforded these isolated wetlands makes them particularly vulnerable to alteration and conversion to other land use types, and compromises the ability of these wetlands to provide suitable habitat for many species (Brinson and Malvarez 2002, Wolfe 1998 as cited in Tiner et al. 2002, Leibowitz 2003, Biebighauser 2007).

Wetland scientists and practitioners frequently rely on assessments of wetland condition to gauge and monitor the ecological integrity of wetlands (U.S. EPA 2002). Specifically, regional-scale assessments often use remotely sensed land use and land cover (LULC) data to assess wetland condition (Tiner 2004, Brown and Vivas 2005, Lane et al. 2012). However, the categorical coarseness inherent in most available LULC data may obscure some important drivers of wetland integrity. When using synoptic land cover data in remote assessments, it is important to understand how the individual LULC classes relate to the biology of specific wetlands. Regionally specific field validation of this relationship is recommended to accurately evaluate wetland condition.

It is likely that many isolated wetlands within the Dougherty have been highly impacted historically and currently by the agricultural and silvicultural land use predominant in the region. To quantify the anthropogenic impacts on isolated wetlands in the region, this study identifies wetlands most degraded by land use, relates land use classes to specific biotic and abiotic variables of condition, and evaluates the influence of land use history on wetland restoration potential.

Literature Review

Wetland Significance and Decline

Globally, the land area covered by wetlands is constantly shifting due to rising sea levels, restriction of natural flood pulses, and other human alterations, but estimates range from 5.3 to 12.8 million square kilometers (Zedler and Kercher 2005). Functionally, wetlands regulate, provide for, and support humans and the biosphere in numerous ways (Millenium Ecosystem Assesment [MEA] 2000). Although wetland function varies according to wetland type and position in the landscape, generally wetlands are recognized as significant providers of filtered water, food, and fuel and fiber resources. Similarly, through regulation of numerous biogeochemical cycles, wetlands serve as important sites of carbon sequestration, flood water retention, and groundwater recharge (Costanza et al. 1989, Costanza et al. 1997, Mitsch and Gosselink 2000, Zedler and Kercher 2005). Cultural, spiritual, and aesthetic services are also highly-valued services provided by wetlands.

These wetland functions which support human health and livelihoods through social, cultural, economic, and environmental factors are collectively known as ecosystem services. Economic valuation of ecosystem services worldwide indicates that wetland systems are among those most valuable to humanity per hectare (Costanza et al. 1997). The combined value of the services provided by wetlands per hectare is disproportionately large when compared with values of common land uses, including agriculture (Turner et al. 1988). Despite growing recognition of the significance of wetlands worldwide, wetlands declined dramatically during the 1900’s in many parts of the world, and in temperate zones in particular. Globally, degradation and loss of wetlands, whether through conversion to other categories of land use or destruction of the wetland hydrology, continues at an alarming rate due to population growth and developmental pressures (Johnston 1994, Millenium Ecosystem Assesment [MEA] 2000).

Within the conterminous United States, wetland area has declined by more than 50% since European colonization (Dahl 1990). In more recent years (1986-1997), wetland area continued to decline, though at a significantly slower rate (Zedler and Kercher 2005). During this period, the greatest proportion of wetland loss (98%) occurred in freshwater wetlands. Agricultural and silvicultural activities were responsible for the greatest portion of freshwater wetland loss (49%; Dahl 2000).

Political policy and public awareness in the United States has been largely responsible for mitigating wetland loss and degradation in recent years (Dahl 2006, 2009). The formulation of the “No Net Loss” policy in the late 1980’s and President Bush’s Wetlands Initiative of 2004, which aims “to attain an overall increase in the quality and quantity of wetlands in America” have made major strides in decreasing the rate of wetland loss in the country (Dahl 2006). Estimates indicate that net wetland area increased for the first time between 1998-2004 (Dahl 2006), although this apparent increase is most likely due to the inclusion of constructed freshwater farm ponds in the tally of wetland area. From 2004 to 2009, the total wetland area remained relatively unchanged (Dahl 2009). However, when wetland gains and losses were calculated for individual wetland types during that time period, some interesting trends emerged. Vegetated freshwater wetlands declined in area from 2004 to 2009, but area of freshwater ponds continued to increase. This trend, although it does not explicitly measure wetland quality, suggests a potential net decrease in quality. Farm pond wetlands are typically created or heavily impacted by humans, and are presumably poor functional equivalents of the natural wetlands they are constructed to replace (Biebighauser 2007, Kudray 2008, De Steven and Lowrance 2011).

Wetland Condition Assessment Methods

In a nationwide effort to quantify and monitor wetland alteration, degradation, and loss, much research has focused on developing wetland assessments to evaluate the ecological integrity of wetlands, and more specifically, their condition and/or function. Ecological integrity, as defined by Karr and Dudley (1981), is an ecosystem's capacity to maintain a "balanced integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to the natural habitat of the region", whereas wetland condition is distinguished from integrity as a relative measurement which indicates the degree of departure from full ecological integrity (Fennessy et al. 2004). The functions performed by any individual wetland may be positively or negatively influenced by disturbance, and so are not necessarily directly related to wetland condition. To quantify ecological integrity is a challenging prospect. Recently, several national-scale projects have focused on measuring wetland condition and function. For example, in 2011, the Environmental Protection Agency carried out a National Wetlands Condition Assessment to evaluate the relative condition of the nation's remaining wetlands. The U.S. Fish and Wildlife Service has recently developed techniques to assess wetland function remotely, using hydrogeomorphic properties to predict wetland function and has already evaluated wetlands within portions of the country (Tiner 2010).

Condition assessments are often designed with sampling components at three different scales, or Levels (Mack et al. 2000, Sutula et al. 2006, North Carolina Wetland Functional Assessment Team [WFAT] 2010). Level 1 assessments are devised to evaluate the wetland efficiently and economically through remote surveys at a regional scales. Level 2 assessments are rapid, on-site qualitative evaluations of the wetland and, often, a surrounding buffer zone. Level 3 assessments are intensive quantitative surveys of indicator taxa and physicochemical properties within the wetland (Stein et al. 2009). Conceptually, inter-level relationships are validated and therefore predictable within this three-tiered framework, permitting a relatively quick and inexpensive assessment of the condition of many wetlands at Level 1, with confirmation using Levels 2 and 3 in independent evaluations of a small subset of sites.

Level 1 landscape-scale assessments generally use indices developed from regional land cover and land use maps to relate wetland context to the likely ecological condition of the wetland. The Landscape Development Intensity (LDI) index is one such method, and has been shown to significantly relate to independent Level 2 and Level 3 assessments in many states (Brown and Vivas 2005, Mack 2006, Reiss and Brown 2007, Stein et al. 2009). Specifically, the LDI is quantified via coefficients which represent human impacts on the landscape. Each type of land use and land cover (LULC) is assigned a value based upon an estimate of the total "emergy," or the amount of available non-renewable energy associated directly or indirectly with the creation and maintenance of each land use type (Odum 1996, Brown and Vivas 2005). The coefficients are scaled from 1 to 10, with the most heavily impacted lands (e.g. high density urban) receiving a 10, and natural areas (e.g., undisturbed forest) receiving a 1 (Brown and Vivas 2005). The LDI of a specific wetland is ascertained by calculating an area-weighted coefficient for a buffer zone of a predetermined width around each wetland averaging the associated index values for the LULC classes present.

Many states have developed regionally-specific rapid assessment methods (RAM's; Level 2 assessments) for wetlands (Brinson 1993, Mack et al. 2000, Fennessy et al. 2004, Schroter et al. 2005, WFAT 2010). These methods categorize important indicators of wetland integrity and processes into readily-apparent characteristics of the biological community, local hydrology, and anthropogenic alteration (e.g. presence of invasive species, drainage ditches, or local erosion). These characteristics of integrity and function are then ranked on a qualitative scale, and inserted into an index which calculates all scores and compares them across wetlands, providing a relative, albeit subjective, measure of the system's integrity. The Ohio Rapid Assessment Method (ORAM) and the Wetlands Rapid Assessment Procedure (WRAP) developed for Florida wetlands are both examples of rapid condition assessment methods that have been validated against independent data at levels 1 and 3 (Mack et al. 2000, Reiss and Brown 2007). In both cases, the wetland condition results of the RAM were significantly related to the results of the other methods, and were suggested as potentially reliable Level 2 methods, accordingly.

Level 3 assessment methods quantitatively assess the ecological integrity of a wetland through intensive surveys of biotic communities and measurable physical and chemical properties. Values relating the species' or property's ecological integrity may be calculated with metrics or assigned based upon professional consensus. Indices are then developed which combine these values across the taxa or properties surveyed.

Intensive assessment of macrophytes are among the most frequently developed and utilized due to their typically rapid response to wetland quality and straightforward sampling methods. Some examples of useful, validated Level 3 macrophyte assessment procedures include Vegetation Index of Biological Integrity (VIBI; Mack 2007), and the Floristic Quality Assessment Index (FQAI; Cohen et al. 2004). Some assessment of macrophytes as biological indicators of "sensitivity" or "tolerance" to alteration are typically incorporated into level 3 indices; studies in Florida with comparable goals based their classification of "sensitive" and "tolerant" on a system of indices and analyses which combined professional opinion with statistical tests (Reiss 2004, Reiss and Brown 2007).

Isolated Wetlands of the Dougherty Plain.

The Dougherty Plain is a physiogeographic subregion of the Coastal Plain characterized by karst topography (Beck and Arden 1983). The region covers approximately 668,940 ha in southwestern Georgia. Historically, this area was dominated by fire-maintained longleaf pine-wiregrass (*Pinus palustris* Mill.-*Aristida beyrichiana* Trin. & Rupr.) savannas with a highly diverse understory (Walker 1993, Drew et al. 1998, Engstrom et al. 2001). Geographically isolated limesink wetlands are a prominent feature of the karst landscape; the average nearest neighbor distance between wetlands is less than 200 meters. (Hendricks and Goodwin 1952, Martin et al. 2012).

The low topographic relief and underlying limestone characteristic of the Dougherty Plain contribute to the frequent occurrence of surficial depressions (an estimated 1.7 wetlands per km^2) across the region (Hendricks and Goodwin 1952, Martin et al. 2012). Slow dissolution of the underlying limestone occurs as the more acidic rainwater percolates into the bedrock, particularly in naturally flat and depressed areas (Hendricks and Goodwin 1952). Eventually the burden of the soil above the weakened limestone causes the soil and limestone to collapse, forming a small depression or pit. This pit promotes further collection of water and subsequent dissolution, resulting in a process of deepening and widening over time. These isolated wetlands can range from small steep-sided pits to large shallow ponds of many hectares (Kirkman et al. 2000), each entirely surrounded by upland, and thus effectively within its own sub-basin, or catchment (Tiner 2003b).

The hydrology of most isolated wetlands is thought to be precipitation-driven (Hendricks and Goodwin 1952), though some studies indicate a connection to the water table in some wetlands (Hendricks 1954, Blood et al. 1997). Clay sediment, which resists percolation of water, collects within these depressions as they age, eventually forming a thick impervious layer (lens) in older ponds (Hendricks 1954). Most isolated wetlands collect and hold water during the wet winter months; in warmer months with net rainfall deficits, evapotranspiration results in the drying-down of these ponds (Hendricks and Goodwin 1952). Some of the deepest wetlands with thick clay lenses, however, may hold water throughout the year (Hendricks and Goodwin 1952, Wharton 1978).

The vegetative diversity in the longleaf pine system represents 40% of all plant species found within the Atlantic and Gulf Coastal Plains (Peet and Allard 1993, Van Lear et al. 2005). Both wetland interiors and the ecotone between wetland and frequently burned upland are particularly diverse (Kirkman et al. 1998, Kirkman et al. 2000, Kaeser and Kirkman 2009). The isolation and ephemerality of these wetlands also make them generally unsuitable habitat for fish, but prime predator-free habitat for a diversity of amphibians and macroinvertebrates, including rare and endangered species (De Steven and Toner 1997, Golladay et al. 1997, Kirkman et al. 1999, Battle and Golladay 2002, Smith et al. 2006).

Isolated wetlands have been divided into three groups, largely determined by age of the depression, period of inundation, fire frequency, landscape, and resulting plant communities (Hendricks and Goodwin 1952, Wharton 1978, Sutter and Kral 1994, Kirkman et al. 2000):

1. Grass-sedge Marshes – These are shallow, open, hyperdiverse marsh-like depressions of herbaceous species, dominated by graminoids. These typically have the shortest hydroperiod, and experience frequent disturbance by fire.

2. Cypress Savannas – The dense understory is composed of a herbaceous community similar to the marshes, with a few species of inundation-tolerant shrubs. The canopy is composed largely of pond cypress (*Taxodium ascendens*), which are dispersed throughout the wetland, creating an open, park-like canopy. Initial establishment of pond cypress requires an extended absence of fire, but the trees are tolerant of frequent fire once mature.
3. Cypress-gum Swamps – These are deep depressions with dense canopies of pond cypress and black gum (*Nyssa sylvatica* var. *biflora*). The deepest areas of these swamps may remain inundated year round. The understory is mostly shaded, the patches of vegetation sparse, and often dominated by shrubs. The longer hydroperiod and the exclusion of a fuel-rich understory in these systems results in infrequent fire.

Land Use History of the Dougherty Plain

In the southeastern United States, humans have greatly influenced vegetation patterns across the landscape since arrival and establishment in the region, about 1200 years BP. Native Americans affected the longleaf forests with fire to clear land, maintain an open forest, and create favorable habitat for wildlife (Carroll et al. 2002, Van Lear et al. 2005). Agriculture, in the form of corn and bean cultivation, was introduced to the region when humans arrived. The decline of native populations and European settlement in the 16th and 17th centuries brought about dramatic changes in the landscape: fire regimes faltered, row-crop and pasture agriculture were introduced. By the early 20th century, most of the piney woods of the southeast had been logged, and the prescribed fire regimes employed at that time typically discouraged regrowth of longleaf pine (Rauscher and Johnsen 2004, Van Lear et al. 2005). The late 20th century saw the expansion and dominance of pine plantations (Turner and Rushcer 1988). High-intensity row crop agriculture expanded dramatically throughout the southeast with widely adopted center pivot irrigation systems in the 1960s and 1970s (Turner and Rushcer 1988, Martin 1999). In Georgia, irrigated agricultural lands expanded most rapidly between 1977 and 1980 (Haire 2005). In 1998 Georgia had nearly 1 million acres of land watered via mechanical irrigation—the largest area east of the Central Plains—and that area continues to increase (Martin 1999, Haire 2005).

Within the Dougherty Plain specifically, Martin et. al (2013) examined patterns of land use and land cover (LULC) change between 1948 and 2007 in a randomly-selected subset of the region. Despite the appearance of little change in the proportions of agricultural and forested LULC, coarsely defined, within the Dougherty Plain, they found that land use intensified significantly, namely through declines in dryland row-crop agriculture and naturally forested lands, and associated increases in irrigated row crop agriculture and pine plantations. They also noted a significant increase in LULC fragmentation throughout the Dougherty Plain, marked by increasing patch densities and more homogeneous patch sizes.

Landscape Change Trajectory Analysis (LCTA) is a recently developed method which quantifies and categorizes the relationships between past and present characteristics of the landscape through the identification of specific paths of transformation over time (Käyhkö 2006). Such studies may incorporate a variety of spatial and temporal variables, including physical characteristics of the land, degree of fragmentation, and land use types. The analysis leads to the identification of major drivers of landscape change, and their associated effects (Käyhkö and Skånes 2008). Due to the complexity and large amount of variation implicit in a continually shifting, spatially diverse landscape, some level of simplification is often necessary to parse out meaningful trends (Lambin et al. 2001). A previous LCTA study of a watershed within an agriculturally-dominated landscape in Canada (Ruiz and Domon 2009) identified an overall trend of increasing homogenization and fragmentation of the land over time. Fifty-one distinct trajectories were identified in this study. When all of these were considered, the "noise" obscured relevant trends; however, a small group of trajectories (*n*=8) accounted for the majority of change in the landscape, and an examination of this subset led to a more meaningful analysis of land use change.

Analysis of land use trends can be further complicated by inconsistencies in categorical resolution among different studies. Previous studies of land use change in the Dougherty Plain have categorized land use coarsely into the broader classes of "Agriculture" and "Pine Forest". These studies showed little to no change within these categories over a span of decades (Turner and Rushcer 1988). Conversely, an analysis of changes in land use composition in the Dougherty Plain by Martin et al. (2013) utilized a finer-scale classification scheme, further separating "Agriculture" into "Irrigated Agriculture" and "Unirrigated Agriculture," and "Pine Forest" into "Natural Forest" and "Planted Pine." As a result, the study demonstrated an intensification of land use that would not have been detected otherwise.

Anthropogenic alteration of the landscape in the past often continues to affect current ecosystem patterns and processes (i.e. land use legacies). Lands used intensively in the past, which have since regenerated into "natural" forests, still exhibit physical and biological signs of their land use histories (Foster et al. 2003). Anthropogenic impacts associated with agricultural land use such as land-clearing, erosion, and nutrient uptake may continue to influence the landscape decades, and even centuries later, resulting in regionally homogenized forest communities, sedimentation of wetlands due to erosion, or depletion and leaching of soil C and

N (Foster et al. 1998, Fuller et al. 1998, Compton and Boone 2000, Craft and Casey 2000, Craft and Chiang 2002).

Land Use and Isolated Wetlands

High-intensity agriculture, both in the form of pine plantations and row-crop fields of peanuts, corn, soybeans, wheat, and cotton, exerts a heavy influence on the landscape of the Dougherty Plain (Turner and Rushcer 1988, Martin et al. 2013). Five counties within the Dougherty Plain account for the majority of all groundwater withdrawals within the Flint River Basin (Couch et al. 1996) due to intensive irrigation in the area. Agriculture has long been considered one of the main threats to remaining wetlands in the United States and across the globe (Heimlich 2003, Tiner 2003a), and likely impacts many of the isolated wetlands within the Dougherty Plain. Martin et al. (2012) developed a model that predicts the occurrence of over 11, 600 isolated wetlands throughout the region. Their model indicates that the mean nearest neighbor distance between wetlands is 180 meters. Thus, it is likely difficult to establish a large center-pivot field, pasture land, or pine plantation in the Dougherty Plain without encountering an isolated wetland.

These wetlands are particularly vulnerable to anthropogenic alteration; approximately half of all isolated wetlands in the Dougherty Plain are small (< 1 ha) (Martin et al. 2012), and therefore more easily drained and trees removed to create more arable land, or dredged and modified such that they no longer create an obstacle for the center pivot machinery. In addition, chemicals and waste associated with these agricultural practices enter the wetlands via runoff or directly via aerial application. Eutrophication is a common problem in wetlands which receive high nutrient loads from agricultural runoff. This can lead to further disruptions to the system, such as encouraging establishment of non-natives (Drexler and Bedford 2002) as well as increases in soil pH and nutrient loads to depths of 1 m (Ewing et al. 2012).

Isolated Wetland Restoration Efforts

Acknowledgment of severe wetland degradation and loss within the United States has led to government-mandated wetland mitigation, with debatable success (MEA 2000, Spieles 2005, Meltz and Copeland 2007). Development plans which alter existing wetlands must compensate for any expected loss of wetland area or function. Typically, this is achieved through one of three methods: enhancement, creation, or restoration.

The Natural Resources Conservation Service (NRCS) initiated the Wetlands Reserve Program (WRP) relatively recently in Georgia. To landowners with agriculturally degraded wetland on their property, the WRP offers monetary incentives to enter into a conservation easement. To date, acceptance into the program has been competitive (Keith Wooster, NRCS, personal communication). The WRP creates a restoration plan for each wetland accepted into the program, and, for longer-term easements (30 years and permanent) offers a one-time payment based upon the area of the enrolled tract. In shorter term easements, the program partially funds the restoration process (De Steven and Gramling 2012).

The restoration potential and cost of wetlands submitted to the program are evaluated based upon a relatively simple, straightforward ranking system, which incorporates environmental and monetary factors of the property (NRCS 2013). Each restoration project often comes with its own unique set of restrictions as well: caveats of the landowner, property line limitations, acceptable applications of funds, and adjacent land use (De Steven and Gramling 2012). Few studies monitoring restoration success or quantification of changes in the ecological integrity of restored WRP depressional wetlands have been conducted in the Coastal Plain (Brinson and Eckles 2010, De Steven and Lowrance 2011, De Steven and Gramling 2012).

In a survey of WRP projects conducted throughout the southeastern US, De Steven and Gramling (2012) report that the majority of depressional wetland restorations were conducted on sites previously used as cropland or pasture. They also found that within Georgia, depressional wetlands were the most common type of wetlands restored through the program. Typically for such projects, hydrologic restoration was accomplished through removal of drainage tiles or plugging drainage ditches. "Macrotopography" of the restored site may have also been altered to increase variation in water depth, and water control structures may have been installed. Vegetation restoration was generally restored passively, though in some cases, wetland tree species (i.e. *Taxodium ascendens* Brongn., pond cypress and *Nyssa biflora* Walter, swamp tupelo) have been planted. Overall, De Steven and Gramling (2012) found that most WRP projects resulted in sites with functional wetland hydrology and habitat, though sites were not necessarily restored with the objective of moving towards an identified "reference" condition.

Given the frequency of passive revegetation approaches in WRP restoration projects, a characterization of the seed bank composition of agricultural depressional wetlands is of interest. Studies of isolated depressional wetlands in the Southeast indicate that the persistent seed banks in these systems may provide a source of diverse, native plant species immediately post-disturbance (Kirkman and Shartiz 1994, Collins and Battaglia 2001, Mulhouse et al. 2005), and in restoration efforts begun long after the initial anthropogenic disturbance (Martin and Kirkman 2009). Many restoration efforts incorporate seed bank studies; persistent seeds in particular are considered an important potential source of "desirable" species which were present at the site prior to anthropogenic disturbance. Results from studies of the restoration potential through revegetation of a disturbed system are conflicted and site dependent; some find that the seed bank is not a viable option for revegetation (Blomqvist et al. 2003, Bossuyt and Honnay 2008, Chaideftou et al. 2011), while others have found that the seed bank could contribute to successful revegetation, if accompanied by additional, complementary management techniques (Bossuyt and Honnay 2008, Martin and Kirkman 2009, Wang et al. 2010, Valkó et al. 2011).

Seed bank seedling emergence experiments are a conventional method for cataloging and quantifying the assemblage of plant species with potential to germinate in a habitat of interest. A seed bank includes both persistent seeds (those which can delay germination for years), and transient seeds (those seeds which delay germination on a seasonal scale) (Thompson and Grime 1979). Transient seed banks are representative of species with seeds which have arrived within the year, typically occurring within the top layer of soil and organic duff, and which are not likely to remain viable after 1-2 years. Persistent seeds are generally assumed to be buried beneath the soil surface through actions of animals, humans, and weather, though the seeds can be found in the soil surface as well (Thompson and Fenner 2000). Persistent seed banks, because they remain viable in the soil for longer periods of time (years to centuries), are important reserves of biodiversity and contribute to the resilience of dynamic, disturbance-dependent ecosystems (Baskin and Baskin 1998).

Justification of Study and Objectives

The widespread expansion of intensive agriculture and silviculture throughout the Dougherty Plain during the past 60 years clearly changed the configuration of land use within the region, resulting in an increasingly fragmented landscape (Martin et al. 2013). Certainly, this intensification of land use has impacted wetland condition across the Dougherty Plain and reduced suitable habitat for isolated wetland-dependent flora and fauna. Consequently, the Dougherty Plain likely contains abundant isolated wetlands that are candidates for restoration programs such as the WRP. However, the impact of anthropogenic land use on the isolated wetlands has yet to be quantified at a regional scale. This study relates land use within the Dougherty Plain to the ecological integrity of isolated wetlands. The second chapter quantifies historic and current patterns of LULC within and among isolated wetlands, and identifies the wetlands that are less-disturbed and most likely to support diverse communities of flora and fauna. Chapter 3 relates common land use classes within the Dougherty Plain to specific biotic and environmental variables associated with wetland condition, and evaluates the relative ability of coarse- and fine-scale land use classification schemes to effectively predict wetland condition. The fourth chapter describes the seed bank composition of agricultural wetlands and assesses the influence of length of time in cultivation on the restoration potential of such wetlands.

Literature Cited

Baskin, C. C. and J. M. Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, Lexington.

Battle, J. M. and S. W. Golladay. 2002. Aquatic invertebrates in hardwood depressions of southwest Georgia. Southeastern Naturalist **1**:149-158.

Beck, B. F. and D. D. Arden. 1983. Hydrology and geomorphology of the Dougherty Plain, southwest Georgia. Southeastern Geological Society, Tallahassee, FL.

Biebighauser, T. R. 2007. Wetland drainage, restoration, and repair / Thomas R. Biebighauser. Lexington : The University Press of Kentucky, c2007.

Blomqvist, M. M., R. M. Bekker, and P. Vos. 2003. Restoration of Ditch Bank Plant Species Richness: The Potential of the Soil Seed Bank. Applied Vegetation Science **6**:179-188.

Blood, E. R., J. S. Phillips, and D. Edwards. 1997. The Role of the Floridian Aquifer in Depressional Wetlands Hydrodynamics and Hydroperiod.*in* Proceedings of the 1997 Georgia Water Resources Conference, Institute of Ecology, University of Georgia, Athens, GA 30602.

Bossuyt, B. and O. Honnay. 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities [electronic resource]. Journal of Vegetation Science **19**:875-884.

Brinson, M. M. 1993. A hydrogeomorphic classification for wetlands. U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS.

Brinson, M. M. and S. D. Eckles. 2010. U.S. Department of Agriculture conservation program and practice effects on wetland ecosystem services: a synthesis. Ecological Applications **21**:S116-S127.

Brinson, M. M. and A. I. Malvarez. 2002. Temperate freshwater wetlands: Types, status and threats. Environmental Conservation **29**:115-133.

Brown, M. T. and M. B. Vivas. 2005. Landscape Development Intensity Index. Environmental Monitoring and Assessment **101**:289-309.

Carroll, W., D., P. R. Kapeluck, R. A. Harper, and D. H. Van Lear. 2002. Background Paper: Historical Overview of the Southern Forest Landscape and Associated Resources. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Chaideftou, E., C. A. Thanos, E. Bergmeier, A. S. Kallimanis, and P. Dimopoulos. 2011. The herb layer restoration potential of the soil seed bank in an overgrazed oak forest. Journal of Biological Research **15**:47-57.

Christie, J. and S. Hausmann. 2003. Various state reactions to the SWANCC decision. Wetlands **23**:653-662.

Cohen, M. J., S. Carstenn, and C. R. Lane. 2004. Floristic Quality Indices For Biotic Assessment Of Depressional Marsh Condition In Florida. Ecological Applications **14**:784-794.

Collins, B. S. and L. L. Battaglia. 2001. Hydrology effects on propagule bank expression and vegetation in six Carolina bays. Community Ecology **2**:21.

Compton, J. E. and R. D. Boone. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology **81**:2314.

Costanza, R., R. dArge, R. deGroot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. Oneill, J. Paruelo, R. G. Raskin, P. Sutton, and M. vandenBelt. 1997. The value of the world's ecosystem services and natural capital. Nature **387**:253-260.

Costanza, R., S. C. Farber, and J. Maxwell. 1989. Valuation and Management of Wetlans Ecosystems. Ecological Economics **1**:335-361.

Couch, C. A., E. H. Hopkins, and P. S. Hardy. 1996. Influences of Environmental Settings on Aquatic Ecosystems in the Apalachicola-Chattahoochee-Flint River Basin.*in* U. S. G. Survey, editor.

Craft, C. B. and W. P. Casey. 2000. Sediment and nutrient accumulation in floodplain and depressional freshwater wetlands of Georgia, USA. Wetlands **20**:323-332.

Craft, C. B. and C. Chiang. 2002. Forms and amounts of soil nitrogen and phosphorus across a longleaf pine-depressional wetland landscape. Soil Science Society of America Journal **66**:1713-1721.

Dahl, T. E. 1990. Wetlands losses in the United States 1780's to 1980's.*in* F. a. W. S. U.S. Department of the Interior, Washington, D.C., editor.

Dahl, T. E. 2000. Status and Trends of Wetlands in the Conterminous United States 1986 to 1997.*in* F. a. W. S. U.S. Department of the Interior, Washington, D.C., editor.

Dahl, T. E. 2006. Status and Trends of Wetlands in the Conterminous United States 1998 to 2004.*in* F. a. W. S. U.S. Department of the Interior, Washington, D.C., editor.

Dahl, T. E. 2009. Status and Trends of Wetlands in the Conterminous United States 2004 to 2009.*in* U. S. F. a. W. Service, editor., Washington D.C.

De Steven, D. and J. Gramling. 2012. Diverse Characteristics of Wetlands Restored under the Wetlands Reserve Program in the Southeastern United States. Wetlands **32**:593-604.

De Steven, D. and R. Lowrance. 2011. Agricultural conservation practices and wetland ecosystem services in the wetland-rich Piedmont-Coastal Plain region. Ecological Applications **21**:S3-S17.

De Steven, D. and M. Toner. 1997. Gradient analysis and classification of carolina bay vegetation: A framework for bay wetlands conservation and restoration.*in* U. S. D. A. F. Service, editor. Savannah River Forest Station, P.O. Box 710, New Ellenton, South Carolina 29802.

Drew, M. B., L. K. Kirkman, and A. K. Gholson, Jr. 1998. The Vascular Flora of Ichauway, Baker County, Georgia: A Remnant Longleaf Pine/Wiregrass Ecosystem. Castanea **63**:1-24.

Drexler, J. Z. and B. L. Bedford. 2002. Pathways of nutrient loading and impacts on plant diversity in a New York peatland. WETLANDS -WILMINGTON- **22**:263-281.

Engstrom, R. T., L. K. Kirkman, and R. J. Mitchell. 2001. Natural History: Longleaf Pine-Wiregrass Ecosystem. Pages 5-18 *in* J. R. Willson, editor. The Fire Forest: Longleaf Pine-Wiregrass Ecosystem. Georgia Wildlife Natural Georgia Series 8, Georgia Wildlife Federation.

Ewing, J. M., M. J. Vepraskas, S. W. Broome, and J. G. White. 2012. Changes in wetland soil morphological and chemical properties after 15, 20, and 30 years of agricultural production. Geoderma **179-180**:73-80.

Fennessy, M. S., A. D. Jacobs, and M. E. Kentula. 2004. Review of Rapid Methods for Assessing Wetland Condition.*in* U.S. Environmental Protection Agency, editor., Washington, D.C.

Foster, D., F. Swanson, J. Aber, I. Burke, N. Brokaw, D. Tilman, and A. Knapp. 2003. The importance of land-use legacies to ecology and conservation. BioScience **53**:77-88.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-Use History as Long-Term Broad-Scale Disturbance: Regional Forest Dynamics in Central New England. Ecosystems **1**:96-119.

Fuller, J. L., D. R. Foster, J. S. McLachlan, and N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems **1**:76-95.

Golladay, S. W., B. W. Taylor, and B. J. Palik. 1997. Invertebrate communities of forested limesink wetlands in southwest Georgia, USA: Habitat use and influence of extended inundation. Wetlands **17**:383-393.

Haire, B. 2005. Georgia Irrigation Expansion Slows. Southeast Farm Press.

Heimlich, R., (ed). 2003. Agricultural Resources and Environmental Indicators.*in* U.S. Department of Agriculture and Economic Research Service, editors.

Hendricks, E. L. 1954. Some Notes on the Relation of Ground-water Levels to Wetland Levels in Limestone Sinks of southwestern Georgia. Transactions, American Geophysical Union **35**:790-804.

Hendricks, E. L. and M. H. Goodwin. 1952. Water-level fluctuations in limestone sinks in southwestern Georgia. U.S. Geological Survey Water-Supply Paper 1110-E.

Johnston, C. 1994. Cumulative impacts to wetlands. Wetlands **14**:49-55.

Kaeser, M. and L. Kirkman. 2009. Estimating total plant species richness in depressional wetlands in the longleaf pine ecosystem. Wetlands **29**:866-874.

Karr, J. and D. Dudley. 1981. Ecological perspective on water quality goals. Environmental Management **5**:55-68.

Käyhkö, N. 2006. Landscape Change Trajectory Analysis (LCTA) in the Assessment of Ecosystem Space-Time Sustainability. IALE-D Annual Conference **Kiel, Germany**: September 27-30.

Käyhkö, N. and H. Skånes. 2008. Retrospective land cover/land use change trajectories as drivers behind the local distribution and abundance patterns of oaks in south-western Finland. Landscape and Urban Planning **88**:12-22.

Kirkman, L. K., M. B. Drew, L. T. West, and E. R. Blood. 1998. Ecotone characterization between upland longleaf pine/wiregrass stands and seasonally-ponded isolated wetlands. Wetlands **18**:346-364.

Kirkman, L. K., P. C. Goebel, L. T. West, M. B. Drew, and B. J. Palik. 2000. Depressional wetland vegetation types: A question of plant community development. Wetlands **20**:373-385.

Kirkman, L. K., S. W. Golladay, L. LaClaire, and R. Sutter. 1999. Biodiversity in southeastern seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society **18**:553-562.

Kirkman, L. K. and R. R. Shartiz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded carolina bays in South Carolina. Ecological Application **4**:177-188.

Kudray, G. M. 2008. Wetlands of the Bitterroot Valley. Helena, Mont. : Montana Natural Heritage Program, c2008.

Lambin, E. F., B. L. Turner, H. J. Geist, S. B. Agbola, A. Angelsen, J. W. Bruce, O. T. Coomes, R. Dirzo, G. Fischer, C. Folke, P. S. George, K. Homewood, J. Imbernon, R. Leemans, X. Li, E. F. Moran, M. Mortimore, P. S. Ramakrishnan, J. F. Richards, H. Skånes, W. Steffen, G. D. Stone, U. Svedin, T. A. Veldkamp, C. Vogel, and J. Xu. 2001. The causes of land-use and land-cover change: moving beyond the myths. Global Environmental Change **11**:261-269.

Lane, C., E. D'Amico, and B. Autrey. 2012. Isolated Wetlands of the Southeastern United States: Abundance and Expected Condition. Wetlands **32**:753-767.

Leibowitz, S. G. 2003. Isolated wetlands and their functions: An ecological perspective. Wetlands **23**:517-531.

Leibowitz, S. G., P. J. Wigington, M. C. Rains, and D. M. Downing. 2008. Non-navigable streams and adjacent wetlands: Addressing science needs following the Supreme Court's Rapanos decision. Frontiers in Ecology and the Environment **6**:364-371.

Mack, J. 2006. Landscape as a predictor of wetland condition: an evaluation of the Landscape Development Index (LDI) with a large reference wetland dataset from Ohio. Environmental Monitoring and Assessment **120**:221-241.

Mack, J. J. 2007. Developing a wetland IBI with statewide application after multiple testing iterations. Ecological Indicators **7**:864-881.

Mack, J. J., M. Micacchion, L. Augusta, and G. R. Sablak. 2000. Vegetation Indices of Biotic Integrity (VIBI) for Wetlands and Calibration of the Ohio Rapid Assessment Method for Wetlands v 5.0. Final report to U.S. EPA. Ohio Environmental Protection Agency, Division of Surface Water, 401 Wetland Ecology Unit,, Columbus, OH.

Martin, D. L. 1999. Adoption of Center Pivot Irrigation. Irrigation Journal **49**:8-10.

Martin, G. I., J. A. Hepinstall, and L. K. Kirkman. 2013. Six decades (1948 - 2007) of landscape change in the Dougherty Plain of Southwest Georgia, USA. Southeastern Geographer **53**.

Martin, G. I., L. K. Kirkman, and J. Hepinstall-Cymerman. 2012. Mapping geographically isolated wetlands in the Dougherty Plain, Georgia, USA. Wetlands **32**:149-160.

Martin, K. L. and L. K. Kirkman. 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the south-eastern USA. Journal of Applied Ecology **46**:906-914.

Meltz, R. and C. Copeland. 2007. The Wetlands Coverage of the Clean Water Act Is Revisited by the Supreme Court: *Rapanos v. United States*.*in* C. R. Service, editor.

Millenium Ecosystem Assesment [MEA]. 2000. Ecosystems and Human Well-Being: Wetlands and Water Synthesis. World Resources Institute, Washington, DC.

Mitsch, W. J. and J. G. Gosselink. 2000. Wetlands. Third Edition edition. John Wiley & Sons, Inc., New York, NY, USA.

Mulhouse, J., L. Burbage, and R. Sharitz. 2005. Seed bank-vegetation relationships in herbaceous Carolina bays: Responses to climatic variability. Wetlands **25**:738-747.

National Resources Conservation Service. 2013. Wetlands Reserve Program. Easements, http://www.nrcs.usda.gov/wps/portal/nrcs/detail/national/programs/easements/wetlands/?cid=nrcs143_008419.

North Carolina Wetland Functional Assessment Team [WFAT]. 2010. N.C. Wetland Assessment Method (NC WAM) User Manual.

Odum, H. T. 1996. Environmental Accounting: Emergy and Environmental Decision Making. John Wiley and Sons, New York, NY.

Peet, R. K. and D. J. Allard. 1993. Longleaf Pine-Dominated Vegetation of the Southern Atlantic and Eastern Gulf Coast Region, USA. Pages 45-82 *in* Tall Timbers Fire Ecology Conference.

Rapanos v United States. 2006. 547 U.S. 715.

Rauscher, H. M. and K. Johnsen, editors. 2004. Southern Forest Science: Past, Present, and Future. U.S.D.A Forest Service, Southern Research Station, Asheville, NC.

Reiss, K. and M. Brown. 2007. Evaluation of Florida Palustrine Wetlands: Application of USEPA Levels 1, 2, and 3 Assessment Methods. EcoHealth **4**:206-218.

Reiss, K. C. 2004. Developing biological indicators for isolated forested wetlands in Florida. UNIVERSITY OF FLORIDA.

Ruiz, J. and G. Domon. 2009. Analysis of landscape pattern change trajectories within areas of intensive agricultural use: case study in a watershed of southern Québec, Canada. Landscape Ecology **24**:419-432.

Schroter, D., W. Cramer, R. Leemans, I. C. Prentice, M. B. Araujo, N. W. Arnell, A. Bondeau, H. Bugmann, T. R. Carter, C. A. Gracia, A. C. de la Vega-Leinert, M. Erhard, F. Ewert, M. Glendining, J. I. House, S. Kankaanpaa, R. J. T. Klein, S. Lavorel, M. Lindner, M. J. Metzger, J. Meyer, T. D. Mitchell, I. Reginster, M. Rounsevell, S. Sabate, S. Sitch, B. Smith, J. Smith, P. Smith, M. T. Sykes, K. Thonicke, W. Thuiller, G. Tuck, S. Zaehle, and B. Zierl. 2005. Ecosystem Service Supply and Vulnerability to Global Change in Europe. Science **310**:1333-1337.

Smith, L. L., D. A. Steen, J. M. Stober, M. C. Freeman, S. W. Golladay, L. M. Conner, and J. Cochrane. 2006. The vertebrate fauna of Ichauway, Baker County, GA. Southeastern Naturalist **5**:599-620.

Spieles, D. J. 2005. Vegetation development in created, restored, and enhanced mitigation wetland banks of the United States. Wetlands : the journal of the Society of the Wetland Scientists **25**:51-63.

Stein, E., A. Fetscher, R. Clark, A. Wiskind, J. Grenier, M. Sutula, J. Collins, and C. Grosso. 2009. Validation of a wetland Rapid Assessment Method: Use of EPA's level 1-2-3 framework for method testing and refinement. Wetlands **29**:648-665.

Sutter, R. D. and R. Kral. 1994. The ecology, status, and conservation of two non-alluvial wetland communities in the South Atlantic and Eastern Gulf coastal plain, USA. Biological Conservation **68**:235-243.

Sutula, M. A., E. D. Stein, J. N. Collins, A. E. Fetscher, and R. Clarke. 2006. A Practical Guide for the Development of a Wetland Assessment Method: The California Experience. Journal of American Water Resources Association **February**:157-175.

Thompson, K. and M. Fenner. 2000. The functional ecology of soil seed banks. Seeds: the ecology of regeneration in plant communities **2**:215-235.

Thompson, K. and J. P. Grime. 1979. Seasonal Variation in the Seed Banks of Herbaceous Species in Ten Contrasting Habitats. The Journal of Ecology **67**:893-921.

Tiner, R. 2004. Remotely-sensed indicators for monitoring the general condition of “natural habitat” in watersheds: an application for Delaware’s Nanticoke River watershed. Ecological Indicators **4**:227-243.

Tiner, R. 2010. NWI Plus: Geospatial Database for Watershed-Level Functional Assessment. National Wetlands Newsletter **32**:4-7.

Tiner, R. W. 2003a. Estimated extent of geographically isolated wetlands in selected areas of the United States. Wetlands **23**:636-652.

Tiner, R. W. 2003b. Geographically isolated wetlands of the United States. Wetlands **23**:494-516.

Tiner, R. W., H. C. Berquist, G. P. DeAlessio, and M. J. Starr. 2002. Geographically Isolated Wetlands: A Preliminary Assessment of their Characteristics and Status in Selected Areas of the United States.*in* F. a. W. S. U.S. Department of the Interior, Northeast Region, Hadley, MA., editor.

Turner, M. G., E. P. Odum, R. Costanza, and T. M. Springer. 1988. Market and Nonmarket Values of the Georgia Landscape. Environmental Management **12**:209-217.

Turner, M. G. and C. L. Rushcer. 1988. Changes in landscape patterns in Georgia, USA. Landscape Ecology **1**:241-251.

U.S. EPA. 2002. Methods for Evaluating Wetland Condition: Developing Metrics and Indexes of Biological Integrity.*in* U. S. E. P. A. Office of Water, Washington, DC, editor.

Valkó, O., P. Török, B. Tóthmérész, and G. Matus. 2011. Restoration Potential in Seed Banks of Acidic Fen and Dry-Mesophilous Meadows: Can Restoration Be Based on Local Seed Banks? Restoration Ecology **19**:9-15.

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. Forest Ecology and Management **211**:150-165.

Walker, J. L. 1993. Rare Vascular Plant Taxa Associated with the Longleaf Pine Ecosystem.*in* Tall Timbers Fire Ecology Conference.

Wang, N., J. Y. Jiao, Y. F. Jia, W. J. Bai, and Z. G. Zhang. 2010. Germinable soil seed banks and the restoration potential of abandoned cropland on the Chinese Hilly-gullied Loess Plateau. Environmental Management **46**:367-377.

Wharton, C. H. 1978. The Natural Environments of Georgia. Geologic and Water Resources Division and Resource Planning Section, Office of Planning and Research, Georgia Department of Natural Resources, Atlanta, Georgia.

Zedler, J. B. and S. Kercher. 2005. Wetland Resources: Status, Trends, Ecosystem Services, and Restorability. Annual Reviews, Palo Alto, CA.

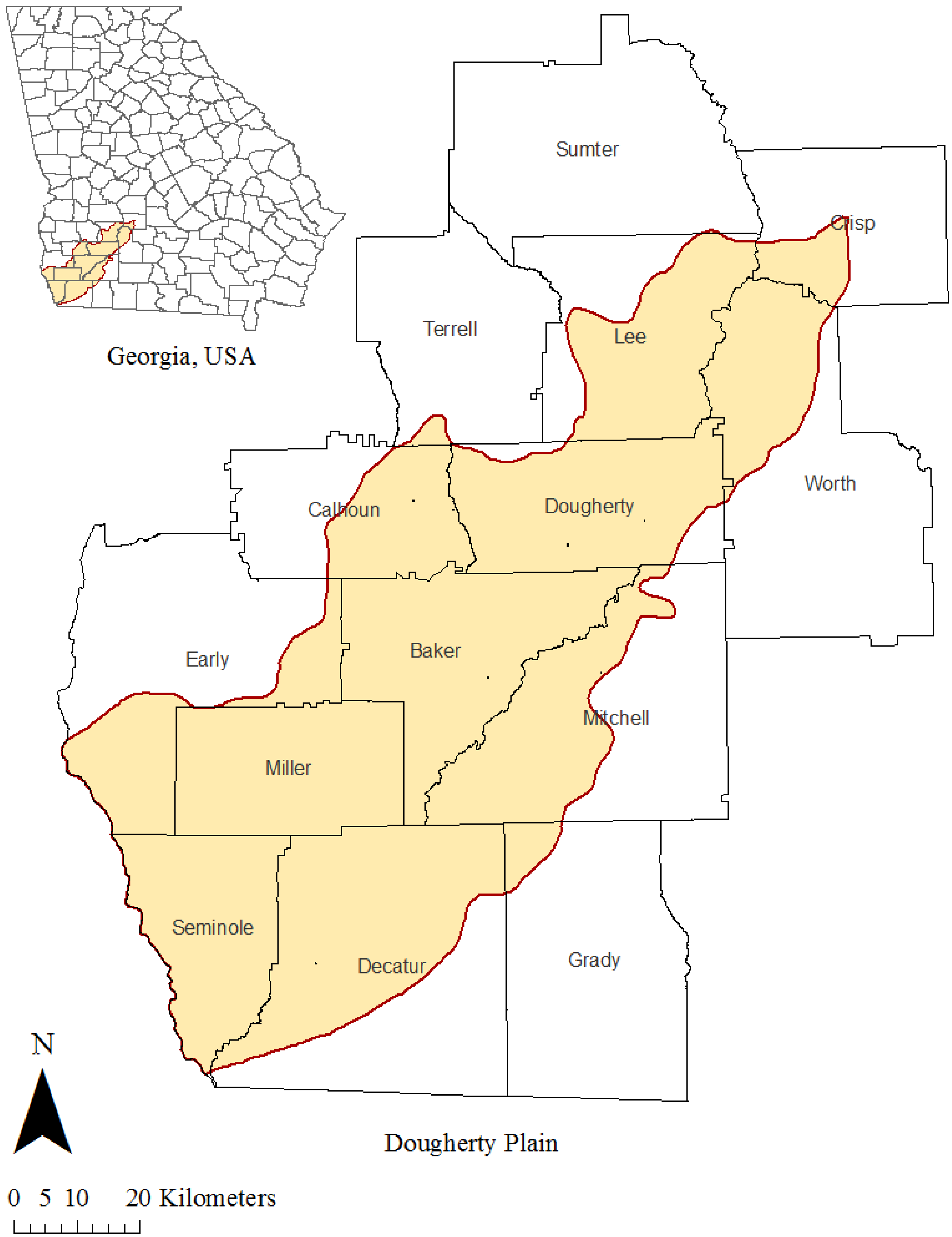

Figure 1.1 Map of the Dougherty Plain and associated counties in southwestern Georgia.

CHAPTER 2

PATTERNS OF LAND USE CHANGE ASSOCIATED WITH GEOGRAPHICALLY ISOLATED WETLANDS OF THE DOUGHERTY PLAIN FROM 1948 TO 2007

Stuber, O.S., Martin, G.I., Hepinstall-Cymerman, J., and Kirkman, L.K. To be submitted to *Ecological Applications*.

Introduction

Geographically isolated wetlands are wetlands that are surrounded entirely by upland (Tiner 2003). The absence of a surficial hydrologic connection to jurisdictional "waters of the United States" means that these wetlands are not federally protected under the Clean Water Act, though they perform many of the same important functions as federally protected wetlands. Studies have demonstrated that they contribute to water storage, nutrient retention, and sediment retention (Tiner et al. 2002). They can also improve water quality and act as recharge zones for underlying aquifers (van der Valk 1989), though specific functions associated with isolated wetlands vary depending upon the local and landscape-scale edaphic features.

In the Coastal Plain, a region with particularly high densities of isolated wetlands, a major function of these wetlands is the provision of habitat for a disproportionately diverse suite of flora and fauna (Whigham 1999, Kirkman et al. 2000, Liner et al. 2008), including several threatened and endangered species. The seasonal cycling between inundation and dry-down provide a unique and variable habitat to which extremely diverse communities of plants, macroinvertebrates, and herpetofauna are adapted (Wiggins et al. 1980, Kirkman et al. 1999, Battle and Golladay 2002).

At the regional scale, connectivity among wetland complexes across the landscape is also an important aspect of habitat provision. In particular, many amphibians depend upon discrete wetland environments for breeding habitat (Semlitsch and Bodie 1998, Semlitsch 2000, Guerry and Hunter 2002, Liner et al. 2008, Kirkman et al. 2013), but utilize forested uplands as their main habitat during the terrestrial phase of their life cycles (Semlitsch 1998, Enge 2002, Kirkman et al. 2013). Forested uplands also provide critical habitat connectivity between wetlands during juvenile dispersal and migration events (Semlitsch 1998, Hanski 1999, Guerry and Hunter 2002, Rothermel 2004). Species with limited vagility may only disperse several hundred meters, whereas other species may be capable of dispersing several kilometers (Smith and Green 2005, McKee 2012). In most cases, amphibians have demonstrated a preference for movement through forested habitat (Cushman 2006) as opposed to pastures and fields, which increase their vulnerability to predators and to dehydration (Rothermel and Semlitsch 2002, Rothermel 2004). Thus, ecological connectivity of wetlands via forest is an important feature of habitat provision and potentially affects the persistence of viable amphibian populations.

The lack of federal protection afforded geographically isolated wetlands makes them particularly vulnerable to alteration and conversion to other land use types, and compromises the ability of these wetlands to provide suitable habitat for many species (Brinson and Malvarez 2002). Generally speaking, such wetlands are often relatively shallow, seasonally dry, and vulnerable to draining, filling, and ditching (Biebighauser 2007). Historically, much of the conversion of wetland area has been attributed to agricultural practices (Dahl 1990, Zedler and Kercher 2005), and the loss of historic isolated wetlands through such anthropogenic alteration has been well documented (Leibowitz 2003, McCauley and Jenkins 2005) More recently, wetland loss has also increasingly been attributed to silvicultural activities (Dahl 2009). Additionally, fragmentation of the landscape associated with development and land use change can also inhibit inter-wetland movement vital to wetland-associated fauna (Amezaga et al. 2002, Rothermel and Semlitsch 2002, Cushman 2006, Roe and Georges 2007).

The Dougherty Plain, a physiographic subregion of the Coastal Plain in southwestern Georgia (Figure 1.1), is a region that has been dominated by agricultural and silvicultural land use for many decades. The region is characterized by karst topography, and has an abundance of isolated wetlands that develop in sinkhole depressions (1.7 wetlands per km^2; Martin et al. 2012).

Martin et al. (2013) recently examined patterns of land use and land cover (LULC) change between 1948 and 2007 using a 10% subsample of the region. Despite the observation of little change in the proportions of agricultural and forest LULC within the Dougherty Plain, they found that land use intensified significantly, namely through declines in dryland row-crop agriculture and naturally forested lands, and associated increases in irrigated row crop agriculture and pine plantations. Martin et al. (2013) also noted a significant increase in LULC fragmentation in their sample, marked by increasing patch densities and more homogeneous patch sizes.

Given the well-documented roles of agricultural and silvicultural land use in wetland conversion and functional loss nationwide, the six decades of LULC intensification and fragmentation in the Dougherty Plain has likely impacted numerous isolated wetlands of the region. In addition to direct conversion of wetlands to anthropogenic land use, landscape fragmentation may have interrupted contiguous forested corridors between wetlands. The goal of this study is to quantify the effect of LULC intensification and fragmentation on the ability of isolated wetlands to provide habitat based on connections through forested corridors. For this study, I consider wetlands to be partially or completely converted to other land uses if the polygons predicted to be wetlands in a previous study (Martin et al. 2012) contain non-wetland land uses associated with anthropogenic activity. Specifically, the objectives are to:

1. Quantify patterns of LULC and LULC change within a subset of isolated wetlands through time (1948-2007), and develop a current (2006) estimate of LULC composition within all wetlands throughout the Dougherty Plain.

2. Examine patterns in habitat connectivity among a subset of wetlands through time (1948-2007), and estimate current (2006) connectivity among all isolated wetlands in the Dougherty Plain.

3. Assess spatial patterns of isolated wetlands in the Dougherty Plain with connectivity via forested corridors as potential habitat for isolated wetland-dependent flora and fauna.

Methods

Study Area

The Dougherty Plain covers approximately 6,690 km^2 in southwestern Georgia; it is bounded to the north by the Fall Line Hills, and to the south and east by the Pelham Escarpment. The Chattahoochee River creates a political border between Georgia and Alabama, and thus defines the western edge of Georgia's Dougherty Plain. Geographically isolated limesink wetlands are a prominent feature of the karst landscape. These wetlands range widely in size and shape, from deep, steep-sided depressions of a few square meters, to expansive, low-lying flats covering many hectares. The average nearest neighbor distance between wetlands is less than 200 meters, and the estimated density is 1.7 wetlands/km^2. (Hendricks and Goodwin 1952, Martin et al. 2012). Generally, however, these wetlands tend to be small and shallow; half of the wetlands in the Dougherty Plain are estimated to be less than less than 1 ha in area (Martin et al. 2012). Historically, the isolated wetlands in the Dougherty Plain were embedded in a landscape dominated by fire-maintained longleaf pine-wiregrass (*Pinus palustris* Mill.-*Aristida beyrichiana* Trin. & Rupr.) savannas with a highly diverse grass-dominated understory (Walker 1993, Drew et al. 1998, Engstrom et al. 2001). Today, although natural forested lands are common, high-intensity cultivation (i.e. pine plantations and row crops) also exerts a heavy influence on the region (Turner and Rushcer 1988, Martin 2010). In intensively cultivated areas, soil disturbance often occurs immediately adjacent to embedded isolated wetlands, and frequently extends through the entire wetland.

Mapping LULC In and Around Isolated Wetlands

For this study, I used a geospatial data layer of predicted isolated wetlands derived from a combination of three geospatial data layers: 1) National Wetland Inventory (NWI) data, 2) USGS Digital Raster Graphic data depicting elevation contour lines and major landscape features, and 3) Soil Survey Geographic (SSURGO) hydric soil data (Martin et al. 2012). More than 11,500 isolated wetlands are predicted to occur in the Dougherty Plain based upon size (> 0.05 ha), lack of connectivity to streams, and location outside of the 100-year floodplain. Validation of the model indicates that it predicts wetlands with > 85% accuracy, and has a specificity (98%) comparable to that of the NWI data. Many of these wetlands have likely been modified through ditching, filling, and draining, so this estimate represents potential rather than actual isolated wetlands.

I quantified historical change in LULC (1948-2007) within isolated wetlands using a subset of wetlands (n=987) located where historical LULC data developed by Martin et al. (2013) was available. This historical dataset consists of LULC data screen-digitized from a chronosequence of aerial photography from the years 1948, 1968, 1993, and 2007. It represents a 10% subsample of the total area of the Dougherty Plain. This subset contains 8.6% of the predicted isolated wetlands within the region from Martin et al. (2012). In addition, I quantified the current (2006) LULC of all wetlands in the Dougherty Plain using the 16-class 2006 National Land Cover Database (NLCD, US Geological Survey 2011). To calculate the composition of

LULC classes within each wetland, the wetland geospatial layer was overlaid with each of the LULC layers developed by Martin et al. (2013) and with the NLCD 2006 data.

The screen-digitized data not only provided historical LULC data that was previously unavailable digitally, but permitted greater resolution of land use categories compared to the NLCD data. Specifically, natural and planted forests can be distinguished, as well as irrigated and dryland row-crops, and orchards. In total, the historical, photo-interpreted data includes 11 LULC classes (Table 2.1). Urban development is not prominent within the study region, thus all developed lands were combined into a single “Developed” category. Within wetlands, old fields and pastures were not distinguishable from natural herbaceous cover, thus these were combined into a single Herbaceous class. After analysis of the historical LULC data with finer categorical resolution, cultivated sub-classes and forested sub-classes were combined post-hoc into composite classes for comparison to the region-wide analysis using the lower class resolution NLCD 2006 data (Table 2.1).

To standardize the NLCD 2006 LULC classes with the subset of historical LULC data, I combined several of the NLCD classes into composite classes: all herbaceous classes were combined into one generic Herbaceous class. Likewise, all forested classes and all developed classes were also combined into Forested and Developed, respectively (Table 2.1). For most synoptic analyses, this simplified classification scheme was used. However, the single Herbaceous class made it impossible to distinguish between anthropogenically dominated herbaceous wetlands (i.e. pasture and old field) and natural herbaceous wetlands. Therefore, anthropogenic disturbance of wetlands dominated by Herbaceous cover was determined based upon the amount of surrounding forest within 100 m. Wetlands surrounded by less Forest (<

50%) were classified as old field or pasture wetlands, and wetlands surrounded by more Forest (> 50%) were classified as naturally herbaceous.

Analytical Approach

To understand the impact of land use intensification and landscape fragmentation on the ability of isolated wetlands to provide habitat for wetland-dependent flora and fauna, I analyzed 1) LULC composition within isolated wetlands and 2) habitat connectivity among wetlands at several spatial and temporal scales. For both analyses, I quantified change through time (1948 – 2007), comparing the historical data in a subset of the Dougherty Plain, and I also quantified current (2006) synoptic patterns using the NLCD data set.

The examination of patterns in LULC at the larger, synoptic scale allowed me to quantify the relationship between wetland size and dominant land use and determine whether smaller isolated wetlands were more vulnerable to anthropogenic disturbance. Likewise, with the synoptic dataset I was able to extend the analysis of connectivity among isolated wetlands to exclude those most affected by anthropogenic disturbance, and create a map of the Dougherty Plain depicting only those isolated wetlands which might provide suitable habitat for isolated wetland-dependent flora and fauna. Finally, I examined how spatial patterns of clustering and autocorrelation among isolated wetlands changed after the removal of wetlands dominated by anthropogenic LULC.

LULC Composition Within Isolated Wetlands

Within each wetland, I determined the area of each LULC class present. I calculated the percentage of total wetland area for each LULC class. I also determined the proportion of wetlands dominated (i.e. a single LULC class covering at least 50% of a wetland) by each land use class.

To calculate the cumulative direct impacts of anthropogenic conversion of isolated wetlands, I pooled all classes associated with human land use (Planted Pine, Herbaceous, all Cultivated classes, Bare, and Developed; Table 2.1). Combining all classes allowed me to detect those wetlands which were not dominated by one specific LULC class, but which nevertheless were largely converted for human use. For this analysis, Herbaceous-dominated wetlands were classified as either anthropogenic or natural herbaceous based upon surrounding forest cover, as described above.

To determine the relationship between wetland size and conversion to anthropogenic land use, I examined the three most common LULC classes occurring within wetlands: Cultivated, Herbaceous, and Forested, and considered 12 size classes of wetlands: <0.5, 0.5-1, 1-2, 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10, and >10 ha. I hypothesized that smaller wetlands were more likely to be dominated by Cultivated land use, due to the apparent ease with which smaller wetlands are converted. To test the null hypothesis of no relationship between wetland size and dominant LULC, I used a chi-square goodness of fit test. The large size of the wetland population being analyzed (n= 11,521) and the extremely left-skewed distribution of wetland sizes lends itself to the sample size-independent, nonparametric goodness of fit analysis (Dowdy et al. 2004). The analysis does require that all expected contingency table values equal at least five, which the data satisfies.

Habitat Connectivity of Isolated Wetlands

I examined the structural connectedness of geographically isolated wetlands via contiguous forested patches using both the subset of historical LULC data to determine change in connectedness over time, and the NLCD 2006 data to assess habitat connectivity region-wide. For each isolated wetland, I calculated two indices of connectedness within a specified distance around each wetland: 1) the number of other isolated wetlands connected to the focal wetland via contiguous forest, and 2) the area of isolated wetlands to which the focal wetland was connected via contiguous forest. Only those isolated wetlands within the specified distance which intersected the same forest patch as the focal wetland were included in the indices (Figure 2.1). For the subset of historical data, I included wetlands within 500 m of the focal wetland, and for the NLCD 2006 data, two scales of connectivity (500 m and 2.5 km) were examined, given the synoptic nature of the data. The 500 m distance represents the maximum distance which a low-vagility amphibian might travel during dispersal events (Smith and Green 2005, Veysey et al. 2011, McKee 2012), whereas the 2.5 km distance represents the potential dispersal distance of high-vagility species (Smith and Green 2005, McKee 2012). To avoid edge effects produced by the spatial limitations of the data, wetlands located near the boundaries of each data set were not used as focal wetlands but were included in connectivity calculations for other focal wetlands (see Appendix A for a more detailed protocol).

When habitat connectivity was examined through time using the historical data, Planted Pine LULC was not included in maps of contiguous Forest LULC because it generally presents a more hostile or less preferable environment for herpetofauna, particularly salamanders, when compared to second-growth forest (Todd 2008, Jennifer Howze, Jones Ecological Research Center, personal communication). However, when connectedness was analyzed using NLCD 2006 LULC data, no separate class existed for Planted Pine, so all forested classes were included and dissolved to create one composite map of Forested LULC throughout the Dougherty Plain. Because forested LULC in NLCD 2006 is spatially represented using relatively coarse, 30mx30m cells, I used the 8-neighbor rule to define patch connectivity (Turner et al. 2001). At both scales of analysis, isolated wetlands themselves were considered a component of ideal habitat in which animals might travel between wetlands, thus if an isolated wetland polygon bridged two otherwise disconnected patches of forest, we considered this a valid connection, and the forested patches were considered contiguous.

Though there are many factors which influence the ability of isolated wetlands to provide suitable habitat, I used the synoptic map of isolated wetlands connected via contiguous forest to create a simple, “first-cut” estimate of isolated wetlands within the Dougherty Plain that could potentially provide habitat at the local wetland scale and at the regional scale for isolated wetland-dependent flora and fauna. To be included in the model, wetlands had to satisfy two criteria: 1) they could not be dominated by anthropogenic land use, and 2) they must be connected to at least one other wetland within 500 m via contiguous forest.

Spatial Pattern Analysis of Connected Wetlands with Potentially Suitable Habitat

Small wetlands (< 1 ha) make up the majority of isolated wetlands in the Dougherty Plain (Martin et al. 2012). If indeed small wetlands are more vulnerable to anthropogenic conversion, a disproportionately large number of small wetlands will have been converted and therefore would be unlikely to provide suitable habitat, affecting observed patterns of clustering and spatial autocorrelation (Martin et al. 2012) as well. To determine if, and how the removal of such “non-habitat” wetlands influenced the spatial patterns of wetland distribution throughout the region, I first examined the size class distribution of wetlands with suitable habitat and compared it to the size class distribution of all isolated wetlands (Martin et al. 2012).

I assessed patterns of regional-scale clustering and autocorrelation using spatial statistics tools in ArcMap 9.2. Average Nearest Neighbor (ANN) analysis was used to determine whether patterns of significant clustering exist in potential suitable habitat wetlands. This analysis calculates the average nearest neighbor distances for centroids representing each wetland, and compares these distances with nearest-neighbor distances derived from randomly-spaced points. An index is then calculated by dividing the observed mean nearest neighbor distance by the expected (random) nearest neighbor distance. Values less than one indicate clustering, and values greater than one indicate dispersion. Assuming normal distribution, a null hypothesis of no pattern, or randomly distributed wetlands, is rejected with Z scores > |1.96|. I also tested for spatial autocorrelation among wetlands based upon wetland size using Moran's I test. Moran's I values can range between -1.0 and 1.0. Values near 1.0 indicate positive spatial autocorrelation, values near -1.0 indicate clustering of unlike features, and values near 0 indicate no pattern. As above, statistical significance is determined using Z Scores. The results of the ANN and Moran's I were compared to results obtained by Martin et al. for all wetlands in the Dougherty Plain.

Results

Historical Trends of LULC Composition within Isolated Wetlands

Forested (Natural Forest and Planted Pine combined) was the most prevalent LULC class within wetlands for all years examined (Table 2.2). However, Natural Forest within wetlands declined steeply between 1968 and 1993, with a loss of 21% of the total area mapped. Conversely, Planted Pine nearly tripled in area during the same period, thus resulting in what appears to be a static cover of Forested LULC overall. The number of wetlands dominated by the Forested LULC also reflects this trend (Table 2.3). In 1948, there were no wetlands dominated by Planted Pine, but by 2007, Planted Pine dominated nearly one third of all Forested wetlands.

Area of Herbaceous LULC within wetlands increased overall during the 60 year study period. Proportionally, it remained the second-largest component of wetland LULC in most years, nearly doubling in total extent from 1948 (472 ha) to 2007 (911 ha). Open Water did cover more area than Herbaceous in 1948, though it is likely that the majority of the land obscured beneath the water would have been considered Herbaceous.

Total area of Cultivated LULC increased consistently throughout the chronosequence from 225 ha (7.33%) in 1948 to 466 ha (15.17%) in 2007. Pecan Orchards represented a small portion of wetland area and dominated a small number of wetlands during this period. Dryland Row-Crop comprised the largest portion of Cultivated LULC between 1948 and 1993, but by 2007 Irrigated Row-Crop had become the largest contributor; it represented nearly 10% of all wetland area (307 ha), and dominated 12.0% of all wetlands. The proportion of wetlands dominated by Anthropogenic LULC classes rose sharply between 1948 and 1968 (27.7% to 45.7%), and continued to rise through 2007 (59.8 %).

Synoptic Analysis of LULC Composition Within Isolated Wetlands

Based on the NLCD 2006 LULC data, more than half (5,907) of all isolated wetlands in the Dougherty Plain were dominated by Forest (Table 2.2). Herbaceous and Cultivated LULC classes composed 21.1% and 14.45% of wetland area, respectively, and the proportion of wetlands dominated by these classes is similar. All remaining classes (Shrub/scrub, Bare, Developed, and Open Water) each represent less than 4% of total wetland area in the Dougherty Plain. When all human-associated LULC classes were combined, Anthropogenic land use dominated nearly half (42.3%) of all wetlands. NLCD 2006 estimates of LULC composition within the subset extent indicate a lower proportion of anthropogenically dominated wetlands compared to 2007 LULC data within the same area. The discrepancy is likely due to the inclusion of Planted Pine in the 2007 estimate of Anthropogenic LULC.

Wetland size was significantly associated with dominance of particular LULC classes. Wetlands in the smallest size class (< 0.5 ha) were positively related to dominance of Cultivated and Herbaceous LULC (X^2= 210.6, p< 0.001 ; X^2= 104.5, p<0.001 respectively), and negatively related to dominance by Forest LULC (X^2= 143.7, p< 0.001; Figure 2.2). In contrast, wetland in the next smallest size class (0.5 – 1 ha) were positively associated with dominance by Herbaceous LULC but negatively associated with dominance by Cultivated and Forest LULC. Only the largest size class (> 10 ha) wetlands were positively associated with dominance of Forest LULC, and these were negatively associated with dominance of Herbaceous and Cultivated LULC.

Historical Habitat Connectivity

Wetland to wetland connectivity via forests declined between 1948 and 2007, particularly among those of intermediate size (Figure 2.3). A sharp increase in wetlands lacking connectivity with other wetlands occurred between 1968 and 1993. Likewise, connectivity among wetlands declined steeply during the same interval. In particular, wetlands connected to less than 10 ha of other wetlands marked the steepest declines. Loss and gain of connected wetlands was focused in several subunits, rather than distributed evenly among them (Figures 2.4-2.7). NLCD 2006 estimates of connectedness within the subset extent are higher in both number and area of connected wetlands when compared to 2007 LULC data within the same area. The discrepancy is likely due to the differences in data resolution and associated rules of connectivity.

Synoptic Habitat Connectivity

Regardless of the scale of analysis (500 m or 2.5 km), about half (51.1% and 46.1%, respectively) of the wetlands lack connections to other isolated wetlands via contiguous forest (Figures 2.8 and 2.9). At the 500 m scale, the average number of wetland-to-wetland connections is 1.49 (including wetlands with no connections to other wetlands), and the mean area of wetlands connected via forest was 10.07 ha. Few (2.0%) of all sampled wetlands were connected to more than 10 other wetlands. At the 2.5 km scale, the average number (13 wetlands) and average total area (60.23 ha) of connected wetlands predictably increased. The most highly connected wetland was connected to 104 others. However, almost 8% were connected to very few (1-2) other wetlands. A visual examination of the highly connected wetlands clearly shows concentrations in several specific areas of the Dougherty Plain at both the 500 m and 2.5 km scales (Figures 2.10 and 2.11), which generally coincide with the locations of large tracts of privately owned forests (natural and planted) and quail plantations. Conversely, wetlands which lack connectivity appear to be distributed more evenly throughout the entire region. The spatially explicit model of connected wetlands that potentially provide habitat for isolated wetland-dependent species identified 3,962 isolated wetlands, or 41.8% of all isolated wetlands within the Dougherty Plain (Figure 2.12).

Spatial Patterns of Connected Wetlands with Potentially Suitable Habitat

A greater proportion of large wetlands (> 10 ha) represent potential suitable habitat for isolated wetland-dependent species, relative to the distribution of all wetlands (Figure 2.13). The Average Nearest Neighbor analysis indicated some significant clustering among wetlands, with an ANN index of 0.64 (Z Score = -43.49, $p < 0.001$). Moran's I test for spatial autocorrelation, however, did not indicate a strong clustering pattern of like-sized wetlands. Despite a significant result (Z Score = 4.31, $p < 0.001$), the Moran's I index is very near 0 (0.02), suggesting that the clustering pattern has no relationship to wetland size, and that the significant result may be a statistical artifact of the very large sample size.

Discussion

Intensification of Land Use in Isolated Wetlands

The results of this study demonstrate that the 60 years of land use intensification and landscape fragmentation in the Dougherty Plain (Martin et al. 2013) ultimately contributed to a significant loss of suitable habitat for isolated wetland-dependent species. The changes in LULC within Dougherty Plain wetlands quantified in this study have implications for isolated wetlands beyond habitat loss, however. Specifically, the intensification of land use within wetlands also strongly suggests a regional trend of declining wetland condition. Though I did not address wetland condition in this study, other studies have repeatedly demonstrated an inverse relationship between the intensity of land use surrounding wetlands and the condition within the wetlands (Brown and Vivas 2005, Mack 2006, Vivas and Brown 2006, Hychka et al. 2007, Chapter 3, this document).

By extension, the intensification of land use quantified in this study warns of a loss of other important aspects of wetland condition at a regional scale, including the physicochemical characteristics (e.g. ephemeral hydroperiods and relatively acidic water) and functional processes (e.g. flood abatement and nutrient storage) associated with wetlands in good condition (Craft and Casey 2000, Fennessy et al. 2004). Studies measuring the condition and function of wetlands which have been converted, in whole or in part, to other forms of land use (agriculture, pine plantations, etc.) report changes in suites of herpetofauna, plant communities, shifts in hydroperiod, and exclusion of fire (Euliss and Mushet 1996, 1999, Rheinhardt et al. 2002, Cushman et al. 2006, Devictor et al. 2007, Chapter 3, this document).

Wetland Size and Disturbance

Though anecdotal evidence and many studies suggest that one characteristic which makes many isolated wetlands vulnerable to alteration is their relatively small size (Semlitsch and Bodie 1998, Martin et al. 2012), I was unable to find a study that statistically documented this trend. The greater vulnerability of small wetlands has huge potential ecological impacts at the landscape scale. Small wetlands are often the most abundant in regions with high densities of isolated wetlands (Bennett and Nelson 1991, Gibbs 1993, Martin et al. 2012). They have also been known to support highly species-rich communities of herpetofauna (Semlitsch and Bodie 1998). Given this, the conversion, or loss of smaller wetlands can lead to disproportionate increases in average inter-wetland distance (Semlitsch 2000), and an associated disruption of the source-sink dynamics that sustain amphibian metapopulations (Cushman 2006).

Connected Wetlands with Potentially Suitable Habitat

The spatially explicit model of connected wetlands with habitat suitable for isolated wetland-dependent species indicates that the region is heterogeneous in its distribution of these habitats. Admittedly, the estimate of potential habitat is generous -- wetlands not dominated by anthropogenic LULC may still be disturbed through indirect processes like sedimentation, nutrient runoff, or the exclusion of fire (Brinson and Malvarez 2002, Gleason et al. 2003, Martin and Kirkman 2009). Nevertheless, the model represents a starting-point for understanding how more than 60 years of land use intensification and fragmentation has shaped the available isolated wetland habitat at a regional scale.

This study clearly shows that smaller wetlands were more likely to be dominated by anthropogenic land use, resulting in their removal from the pool of wetlands that can potentially support wetland-dependent species. The spatial clustering exhibited by the connected wetlands with suitable habitat is likely due to the association of many of the modeled wetlands with larger patches of contiguous public and private forests. The apparent lack of spatial autocorrelation based on wetland size exhibited in the suitable habitat model may be a result of underlying physiogeographic patterns and associated land use. When all predicted isolated wetlands were examined, the clusters of wetlands which exhibited significant spatial autocorrelation were mostly located in the center of the Dougherty Plain, where irrigated agricultural fields are particularly dominant (Martin et al. 2012). Thus, the high intensity of land use in that region likely led to the exclusion of more wetlands from the suitable habitat model, potentially disrupting original patterns of spatial clustering. Alternatively, averaging spatial patterns at the regional scale may have resulted in obscured localized patterns of autocorrelation and disaggregation.

The Role of Center Pivot Agriculture

Agricultural land use (including pasture) has long been recognized as a major driver of wetland loss (Dahl 1990, Millenium Ecosystem Assesment [MEA] 2000, Heimlich 2003), and this pattern certainly holds true within the Dougherty Plain. In this region specifically, the majority of the loss of wetland habitat on cultivated land is attributable to irrigated row-crop agriculture. Center pivot irrigation is the most common irrigation method used in southwestern Georgia by far (Haire 2005, Hook et al. 2010). For center pivot systems to function, wetlands within agricultural fields are typically cleared of vegetation, and if necessary, a berm is constructed through the wetland so that the machinery can move across it.

Center pivot irrigation technology was also likely an important driver of recent declines in wetland connectivity. The steepest decline in wetland connectivity I observed corresponds to a significant decrease in the proportion of forest within the sampled area (Martin et al. 2013). This time period also coincides with the widespread adoption of center pivot irrigation technology in the late 1970's (Martin 1999). A considerable portion of forested land (18.7%) was converted to irrigated row-crop after center pivot was introduced to the Dougherty Plain (Martin et al. 2013).

Comparing the Dougherty Plain to Similar Regions

The Dougherty Plain has experienced proportionally less wetland loss due to anthropogenic conversion relative to similar agricultural regions with high densities of isolated wetlands. In some regions, (e.g. Carolina bays of South Carolina (Bennett and Nelson 1991), prairie potholes of Iowa (van der Valk pers. comm. as cited in Leibowitz 2003) and Illinois (McCauley and Jenkins 2005), and vernal pools of southern California (Bauder and Wier 1990 as cited in King 1998) estimates of wetland loss range upwards of 90%. Rhazi et al. (2012) however, reported comparable levels of wetland loss for Mediterranean temporary pools in western Morocco. As little as 5-7% of Playa lakes in the Southern High Plains region have been converted to other land uses (David Haukos pers. comm. as cited in Leibowitz 2003).

The high proportion of Forested land cover within the Dougherty Plain may be responsible for the comparably low levels of wetland conversion. Though Natural Forest wetland area declined during the years examined in this study, the proportion of Natural Forest remained high relative to other land use classes, and relative to historical proportions of forest in a similar study. Kirkman et al. (1996) quantified LULC composition within Carolina bays in 1951 and found that 28% of the area within Carolina bays was forested, which is considerably less than the proportion in Natural Forest in 1948 for wetlands in this study (53%). This suggests that, at least initially, this region of Georgia may not have been cultivated as extensively as similar landscapes within other areas of the Coastal Plain.

Limitations of the Study

The LULC data sets used in this study differed from each other in categorical and spatial resolution and in extent. The results, therefore, must be interpreted with these differences in mind. Specifically, LULC patterns within wetlands representing a small portion of the NLCD 2006 cell size (0.09 ha) may have been obscured (Cunningham 2006). A comparison of the proportion of LULC classes within wetlands as estimated by NLCD and screen-digitized data indicates that the coarser NLCD data likely presents a conservative estimate of wetland conversion to cultivated and herbaceous land use classes.

Similarly, the estimates of connectivity must be considered with the spatial resolution of the dataset in mind. NLCD data does not always identify linear barriers such as roads. Therefore, the synoptic analysis may include instances where a contiguous forested patch “crosses” a known road, thereby potentially inflating the estimate of connectivity. Additionally, pine plantations were included in the coarser synoptic measures of contiguous forest. The synoptic estimates of wetland connectivity should therefore be considered generously inclusive.

Conclusions

The rising dominance of anthropogenic land use within the isolated wetlands combined with the decline in contiguous forested corridors between wetlands has created a scenario with major implications for the condition and function of these wetlands, and the flora and fauna that depend upon them. Specifically, this study reinforces the vulnerability of small wetlands in an agricultural landscape, and highlights the role of center pivot agriculture as a potentially important driver of wetland conversion and loss of habitat connectivity. Ultimately, this study represents a useful initial estimate of the extent of degradation and changes to isolated wetlands within the Dougherty Plain, and can serve as a baseline for future conservation efforts and regional wetland assessments.

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Literature Cited

Amezaga, J. M., L. Santamaría, and A. J. Green. 2002. Biotic wetland connectivity—supporting a new approach for wetland policy. Acta Oecologica **23**:213-222.

Battle, J. M. and S. W. Golladay. 2002. Aquatic invertebrates in hardwood depressions of southwest Georgia. Southeastern Naturalist **1**:149-158.

Bennett, S. H. and J. B. Nelson. 1991. Distribution and status of Carolina bays in South Carolina. South Carolina Wildlife and Marine Resources Department, Nongame and Heritage Trust Section, Columbia, SC.

Biebighauser, T. R. 2007. Wetland drainage, restoration, and repair / Thomas R. Biebighauser. Lexington : The University Press of Kentucky, c2007.

Brinson, M. M. and A. I. Malvarez. 2002. Temperate freshwater wetlands: Types, status and threats. Environmental Conservation **29**:115-133.

Brown, M. T. and M. B. Vivas. 2005. Landscape Development Intensity Index. Environmental Monitoring and Assessment **101**:289-309.

Craft, C. B. and W. P. Casey. 2000. Sediment and nutrient accumulation in floodplain and depressional freshwater wetlands of Georgia, USA. Wetlands **20**:323-332.

Cunningham, M. A. 2006. Accuracy assessment of digitized and classified land cover data for wildlife habitat. Landscape and Urban Planning **78**:217-228.

Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: A review and prospectus. Biological Conservation **128**:231-240.

Cushman, S. A., K. S. McKelvey, J. Hayden, and M. K. Schwartz. 2006. Gene Flow in Complex Landscapes: Testing Multiple Hypotheses with Causal Modeling. American Naturalist **168**:486-499.

Dahl, T. E. 1990. Wetlands losses in the United States 1780's to 1980's.*in* F. a. W. S. U.S. Department of the Interior, Washington, D.C., editor.

Dahl, T. E. 2009. Status and Trends of Wetlands in the Conterminous United States 2004 to 2009.*in* U. S. F. a. W. Service, editor., Washington D.C.

Devictor, V., J. Moret, and N. Machon. 2007. Impact of Ploughing on Soil Seed Bank Dynamics in Temporary Pools. Plant Ecology:45.

Dowdy, S., S. Wearden, and D. Chilko. 2004. Statistics for research. Third edition. Wiley-interscience, Hoboken, New Jersey.

Drew, M. B., L. K. Kirkman, and A. K. Gholson, Jr. 1998. The Vascular Flora of Ichauway, Baker County, Georgia: A Remnant Longleaf Pine/Wiregrass Ecosystem. Castanea **63**:1-24.

Enge, K. M. 2002. Herpetofaunal drift-fence survey of two seepage bogs in Okaloosa County, Florida. Florida Scientist **65**:67-82.

Engstrom, R. T., L. K. Kirkman, and R. J. Mitchell. 2001. Natural History: Longleaf Pine-Wiregrass Ecosystem. Pages 5-18 *in* J. R. Willson, editor. The Fire Forest: Longleaf Pine-Wiregrass Ecosystem. Georgia Wildlife Natural Georgia Series 8, Georgia Wildlife Federation.

Euliss, N. H. and D. M. Mushet. 1996. Water-level Fluctuation in Wetlands as a Function of Landscape Condition in the Prairie Pothole Region. Wetlands **16**:587-593.

Euliss, N. H. and D. M. Mushet. 1999. Influence of agriculture on aquatic invertebrate communities of temporary wetlands in the Prairie Pothole Region of North Dakota, USA. Wetlands **19**:578-583.

Fennessy, M. S., A. D. Jacobs, and M. E. Kentula. 2004. Review of Rapid Methods for Assessing Wetland Condition.*in* U.S. Environmental Protection Agency, editor., Washington, D.C.

Gibbs, J. 1993. Importance of small wetlands for the persistence of local populations of wetland-associated animals. Wetlands **13**:25-31.

Gleason, R. A., N. H. Euliss, D. E. Hubbard, and W. G. Duffy. 2003. Effects of Sediment Load on Emergence of Aquatic Invertebrates and Plants From Wetland Soil Egg and Seed Banks. Wetlands **23**:26-34.

Guerry, A. D. and M. L. Hunter. 2002. Amphibian Distributions in a Landscape of Forests and Agriculture: an Examination of Landscape Composition and Conf iguration. Conservation Biology **16**:745-754.

Haire, B. 2005. Georgia Irrigation Expansion Slows. Southeast Farm Press.

Hanski, I. 1999. Metapopulation Ecology. Oxford University Press, Oxford, UK.

Heimlich, R., (ed). 2003. Agricultural Resources and Environmental Indicators.*in* U.S. Department of Agriculture and Economic Research Service, editors.

Hendricks, E. L. and M. H. Goodwin. 1952. Water-level fluctuations in limestone sinks in southwestern Georgia. U.S. Geological Survey Water-Supply Paper 1110-E.

Hook, J. E., G. Hoogenboom, J. Paz, J. Mullen, J. Bergstrom, and M. Risse. 2010. Agricultural Irrigation Water Demand: Georgia's Major and Minor Crops 2011 through 2050. National Environmentally Sound Production Agriculture Laboratory (NESPAL), University of Georgia.

Hychka, K. C., D. H. Wardrop, and R. P. Brooks. 2007. Enhancing a landscape assessment with intensive data: a case study in the Upper Juniata watershed. Wetlands **27**:446-461.

King, J. L. 1998. Loss of diversity as a consequence of habitat destruction in California vernal pools. Pages 119-123 *in* Ecology, conservation and management of vernal pool ecosystems-proceedings from a 1996 conference. California Native Plant Society, Sacramento, California.

Kirkman, L. K., P. C. Goebel, L. T. West, M. B. Drew, and B. J. Palik. 2000. Depressional wetland vegetation types: A question of plant community development. Wetlands **20**:373-385.

Kirkman, L. K., S. W. Golladay, L. LaClaire, and R. Sutter. 1999. Biodiversity in southeastern seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society **18**:553-562.

Kirkman, L. K., R. L. Lide, G. Wein, and R. R. Shartiz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western coastal plain of South Carolina. Wetlands **16**:564-576.

Kirkman, L. K., L. L. Smith, and S. W. Golladay. 2013. Southeastern Depressional Wetlands.*in* L. K. Kirkman, editor. The Natural Communities of Georgia. Athens : University of Georgia Press.

Leibowitz, S. G. 2003. Isolated wetlands and their functions: An ecological perspective. Wetlands **23**:517-531.

Liner, A. E., L. L. Smith, S. W. Golladay, S. B. Castleberry, and J. W. Gibbons. 2008. Amphibian Distributions within Three Types of Isolated Wetlands in Southwest Georgia. American Midland Naturalist:69.

Mack, J. 2006. Landscape as a predictor of wetland condition: an evaluation of the Landscape Development Index (LDI) with a large reference wetland dataset from Ohio. Environmental Monitoring and Assessment **120**:221-241.

Martin, D. L. 1999. Adoption of Center Pivot Irrigation. Irrigation Journal **49**:8-10.

Martin, G. I. 2010. Evaluating the location, extent, and condition of isolated wetlands in the Dougherty Plain, Georgia, USA [electronic resource] / by Glenn I. Martin. 2010.

Martin, G. I., J. A. Hepinstall, and L. K. Kirkman. 2013. Six decades (1948 - 2007) of landscape change in the Dougherty Plain of Southwest Georgia, USA. Southeastern Geographer **53**.

Martin, G. I., L. K. Kirkman, and J. Hepinstall-Cymerman. 2012. Mapping geographically isolated wetlands in the Dougherty Plain, Georgia, USA. Wetlands **32**:149-160.

Martin, K. L. and L. K. Kirkman. 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the south-eastern USA. Journal of Applied Ecology **46**:906-914.

McCauley, L. A. and D. G. Jenkins. 2005. GIS-based estimates of former and current depressional wetlands in an agricultural landscape. Ecological Applications **15**:1199-1208.

McKee, A. M. 2012. Correlations between community diversity and within-species genetic diversity in an amphibian assemblage: Potential processes and implications for conservation management. University of Georgia, Athens, GA.

Millenium Ecosystem Assesment [MEA]. 2000. Ecosystems and Human Well-Being: Wetlands and Water Synthesis. World Resources Institute, Washington, DC.

Rhazi, L., P. Grillas, E.-R. Saber, M. Rhazi, L. Brendonck, and A. Waterkeyn. 2012. Vegetation of Mediterranean temporary pools: a fading jewel? Hydrobiologia **689**:23-36.

Rheinhardt, R. D., M. C. Rheinhardt, and M. M. Brinson. 2002. A regional guidebook for applying the hydrogeomorphic approach to assessing wetland functions of wet pine flats on mineral soils in the Atlantic and Gulf Coastal Plains. DTIC Document.

Roe, J. H. and A. Georges. 2007. Heterogeneous wetland complexes, buffer zones, and travel corridors: Landscape management for freshwater reptiles. Biological Conservation **135**:67-76.

Rothermel, B. B. 2004. Migratory Success of Juveniles: A Potential Constraint on Connectivity for Pond-Breeding Amphibians. Ecological Applications **14**:1535-1546.

Rothermel, B. B. and R. D. Semlitsch. 2002. An Experimental Investigation of Landscape Resistance of Forest versus Old-Field Habitats to Emigrating Juvenile Amphibians. Conservation Biology **16**:1324-1332.

Semlitsch, R. D. 1998. Biological Delineation of Terrestrial Buffer Zones for Pond-Breeding Salamanders. Conservation Biology **5**:1113-1119.

Semlitsch, R. D. 2000. Size does matter: the value of small isolated wetlands. National Wetlands Newsletter **22**:5.

Semlitsch, R. D. and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology **12**:1129-1133.

Smith, M. A. and D. M. Green. 2005. Dispersal and the Metapopulation Paradigm in Amphibian Ecology and Conservation: Are All Amphibian Populations Metapopulations? Ecography:110.

Tiner, R. W. 2003. Estimated extent of geographically isolated wetlands in selected areas of the United States. Wetlands **23**:636-652.

Tiner, R. W., H. C. Berquist, G. P. DeAlessio, and M. J. Starr. 2002. Geographically Isolated Wetlands: A Preliminary Assessment of their Characteristics and Status in Selected Areas of the United States.*in* F. a. W. S. U.S. Department of the Interior, Northeast Region, Hadley, MA., editor.

Todd, B. D. 2008. Effects of forest harvesting on reptiles and amphibians of the southeastern United States [electronic resource] / by Brian D. Todd. 2008.

Turner, M. G., R. H. Gardner, and R. V. O'Neill. 2001. Landscape ecology in theory and practice: pattern and process. Springer Science+Business Media, LLC, New York City, NY.

Turner, M. G. and C. L. Rushcer. 1988. Changes in landscape patterns in Georgia, USA. Landscape Ecology **1**:241-251.

van der Valk, A. 1989. Northern prairie wetlands. Iowa State University Press.

Veysey, J. S., S. D. Mattfeldt, and K. J. Babbitt. 2011. Comparative influence of isolation, landscape, and wetland characteristics on egg-mass abundance of two pool-breeding amphibian species. Landscape Ecology **26**:661-672.

Vivas, M. B. and M. T. Brown. 2006. Areal Empower Density and Landscape Development Intensity (LDI) Indices for Wetlands of the Bayou Meto Watershed, Arkansas. Howard T. Odum Center for Wetlands, University of Florida, Gainesville, FL.

Walker, J. L. 1993. Rare Vascular Plant Taxa Associated with the Longleaf Pine Ecosystem.*in* Tall Timbers Fire Ecology Conference.

Whigham, D. F. 1999. Ecological issues related to wetland preservation, restoration, creation and assessment. Science of the Total Environment **240**:31-40.

Wiggins, G. B., R. J. Mackay, and I. M. Smith. 1980. Evolutionary and ecological strategies of animals in annual temporary pools. Archiv für Hydrobiologie supplement **58**:206.

Zedler, J. B. and S. Kercher. 2005. Wetland Resources: Status, Trends, Ecosystem Services, and Restorability. Annual Reviews, Palo Alto, CA.

Table 2.1 Land use and land cover (LULC) crosswalk table.

Composite LULC Classes[a]	NLCD 2006	Photo-interpreted (1948-2007)
Forested	Deciduous Forest, Evergreen Forest, Mixed Forest, Woody Wetlands	Natural Forest[b]
		Planted Pine
Scrub/Shrub	Scrub/Shrub	--
Herbaceous	Grassland, Pasture/Hay, Emergent Herbaceous Wetlands	Herbaceous
Cultivated	Cultivated Crops	Irrigated Row-Crop
		Dryland Row-Crop
		Pecan Orchard
Bare	Barren Land	Bare
Developed	All Developed classes (Open Space, Low Intensity, Medium Intensity, High Intensity)	Developed, Roads
Open Water	Open Water	Open Water

[a] Composite LULC classes represent the broader categories into which both the NLCD 2006 data and the photo-interpreted LULC data were grouped to make the datasets comparable to one another.
[b] LULC sub-classes, shown here in separate rows, were analyzed separately and as part of the composite classes.

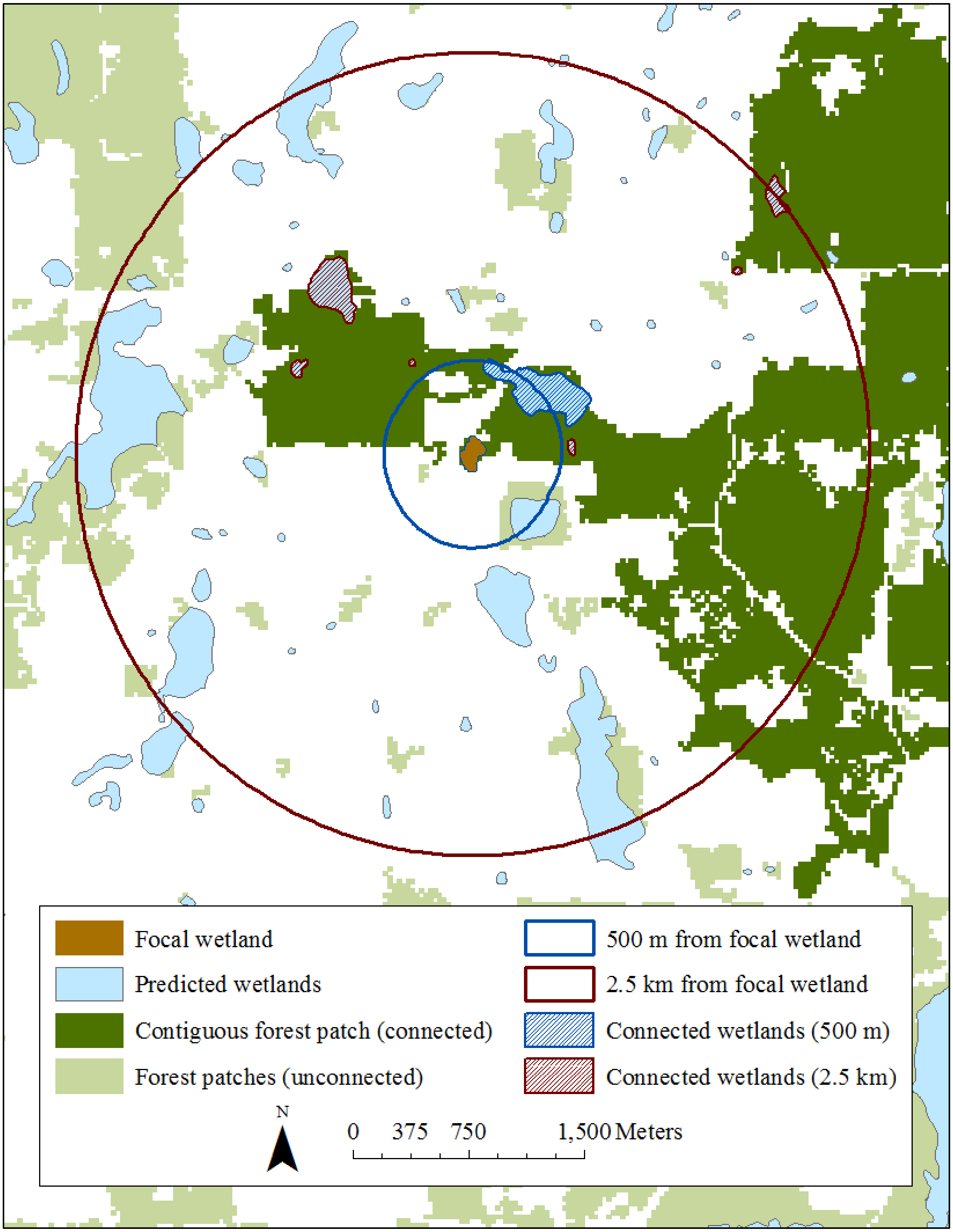


Figure 2.1 Map depicting an example of the schematic connectivity analysis at two scales (500 m and 2.5 km) for a focal wetland.

Table 2.2 Area (ha) and percent of wetland area sampled (%) covered by LULC classes within isolated wetlands within historic subsamples and throughout the Dougherty Plain.

	1948[a]		1968		1993		2007		NLCD 2006[b] (subset only)		NLCD 2006 (Dough. Plain)	
LULC Class	ha	%	ha	%	ha	%	ha	%	ha	%	ha	%
Forested	1641	53.4	1780	57.9	1578	51.4	1568	51.0	1715	55.8	23601	55.6
Natural Forest[c]	1630	53.0	1698	55.2	1344	43.7	1286	41.9	--	--	--	--
Planted Pine	11	0.3	82	2.7	234	7.6	282	9.2	--	--	--	--
Herbaceous	472	15.4	856	27.9	751	24.4	911	29.6	705	22.9	8938	21.1
Shrub/Scrub	--	--	--	--	--	--	--	--	58	1.9	854	2.0
Cultivated	225	7.3	306	10.0	430	14.0	466	15.2	409	13.3	6129	14.4
Irrigated Row-Crops	--	--	--	--	164	5.3	307	10.0	--	--	--	--
Dryland Row-Crops	180	5.9	253	8.2	200	6.5	72	2.3	--	--	--	--
Pecan Orchard	45	1.5	53	1.7	66	2.2	88	2.9	--	--	--	--
Barren Land	6	0.2	5	0.2	2	0.1	6	0.2	13	0.4	278	0.7
Developed	26	0.8	28	0.9	37	1.2	42	1.4	89	2.9	1628	3.8
Open Water	703	22.9	97	3.2	275	8.9	80	2.6	85	2.8	1002	2.4

[a] Photo-interpreted data was used for years 1948, 1968, 1993, and 2007 and represented a subset of wetlands (3,073 ha total) within the Dougherty Plain.
[b] LULC area derived from NLCD 2006 data was calculated for the subset of wetlands and for the total area (42, 429 ha) of all predicted isolated wetlands within the Dougherty Plain.
[c] Indented LULC sub-classes were analyzed individually but were also combined to calculate totals for composite LULC groups.

Table 2.3 Total number and percent of wetlands dominated by LULC classes within historic subsamples and throughout the Dougherty Plain.

	1948[a]		1968		1993		2007		NLCD2006[b] (subset only)		NLCD2006 (Dough. Plain)	
LULC Class	Count	%	Count	%	Count	%	Count	%	Count	%	Count	%
Forested	467	47.3	525	53.2	466	47.2	478	48.4	520	52.7	5907	51.3
Natural Forest[c]	467	47.3	498	50.5	367	37.2	349	35.4	--	--	--	--
Planted Pine†	0	0.0	24	2.4	90	9.1	117	11.9	--	--	--	--
Herbaceous†	165	16.7	261	26.4	248	25.1	211	21.4	217	22.0	2068	17.9
Shrub/Scrub	--	--	--	--	--	--	--	--	14	1.4	178	1.5
Cultivated†	97	9.8	170	17.2	172	17.4	225	22.8	145	14.7	1982	17.2
Irrigated Row-Crop†	N/A	0.0	N/A	0.0	58	5.9	118	12.0	--	--	--	--
Dryland Row-Crop†	77	7.8	129	13.1	76	7.7	49	5.0	--	--	--	--
Pecan Orchard†	20	2.0	40	4.1	35	3.5	51	5.2	--	--	--	--
Bare†	0	0.0	0	0.0	3	0.3	1	0.1	6	0.6	60	0.5
Developed†	3	0.3	1	0.1	10	1.0	16	1.6	24	2.4	482	4.2
Open Water	215	21.8	7	0.7	57	5.8	17	1.7	11	1.1	74	0.6
Anthropogenic	273	27.7	451	45.7	523	53.0	590	59.8	393	39.8	4873	42.3

[a]Photo-interpreted data was used for years 1948, 1968, 1993, and 2007 and represented a subsample of 987 wetlands within the Dougherty Plain.
[b] Total number of wetlands dominated by each NLCD 2006 class was calculated for the subset of wetlands, and for all predicted isolated wetlands within the Dougherty Plain (n = 11,521).
[c] Indented LULC sub-classes were analyzed individually but were also combined to calculate totals for composite LULC groups.
† = land use classes included, in whole or in part, in cumulative estimate of wetlands dominated by Anthropogenic land use.

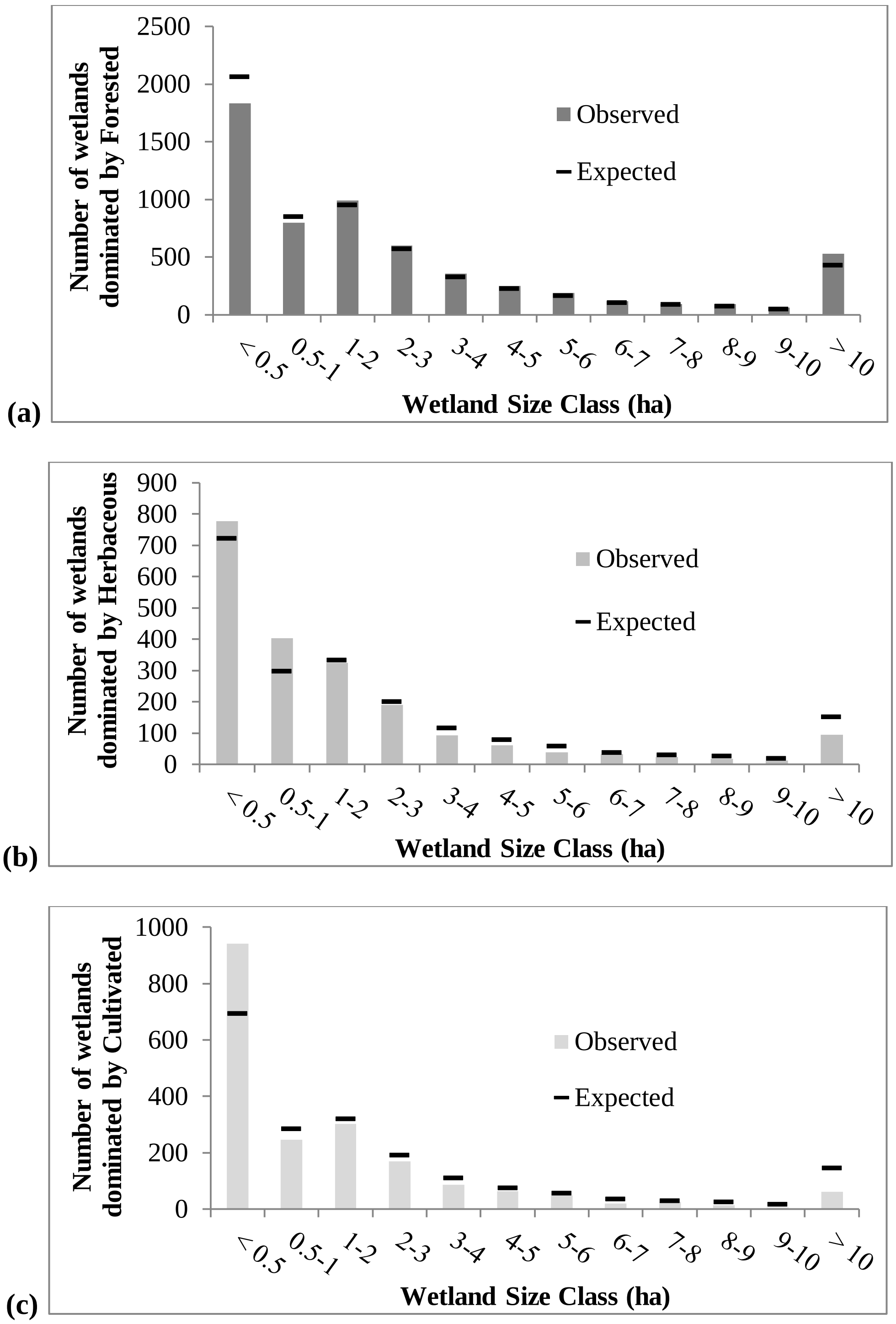
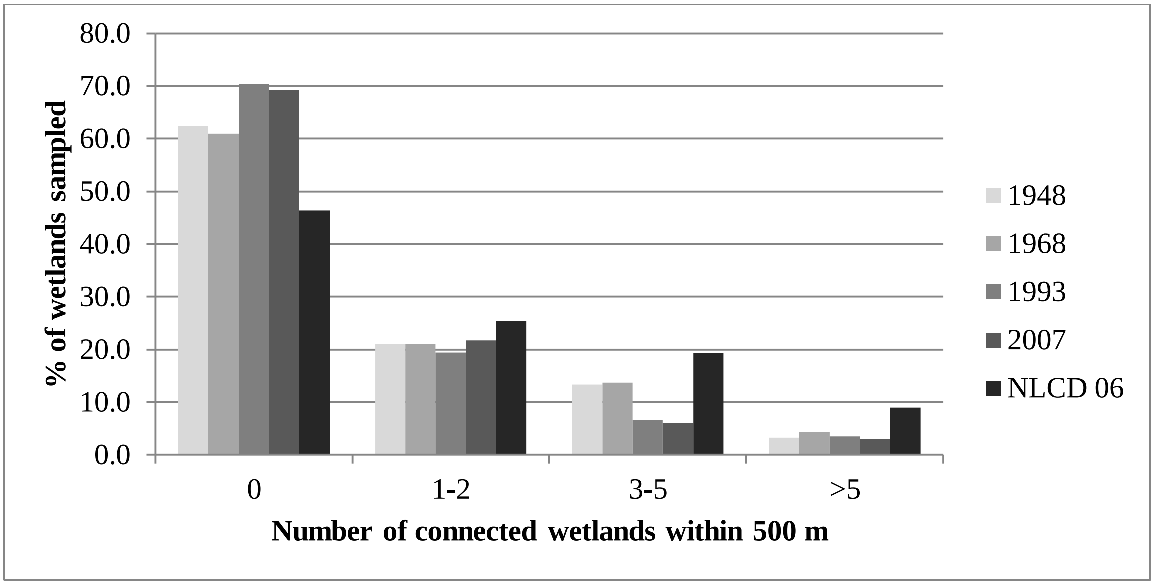
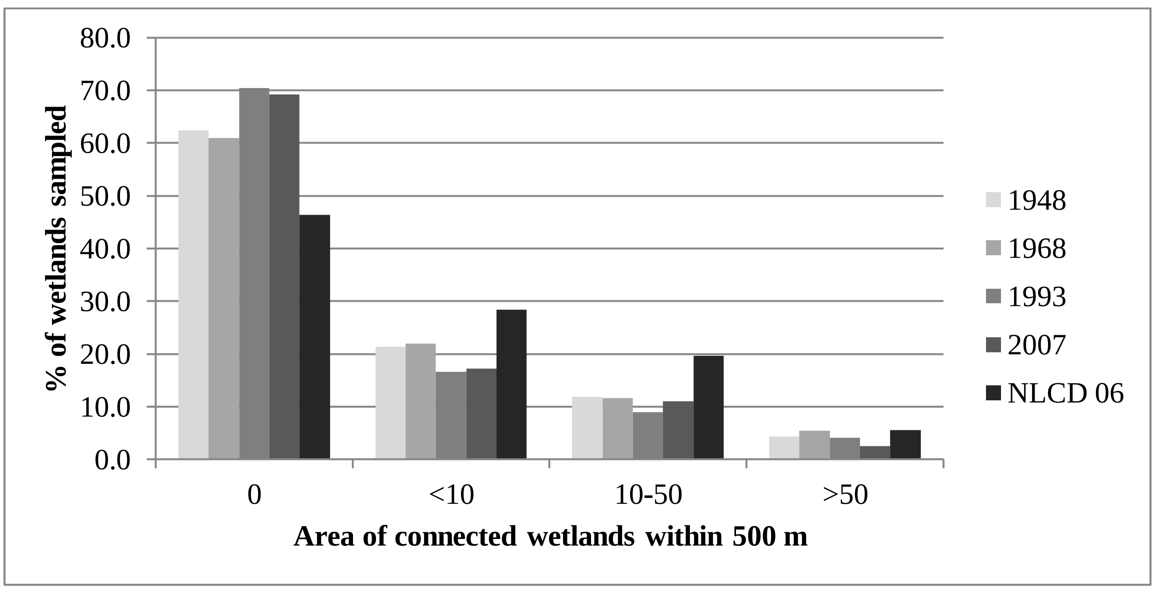


Figure 2.2 Bar graphs depicting the frequency table values for expected and observed number of wetlands dominated by the composite LULC groups: a) Forested, b) Herbaceous, and c) Cultivated. Frequencies were calculated using NLCD 2006 data for all modeled isolated wetlands within the Dougherty Plain.



(a)



(b)

Figure 2.3 Histograms comparing the proportion of connected isolated wetlands in the Dougherty Plain through time. Wetlands are assigned to bins based on indices of connectedness assessed within 500 meters of contiguous forest. Graph **(a)** depicts the number of other wetlands to which each wetland is connected, and **(b)** the total area of other wetlands to which each wetland is connected.

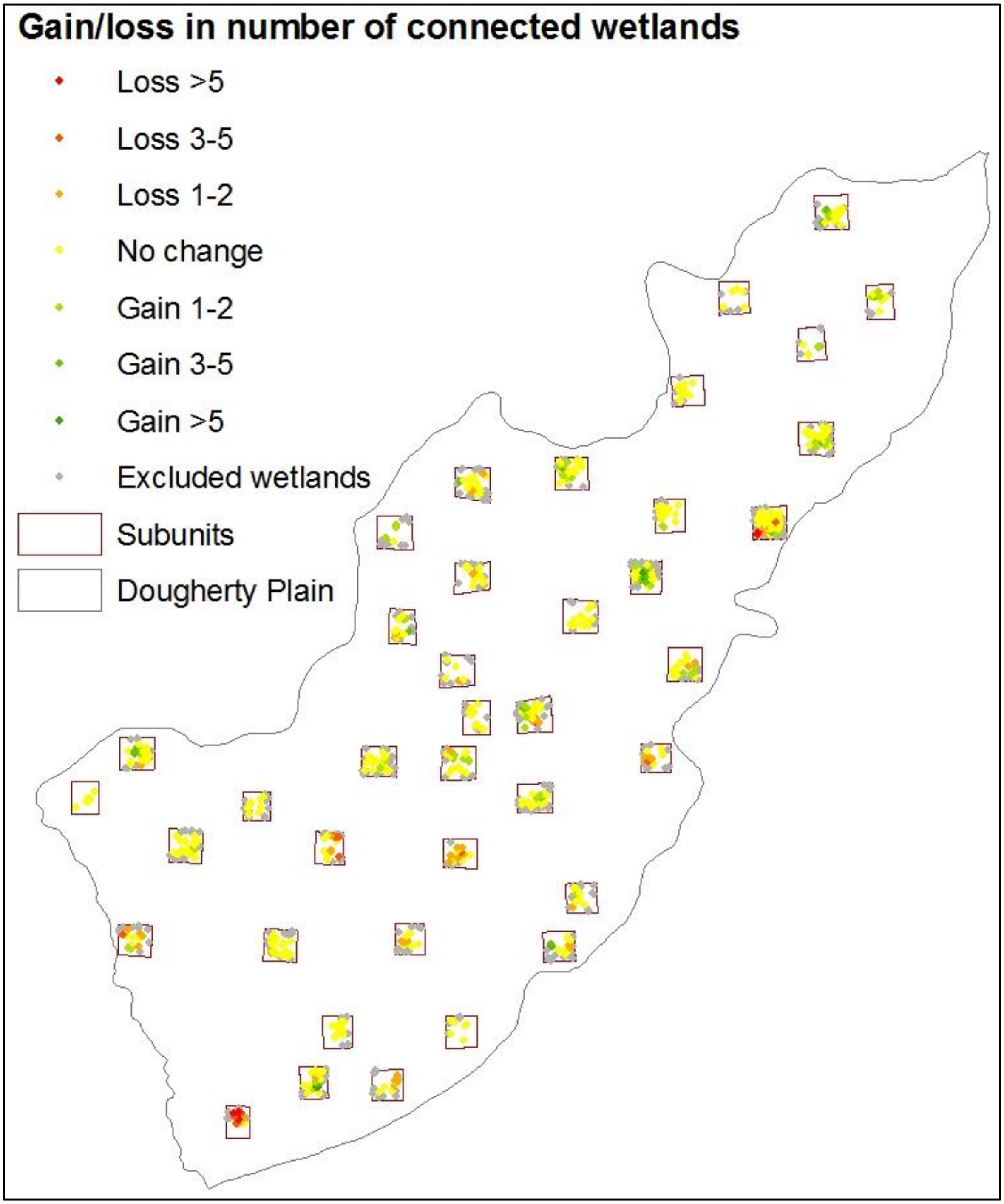


Figure 2.4 Change in isolated wetland connectedness via contiguous forest (500 m scale) within a subset of the Dougherty Plain, 1948-1968.

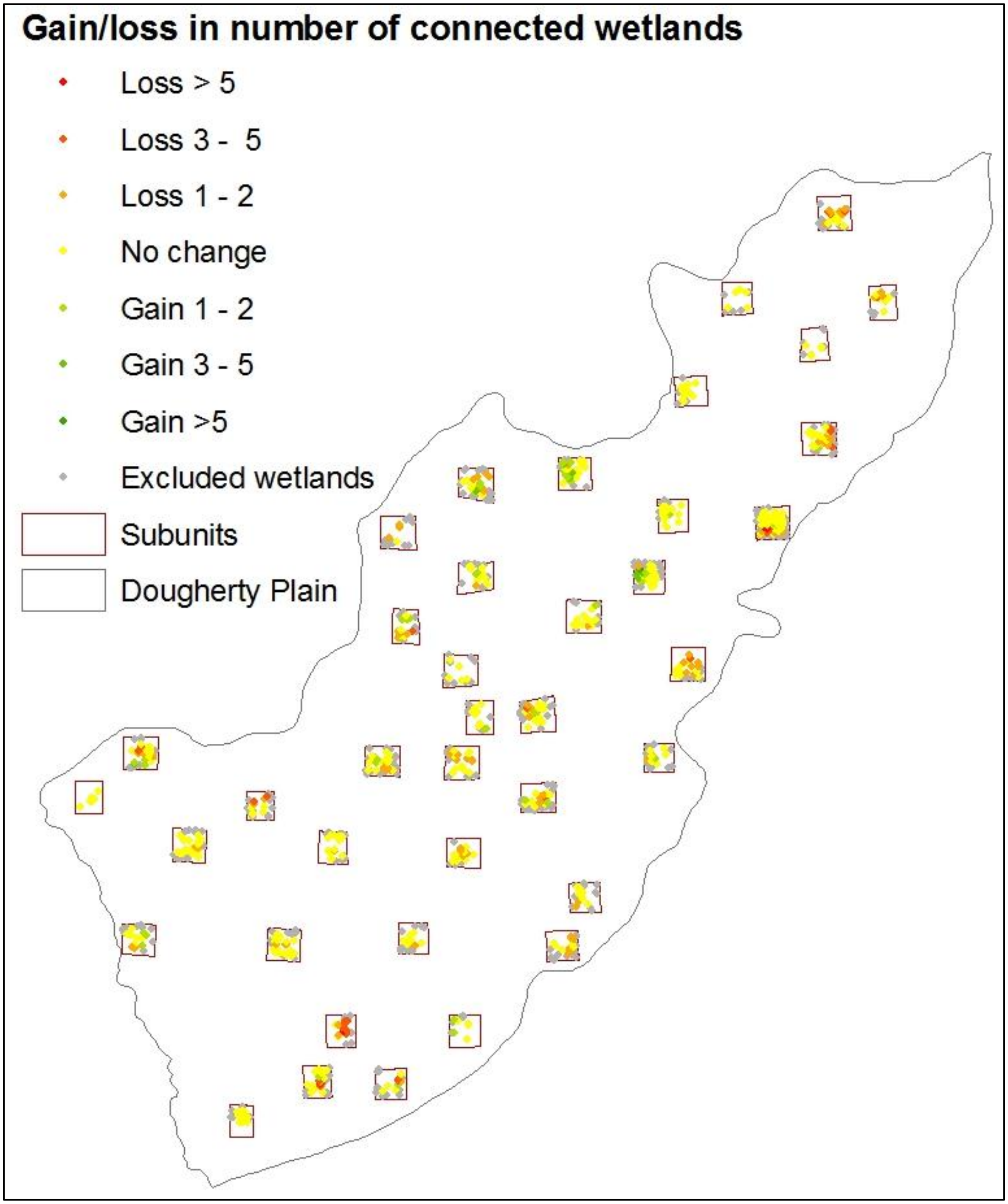


Figure 2.5 Change in isolated wetland connectedness via contiguous forest (500 m scale) within a subset of the Dougherty Plain, 1968-1993.

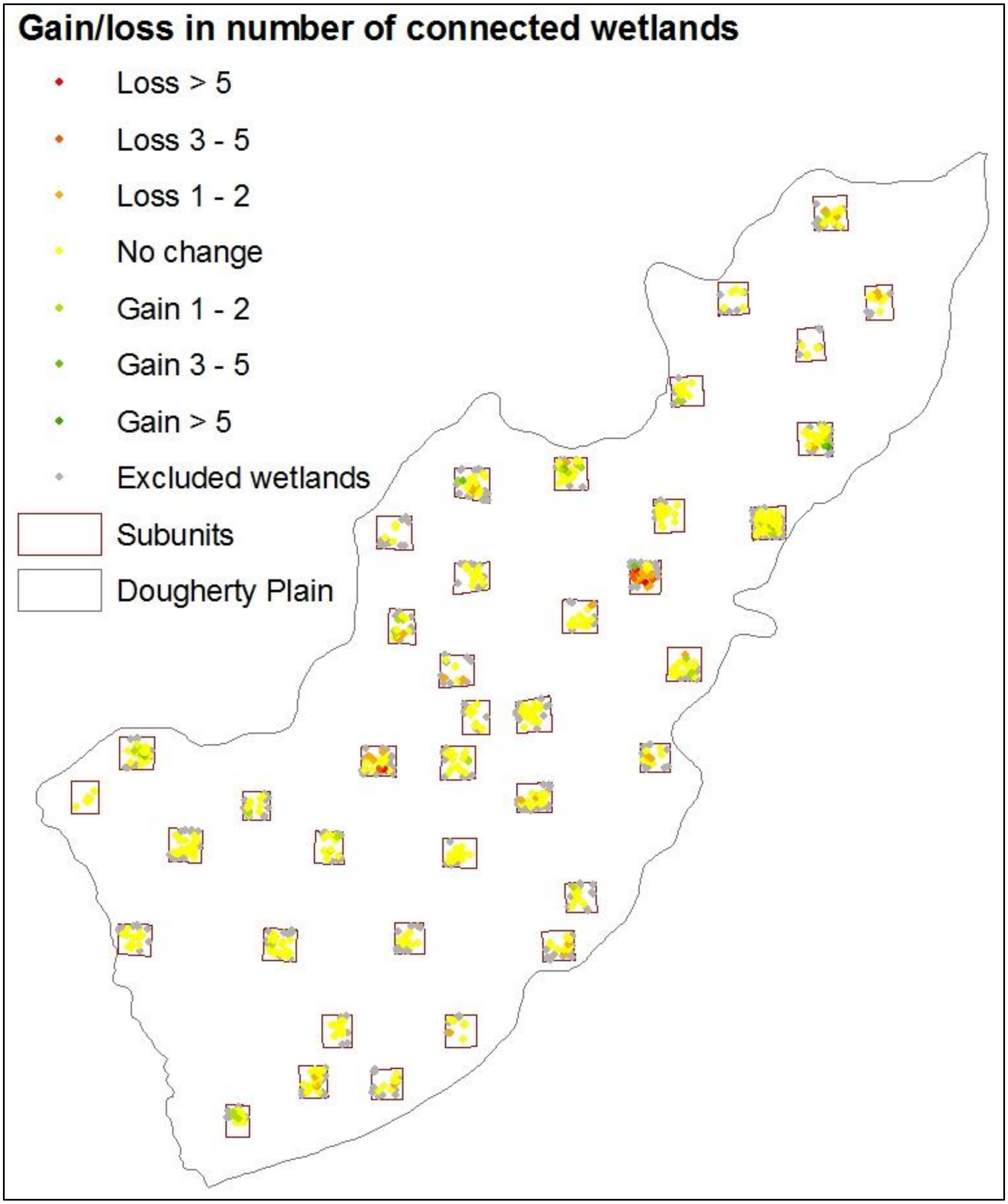


Figure 2.6 Change in isolated wetland connectedness via contiguous forest (500 m scale) within a subset of the Dougherty Plain, 1993-2007.

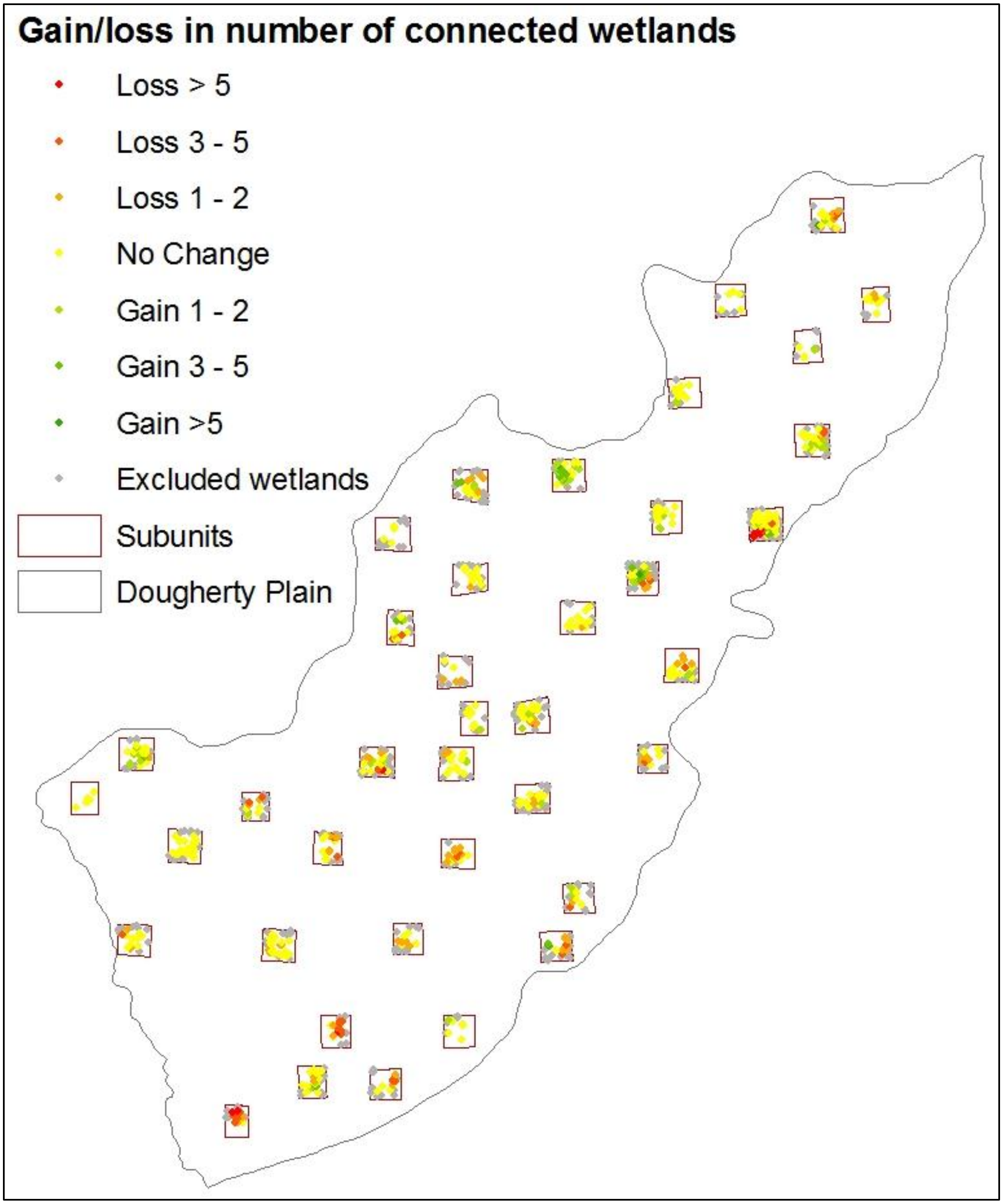
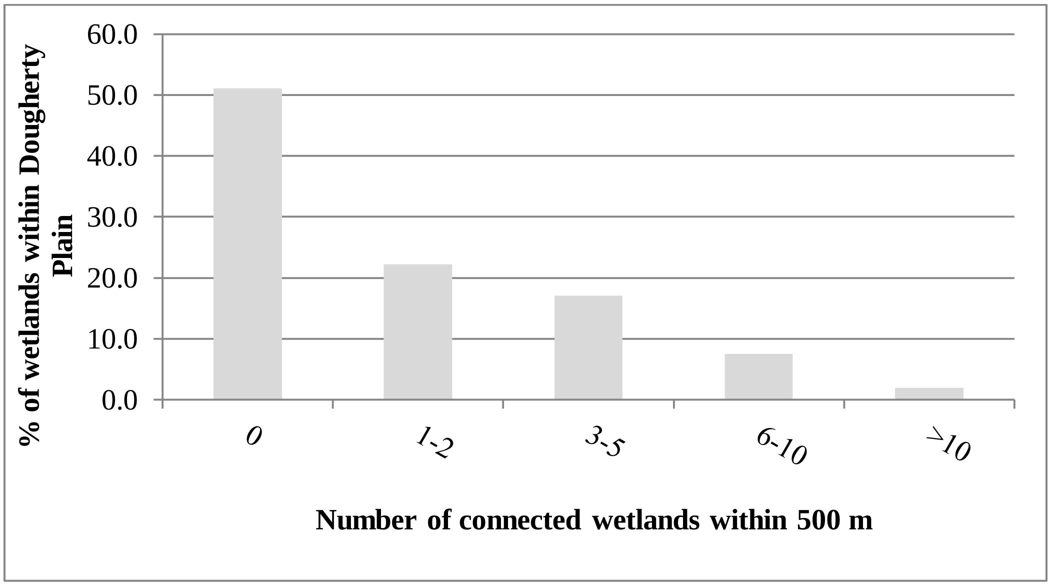
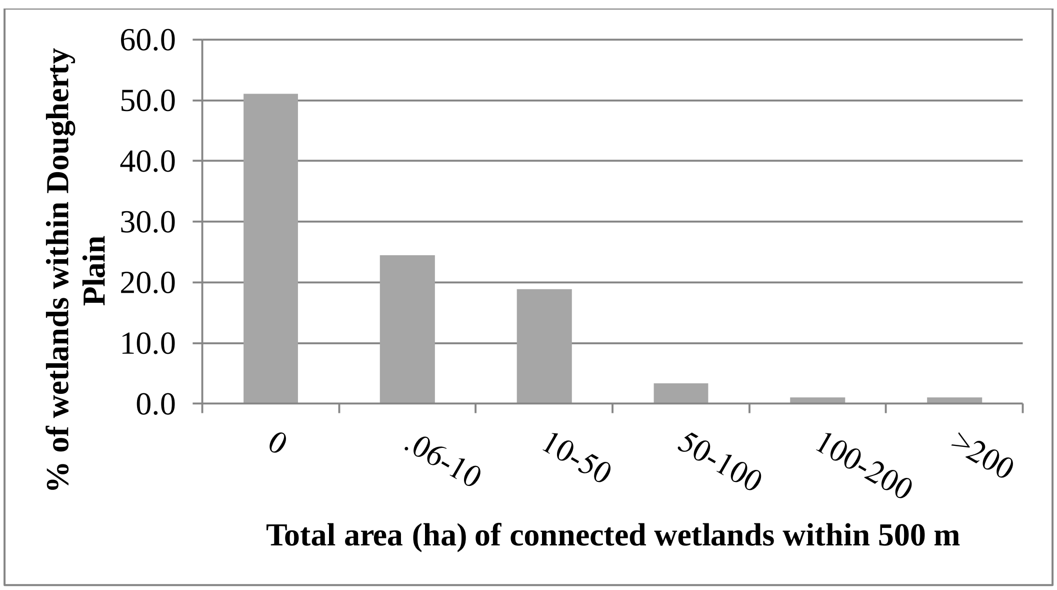


Figure 2.7 Change in isolated wetland connectedness via contiguous forest (500 m scale) within a subset of the Dougherty Plain, 1948-2007.

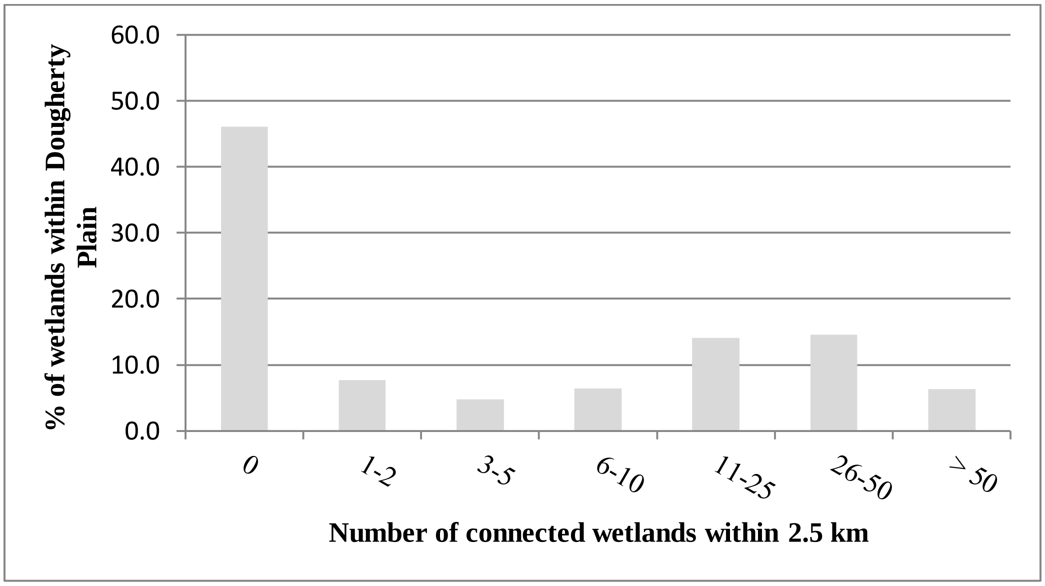


(a)

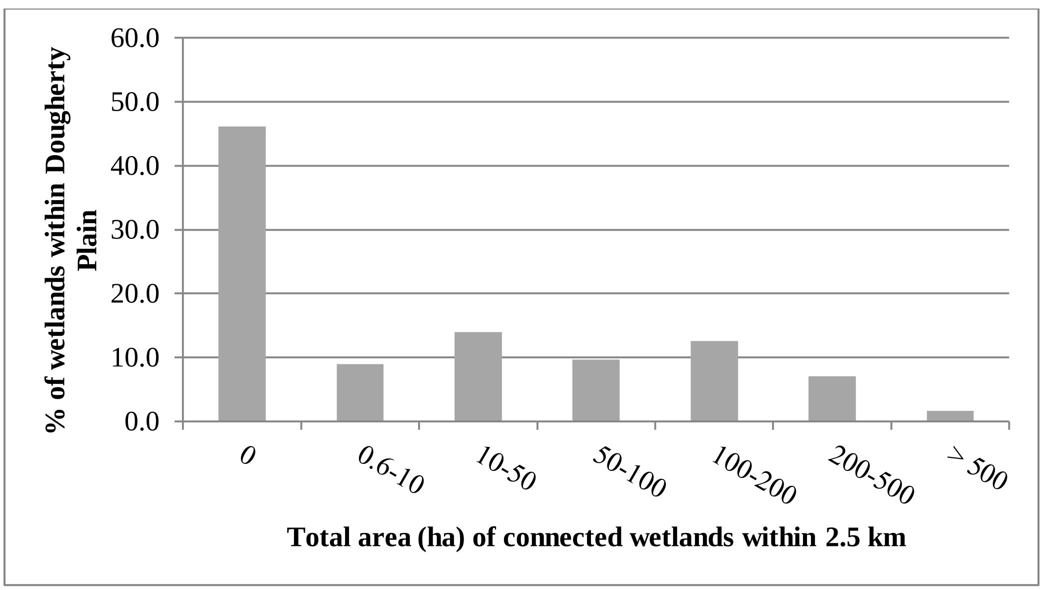


(b)

Figure 2.8 Histograms depicting the proportion of isolated wetlands in the Dougherty Plain assigned to bins based on indices of connectedness assessed within 500 meters through contiguous forest. Graph **(a)** depicts the number of other wetlands to which each wetland is connected, and **(b)** the total area of other wetlands to which each wetland is connected.



(a)



(b)

Figure 2.9 Histograms depicting the proportion of isolated wetlands in the Dougherty Plain assigned to bins based on indices of connectedness assessed within 2.5 km through contiguous forest. Graph **(a)** depicts the number of other wetlands to which each wetland is connected, and **(b)** the total area of other wetlands to which each wetland is connected.

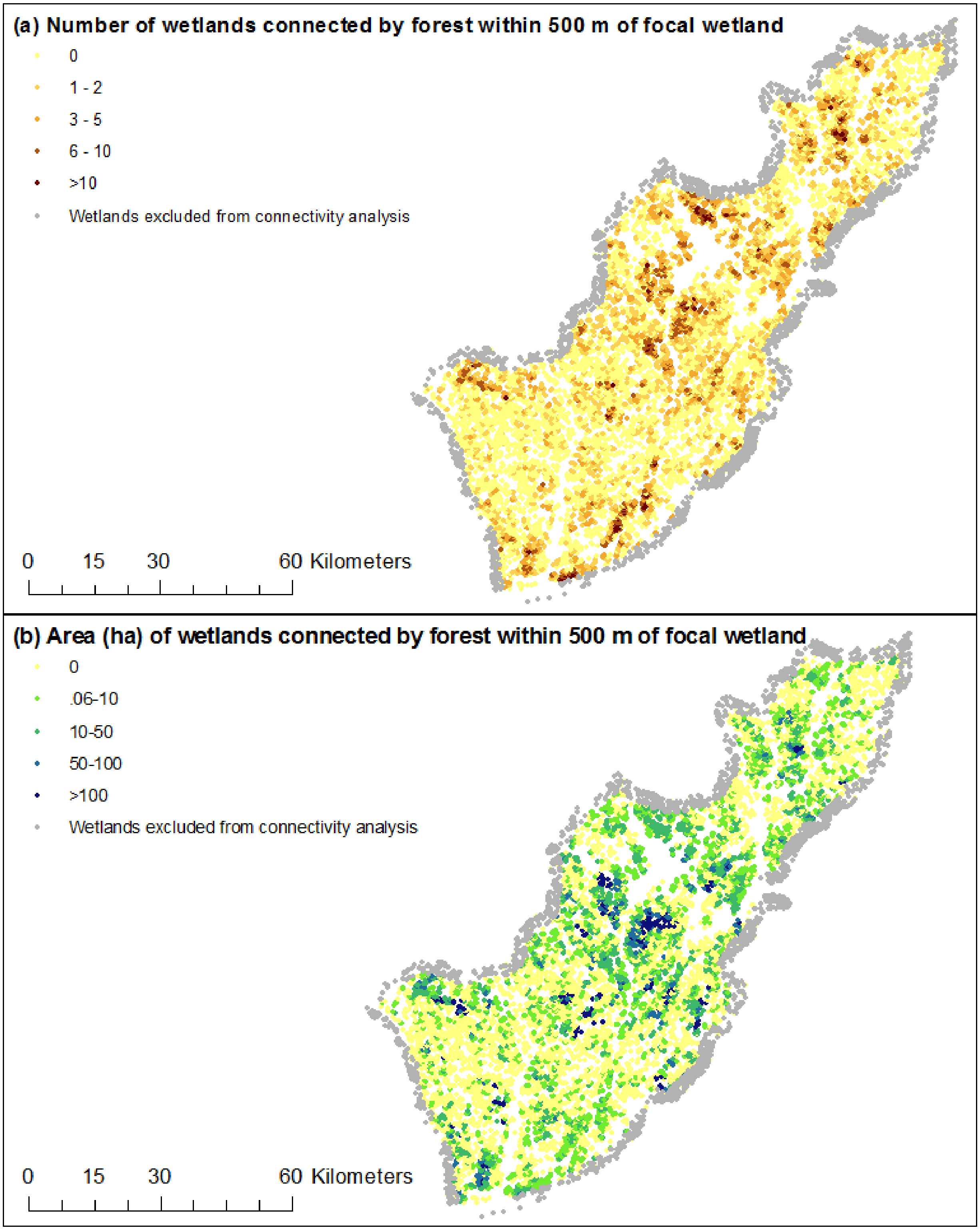


Figure 2.10 Spatial distribution of the indices of connectedness assessed within 500m for individual wetlands within the Dougherty Plain: **(a)** number of connected wetlands and **(b)** total area (ha) of connected wetlands.

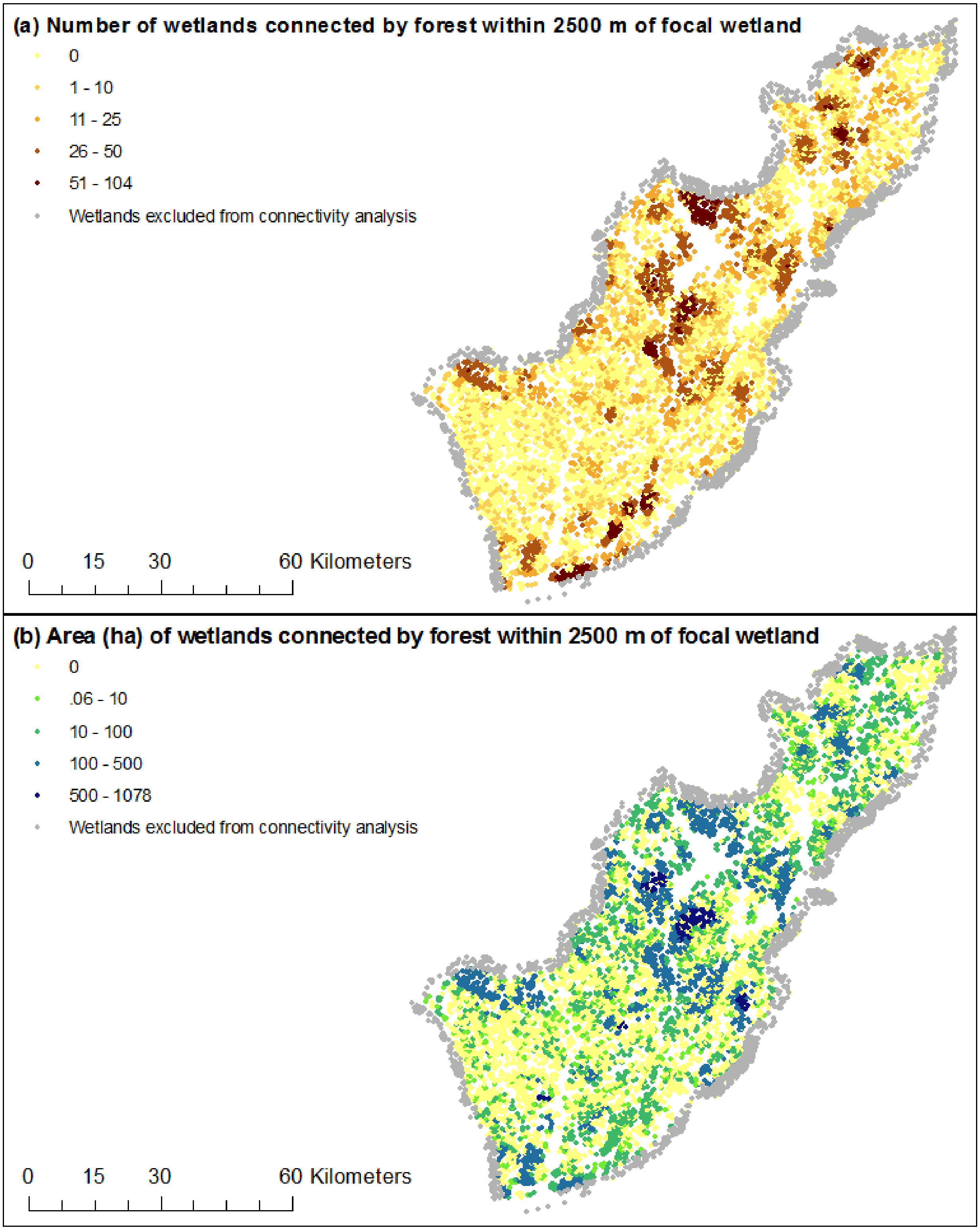


Figure 2.11 Spatial distribution of the indices of connectedness assessed within 2.5 km for individual wetlands within the Dougherty Plain: **(a)** number of connected wetlands and **(b)** total area (ha) of connected wetlands.

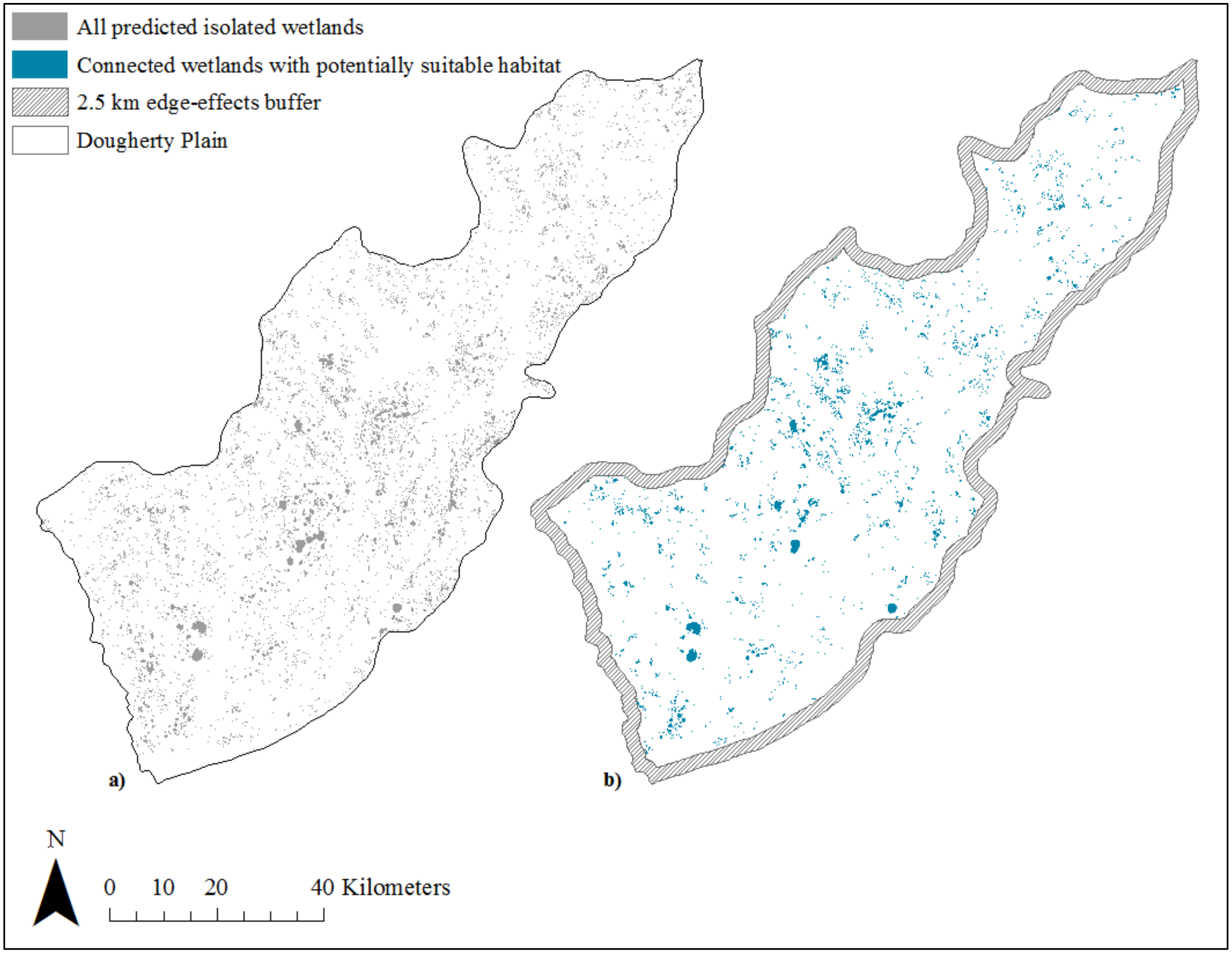


Figure 2.12 Maps of the Dougherty Plain depicting a) all isolated wetlands predicted by the Combined Model (n = 11,521; Martin, 2011), and b) isolated wetlands connected via forest (within 500 m) with potentially suitable habitat (n = 3,962). To avoid edge effects, wetlands falling within shaded buffer were not included.

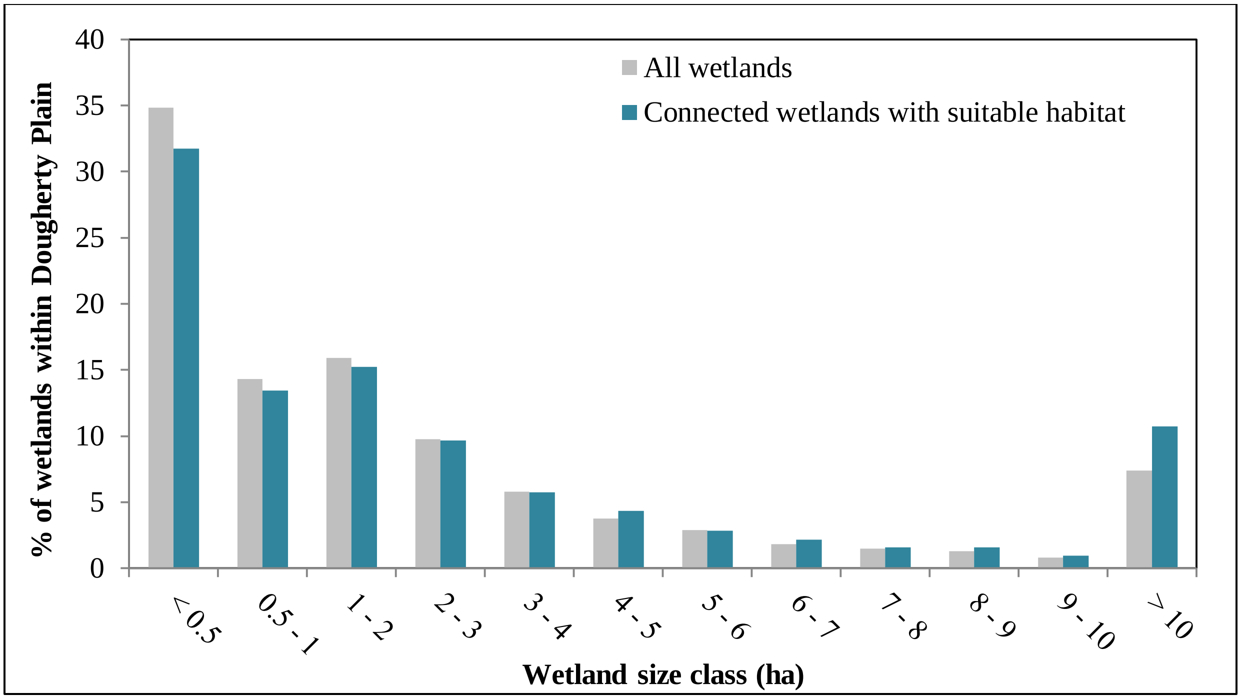


Figure 2.13 A comparison of size class distribution between all isolated wetlands in the Dougherty Plain and the model of connected wetlands with potentially suitable habitat for isolated wetland-dependent species.

CHAPTER 3

RELATING REMOTELY SENSED LAND USE IN THE DOUGHERTY PLAIN TO THE MACROPHYTE COMMUNITIES AND WATER CHEMISTRY OF GEOGRAPHICALLY ISOLATED WETLANDS

Stuber, O.S., Martin, G.I., Kirkman, L.K., and Hepinstall-Cymerman, J. To be submitted to *Wetlands.*

Introduction

Wetland condition is the ultimate result of the "integration of the chemical, physical, and biological processes that maintain the system over time" (Fennessy et al. 2004). Anthropogenic use of the landscape can disrupt these processes, often in predictable ways, leading to declines in wetland condition. Currently, there is considerable interest in using remotely-sensed data to assess wetland condition based on characteristics of the surrounding landscape. Such data is typically available across large spatial extents, and can be interpreted and analyzed using a Geographic Information System (GIS) from a desktop computer and thus provide an efficient way to gauge wetland condition throughout an entire region using standardized criteria. For example, Tiner (2004) developed remotely assessed indices of wetland buffer integrity, wetland extent, and wetland disturbance based upon the proportion of natural and disturbed wetland area that were then combined with other similarly designed indices to evaluate the integrity of the Nanticoke River watershed in Delaware. Similarly, Lane et al. (2012) used remotely sensed land use and land cover (LULC) data in conjunction with the Landscape Development Intensity Index (LDI; Brown and Vivas 2005) to predict the condition of geographically isolated wetlands across eight states in the southeastern United States.

Often, remote assessment of wetland condition is conducted as part of a three-tiered wetland assessment scheme. Remote assessments are referred to as Level 1. Level 2 assessments incorporates rapid, on-site evaluations of wetland condition, and Level 3 assessments involve intensive sampling of biotic and environmental variables related to wetland condition (U.S. Environmental Protection Agency, U.S. EPA 2002). Most, if not all, Level 1 wetland condition assessments incorporate land use and land cover (LULC) data to determine the degree of human disturbance, or stress, impacting each wetland (e.g. Lopez and Fennessy 2002, U.S. EPA 2002, Brown and Vivas 2005, Phillips et al. 2005, Hychka et al. 2007)). LULC-based evaluations of disturbance or stress are then related to indices of biological integrity (IBI's) or other important environmental and biological indicators of wetland condition identified through intensive sampling (U.S. EPA 2002, Stein et al. 2009). The utility of Level 1 assessments is determined by the strength of relationships between landscape indicators of condition and local, biological and environmental indicators of condition. For example, the LDI index is a Level 1 assessment method that predicts the ecological integrity of individual wetlands based upon estimates of the intensity of human development in the surrounding landscape (Brown and Vivas 2005). Previous studies have demonstrated strong correlations between LDI-based estimates of wetland condition and independent, more intensive assessments of condition (Brown and Vivas 2005, Mack 2006, Reiss and Brown 2007, Stein et al. 2009).

Some indices, such as the LDI, are cumulative, and generate predictions of wetland condition based upon the combined influence of LULC and other landscape variables being considered (e.g. slope, density of roads, presence of dams). However, the intensity of development and types of disturbance can vary widely between specific land use classes and may influence wetland condition through different processes. Understanding the relationships between specific classes of land use and relevant biological and environmental variables that are often used to determine wetland condition may help identify the most important mechanisms by which land use influences wetland condition and reveal the most useful landscape variables to predict wetland condition.

Class resolution of LULC data (i.e., the number and differentiation of land use and land cover types) is another important consideration when determining influence of LULC on individual wetlands. Often, the best available LULC data for a region may be relatively coarse.

Some regional-scale assessment methods, such as the LDI index, are structured for a relatively fine resolution of LULC categories, but are flexible and can be merged and adapted for coarser data sets, such as the United States' National Land Cover Data released for 2006 (NLCD 2006; Lane et al. 2012). However, coarse categorical resolution could potentially obscure important relationships between the disparate impacts of land use on wetland condition when several distinct types of land use are combined.

Wetland condition influences a wetland's ability to perform important ecological functions and ultimately maintain ecological integrity within the larger landscape (Fennessy et al. 2004). Research has shown that isolated wetlands provide numerous important functions, including nutrient storage (Whigham and Jordan 2003), flood attenuation, and provision of habitat supporting high levels of biodiversity (Semlitsch et al. 1996, Whigham 1999, Kirkman et al. 2000, Tiner et al. 2002, Leibowitz 2003). Despite the fact that these functions are similar to those of wetlands protected under the Clean Water Act (CWA; Meltz and Copeland 2007), these wetlands lack federal protection due to the absence of an obvious surficial hydrologic connection to jurisdictional waters (i.e. an ecological nexus (*Rapanos v United States* 2006); also see Chapter 1). Additionally, isolated wetlands are particularly vulnerable to anthropogenic alteration; they are often relatively small and shallow, and therefore easily dredged, drained, filled, or otherwise modified (Biebighauser 2007 also see Chapter 2). Thus, accurately predicting and monitoring the condition of geographically isolated wetlands is particularly important for their conservation.

Overall, the objective of this study was to examine the relationships between land use and isolated wetland condition. To do this, I compared plant community composition and water quality among isolated wetlands influenced by different classes of land use. I focused on five specific land use classes: Forest, Planted Pine, Pecan Orchard, Dryland (i.e. unirrigated) Row-crop, and Irrigated Row-crop. Reference wetlands were also included to provide a baseline for comparison. Specifically, the objectives for this study were:

1) Characterize biotic and environmental variables and factors associated with each land use class and with reference sites.
2) Identify species indicative of disturbance and reference conditions.
3) Determine the level of land use class resolution that best predicts wetland condition.

Methods

Study Area

The study was conducted in the Dougherty Plain, a physiogeographic subregion of the Coastal Plain characterized by karst topography (Beck and Arden 1983), which covers approximately 6,690 km^2 in southwestern Georgia (Figure 1.1). Geographically isolated limesink wetlands are a prominent feature of the karst landscape; the average nearest neighbor distance between wetlands is less than 200 meters. (Hendricks and Goodwin 1952, Kirkman et al. 1996, Kirkman et al. 1999, Tiner 2003, Martin et al. 2012). Historically, the Dougherty Plain was dominated by fire-maintained longleaf pine-wiregrass (*Pinus palustris* Mill.-*Aristida beyrichiana* Trin. & Rupr.) savannas with a highly diverse understory (Walker 1993, Drew et al. 1998, Engstrom et al. 2001). Today, high-intensity agriculture, both in the form of pine plantations and row crops exerts a heavy influence on the landscape of the region (Turner and Rushcer 1988, Couch et al. 1996, Martin et al. 2013). Natural forested lands are also common (Turner and Rushcer 1988, Martin et al. 2013).

Wetland Selection and Delineation

Potential wetland sampling sites were identified across the study area using recent (2010) aerial photography from the National Agriculture Imagery Program (NAIP) and a spatial model developed by Martin et al (2012) that predicts the location and extent of isolated wetlands throughout the Dougherty Plain. I selected 32 wetlands for vegetation and water quality sampling based upon the class of dominant land use in the surrounding upland. Wetland size and permission for site access were also factors in site selection. The land surrounding the study wetlands was dominated by one of five common classes of land use: Planted Pine, Irrigated Row-crop agriculture, Dryland Row-crop agriculture, Pecan Orchards, and Forest. A land use was considered “dominant” if it composed more than 50% of a 100 meter-wide zone surrounding the isolated wetland. In most cases, the dominant land use covered at least 70% of the surrounding upland. In this chapter, I will hereafter refer to wetlands by the land use that dominates the surrounding uplands, which does not necessarily imply that it represents the land use within the wetland. Land use was determined through photo-interpretation of high-resolution 2010 NAIP photography, with a 1 m ground sample distance (pixel), and 6m horizontal accuracy.

Additionally, for this study, I included vegetation and water quality data collected from 28 wetlands in a previous study (Martin 2010), including nine wetlands in Reference condition. Non-reference wetlands were included from this prior study only if they met the same criteria of land use dominance specified above. Reference wetlands were located on the property of the Joseph W. Jones Ecological Research Center, a 12,000 ha ecological reserve dominated by fire-maintained longleaf pine stands. Isolated wetlands located on this site have a known history of frequent prescribed fire and represent some of the best examples of ecologically intact isolated wetlands in the region.

In total, 60 wetlands ranging in size from 0.05 to 6.87 ha were included in this study. The distribution of wetlands among surrounding land use types were: Planted Pine (n=13), Irrigated Row-crop (n=8), Dryland Row-crop (n=7), Pecan Orchard (n=11), Forest (n=12), and Reference (n=9).

Wetland boundaries were delineated in the field by collecting points along the upland-wetland boundary with a TDS Nomad GPS unit (Tripod Data Systems, Westminster, CO, USA) operating with a Crescent A100 Smart Antenna (Hemisphere GPS, Calgary, AB, CAN) with estimated sub-meter horizontal accuracy. To determine wetland boundaries, I used hydric soil indicators (Natural Resources Conservation Service 2010) whenever possible; often anthropogenic alteration of the site led to unreliable hydrologic and macrophyte indicators. In a few cases, hydric soil indicators were obscured due to a combination of topographic alterations and sandy soil types. In these situations, I relied on macrophyte indicators and local changes in slope to determine a boundary. Wetlands that did not fulfill any of these delineation criteria were not included among my final sample sites.

Boundary points were imported into ArcMAP 9.2 (Environmental Systems Research Institute, Redlands, CA, USA), converted to polygons, and “smoothed” to create a vector layer of all delineated wetland sites. In all cases, the field-delineated boundary did not precisely follow the boundary predicted by the Combined Model of Martin et al. (2012). Buffers were recreated to fit the field-verified wetland boundaries, and the dominant land use classes ultimately used to categorize wetlands were mapped using NAIP 2010 imagery.

Vegetation Sampling

I sampled vegetation in 32 wetlands from August-October 2011 using the same methodology of Martin (2010) for the 28 wetlands sampled in August-November 2009. Sampling points were distributed randomly throughout the wetlands. The number of points per wetland was scaled by wetland area, and ranged from 5 points in the smallest wetland (0.05 ha) to 24 points per wetland for the largest (6.87 ha). At each sampling point, all species within a 1 m^2 plot were recorded, and abundance of each species was estimated using 6 cover classes (1=<1%, 2=1-5%, 3=6-15%, 4=16-30%, 5=31-60%, 6=61-100%). I also conducted point-quarter sampling within a 10 m radius at each point to obtain an estimate of the woody vegetation community. Diameter at breast height (i.e., 1.3 m) was recorded for individuals with a diameter of at least 3 cm.

Descriptive plant community metrics were calculated for each wetland using relative coverage values for each species recorded. Coverage values were determined based on the median value of each cover class, and averaged across all plots in each wetland. Metrics included: richness, Shannon's diversity index (*H'*), percent cover of native perennials, percent cover of exotic species, ratio of annual to perennial cover, percent cover of woody species, percent cover of vine species, percent cover of herbaceous species, and percent cover of wetland species (includes facultative wet and obligate species; plants.usda.gov/wetland.html).

Water Chemistry

Water samples for all wetlands were collected from late winter through early summer, with the goal of capturing water quality during the typical natural hydroperiod for seasonally ponded isolated wetlands in the region. Water samples were collected three times between February and May 2010 in 28 wetlands (Martin 2010). In 2012, I collected water from 31 wetlands (most were not the same wetlands sampled in 2010) between February and June. Due to severe drought conditions, wetlands in the region were relatively dry. Thus, I specifically collected samples within a week after major rain events, during which rainfall exceeded 2 inches. Despite this modified sampling approach, some wetlands did not pond water during the study period, or access to the property was restricted. Each water sample was composed of three subsamples collected in 1 L acid-washed polyethylene bottles from random locations at each wetland. When standing water existed in several discrete ponded areas within a wetland, an effort was made to collect at least one subsample within each area. Samples were stored on ice during transit to the lab, where they were stored at 4° C until processed.

Prior to analyses, subsamples were poured through a 2 mm sieve to remove large debris (e.g., leaves, small twigs) from the water sample. Due to the very shallow depth of some of the ponded areas, it was often difficult to exclude such floating debris from the samples. All subsamples of the water samples were analyzed for NH_4, NO_3, PO_4, pH, ash-free dry mass (AFDM), and total dry mass (TDM). Results from each subsample were combined to obtain an average value per site for each collection date. To provide a measure of the quality of our results, blanks composed of deionized water were processed for each of the above parameters (except pH) following the protocols described below. To assure the quality of our pH measurements, we calibrated our instruments using two buffers at pH 4 and 7.

Subsamples were vacuum filtered through a fiberglass prefilter within two days of collection. Prior to filtering, filters were ashed at 500° C and weighed. The volume of water processed through each filter was recorded, and filters were dried and weighed to quantify dry mass suspended within the water column. To quantify inorganic suspended material, the filters were then ashed once more at 500° C for 1.5 – 2 hours to remove all organic dry mass and then weighed. Filtered subsamples were analyzed for NO_3, PO_4, and NH_4 using a Lachat Quickchem 8500. Unfiltered portions of each subsample were brought to room temperature and pH was measured using an Accumet Basic AB15 pH meter.

Analytical Approach

First, to examine the relationship between land use, macrophyte community composition, and water quality within isolated wetlands, I used two methods of ordination (non-metric multidimensional scaling [NMS] and principal components analysis [PCA]) to identify the driving community and environmental variables that distinguished land use groups (Clarke 1993). I used Indicator Species Analysis (ISA) to generate a list of macrophyte species strongly associated with each land use. All multivariate analyses were performed using PC-ORD version 6.0 (McCune and Mefford 2011). I used NMS to graphically represent differences between species' relative abundances within each wetland. NMS ordination is generally well-suited for heterogeneous, non-normal community data and does not assume linear relationships among variables (McCune et al. 2002). PCA ordination, which assumes a linear relationship between variables, was used to graphically represent differences between wetlands based on water quality (McCune et al. 2002). Wetlands that did not pond water during the course of the study were deleted from water quality analyses. Differences in mean values of variables that were strongly correlated with ordination axes were tested among land use classes using analysis of variance (ANOVA). Where a significant difference was detected, I performed Tukey's Multiple Pairwise Comparison tests with Bonferroni correction to compare means.

NMS and PCA ordination results were interpreted in conjunction with multi-response permutation procedures (MRPP) to determine whether wetlands grouped by land use differed significantly based upon cumulative measures of macrophyte community and water quality.

Finally, MRPPs were again used to test alternate land use classification scenarios, and identify which scenario best predicted significant differences in wetland condition.

Biological and Environmental Variables and Wetland Condition

Prior to conducting NMS ordinations, species abundances were log-transformed to improve normality. Additionally, I removed species which occurred in less than 5% of the sites to decrease statistical “noise” caused by infrequent or rare species (McCune et al. 2002). To reduce the influence of absolute vegetative cover (i.e. sparse or empty plots common in closed-canopy wetlands, full plots in open canopy wetlands), and allow comparison of the relative contribution of species to their communities across both canopy types, I relativized species cover by total vegetative cover within each wetland. I also conducted NMS ordination procedures separately for open-canopy wetlands (≤ 50% canopy cover) and for closed-canopy wetlands (≥ 50% canopy cover). I used Sorenson distance measures and random starting configurations for all NMS ordinations. For each ordination, between 100–500 runs with real data were conducted with at least100 iterations each to obtain a solution with low stress and high stability. Monte Carlo tests were performed 50–100 times with random data for each ordination to determine whether the ordination procedure produced a solution that was more stable and had lower stress than would be achieved with random data. Ordination solutions were assessed using NMS scree plots, which plot solution stress against dimensionality. For all analyses, I selected the lowest dimensionality with an acceptable level of stress, where further stress reduction through additional dimensions was relatively minor. All solutions selected had high stability (instability < 0.0005; McCune et al. 2002).

I conducted PCA ordinations for each year (2010 and 2012) using normalized water quality variables to construct cross-product matrices based upon Pearson’s correlation coefficients. All axes that satisfied the broken stick criteria were interpreted (Jackson 1993). In both years, extreme outlier values from a single cattle pasture wetland strongly skewed the results, so these data were removed from subsequent PCA analyses.

To examine whether wetland condition significantly differed among land use groups, MRPP analyses were performed in conjunction with each of the ordinations. MRPP is a non-parametric procedure that tests a null hypothesis of no difference between groups, and produces a measure of the chance-corrected within-group agreement (*A*). An *A* of 1 indicates all objects within a group are identical, and an *A* of 0 indicates that heterogeneity within groups equals that expected by chance. In community ecology, an *A* statistic of 0.3 shows relatively high similarity among members within groups, whereas an *A* of 0.1 is more indicative of chance, but may still result in significantly different groups (McCune et al. 2002). Parameters for each MRPP corresponded with the parameters of the associated ordination. I used Sorenson distance measures and rank-transformed data when conducting MRPPs to best represent the NMS graphical results, whereas Euclidean distance measures and non-rank-transformed data were used to produce MRPPs results comparable to PCA ordinations.

To clarify how each land use type is influencing the macrophyte communities and water quality within isolated wetlands, the community metrics, individual species, and water quality variables most strongly correlated to the ordination solutions were identified. For NMS ordinations, community metrics and individual species which had an $r^2 > 0.2$ were included in further analyses. For PCA ordinations, only those variables which were most strongly correlated with one of the interpretable axes were included in further comparisons.

To demonstrate how, and to what degree, land use influences these selected variables, I conducted ANOVA comparisons of environmental variables between LULC groups. To reduce the number of ANOVA comparisons, I first eliminated redundant variables. Variables that were strongly correlated with one another (Pearson's rho > |0.70|) were identified, and the variable with the weaker relationship to an ordination axis was eliminated from ANOVA comparisons. Additionally, individual species related to the NMS axes where $r^2 < 0.4$ were also eliminated. All variables which did not meet initial assumptions of normality were transformed. Because the goal of these analyses is descriptive, I interpreted results of the Tukey comparisons for both an α of 0.05 and for the Bonferroni corrected α values, though only comparisons which satisfied the Bonferroni correction were considered significant.

Indicator Species Analysis was performed on the 60 wetlands to identify species strongly associated with each land use and with reference conditions (Dufrene and Legendre 1997). To determine whether land use class is associated with different suites of species in open- and closed-canopy wetlands, ISA was conducted separately on open-canopy and closed-canopy wetlands as well. The ISA evaluates the fidelity of each species to pre-determined groups (in this case, land use), and assigns each species an indicator value (IV) ranging from 0 to 100. A species with an IV of 0 gives no indication of association with that group, whereas an IV of 100 means the species is always found only within that group. Species' IVs are tested for significance using a Monte Carlo randomization technique.

Land Use Classification Comparisons

To determine optimal land use classification for predicting wetland condition, I examined four alternate scenarios of land use classification (Table 3.1). To test for differences between land use groups in each scenario, I used MRPP to assess whether land use groups were statistically dissimilar. To clarify whether certain distinctions in land use class actually correspond to distinctions in wetland condition, within-group agreement (*A*) was compared among scenarios, as was the proportion of significantly different pairwise comparisons.

I evaluated the relative ability of each alternate grouping scenario to characterize wetlands based on either macrophyte community or water quality by comparing three specific results from each analysis. First, I determined whether each scenario actually produced significantly different groups by comparing the *p*-values from each MRPP. Next, the similarity of wetland condition within each group was compared using the *A* statistic generated by the MRPP. Finally, to identify which scenario maximizes the significant differences between groups of wetlands, I compared the ratio of significant to insignificant p-values of group pairwise comparisons with Bonferroni correction. I used all 60 wetlands to compare classification scenarios with community data. To examine the effectiveness of classification scenarios on water quality, I used only wetlands sampled in 2010; patterns from 2012 data were likely influenced by extreme drought.

Results

Vegetation

A total of 375 vascular plant species were identified in the 60 wetlands. Richness varied widely, ranging from 3 species in a Dryland Row-crop wetland, to 68 species in a Forest wetland. Of the species present, 38 were non-native (10.1%) and most of these (89 %) were found in Orchard and Irrigated Row-crop wetlands. Nearly half of the species were either obligate wetland (79) or facultative wetland (93) species, and the remaining were mostly facultative species (see Appendix B). Average richness (± SE) in open-canopy wetlands and closed-canopy wetlands was similar, with 28 (±2.6) and 23 (±2.5) species, respectively.

Vegetative composition differed in ordination space between reference sites and more disturbed sites, although there was considerable overlap among several land use categories. (Figure 3.1). The NMS ordination for all 60 wetlands produced a two-dimensional solution with an acceptable stress value (15.512). Percent cover of native perennial and percent cover of exotic species was strongly related to the 1st axis (r^2 = 0.64 and 0.416, respectively). These two metrics were also highly correlated (Table 3.2). These variables effectively created a gradient along the 1st axis, where Irrigated Row-crop wetlands were associated with lower cover of native perennials, and Planted Pine and Reference wetlands were associated with the greatest cover. Shannon's diversity index and relative cover of wetland species were important wetland community characteristics associated with the second axis, where Reference wetlands have notably greater Shannon's diversity than those surrounded by Planted Pine, and a greater abundance of wetland species (% cover of species with wetland status) when compared to Forest, Dryland Row-crop, and Irrigated Row-crop wetlands (Table 3.2). Percent cover of herbaceous species, though associated with the second axis, did not differ significantly among land use classes. The abundance of both *Rhexia mariana* L. (Maryland meadowbeauty) and *Leersia hexandra* Sw. (southern cutgrass) was positively associated with Reference wetlands. The MRPP results associated with the ordination indicated that the grouping pattern was significant (p <0.001), and within-group agreement was relatively high for community data (A = 0.291). Pairwise comparison of groups showed that overall, Reference wetlands were significantly different from all other groups, and that Forest and Planted Pine wetlands each differed significantly from both the Pecan Orchard and Irrigated Row-crop wetlands (Table 3.5).

The comparison of open-canopy wetland vegetation communities led to a clearer separation of land use classes in ordination space (Figure 3.3). The 2-dimensional NMS ordination solution for open-canopy wetlands had sufficiently low stress (15.534). Percent cover of native perennials and exotic species again acted as important driving variables, and were related to axes 1 (r^2 = .508) and 2 (r^2 = .382) respectively (Table 3.3). Similarly, the ratio of annual to perennial cover was associated with the second axis. Reference and Planted Pine wetlands had a notably higher cover of native perennials, and a lower annual/perennial ratio when compared to Dryland and Irrigated Row-crop wetlands. Percent cover of exotic species significantly distinguished Reference wetlands from Pecan Orchard wetlands, with the other land use groups positioned along a gradient in between. Shannon’s diversity and richness were also important drivers along the first axis, and were highly correlated to each other, though Shannon’s diversity was not significantly greater in any land use group. Eight species showed strong correlation with the ordination axes, though all were highly correlated with other species or community metrics, so I examined the differences between groups for three: *Dichanthelim leucothrix* (Nash) Freckmann (rough panicgrass), *Leersia hexandra* Sw. (southern cutgrass), and *Viola lanceolata* L. (bog white violet). All of these species were found in notably higher abundances in Reference wetlands as compared to Irrigated Row-crop and Pecan Orchard sites (Table 3.3). MRPP results indicate significantly different groups ($p < 0.001$) and a very high A (0.3902; Table 3.5). Reference, Forest, and Planted Pine wetlands differed significantly in overall community composition from Pecan Orchard wetlands, and Reference wetlands also differed significantly from Irrigated Row-crop wetlands.

When the plant communities of closed-canopy wetlands were compared in ordination space, there was much overlap among land use groups. Only Reference wetlands remained clearly separate (Figure 3.3). The land use groups Irrigated Row-crop and Pecan Orchard were each represented by very few sample wetlands (1 and 2, respectively). The NMS ordination for closed-canopy wetlands produced a three-dimensional solution with a stress of 14.006, where the third axis represents much of the variation (Table 3.5). Many community metrics and species had strong associations to the ordination axes (Table 3.4). Shannon's diversity index, percent cover of wetland species, and percent cover of herbaceous species were among the community metrics most strongly associated with the ordination axes, and appear to drive the distinction between Reference wetlands and other land use groups. Reference wetlands were notably more diverse, and had a greater cover of *Rubus cuneifolius* Pursh (sand blackberry) when compared to Planted Pine wetlands. Otherwise, no metrics or species distinguished the land use groups. The MRPP results indicate significantly different groups for these closed-canopy wetlands ($p = 0.004$), but A is somewhat low (0.1976), indicating that the similarity in community composition found within groups is closer to what is expected by chance (Table 3.5). Plant community in Reference sites was significantly different from wetlands surrounded by Forest and by Planted Pine. Irrigated Row-crop LULC was not included in the MRPP analysis because it was only represented by one wetland.

Water Quality

Water quality measures varied considerably among wetlands, and between years, often by orders of magnitude (see Appendix B). For example, in 2010, phosphate levels ranged between 0.38 to 572 µg/L, and nitrate levels ranged between 0 and 2690.5 µg/L. In 2012, the range of nutrient loads increased. The dramatic differences between years and high values measured in 2012 are likely a result of the drought; typically, the wetlands sampled in 2012 had water concentrated in only the deepest areas, in small, discrete puddles.

When wetland water quality in 2010 was compared in ordination space, wetlands separated generally according to land use, though there was some overlap. PCA ordination produced three interpretable axes, based on the broken-stick criteria (Jackson 1993). Cumulatively, the axes represented 89.61% of the variance in water quality among all wetlands sampled (Table 3.7). All water quality variables sampled in 2010 were strongly associated with one of the three principal component axes. Four variables were strongly associated with the first component axis: PO_4, pH, AFDM and TDM (Table 3.6). However, PO_4 and pH were highly correlated, as were AFDM and TDM, so of these variables I selected pH and TDM to compare among groups using ANOVA. Graphically, Pecan Orchard and Irrigated Row-crop wetlands were distinguished from other classes due to higher pH, and, correspondingly, more PO_4 compared to reference wetlands. PO_4 and pH of Planted Pine and Forest wetlands tended to fall between Pecan Orchard and Irrigated Row-crop wetlands (Figure 3.4). Multiple comparisons indicated that the pH of Reference sites was lower than Irrigated Row-crop and Pecan Orchard sites. Planted Pine had a lower pH than Pecan Orchard wetlands. Irrigated Row-crop sites had greater TDM than wetlands surrounded by Planted Pine, Reference, and Pecan Orchard. NH_4 was most strongly associated with the second component axis, but did not differ significantly among land use groups. Though NO_3 content was greater in Pecan Orchard wetlands, this may be simply an artifact of a single elevated value and a small sample size. The MRPP analysis indicated significant differences among groups ($p < 0.001$), and a reasonable level of within-group agreement ($A = 0.252$). Reference sites differed significantly from Irrigated Row-crop and Pecan Orchard wetlands.

No strong patterns in the water quality data collected in 2012 were observed among land use classes of wetlands (Figure 3.5; Table 3.6). Only one axis was interpretable from the PCA ordination, explaining 44.60% of the variance (Table 3.7). The MRPP analysis indicated significant grouping of wetlands ($p = 0.002$), but the within-group agreement was low ($A =$

0.1232). Water quality within Pecan Orchards differed significantly from Reference and Planted Pine sites.

Indicator Species

The ISA of all 60 wetlands identified 57 indicator species in total, half of which were strongly associated Reference wetlands (Table 3.8). In general, ISA analyses produced relatively lengthy lists of indicator species for Reference, Pecan Orchard, and Irrigated Row-crop wetlands. Most of the species associated with Reference wetlands were perennials with obligate or facultative wet status. Pecan Orchard and Irrigated Row-crop wetlands were largely associated facultative weedy annuals. Forest, Planted Pine, and Dryland Row-crop wetlands had few to no indicator species, suggesting that most of the species composing the communities within these wetlands are common among other land use groups as well. Some indicator species suggested a drier environment; open-canopy Forest wetlands were strongly associated with *Quercus* (oak) species, and closed-canopy Pecan Orchard and Dryland Row-crop were each associated with woody facultative or upland species.

Land Use Classifications

Of the alternate classification scenarios I examined, all predicted some significant distinctions in condition among land use groups, both in macrophyte communities and in water quality (Table 3.9). Yet, there was no scenario that consistently performed the best when considering both within-group agreement and the ratio of significant pairwise comparisons. Original *a-priori* land use classes best predicted within-group agreement for both community characteristics and water quality, though all alternate classifications were relatively comparable. Scenarios which combined agricultural land use classes (both III and IV) best predicted significant differences in wetland condition based on macrophyte community composition (Table

3.9). Scenario II, which combined natural and commercial forests, best predicted differences in wetland condition based upon water quality.

Discussion

This study identifies biologically meaningful relationships between land use and the macrophyte communities and water quality of isolated wetlands, and demonstrates the influence of underlying classification schemes on remote assessments of wetland condition. Distinct impacts on biotic and environmental characteristics of isolated wetlands were identified for land uses classified at a fine scale, though results indicate that such fine-scaled classification may not be necessary when assessing impacts of land use on overall wetland condition. Additionally, discrepancies in patterns among similar land use classes and between wetland canopy types highlighted the importance of considering factors beyond current LULC when estimating wetland condition.

Land Use and Wetland Condition

Overall, the results of this study support the use of LULC data to develop an objective gradient of anthropogenic stress which can then be used to predict wetland condition, a method common among remote wetland condition assessments (Tiner 2004, Brown and Vivas 2005, Lane et al. 2012). By characterizing the relationships between individual land use classes and wetland condition, this study confirmed that each land use class is indeed associated with a certain degree and direction of change from the reference condition of isolated wetlands.

In general, the specific characteristics of wetland condition associated with each land use class were consistent with previous studies. The association of Reference wetlands with greater levels of diversity, higher cover of native perennials, and low pH corroborates many descriptive studies of relatively undisturbed isolated wetlands (Newman and Schalles 1990, Bennett and Nelson 1991, Battle and Golladay 2001, Sharitz 2003, Whigham and Jordan 2003, Kaeser and Kirkman 2009). Likewise, the association of agricultural land use classes (Irrigated Row-crop, Dryland Row-crop, and Pecan Orchard) with a higher cover of exotic species and increased nutrient loads is demonstrated by many other studies as well, and can be attributed to the high levels of disturbance associated with agricultural management practices, such as plowing, irrigation berm construction, mowing, and application of herbicides and fertilizers (Neely and Baker 1989, Ewel 1990, Craft and Casey 2000, Craft and Chiang 2002).

Not all agricultural classes influenced wetlands via the same mechanisms, however. The association of Irrigated Row-crop wetlands with higher sediment loads compared to Pecan Orchard wetlands demonstrated a fine-scale distinction between these two classes of agriculture, a distinction almost certainly due to the plowing and planting processes which frequently disturb the soil in row-crop agricultural landscapes (Gleason and Euliss 1998, Skagen et al. 2008), but which occur infrequently in Pecan Orchards. High sedimentation rates have been documented in isolated wetlands in similar cultivated landscapes. Luo et al. (1997) estimated that isolated wetlands within the Southern High Plains region could fill within 95 years, and Gleason (2001) estimated that more than half of the cultivated prairie potholes will be lost to sedimentation within the next 200 years at the current rate of sedimentation.

Most interesting, however, were the relationships between wetland condition and forested LULC classes (Reference, Forest, and Planted Pine), which suggested that remote assessments based solely upon surrounding land use may not always predict wetland condition sufficiently. Specifically, fire history, a prominent driver of vegetation communities in Reference wetlands, was likely more influential than surrounding LULC in determining condition among wetlands surrounded by different classes of forest. In relatively undisturbed landscapes in the Coastal Plain, the interaction of fire and hydrology promotes and sustains species-rich communities within isolated wetlands (Kirkman 1995, Kirkman et al. 2000). In fact, some wetland-associated species, including the endangered *Schwalbea Americana* L. (American chaffseed), require frequent fire to maintain viable populations (Kirkman et al. 1998). Within the Dougherty Plain, the interaction of fire and hydrology leads to the development of different isolated wetland ecosystem types, ranging from grass-sedge marshes to cypress-gum swamps (Kirkman et al. 2000).

Total exclusion of fire, however, can lead to hardwood establishment and eventual dominance (typically by *Quercus* [oak] species), ultimately resulting in the development of an alternate ecosystem state (Martin and Kirkman 2009). Within such hardwood depressions, the oaks increase drawdown of the water table at the catchment scale (Clayton and Hicks 2007, Brian Clayton, Jones Ecological Research Center, personal communication) and shade out the understory (Kirkman et al. 2004), resulting in drier depressions with very low understory richness. A history of fire exclusion, therefore, most likely led to the development of communities with lower diversity in Planted Pine wetlands and a lower cover of wetland species in Forest wetlands, relative to Reference. Oak encroachment, as a result of fire exclusion, also probably led to the association of open-canopy Forest wetlands with two oak indicator species. Finally, differences in overall community composition were most apparent among closed-canopy Forest and Planted Pine wetlands and Reference sites, whereas there were no differences among open-canopy wetlands of those LULC classes. This discrepancy suggests that, where isolated wetlands are burned regularly (as evidenced by the maintenance of open-canopy wetlands), neither Forest nor Planted Pine LULC have a significant impact on the vegetation communities of isolated wetlands.

A land management culture of prescribed fire has long existed in the Coastal Plain pine forests, and programs promoting prescribed fire have been in place since the 1950's (Johnson and Hale 2000, Waldrop et al. 2012). Even within regularly burned forested landscapes, however, natural and artificial barriers can prevent fires from burning the interior of isolated wetlands. Many forested properties, particularly plantations that manage for turkey and quail, burn uplands in winter to avoid damaging ground-nesting bird habitat (Stoddard 1935, Johnson and Hale 2000). This practice of dormant season burning coincides with the time of year wetlands are typically inundated (Kirkman et al. 2000), thus potentially resulting in the exclusion of fire from wetlands. Similarly, a common practice among landowners in the region is to create barren firebreaks by disking the soil around the margins of isolated wetlands, which, if maintained, also effectively exclude fire from the wetland.

Predicting Overall Wetland Condition

Despite the fine-scale distinctions I detected in specific biological and environmental variables among land use classes, coarser classification scenarios best predicted significant differences in overall wetland condition. This suggests that relatively coarse, nationally available data sets such as the National Land Cover Data (NLCD) have sufficient class resolution to accurately predict relative differences in condition among isolated wetlands.

Other wetland assessments have demonstrated the utility of coarser classification schemes when predicting overall condition, initially estimating condition with finer-scale data but ultimately employing a coarse scale to classify wetlands into two or three levels based on condition. Lane et al. (2012) estimated isolated wetland condition using 9 levels of LDI-based land use classification, but ultimately grouped wetlands into two condition classes: “impaired” and “reference”. Similarly, Cohen et al. (2005) assessed wetland condition based upon numerous vegetative metrics, but the best model developed from these metrics grouped wetlands into three condition classes: minimally, moderately, and severely disturbed. Thus, if wetland condition is often modeled at a coarse scale, it follows that coarse scale LULC data is sufficient to predict condition.

However, the predictive power of coarse versus fine scale LULC data may vary regionally. Lawler et al. (2004) compared predictive models of avian habitat and species richness throughout the United States based on fine-scale and coarse-scale LULC data. They found that the scale of classification strongly influenced predictions of species richness in certain eco-regions, but in other regions the scale of classification made little difference. Similarly, the most appropriate classification scale for LULC-based assessments of wetland condition may vary from region to region, based on underlying ecological and cultural drivers (e.g. the role of fire in maintaining wetland species richness, or the predominance of irrigated agriculture in the Southeast).

Limitations

Cattle pasture was not included in this study, though it likely represents a considerable portion of land use in the region, particularly in and around isolated wetlands (Chapter 2, this document). This was largely because the remote identification of cattle pasture in this region is often unreliable. Additionally, cattle pasture as a land use classification can be ephemeral. Some row-crop agriculture fields are seasonally converted to cattle pasture, so it is difficult to disentangle the separate influences of these two land use classes. Previous studies which examine the condition of isolated wetlands embedded in intensive cattle pastures show trends of enriched phosphate content and greater physical disturbance (Gathumbi et al. 2005), as well as decreased native species richness (Boughton et al. 2010). It is likely that in the Dougherty Plain, such wetlands would have conditions similar to wetlands influenced by other agricultural classes, although perhaps more extreme.

To prevent the influence of geographic position or the management practices of a few individuals from biasing the study, I attempted to include wetlands located throughout the Dougherty Plain, and managed by a variety of landowners in each land use category. Reference wetlands, however, are all managed with similar methods on the same private property. Inclusion of other wetlands deemed as best existing specimens of these isolated wetlands on other properties would provide a better and more complete comparison between Reference, Planted Pine and Forest sites, in particular.

Future Directions

Wetland condition assessment methods often incorporate multiple biological and environmental measures of ecological condition (U.S. EPA 2002). The clear next step would be to combine water quality and plant community data in NMS and MRPP analyses to determine how LULC relates to a more complete estimate of wetland condition. Since there was no single classification scenario that best predicted wetland condition based on both plant community and water quality, this would help identify which classification scenario performs best overall. Water quality data collected from these study wetlands in a year of average rainfall could supplement the existing vegetation dataset and make possible a more complete multivariate comparison of the influence of land use on wetland condition.

Finally, by clarifying the relationships between LULC and wetland condition within the Dougherty Plain and highlighting the role of fire history in shaping wetland communities, wetland condition can be assessed throughout the region using the model of predicted isolated wetlands developed by Martin et al. (2012). By combining both LULC data and indicators of fire history (i.e. hardwood cover), predictions of wetland condition may be capable of more than simply identifying “least disturbed” wetlands. Rather, relatively accurate models can be developed that identify wetlands in reference condition and locate areas of high conservation interest throughout the region.

Conclusion

This study identifies biologically relevant relationships between specific, fine-scale classes of land use within the Dougherty Plain, and the condition of isolated wetlands, and demonstrated the utility of coarser LULC classification schemes in predicting wetland condition. Overall, wetlands influenced by agricultural land use classes differed the most from Reference wetlands in both plant community composition and water quality. However, the differences between the plant communities of Forest and Reference wetlands were the most illuminating, and highlighted the role of fire and fire history in determining current wetland condition. These results suggest that using only land use to predict wetland condition fails to incorporate all relevant factors. The knowledge gained from this study will support future accurate assessments of wetland condition at a regional level and enable remote identification of wetlands in reference condition based on surrounding land use and evidence of fire history.

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Literature Cited

Battle, J. and S. W. Golladay. 2001. Hydroperiod influence on breakdown of leaf litter in cypress-gum wetlands. American Midland Naturalist **146**:128-145.

Beck, B. F. and D. D. Arden. 1983. Hydrology and geomorphology of the Dougherty Plain, southwest Georgia. Southeastern Geological Society, Tallahassee, FL.

Bennett, S. H. and J. B. Nelson. 1991. Distribution and status of Carolina bays in South Carolina. South Carolina Wildlife and Marine Resources Department, Nongame and Heritage Trust Section, Columbia, SC.

Biebighauser, T. R. 2007. Wetland drainage, restoration, and repair / Thomas R. Biebighauser. Lexington : The University Press of Kentucky, c2007.

Boughton, E. H., P. F. Quintana-Ascencio, P. J. Bohlen, D. G. Jenkins, and R. Pickert. 2010. Land-use and isolation interact to affect wetland plant assemblages. Ecography **33**:461-470.

Brown, M. T. and M. B. Vivas. 2005. Landscape Development Intensity Index. Environmental Monitoring and Assessment **101**:289-309.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**:117.

Clayton, B. and D. W. Hicks. 2007. Hydrologic Monitoring of a Hardwood Encroached, Isolated Depressional Wetland, Southwest Georgia. Proceedings of the 2007 Georgia Water Resources Conference, University of Georgia.

Cohen, M. J., C. R. Lane, K. C. Reiss, J. A. Surdick, E. Bardi, and M. T. Brown. 2005. Vegetation based classification trees for rapid assessment of isolated wetland condition. Ecological Indicators **5**:189-206.

Couch, C. A., E. H. Hopkins, and P. S. Hardy. 1996. Influences of Environmental Settings on Aquatic Ecosystems in the Apalachicola-Chattahoochee-Flint River Basin.*in* U. S. G. Survey, editor.

Craft, C. B. and W. P. Casey. 2000. Sediment and nutrient accumulation in floodplain and depressional freshwater wetlands of Georgia, USA. Wetlands **20**:323-332.

Craft, C. B. and C. Chiang. 2002. Forms and amounts of soil nitrogen and phosphorus across a longleaf pine-depressional wetland landscape. Soil Science Society of America Journal **66**:1713-1721.

Drew, M. B., L. K. Kirkman, and A. K. Gholson, Jr. 1998. The Vascular Flora of Ichauway, Baker County, Georgia: A Remnant Longleaf Pine/Wiregrass Ecosystem. Castanea **63**:1-24.

Dufrene, M. and P. Legendre. 1997. Species Assemblages and Indicator Species: The Need for a Flexible Asymmetrical Approach. Ecological Monograms **67**:345-366.

Engstrom, R. T., L. K. Kirkman, and R. J. Mitchell. 2001. Natural History: Longleaf Pine-Wiregrass Ecosystem. Pages 5-18 *in* J. R. Willson, editor. The Fire Forest: Longleaf Pine-Wiregrass Ecosystem. Georgia Wildlife Natural Georgia Series 8, Georgia Wildlife Federation.

Ewel, K. C. 1990. Swamps. Pages 281-317 *in* R. L. Myers and J. J. Ewel, editors. Ecosystems of Florida. University of Florida Press, Orlando, FL, USA.

Fennessy, M. S., A. D. Jacobs, and M. E. Kentula. 2004. Review of Rapid Methods for Assessing Wetland Condition.*in* U.S. Environmental Protection Agency, editor., Washington, D.C.

Gathumbi, S. M., P. J. Bohlen, and D. A. Graetz. 2005. Nutrient Enrichment of Wetland Vegetation and Sediments in Subtropical Pastures. Soil Sci. Soc. Am. J. **69**:539-548.

Gleason, R. A. 2001. Invertebrate egg and plant seed banks in natural, restored, and drained wetlands in the prairie pothole region (USA) and potential effects of sedimentation on recolonization of hydrophytes and aquatic invertebrates. Biological Sciences, South Dakota State University.

Gleason, R. A. and N. H. Euliss. 1998. Sedimentation of Prairie Wetlands. Great Plains Research **8**:97-112.

Hendricks, E. L. and M. H. Goodwin. 1952. Water-level fluctuations in limestone sinks in southwestern Georgia. U.S. Geological Survey Water-Supply Paper 1110-E.

Hychka, K. C., D. H. Wardrop, and R. P. Brooks. 2007. Enhancing a landscape assessment with intensive data: a case study in the Upper Juniata watershed. Wetlands **27**:446-461.

Jackson, D. A. 1993. Stopping Rules in Principal Components Analysis: A Comparison of Heuristical and Statistical Approaches. Ecology **74**:2204-2214.

Johnson, A. S. and P. E. Hale. 2000. The historical foundations of prescribed burning for wildlife: a Southeastern perspective. Page 11 *in* The Role of Fire in Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions Proceedings of a Special Workshop. Citeseer.

Kaeser, M. and L. Kirkman. 2009. Estimating total plant species richness in depressional wetlands in the longleaf pine ecosystem. Wetlands **29**:866-874.

Kirkman, L. K. 1995. Impacts of fires and hydrological regimes on vegetation in depression wetlands of southeastern USA. Pages 10-20 *in* S. I. Cerulean and R. T. Engstrom, editors. Proceedings of the Tall Timbers Fire Ecology Conference, No. 19, Tall Timbers Research Station, Tallahassee, FL, USA.

Kirkman, L. K., M. B. Drew, and D. Edwards. 1998. Effects of experimental fire regimes on the population dynamics of shape Schwalbea americana L. Plant Ecology **137**:115-137.

Kirkman, L. K., P. C. Goebel, B. J. Palik, and L. T. West. 2004. Predicting plant species diversity in a longleaf pine landscape. Ecoscience **11**:80-93.

Kirkman, L. K., P. C. Goebel, L. T. West, M. B. Drew, and B. J. Palik. 2000. Depressional wetland vegetation types: A question of plant community development. Wetlands **20**:373-385.

Kirkman, L. K., S. W. Golladay, L. LaClaire, and R. Sutter. 1999. Biodiversity in southeastern seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society **18**:553-562.

Kirkman, L. K., R. L. Lide, G. Wein, and R. R. Shartiz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western coastal plain of South Carolina. Wetlands **16**:564-576.

Lane, C., E. D'Amico, and B. Autrey. 2012. Isolated Wetlands of the Southeastern United States: Abundance and Expected Condition. Wetlands **32**:753-767.

Lawler, J. J., R. J. O'Connor, C. T. Hunsaker, K. B. Jones, T. R. Loveland, and D. White. 2004. The effects of habitat resolution on models of avian diversity and distributions: a comparison of two land-cover classifications. Landscape Ecology **19**:515-530.

Leibowitz, S. G. 2003. Isolated wetlands and their functions: An ecological perspective. Wetlands **23**:517-531.

Lopez, R. D. and M. S. Fennessy. 2002. Testing the Floristic Quality Assessment Index as an indicator of wetland condition. Ecological Application **12**:487-497.

Luo, H.-R., L. M. Smith, B. L. Allen, and D. A. Haukos. 1997. Effects of Sedimentation on Playa Wetland Volume. Ecological Applications:247.

Mack, J. 2006. Landscape as a predictor of wetland condition: an evaluation of the Landscape Development Index (LDI) with a large reference wetland dataset from Ohio. Environmental Monitoring and Assessment **120**:221-241.

Martin, G. I. 2010. Evaluating the location, extent, and condition of isolated wetlands in the Dougherty Plain, Georgia, USA [electronic resource] / by Glenn I. Martin. 2010.

Martin, G. I., J. A. Hepinstall, and L. K. Kirkman. 2013. Six decades (1948 - 2007) of landscape change in the Dougherty Plain of Southwest Georgia, USA. Southeastern Geographer **53**.

Martin, G. I., L. K. Kirkman, and J. Hepinstall-Cymerman. 2012. Mapping geographically isolated wetlands in the Dougherty Plain, Georgia, USA. Wetlands **32**:149-160.

Martin, K. L. and L. K. Kirkman. 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the south-eastern USA. Journal of Applied Ecology **46**:906-914.

McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities. MjM Software Design Gleneden Beach, Oregon.

McCune, B. and M. J. Mefford. 2011. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach, Oregon, USA.

Meltz, R. and C. Copeland. 2007. The Wetlands Coverage of the Clean Water Act Is Revisited by the Supreme Court: *Rapanos v. United States*.*in* C. R. Service, editor.

Natural Resources Conservation Service. 2010. Field Indicators of Hydric Soils in the United States, Version 7.0.*in* L. M. Vasilas, G. W. Hurt, and C. V. Noble, editors.

Neely, R. K. and J. L. Baker. 1989. Nitrogen and phosphorus dynamics and the fate of agricultural runoff in Northern Prairie Wetlands. Pages 92-131 Northern Prairie Wetlands B2 - Northern Prairie Wetlands. Iowa State University Press, Ames, IA.

Newman, M. C. and J. F. Schalles. 1990. The water chemistry of Carolina bays: A regional survey. Pages 147-168.

Phillips, R. L., O. Beeri, and E. S. DeKeyser. 2005. Remote Wetland Assessment For Missouri Coteau Prairie Glacial Basins. Wetlands **25**:335-349.

Rapanos v United States. 2006. 547 U.S. 715.

Reiss, K. and M. Brown. 2007. Evaluation of Florida Palustrine Wetlands: Application of USEPA Levels 1, 2, and 3 Assessment Methods. EcoHealth **4**:206-218.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Chapter 9 - Structure and Dynamics of an Amphibian Community: Evidence from a 16-Year Study of a Natural Pond. Pages 217-248 *in* L. C. Martin and A. S. Jeffrey, editors. Long-Term Studies of Vertebrate Communities. Academic Press, San Diego.

Sharitz, R. R. 2003. Carolina Bay Wetlands: Unique Habitats Of The Southeastern United States. Wetlands **23**:550-562.

Skagen, S. K., C. P. Melcher, and D. A. Haukos. 2008. Reducing sedimentation of depressional wetlands in agricultural landscapes. Wetlands **28**:594-604.

Stein, E., A. Fetscher, R. Clark, A. Wiskind, J. Grenier, M. Sutula, J. Collins, and C. Grosso. 2009. Validation of a wetland Rapid Assessment Method: Use of EPA's level 1-2-3 framework for method testing and refinement. Wetlands **29**:648-665.

Stoddard, H. L. 1935. Use of controlled fire in southeastern upland game management. Journal of Forestry **33**:336-351.

Tiner, R. 2004. Remotely-sensed indicators for monitoring the general condition of "natural habitat" in watersheds: an application for Delaware's Nanticoke River watershed. Ecological Indicators **4**:227-243.

Tiner, R. W. 2003. Estimated extent of geographically isolated wetlands in selected areas of the United States. Wetlands **23**:636-652.

Tiner, R. W., H. C. Berquist, G. P. DeAlessio, and M. J. Starr. 2002. Geographically Isolated Wetlands: A Preliminary Assessment of their Characteristics and Status in Selected Areas of the United States.*in* F. a. W. S. U.S. Department of the Interior, Northeast Region, Hadley, MA., editor.

Turner, M. G. and C. L. Rushcer. 1988. Changes in landscape patterns in Georgia, USA. Landscape Ecology **1**:241-251.

U.S. EPA. 2002. Methods for Evaluating Wetland Condition: Developing Metrics and Indexes of Biological Integrity.*in* U. S. E. P. A. Office of Water, Washington, DC, editor.

Waldrop, T. A., S. L. Goodrick, C. A. Harper, G. Towne, and M. J. Dixon. 2012. Introduction To Prescribed Fire In Southern Ecosystems.*in* U. S. D. o. Agriculture, editor. Southern Research Station, Asheville, NC.

Walker, J. L. 1993. Rare Vascular Plant Taxa Associated with the Longleaf Pine Ecosystem.*in* Tall Timbers Fire Ecology Conference.

Whigham, D. F. 1999. Ecological issues related to wetland preservation, restoration, creation and assessment. Science of the Total Environment **240**:31-40.

Whigham, D. F. and T. E. Jordan. 2003. Isolated wetlands and water quality. Wetlands **23**:541-549.

Table 3.1 Alternate LULC classification scenarios.

Classification Scenario	*n* classes	Land Use Groups	Justification for combining groups
Original	6	Ref, Fors, Pine, Orch, Dry, Irr	n/a
I	5	Ref, Fors, Pine, Dry, [Orch + Irr]	irrigated systems
II	4	[Ref + Fors + Pine], Orch, Dry, Irr	forested community
III	5	Ref, Fors, Pine, Orch, [Dry + Irr]	row-crop agriculture
IV	4	Ref, Fors, Pine, [Orch + Dry + Irr]	general agriculture

[a]LULC classes are represented with codes: Ref = Reference, Fors = Forest, Pine = Planted Pine, Orch = Pecan Orchard, Dry = Dryland Row-crop, and Irr = Irrigated Row-crop

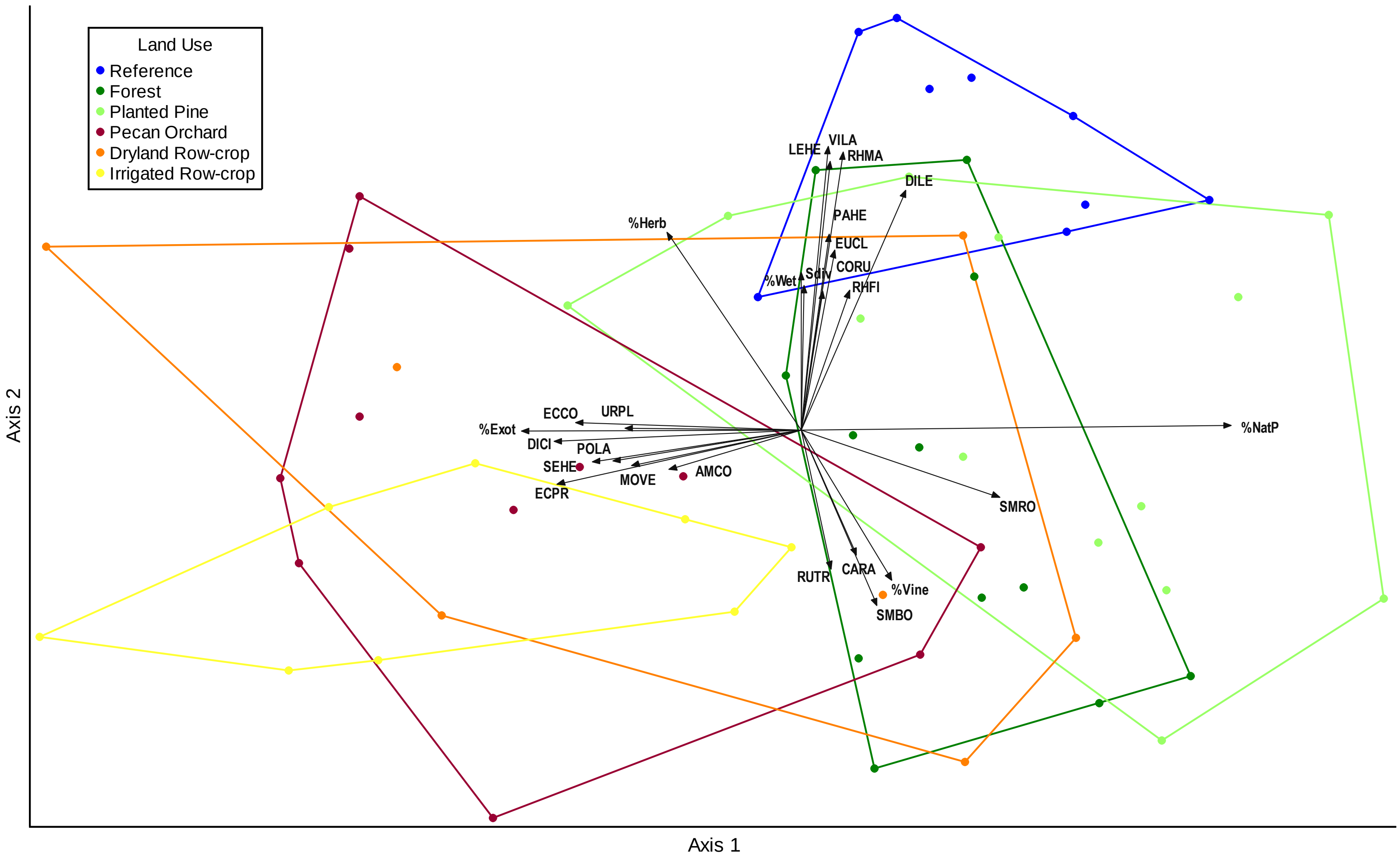

Figure 3.1 A joint plot displaying the results of an NMS ordination of the relative cover of macrophyte species within isolated wetlands surrounded by a dominant land use class. Wetlands are grouped by land use class. Cumulatively, this solution represents 64.8% of the variance among wetlands (Axis 1 r^2 = 0.418, Axis 2 r^2 = 0.230). Each vector represents a community metric or individual species related (cutoff r^2 = 0.200) to the ordination axes. Stress =15.512 and instability = 0.0004. For species and community metrics codes, refer to Table 3.4

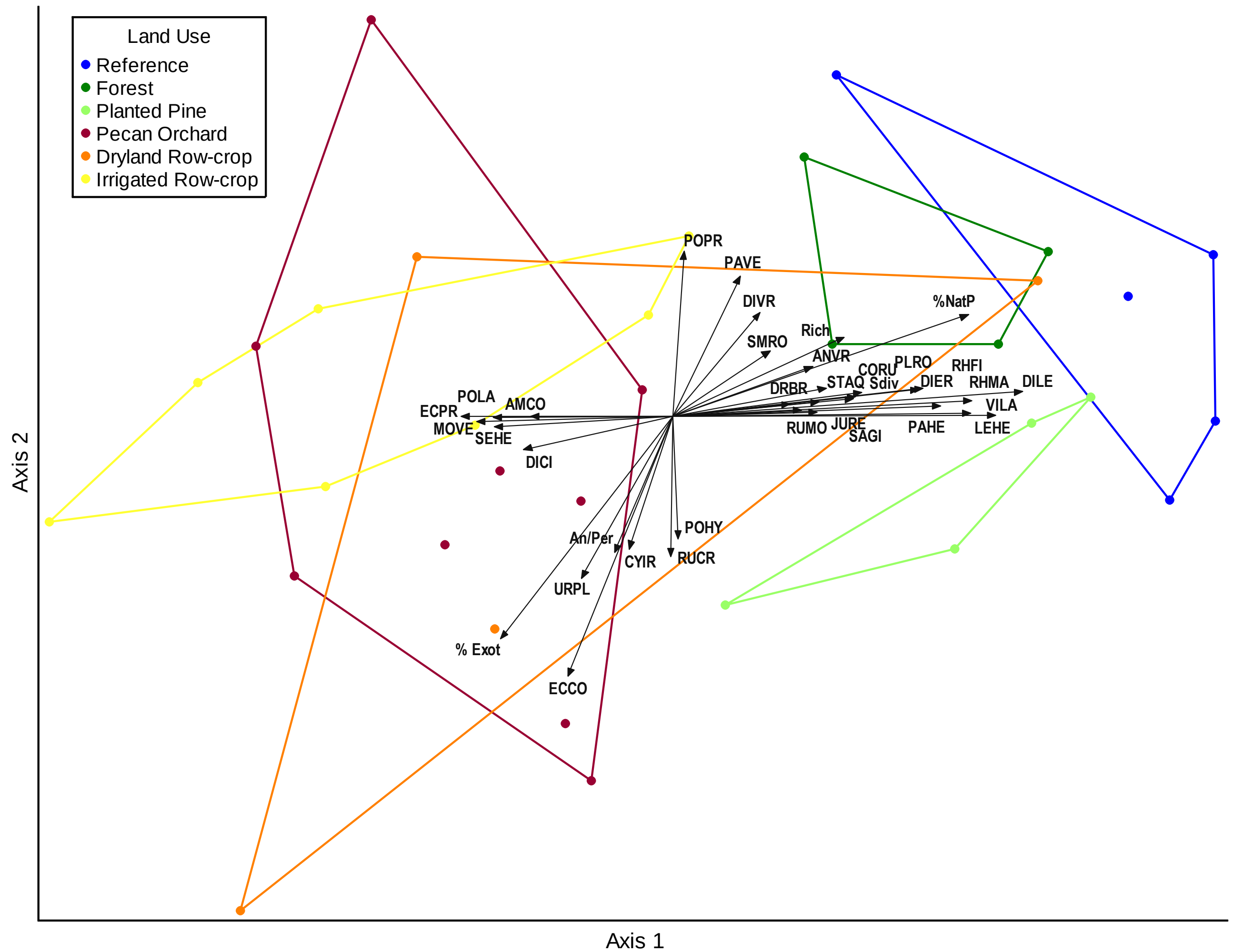

Figure 3.2 A joint plot displaying the results of an NMS ordination of the relative cover of macrophyte species within open-canopy isolated wetlands surrounded by a dominant land use class. Wetlands are grouped by land use class. Cumulatively, this solution represents 69.3% of the variance among wetlands (Axis 1 $r^2 = 0.553$, Axis 2 $r^2 = 0.140$). Each vector represents a community metric or individual species related (cutoff $r^2 = 0.200$) to the ordination axes. Stress = 15.534 and instability = 0.0002. For species and community metrics codes, refer to Table 3.4

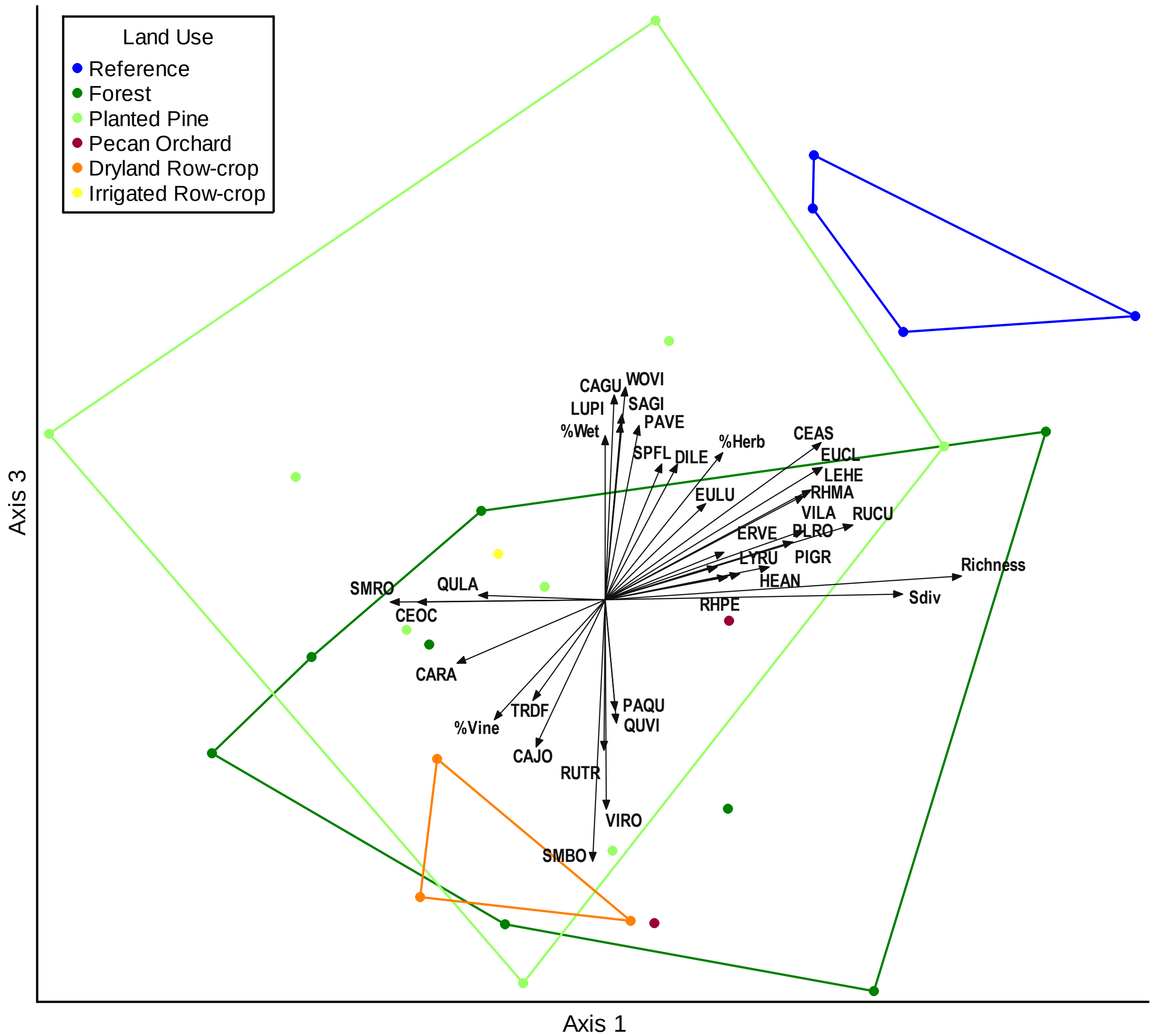

Figure 3.3 A joint plot displaying the results of a 3-dimensional NMS ordination of the relative cover of macrophyte species within closed-canopy isolated wetlands surrounded by a dominant land use class. Wetlands are grouped by land use class. Cumulatively, this solution represents 77.1% of the variance among wetlands (Axis 1 r^2 = 0.242, Axis 2 r^2 = 0.150, Axis 3 r^2 = 0.379). Each vector represents a community metric or individual species related (cutoff r^2 = 0.200) to the ordination axes. Stress = 14.006 and instability = 0.0005. For species and community metrics codes, refer to Table 3.4.

Table 3.2 List of community metrics and species abundance that showed a relationship ($r^2 > 0.200$) to NMS ordination axes when all wetlands were compared. ANOVA analyses were conducted on all metrics, and on species where $r^2 > 0.400$. Tukey's multiple comparison procedures were performed on variables with significant ANOVA results. Statistically significant differences among groups were determined with Bonferroni-corrected alpha values, and denoted with alphabetic subscripts. Pairwise comparisons with notable but non-statistical differences ($\alpha = 0.05$) were also included and denoted with numeric subscripts (1 of 2).

Category	Dependent Variable	Code	NMS Axis	R^2	F value	*p*-value	Multiple comparisons (Bonferroni α=0.003)
Community Metrics	Shannon's Diversity	Sdiv	2	0.22	3.08	0.016	Pine_1 Ref_2
	% cover of native perennials	%NatP	1	0.64	6.57	<0.001	Irr_{a1} $\text{Dry}_{1,2}$ $\text{Fors}_{2,3}$ Ref_{b3} Pine_{b3}
	% cover of species with wetland status	%Wet	2	0.23	3.10	0.016	Irr_1 Dry_1 Fors_1 Ref_2
	% cover of exotic species	%Exot	1	0.42	see %NatP		---
	% cover of vines	%Vine	2	0.22	see %Herb		---
	% cover of herbaceous species	%Herb	2	0.29	1.70	0.152	---
Species	*Coelorachis rugosa*	CORU	2	0.21	---	---	---
	Digitaria ciliaris	DICI	1	0.37	---	---	---
	Dichanthelium Leucothrix	DILE	2	0.36	---	---	---
	Echinochloa colona	ECCO	1	0.34	---	---	---
	Eclipta prostrata	ECPR	1	0.36	---	---	---
	Euthamia caroliniana	EUCL	2	0.27	---	---	---
	Leersia hexandra	LEHE	2	0.42	5.76	< 0.001	Irr_a Orch_a Dry_1 Fors_1 $\text{Ref}_{b,2}$
	Mollugo verticillata	MOVE	1	0.25	---	---	---
	Panicum hemitomon	PAHE	2	0.29	---	---	---
	Polygonum lapathifolium	POLA	1	0.31	---	---	---
	Rhynchospora filifolia	RHFI	2	0.29	---	---	---
	Rhexia mariana	RHMA	2	0.41	6.78	<.001	Dry_a Irr_a Orch_a Pine_a Ref_b
	Rubus trivialis	RUTR	2	0.21	---	---	---
	Sesbania herbacea	SEHE	1	0.28	---	---	---
	Smilax bona-nox	SMBO	2	0.26	---	---	---
	Smilax rotundifolia	SMRO	1	0.30	---	---	---

Table 3.3 Open-canopy wetland community metrics and species abundance that showed a relationship ($r^2 > 0.200$) to NMS ordination axes. ANOVA analyses were conducted on all metrics, and on species where $r^2 > 0.400$. Tukey's multiple comparison procedures were performed on variables with significant ANOVA results. Statistically significant differences among groups were determined with Bonferroni-corrected alpha values, and denoted with alphabetic subscripts. Pairwise comparisons with notable but non-statistical differences ($\alpha = 0.05$) were also included and denoted with numeric subscripts. (1 of 2)

Category	Dependent Variable	Code	NMS Axis	R^2	F value	*p*-value	Multiple comparisons (Bonferroni α=0.003)
Community Metrics	Richness	Rich	1	0.29	see Sdiv		---
	Shannon's Diversity	Sdiv	1	0.31	1.79	0.148	---
	% cover of native perennials	%NatP	1	0.51	7.02	< 0.001	Dry_a Irr_1 $Pine_{b,2}$ $Ref_{b,2}$
	% cover of exotic species	%Exot	2	0.38	8.42	< 0.001	$Ref_{a,1}$ $Pine_{1,2}$ $Fors_{1,2}$ $Dry_{2,3}$ $Irr_{2,3}$ $Orch_{b,3}$
	Annual/perennial ratio	An/Per	2	0.23	4.47	0.004	$Pine_1$ $Ref_{1,2}$ Irr_3 $Dry_{2,3}$
Species	*Ammania coccinea*	AMCO	1	0.24	---	---	---
	Andropogon virginicus	ANVR	1	0.24	---	---	---
	Coelorachis rugosa	CORU	1	0.32	---	---	---
	Cyperus iria	CYIR	2	0.23	---	---	---
	Digitaria ciliaris	DICI	1	0.26	---	---	---
	Dichanthelium erectifolium	DIER	1	0.42	see DILE		---
	Dichanthelium Leucothrix	DILE	1	0.60	5.08	0.002	Irr_1 $Orch_1$ Ref_2
	Drosera brevifolia	DRBR	1	0.20	---	---	---
	Echinochloa colona	ECCO	2	0.45	see %Exot		---
	Eclipta prostrata	ECPR	1	0.36	---	---	---
	Juncus repens	JURE	1	0.22	---	---	---
	Leersia hexandra	LEHE	1	0.55	5.07	0.002	Irr_1 $Orch_1$ $Pine_2$ Ref_2
	Mollugo verticillata	MOVE	1	0.31	---	---	---

Table 3.3 Continued (2 of 2).

Category	Dependent Variable	Code	NMS Axis	R^2	F value	*p*-value	Multiple comparisons (Bonferroni α=0.003)
Species (Continued)	*Panicum hemitomon*	PAHE	1	0.51	see DILE, LEHE		---
	Panicum verrucosum	PAVE	2	0.24	---	---	---
	Pluchea rosea	PLRO	1	0.26	---	---	---
	Polygonum hydropiperoides	POHY	2	0.21	---	---	---
	Polygonum lapathifolium	POLA	1	0.34	---	---	---
	Polypremum procumbens	POPR	2	0.28	---	---	---
	Rhynchospora filifolia	RHFI	1	0.43	see VILA		---
	Rhexia mariana	RHMA	1	0.51	see DILE		---
	Rumex crispus	RUCR	2	0.24	---	---	---
	Rudbeckia mohrii	RUMO	1	0.25	---	---	---
	Saccharum giganteum	SAGI	1	0.25	---	---	---
	Sesbania herbacea	SEHE	1	0.31	---	---	---
	Stylisma aquatica	STAQ	1	0.31	---	---	---
	Urochloa platyphylla	URPL	2	0.28	---	---	---
	Viola lanceolata	VILA	1	0.46	8.83	<0.001	Irr_a $Orch_a$ Dry_a $Fors_a$ $Pine_1$ $Ref_{b,2}$

Table 3.4 Closed-canopy wetland community metrics and species abundance that showed a relationship ($r^2 > 0.200$) to NMS ordination axes. ANOVA analyses were conducted on all metrics, and on species where $r^2 > 0.400$. Tukey's multiple comparison procedures were performed on variables with significant ANOVA results. Statistically significant differences among groups were determined with Bonferroni-corrected alpha values, and denoted with alphabetic subscripts. Pairwise comparisons with notable but non-statistical differences ($\alpha = 0.05$) were also included and denoted with numeric subscripts. (1 of 2)

Category	Dependent Variable	Code	NMS Axis	R^2	F value	*p*-value	Multiple comparisons (Bonferroni α=0.005)
Community Metrics	Richness	Rich	1	0.66	2.78	0.067	---
	Shannon's Diversity	Sdiv	1	0.55	3.61	0.031	$Pine_1$ Ref_2
	% cover of species with wetland status	%Wet	3	0.30	2.19	0.120	---
	% cover of vines	%Vine	2	0.29	see %Herb		---
	% cover of herbaceous species	%Herb	3	0.27	1.86	0.170	---
Species	*Carex glaucescens*	CAGU	3	0.38	---	---	---
	Carex joorii	CAJO	3	0.27	---	---	---
	Campsis radicans	CARA	2	0.29	---	---	---
	Centella asiatica	CEAS	1	0.40	---	---	---
	Cephalanthus occidentalis	CEOC	1	0.35	---	---	---
	Celtis occidentalis	CEOD	2	0.26	---	---	---
	Dichanthelium Leucothrix	DILE	3	0.25	---	---	---
	Eclipta prostrata	ECPR	2	0.20	---	---	---
	Erigeron vernus	ERVE	1	0.22	---	---	---
	Euthamia caroliniana	EUCL	1	0.40	---	---	---
	Helianthus angustifolius	HEAN	1	0.25	---	---	---
	Juncus effusus	JUEF	2	0.29	---	---	---
	Leersia hexandra	LEHE	1	0.38	---	---	---
	Lonicera japonica	LOJA	2	0.23	---	---	---
	Ludwigia pilosa	LUPI	3	0.33	---	---	---
	Lycopus rubellus	LYRU	1	0.21	---	---	---
	Nyssa sylvatica	NYSY	2	0.25	---	---	---

Table 3.4 Continued (2 of 2).

Category	Dependent Variable	Code	NMS Axis	R^2	F value	*p*-value	Multiple comparisons (Bonferroni α=0.005)
	Parthenocissus quinquefolia	PAQU	2	0.22	---	---	---
	Panicum verrucosum	PAVE	3	0.32	---	---	---
	Pityopsis graminifolia	PIGR	1	0.30	---	---	---
	Pluchea rosea	PLRO	1	0.35	---	---	---
	Quercus laurifolia	QULA	1	0.23	---	---	---
	Quercus nigra	QUNI	2	0.22	---	---	---
	Quercus virginiana	QUVI	3	0.23	---	---	---
	Rhynchospora filifolia	RHFI	2	0.22	---	---	---
	Rhexia mariana	RHMA	1	0.37	---	---	---
Species (Continued)	*Rhynchospora perplexa*	RHPE	1	0.23	---	---	---
	Rubus cuneifolius	RUCU	1	0.46	4.05	0.021	Pine_1 Ref_2
	Rubus trivialis	RUTR	2	0.31	---	---	---
	Saccharum giganteum	SAGI	3	0.34	---	---	---
	Senna obtusifolia	SEOB	2	0.20	---	---	---
	Smilax bona-nox	SMBO	3	0.48	2.72	0.072	---
	Smilax rotundifolia	SMRO	1	0.40		---	---
	Sporobolus floridanus	SPFL	3	0.25	---	---	---
	Viola lanceolata	VILA	1	0.37	---	---	---
	Vitis rotundifolia	VIRO	3	0.39	---	---	---
	Woodwardia virginca	WOVI	3	0.39	---	---	---

Table 3.5 Results of the MRPP analyses and associated Multiple Comparison procedures performed on isolated wetland macrophyte communities.

	Surrounding Land use	N	NMS Ordination				MRPP		
			Axes	**R^2**	***p*-value**	**stress**	**A**	***p*-value**	**significantly different groups[a]**
All Wetlands	Reference	9	1	0.418	0.0196	15.51	0.291	<0.001	Ref$_a$, For$_b$, Pine$_b$, Orch$_c$, Dry$_{bc}$, Irr$_c$
	Forest	12							
	Planted Pine	13	2	0.230					
	Pecan Orchard	11							
	Dryland Row Crop	7	---	---					
	Irrigated Row Crop	8							
Open-Canopy Wetlands	Reference	5	1	0.553	0.0099	15.53	0.39	<0.001	Ref$_a$, For$_{ab}$, Pine$_{ab}$, Orch$_c$, Dry$_{ac}$, Irr$_{bc}$
	Forest	4							
	Planted Pine	4	2	0.14					
	Pecan Orchard	9							
	Dryland Row Crop	4	---	---					
	Irrigated Row Crop	7							
Closed-Canopy Wetlands	Reference	4	1	0.242	0.0040	14.01	0.198	0.004	Ref$_a$, Fors$_b$, Pine$_b$, Orch$_{ab}$, Dry$_{ab}$
	Forest	8							
	Planted Pine	9	2	0.150					
	Pecan Orchard	2							
	Dryland Row Crop	3	3	0.379					
	Irrigated Row Crop[b]	1							

[a] Significance differences between pairs of groups were evaluated with Bonferroni adjusted alpha values. Classes with different subscripts differ.
[b] Irrigated Row-crop was not included in the closed-canopy MRPP because it was only represented by one wetland.

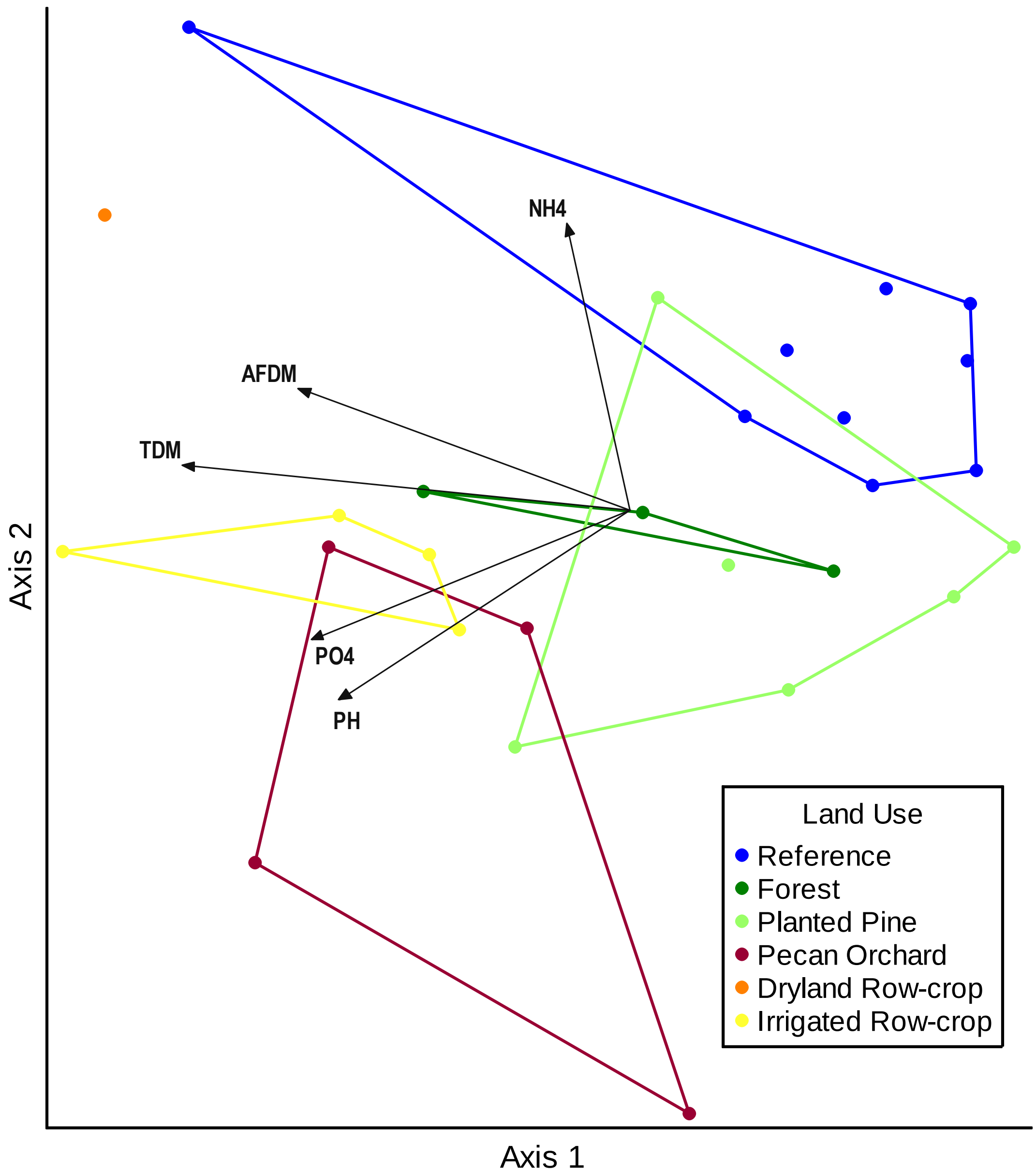

Figure 3.4 A joint plot displaying the results of a 3-dimensional PCA ordination of isolated wetland water in 2010. Wetlands are grouped by the class of dominant surrounding land use. Cumulatively, this solution represents 89.6% of the variance among wetlands (Axis 1 = 46.1, Axis 2 = 24.8, Axis 3 = 18.7). Each vector represents a water quality variable related (cutoff r^2 = 0.200) to the ordination axes. For water quality codes, refer to Table 3.5.

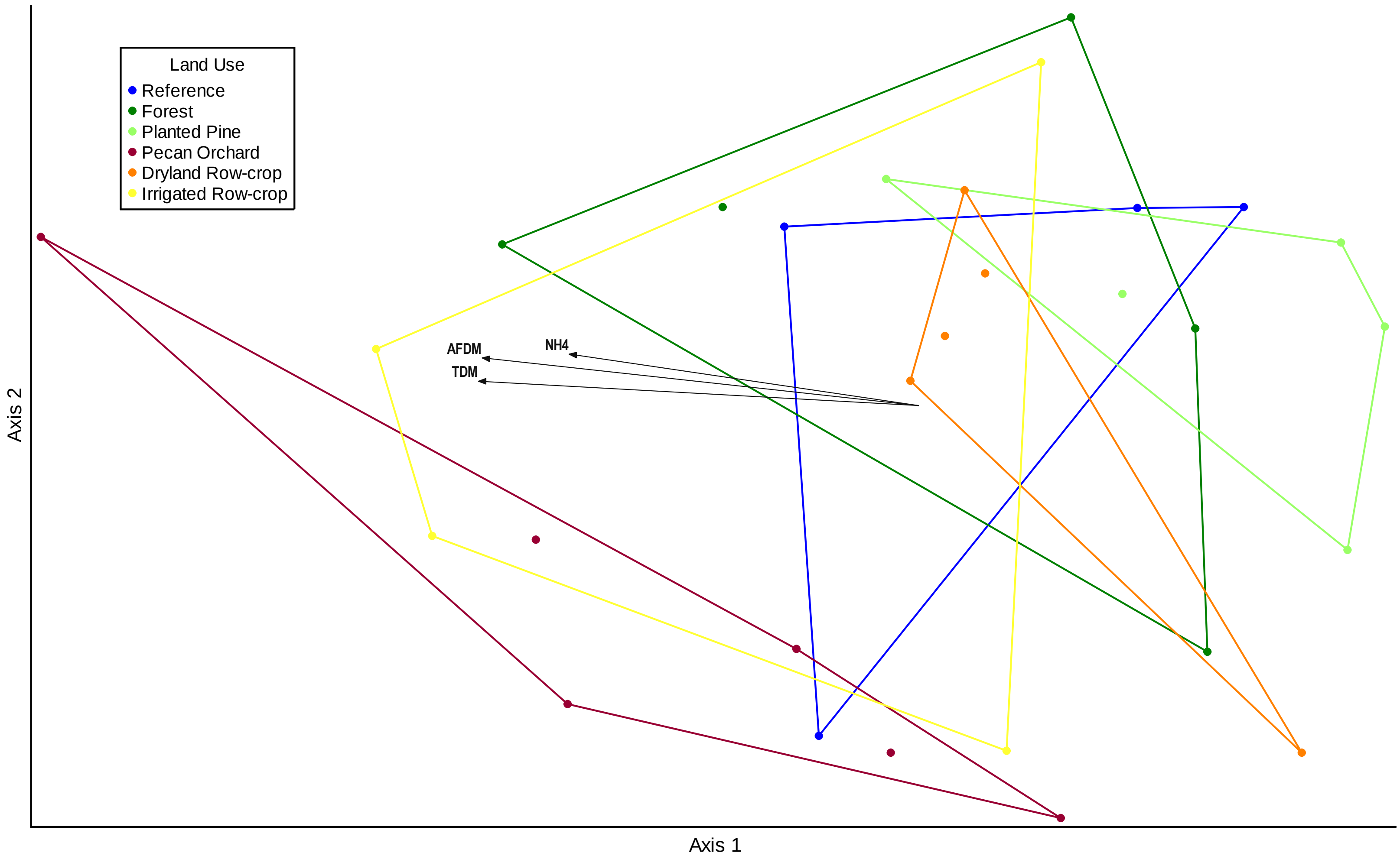

Figure 3.5 A joint plot displaying the results of a PCA ordination of isolated wetland water quality in 2012. Axis 1 represents the only interpretable axis in this solution, and represents 44.6% of the total variance among wetlands. Wetlands are grouped by the class of dominant surrounding land use. Each vector represents a water quality variable related (cutoff $r^2 = 0.200$) to the ordination axes. For water quality codes, refer to Table 3.5.

Table 3.6 List of water quality variables from 2010 and 2012 that were most strongly correlated to interpretable Principal Component axes. ANOVA analyses were conducted on each of these variables, and Tukey's multiple comparison procedures were performed on variables with significant ANOVA results. Statistically significant differences among groups were determined with Bonferroni-corrected alpha values, and denoted with alphabetic subscripts. Pairwise comparisons with notable but non-statistical differences (α = 0.05) were also included and with numeric subscripts. AFDM = Ash free dry mass, TDM = Total dry mass.

Dependent Variable	**2010**					**2012**				
	PC Axis	V vector	F value	*p* -value	Multiple comparisons (Bonferroni α=0.005)	PC Axis	V vector	F value	*p* -value	Multiple comparisons (Bonferroni α=0.005)
PO4	1	-0.767	6.65	0.001		---	---	---	---	---
NO3	3	-0.882	3.57	0.023	Fors_1 Ref_1 Orch_2	---	---	---	---	---
NH4	2	-0.728	0.42	0.804	---	1	-0.760	0.55	0.740	---
AFDM	1	-0.782	see TDM		---	1	-0.849	see TDM		---
TDM	1	-0.908	5.16	0.005	Pine_a Ref_1 Orch_1 $\text{Irr}_{b,2}$	1	-0.853	2.47	0.062	---
PH	1	-0.733	14.51	<0.001	$\text{Ref}_{a,1}$ $\text{Pine}_{a,b}$ Fors_2 $\text{Irr}_{b,c}$ Orch_c	---	---	---	---	---

Table 3.7 Results of the PCA and MRPP analyses and associated Multiple Comparison procedures performed on isolated wetland water quality in 2010 and 2012.

Year	Surrounding Land use	N	PCA Ordination: PC Axes	Eigenvalue	% variance	*p*-value	MRPP: *A*	*p*-value	significant groups[a]
2010	Reference	9	1	2.763	46.052	0.001	0.2520	<0.001	Ref_a, $Fors_{ab}$, $Pine_{ab}$, $Orch_b$, Dry_{ab}, Irr_b
	Forest	3							
	Planted Pine	6	2	1.49	24.829	0.073			
	Pecan Orchard	4							
	Dryland Row Crop	1	3	1.124	18.725	0.242			
	Irrigated Row Crop	4							
2012	Reference	4	1	2.676	44.596	0.001	0.1232	0.002	Ref_a, $Fors_{ab}$, $Pine_a$, $Orch_b$, Dry_{ab}, Irr_{ab}
	Forest	6							
	Planted Pine	5	---	---	---	---			
	Pecan Orchard	6							
	Dryland Row Crop	4	---	---	---	---			
	Irrigated Row Crop	4							

[a] Significance differences between pairs of groups were evaluated with Bonferroni adjusted alpha values and are indicated by different subscripts.

Table 3.8 Indicator species within isolated wetlands with strong associations to specific land use classes within the Dougherty Plain (1 of 3).

Dominant Surrounding Land Use	Species	Code	Wetland Status	Status	All Wetlands		Open-canopy Wetlands		Closed-canopy Wetlands	
					IV	*p*	IV	*p*	IV	p
Reference	*Amphicarpum muhlenbergianum*	AMMU	FACW	NP	30.1	0.0176	60	0.016	---	---
	Aristida palustris	ARPA	OBL	NP	33.3	0.0052	---	---	---	---
	Carex glaucescens	CAGU	OBL	NP	---	---	---	---	49.7	0.0296
	Centella asiatica	CEAS	FACW	NP	52.4	<0.001	---	---	96.7	<0.001
	Coelorachis rugosa	CORU	OBL	NP	34.3	0.008	45.4	0.030	---	---
	Dichanthelium Leucothrix	DILE	---	NP	52.8	0.001	---	---	71.5	0.031
	Drosera brevifolia	DRBR	OBL	NP	33.3	0.0064	60	0.016	---	---
	Echinodorus tenellus	ECTE	OBL	NP	29.2	0.0316	48.4	0.049	---	---
	Eriocaulon compressum	ERCO	OBL	NP	33.3	0.0066	---	---	---	---
	Erigeron vernus	ERVE	OBL	NP	---	---	---	---	50	0.038
	Euthamia caroliniana	EUCL	FACU	NP	43.6	0.0018	---	---	71.8	0.015
	Eupatorium leucolepis	EULU	FACW+	NP	33.3	0.0076	---	---	75	0.0094
	Eupatorium mohrii	EUMO	FACW-	NP	44.4	<0.001	---	---	50	0.038
	Leersia hexandra	LEHE	OBL	NP	63.5	<0.001	---	---	72.2	0.0192
	Leucothoe racemosa	LERA	FACW	NP	---	---	---	---	47.1	0.038
	Ludwigia pilosa	LUPI	OBL	NP	31.8	0.03	---	---	---	---
	Lycopus rubellus	LYRU	OBL	NP	---	---	---	---	50	0.038
	Panicum anceps	PAAN	FAC-	NP	25	0.0354	---	---	---	---
	Panicum hemitomon	PAHE	OBL	NP	30.5	0.0234	---	---	---	---
	Piriqueta cistoides	PICI	---	NP	27.6	0.0192	49.6	0.021	---	---
	Pluchea rosea	PLRO	FACW	NP	---	---	---	---	45.7	0.036
	Proserpinaca pectinata	PRPE	OBL	NP	32	0.0136	---	---	---	---
	Rhynchospora filifolia	RHFI	FACW-	NP	39.4	0.0036	59.2	0.008	---	---
	Rhynchospora globularis	RHGG	FACW	NP	43.1	<0.001	80	0.002	---	---
	Rhexia mariana	RHMA	FACW+	NP	42.7	0.002	---	---	---	---

Table 3.8 Continued (2 of 3).

Dominant Surrounding Land Use	Species	Code	Wetland Status	Status	All Wetlands		Open-canopy Wetlands		Closed-canopy Wetlands	
					IV	*p*	IV	*p*	IV	p
Reference (continued)	*Rhexia virginica*	RHVI	FACW+	NP	32.4	0.0144	---	---	50	0.036
	Rubus cuneifolius	RUCU	FACU	NP	---	---	---	---	64.7	0.0332
	Rudbeckia mohrii	RUMO	FACW+	NP	37.2	0.0026	---	---	---	---
	Scleria reticularis	SCRE	OBL	NP	31.3	0.0198	---	---	---	---
	Sporobolus floridanus	SPFL	FAC	NP	44.4	<0.001	---	---	75	0.012
	Stylisma aquatica	STAQ	FACW+	NP	42.9	0.0016	58.7	0.011	---	---
	Viola lanceolata	VILA	OBL	NP	74.3	<0.001	74.5	0.005	72.7	0.0158
	Woodwardia virginca	WOVI	OBL	NP	28.5	0.0224	---	---	67.6	0.02
	Xyris jupicai	XYJU	OBL	NP	22.2	0.0494	---	---	---	---
Forest	*Cephalanthus occidentalis*	CEOC	OBL	NP	32.6	0.0464	---	---	---	---
	Hypericum hypericoides	HYHY	FAC	NP	27.5	0.0242	---	---	---	---
	Smilax bona-nox	SMBO	FAC	NP	41.6	0.0084	---	---	---	---
	Eupatorium capillifolium	EUCA	FACU	NA	---	---	65.3	0.014	---	---
	Juncus repens	JURE	OBL	NP	---	---	48.7	0.034	---	---
	Quercus laurifolia	QULA	FACW	NP	---	---	61.5	0.017	---	---
	Quercus virginiana	QUVI	FACU+	NP	---	---	49.7	0.019	---	---
Planted Pine	*Carex glaucescens*	CAGU	OBL	NP	---	---	38.5	0.047	---	---
	Cephalanthus occidentalis	CEOC	OBL	NP	---	---	59	0.008	---	---
	Croton elliottii	CREO	FACW+	NP	---	---	68.5	0.017	---	---
Pecan Orchard	*Ambrosia artemisiifolia*	AMAT	FACU	NA	---	---	---	---	100	0.0038
	Boehmeria cylindrica	BOCY	FACW+	NP	32.6	0.0126	---	---	---	---
	Commelina communis	COCO	FAC	EA	36.4	0.0032	---	---	---	---
	Cuphea carthagenensis	CUCR	FACW	EA	27.3	0.0174	---	---	---	---
	Cyperus compressus	CYCO	FACW	NA	26.3	0.0454	---	---	---	---
	Cynodon dactylon	CYDA	FACU	EP	36.4	0.0024	44.4	0.043	---	---

Table 3.8 Continued (3 of 3).

Dominant Surrounding Land Use	Species	Code	Wetland Status	Status	All Wetlands		Open-canopy Wetlands		Closed-canopy Wetlands	
					IV	*p*	IV	*p*	IV	p
Pecan Orchard (continued)	*Cyperus retrorsus*	CYRR	FACU+	NP	24.2	0.0366	---	---	---	---
	Cyperus virens	CYVI	FACW	NP	36.4	0.005	44.4	0.029	---	---
	Digitaria ciliaris	DICI	---	EA	28.3	0.0416	---	---	---	---
	Echinochloa colona	ECCO	FACW	EA	43.9	0.0034	50.5	0.04	---	---
	Geranium carolinianum	GECA	---	NA	23.8	0.0376	---	---	---	---
	Juncus effusus	JUEF	FACW+	NP	27.1	0.0344	---	---	---	---
	Ludwigia palustris	LUPA	OBL	NP	44.3	0.002	55.6	0.035	---	---
	Modiola caroliniana	MOCA	FACU+	NP	27.3	0.0164	---	---	---	---
	Paspalum urvillei	PAUR	FAC	NP	27.2	0.0324	---	---	---	---
	Polygonum hydropiperoides	POHY	OBL	NP	42.4	0.0294	---	---	---	---
	Prunus serotina	PRSE	FACU	NP	---	---	---	---	98.1	0.0032
	Rumex verticillatus	RUVE	FACW+	NP	24.2	0.0348	---	---	---	---
Dryland Row-crop	*Ampelopsis arborea*	AMAE	FAC+	NP	---	---	---	---	61.5	0.0302
Irrigated Row-crop	*Ammania coccinea*	AMCO	FACW+	NP	50	<0.001	57.1	0.021	---	---
	Cyperus iria	CYIR	FACW	EA	28.2	0.0472	---	---	---	---
	Cyperus rotundus	CYRT	FAC-	EP	25	0.0156	---	---	---	---
	Eclipta prostrata	ECPR	FACW-	NP	58.3	<0.001	54.1	0.022	---	---
	Gossypium hirsutum	GOHI	---	NP	25	0.0126	---	---	---	---
	Melochia corchorifolia	MECO	FAC	NP	20.9	0.0486	---	---	---	---
	Mollugo verticillata	MOVE	FAC	EA	67.3	<0.001	71.5	0.015	---	---
	Paspalum boscianum	PABO	FACW	NP	25	0.0182	---	---	---	---
	Polygonum lapathifolium	POLA	FACW	NA	50.9	<0.001	57.4	0.017	---	---
	Sida rhombifolia	SIRH	FACU	NA	49.4	0.0036	---	---	---	---

Table 3.9 A comparison of land use classification scenarios using MRPP and Tukey's Multiple Comparison procedure with Bonferroni-corrected α values. "Sig ratio" provides a measure of how well each scenario distinguishes between groups by denoting the ratio of significantly different pairwise comparisons relative to those which were not significant. The effectiveness of alternate grouping scenarios is considered for both macrophyte community and water quality.

Classification Scenarios	Macrophyte Community				2010 Water Quality[a]			
	A	*p*-value	α	sig ratio	A	*p*-value	α	sig ratio
Original	0.2909	<0.001	0.00333	9/15	0.2520	<0.001	0.005	2/10
I	0.2747	<0.001	0.005	6/10	0.2316	<0.001	0.00833	3/6
II	0.2316	<0.001	0.00833	2/6	0.2139	<0.001	0.01667	2/3
III	0.2738	<0.001	0.005	8/10	0.2520	<0.001	0.005	2/10
IV	0.2586	<0.001	0.00833	5/6	0.2316	<0.001	0.00833	3/6

[a] In 2010, only one Dryland Row-crop wetland was sampled for water quality and so could not be included in MRPP analyses. With the absence of Dryland Row-Crop, Scenarios III and IV become redundant with the Original Scenario and Scenario I, respectively.

CHAPTER 4

THE INFLUENCE OF AGRICULTURAL LAND USE HISTORY ON SEED BANK COMPOSITION OF ISOLATED WETLANDS

Stuber, O.S., Kirkman, L.K., and Hepinstall-Cymerman, J. To be submitted to *Wetlands*.

Introduction

Anthropogenic alteration of the landscape in the past often continues to affect ecosystem patterns and processes (i.e., “land use legacies”). For example, impacts associated with agricultural land use such as land-clearing, erosion, and nutrient uptake may continue to influence the landscape decades, and even centuries later, with resulting evidence such as regionally homogenized plant communities and depletion and leaching of soil in forested landscapes, as well as accumulation of sediment, organic C, and N in wetland landscapes (Foster et al. 1998, Fuller et al. 1998, Compton and Boone 2000, Craft and Casey 2000). The influence of historical land use can be particularly evident in seed bank community composition. Plue et al. (2008) demonstrated that anthropogenic activity continues to influence seed bank richness via increased phosphorous levels 1600 years after the last human settlements on the land. More directly, several studies have shown that grasslands with a history of agriculture tend to have high-density seed banks, similar to the large seed banks found in arable lands (Lavorel et al. 1993, Luzuriaga et al. 2005), whereas minimally-disturbed grasslands, such as California bunchgrass, can be associated with relatively smaller seed banks (Major and Pyott 1966).

Seed bank studies are a conventional method for cataloging and quantifying the assemblage of plant species with potential to germinate in a site. A seed bank includes both persistent seeds and transient seeds (Thompson and Grime 1979). Transient seed banks are representative of those species whose seeds have arrived within the year, typically occurring within the top layer of soil and organic duff, and which are not likely to remain viable over a long period of time. Persistent seeds are generally assumed to be buried beneath the soil surface through actions of animals, humans, and weather, though the seeds can be found in the soil surface as well (Thompson and Fenner 2000). Persistent seed banks, because they remain viable in the soil for longer periods of time, are important reserves of biodiversity and contribute to the resilience of dynamic, disturbance-dependent ecosystems (Baskin and Baskin 1998). They are considered an important potential source of “desirable” species which were present at a site prior to anthropogenic disturbance; consequently, many restoration efforts incorporate seed bank studies.

Studies of isolated depressional wetlands in the Southeast indicate that the persistent seed banks provide a source of propagules of diverse, native plant species that may play a role in revegetation immediately post-disturbance (Kirkman and Shartiz 1994) and in some cases long after the initial anthropogenic disturbance (Martin and Kirkman 2009, De Steven and Lowrance 2011). The restoration potential via passive methods that rely on the seed bank is site dependent; in some situations, such as when the seed bank contains low densities of target species, the seed bank is not a viable option for revegetation (Blomqvist et al. 2003, Bossuyt and Honnay 2008, Chaideftou et al. 2011), while others have found that the seed bank could contribute to successful revegetation, if accompanied by additional, complementary management techniques (Bossuyt and Honnay 2008, Martin and Kirkman 2009, Wang et al. 2010, Valkó et al. 2011).

In this study, we examine the role of agricultural land use history on the composition of the soil seed bank in isolated depressional wetlands currently located within irrigated agricultural fields within the Dougherty Plain. Because these wetlands are subjected to seasonal physical disturbance via tilling and plowing, as well as atypical hydroperiods associated with seasonal irrigation, wetland vegetation communities are species poor relative to reference sites (See Chapter 3). My objective is to determine if restoration potential varies depending on the length of time which a wetland has been disturbed by agricultural practices (60 years versus approximately 30 years). The conclusions from this experiment will be of interest to the

Wetlands Reserve Program (WRP) of the National Resources Conservation Service (NRCS), which must prioritize degraded wetlands as candidates for restoration.

Methods

Study Area

The Dougherty Plain is a physiogeographic subregion of the Coastal Plain characterized by karst topography (Beck and Arden 1983), and covers approximately 6,690 km^2 in southwestern Georgia. Geographically isolated limesink wetlands are a prominent feature of the karst landscape; the average nearest neighbor distance between wetlands is less than 200 meters. (Hendricks and Goodwin 1952, Kirkman et al. 1996, Kirkman et al. 1999, Tiner 2003, Martin et al. 2012). Historically, this region was dominated by fire-maintained longleaf pine-wiregrass (*Pinus palustris* Mill.-*Aristida beyrichiana* Trin. & Rupr.) savannas with a highly diverse understory (Walker 1993, Drew et al. 1998, Engstrom et al. 2001). Today, row crop agriculture is of major economic importance, and constitutes approximately a third of the land use of the Dougherty Plain. A majority of the agricultural land is irrigated with center pivot systems. Agriculture has been practiced in Georgia for centuries, but irrigated agricultural lands expanded most rapidly in the state between 1977 and 1980 (Haire 2005) following the introduction of center pivot irrigation technology.

Wetland Selection and Delineation

Potential wetland sampling sites were identified within 39 randomly-stratified subunits, comprising a total 10% of the Dougherty Plain, for which photo-interpreted historical LULC data was available for the years 1948, 1968, 1993, and 2007. I selected 6 wetlands currently surrounded by agriculture for seed bank sampling based upon the historical trajectory in the surrounding upland. Three wetlands were selected in each of 2 focal trajectories: 1) natural forest converted to irrigated agriculture between 1968 and 1993 (30 years of cultivation), and 2) unirrigated agriculture (dryland row-crop or pasture) converted to irrigated row-crop agriculture between 1968 and 1993 (60 years of cultivation). Presumably, the land surrounding study sites was converted to irrigated agriculture following the popularization of center pivot irrigation technology in the late 1970's and early 1980's.

In most cases, wetlands were delineated in the field by collecting points along the wetland boundary with a TDS Nomad GPS unit (Tripod Data Systems, Westminster, CO, USA) operating with a Crescent A100 Smart Antenna (Hemisphere GPS, Calgary, AB, CAN) with estimated sub-meter horizontal accuracy. To determine the wetland boundary, I used the presence of hydric soil indicators (NRCS, 2010); often the hydrology and vegetation were unreliable indicators as a result of anthropogenic alteration of the site. Boundary points were imported into ArcMAP 9.2 (Environmental Systems Research Institute, Redlands, CA, USA), converted to polygons, and "smoothed" to create a vector layer of all delineated wetland sites. In a few cases, none of the standard wetland indicators were present due to the degree of soil disturbance. To delineate the boundary for these wetland sites, I interpreted high-resolution NAIP photography from 2010. I observed color, texture, and pattern of the soils and vegetation associated with field-delineated agricultural wetland boundaries, and delineated the remaining wetlands using the same visual cues. Wetlands selected for study varied in shape from circular to oblong, and ranged in area from 0.4 – 2.3 ha, which is representative of the majority of isolated wetlands in the Dougherty Plain.

Data Collection

Seed bank soil samples were collected in November and December 2011. At each wetland, we established a sampling transect along a randomly selected bearing such that each transect extended from one edge of the wetland, through the center, and past the wetland boundary to the opposite edge into the surrounding upland. Transect lengths varied from 94 to 219 meters, depending upon wetland size and shape. Sampling points were placed every 15 m along each transect, including one sampling point anchored in the upland at each transect end. To avoid sampling in areas where the original topsoil was obviously removed or deeply buried, sampling points which fell in areas of drastic topographical alteration (e.g. deeply dredged areas or pivot berms) were offset along secondary transects perpendicular to the main transect, and placed at the nearest location where original topsoil was still presumably present, albeit altered by regular tilling or sedimentation (Figure 4.1). Five cylindrical soil cores (10 cm deep by 7 cm diameter) were collected from within a $1 m^2$ frame at each sampling point, and the soil was homogenized into a single sample.

Seed bank community composition was assessed with data from a standard seedling emergence study conducted from January to August 2012. Soil samples were stored at 4° C until they could be processed through a series of sieves to remove vegetative propagules. Each sample was spread on a layer of potting soil in plastic tubs with holes in the bottom for drainage. Tubs were arranged randomly in the greenhouse and watered regularly with reverse osmosis-filtered water and maintained at ambient temperature. Seedlings were identified every 2 – 4 weeks and discarded. Unidentified seedlings were transplanted to separate pots and grown until they were mature enough to be identified.

To compare seed bank composition with standing vegetation, standing vegetation was also sampled at two of the sample wetlands of similar size (ca. 1.5 ha) with different historical trajectories. Twelve sampling points were randomly distributed throughout each wetland. At each sampling point, all species within a $1 m^2$ plot were recorded, and abundance of each species was estimated using 6 cover classes (1=<1%, 2=1-5%, 3=6-15%, 4=16-30%, 5=31-60%, 6=61-100%).

Data Analysis

To compare the seed bank communities among wetlands and between land use histories, descriptive community metrics based on abundance were calculated for the seed bank in each wetland and included: seedling density (per m^2), richness, % exotic species, annual/perennial ratio, % herbaceous species, % hydrophytes (including obligate and facultative wet species), and % native hydrophyte perennials. Species abundance was derived from the proportion of germinants of each species relative to the total number of germinants in each wetland. Similarly, community metrics were also calculated for standing vegetation in wetlands where groundcover was sampled. Abundance of species present in the groundcover was calculated based on percent cover and averaged across all plots in each wetland.

To compare overall community composition between the two land use histories, I used non-metric multidimensional scaling (NMS) procedure in PC-ORD (McCune and Mefford 2011). Most species identified were present at very low relative abundances (< 1% of the seed bank) due to the prolific germination of a few species. Species which represented < 1% of a wetland's seed bank community were removed for ordinations, and abundances were log-transformed to improve normality. Two-sided T-tests were used to compare the community metrics of land use history groups. Metrics were transformed using either arc sin square root or logarithmic functions to best improve normality. Percent similarity between ground cover and seed bank communities was determined using Sorenson's similarity index.

Results

A total of 92 species were observed within the seed banks of the wetlands sampled and three seedlings that were not identified to the species level. Mean (± SE) seedling density was 31,701 (±9,020) per m^2. The distribution of species and total individuals varied considerably by wetland. Few species dominated the seed bank of any wetland. Of the total species, only 9 composed more than 10% of the seed bank community in at least one wetland. *Polygonum lapathifolium* L. (curlytop knotweed), an annual herb, was the most abundant species, with a mean (± SE) seedling density of 9,078 (± 4,773) per m^2, and was present in all six wetlands. Several other herbaceous species were present at mean densities greater than 1000 seedlings/m^2, and were found in all wetlands: *Echinochloa crus-galli* (L.) P. Beauv. (barnyard grass), *Eclipta prostrata* (L.) L. (false daisy), *Lindernia dubia* (L.) Pennell (yellowseed false pimpernel), *Panicum dichotomiflorum* Michx. (fall panicgrass), and *Veronica peregrina* L. (purslane speedwell). Seventy-six species contributed less than an average of 1% to seedling density in any wetland.

No consistent patterns in seed bank composition based on agricultural history were observed based on the NMS ordinations. The procedure was unable to generate a solution, likely due to low sample size and highly heterogeneous data. There were no significant differences between the community metrics of each land use history group, therefore all further results combine the seed bank community data for all wetlands.

The seed banks in these wetlands were almost entirely composed of herbaceous species (Table 4.2). Wetland seed bank richness averaged 53 species per wetland. Exotic species composed nearly ¼ of the total seed bank. The average annual/perennial ratio was 1.9. In general, hydrophytes were abundant, composing more than 75% of the seed bank on average.

Specifically, native perennial hydrophytes represented about 1/3 of the seed bank community on average. Only 14 taxa occurred relatively frequently (present in ≥ 3 wetlands with $\geq 1\%$ abundance). Of the frequent taxa, all were herbaceous, and more than half were hydrophytes (Table 4.1). Only 4 of the frequently occurring species were exotic.

The Seed Bank-Vegetation Relationship

The standing vegetation within the wetlands differed considerably from the seed bank in the wetlands in which ground cover was sampled. In both wetlands sampled, groundcover species richness was n=27, compared to an average richness of n=58 in the seed banks. Species which were present aboveground, but absent in the emergent seed bank included: *Cyperus rotundus* L. (nutgrass), *Diospyros virginiana* L. (common persimmon), and *Gossypium hirsutum* L. (upland cotton; Table 4.1). Overall, percent similarity between the standing vegetation and the seed bank was 34%. Similar to the seed bank, the ground cover in both wetlands was dominated by herbaceous species (Table 4.2). The cover of hydrophytes varied dramatically between wetlands (7% - 61%), as did the cover of exotic species (26% - 69%), where the wetland with lower coverage of hydrophytes also had a greater abundance of exotic species. Native perennial hydrophytes were present in similar abundances at both sites (3% - 6%).

Discussion

Historic vs. Current Land Use

No consistent patterns in composition of the soil seed bank of the isolated wetlands in this study could be attributed to length of time in cultivation. The agricultural practice of plowing is generally associated with the physical removal of seeds and propagules from the seed bank (Tørresen and Skuterud 2002), as well as redistribution and dilution of the seed bank to at least

12 cm below the surface (Luzuriaga et al. 2005). Accordingly, studies have demonstrated major shifts in seed bank composition following agricultural disturbance (Buhler 1995, Colbach et al. 2000). Results from this study indicate that decades of repetitive cultivation eliminates legacy effects of different land use histories on the wetland seed bank communities. Thus, I found no evidence to warrant the prioritization of agricultural wetlands for restoration based upon length of time in cultivation.

Implications for Restoration

Though many of the most abundant species were annual species typically associated with disturbance, seed bank communities as a whole were overwhelmingly dominated by herbaceous species, a considerable portion of which were native hydrophytes. The seed bank of historically-cultivated Carolina bays censused by De Steven et al (2006) showed similar proportions of herbaceous and wetland taxa. Additionally, the presence in the seed bank of native perennials commonly found in less disturbed wetlands (e.g. *Rhexia mariana* L. (Maryland meadowbeauty), *Juncus repens* Michx. (lesser creeping rush), and *Ludwigia palustris* (L.) Elliott (marsh seedbox), and their absence from the aboveground vegetation suggests that species which were likely present prior to cultivation may continue to persist in the seed bank. Indeed, DeVictor et al (2007) demonstrated that seeds within an actively cultivated portion of a seasonal pool were merely buried in the lower strata of the topsoil, and remained viable. Thus, the seed bank within agricultural isolated wetlands may be an effective source for the establishment of functional hydrophytes.

The majority of depression wetlands restored through the WRP begin as agricultural wetlands, and within Georgia, depression wetlands are the most common wetland type enrolled in the WRP (De Steven and Gramling 2012). Typically, after altering the topography to restore the original hydrology, the restoration is left to passive revegetation, though in some cases wetland trees may be planted as well. De Steven and Lowrence (2011) observed that the goals of the WRP restoration projects may not necessarily include returning wetlands to a reference community. Rather, the program aims to broadly restore wetland function, with a focus on restoring or changing the hydrology to suit the landowner's preferences, and to increase wildlife habitat. With these goals in mind, the overall dominance of hydrophytes and native species in the seed banks indicates that agricultural wetland seed banks may in fact be a relatively good source for passive seedling recruitment and establishment following restoration of the hydrologic regime.

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Literature Cited

Baskin, C. C. and J. M. Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. Academic Press, Lexington.

Beck, B. F. and D. D. Arden. 1983. Hydrology and geomorphology of the Dougherty Plain, southwest Georgia. Southeastern Geological Society, Tallahassee, FL.

Blomqvist, M. M., R. M. Bekker, and P. Vos. 2003. Restoration of Ditch Bank Plant Species Richness: The Potential of the Soil Seed Bank. Applied Vegetation Science **6**:179-188.

Bossuyt, B. and O. Honnay. 2008. Can the seed bank be used for ecological restoration? An overview of seed bank characteristics in European communities [electronic resource]. Journal of Vegetation Science **19**:875-884.

Buhler, D. D. 1995. Influence of tillage systems on weed population dynamics and management in corn and soybean in the central USA. Crop science **35**:1247-1258.

Chaideftou, E., C. A. Thanos, E. Bergmeier, A. S. Kallimanis, and P. Dimopoulos. 2011. The herb layer restoration potential of the soil seed bank in an overgrazed oak forest. Journal of Biological Research **15**:47-57.

Colbach, N., J. Roger-Estrade, B. Chauvel, and J. Caneill. 2000. Modelling vertical and lateral seed bank movements during mouldboard ploughing. European Journal of Agronomy **13**:111-124.

Compton, J. E. and R. D. Boone. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology **81**:2314.

Craft, C. B. and W. P. Casey. 2000. Sediment and nutrient accumulation in floodplain and depressional freshwater wetlands of Georgia, USA. Wetlands **20**:323-332.

De Steven, D. and J. Gramling. 2012. Diverse Characteristics of Wetlands Restored under the Wetlands Reserve Program in the Southeastern United States. Wetlands **32**:593-604.

De Steven, D. and R. Lowrance. 2011. Agricultural conservation practices and wetland ecosystem services in the wetland-rich Piedmont-Coastal Plain region. Ecological Applications **21**:S3-S17.

De Steven, D., R. R. Sharitz, J. H. Singer, and C. D. Barton. 2006. Testing a passive revegetation approach for restoring coastal plain depression wetlands. Restoration Ecology **14**:452-460.

Devictor, V., J. Moret, and N. Machon. 2007. Impact of Ploughing on Soil Seed Bank Dynamics in Temporary Pools. Plant Ecology:45.

Drew, M. B., L. K. Kirkman, and A. K. Gholson, Jr. 1998. The Vascular Flora of Ichauway, Baker County, Georgia: A Remnant Longleaf Pine/Wiregrass Ecosystem. Castanea **63**:1-24.

Engstrom, R. T., L. K. Kirkman, and R. J. Mitchell. 2001. Natural History: Longleaf Pine-Wiregrass Ecosystem. Pages 5-18 *in* J. R. Willson, editor. The Fire Forest: Longleaf Pine-Wiregrass Ecosystem. Georgia Wildlife Natural Georgia Series 8, Georgia Wildlife Federation.

Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-Use History as Long-Term Broad-Scale Disturbance: Regional Forest Dynamics in Central New England. Ecosystems **1**:96-119.

Fuller, J. L., D. R. Foster, J. S. McLachlan, and N. Drake. 1998. Impact of human activity on regional forest composition and dynamics in central New England. Ecosystems **1**:76-95.

Haire, B. 2005. Georgia Irrigation Expansion Slows. Southeast Farm Press.

Hendricks, E. L. and M. H. Goodwin. 1952. Water-level fluctuations in limestone sinks in southwestern Georgia. U.S. Geological Survey Water-Supply Paper 1110-E.

Kirkman, L. K., S. W. Golladay, L. LaClaire, and R. Sutter. 1999. Biodiversity in southeastern seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society **18**:553-562.

Kirkman, L. K., R. L. Lide, G. Wein, and R. R. Shartiz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western coastal plain of South Carolina. Wetlands **16**:564-576.

Kirkman, L. K. and R. R. Shartiz. 1994. Vegetation disturbance and maintenance of diversity in intermittently flooded carolina bays in South Carolina. Ecological Application **4**:177-188.

Lavorel, S., M. Debussche, J.-D. Lebreton, and J. Lepart. 1993. Seasonal Patterns in the Seed Bank of Mediterranean Old-Fields. Oikos:114.

Luzuriaga, A. L., A. Escudero, J. M. Olano, and J. Loidi. 2005. Regenerative role of seed banks following an intense soil disturbance. Acta Oecologica **27**:57-66.

Major, J. and W. T. Pyott. 1966. Buried, Viable Seeds in Two California Bunchgrass Sites and Their Bearing on the Definition of a Flora. Vegetatio:253.

Martin, G. I., L. K. Kirkman, and J. Hepinstall-Cymerman. 2012. Mapping geographically isolated wetlands in the Dougherty Plain, Georgia, USA. Wetlands **32**:149-160.

Martin, K. L. and L. K. Kirkman. 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the south-eastern USA. Journal of Applied Ecology **46**:906-914.

McCune, B. and M. J. Mefford. 2011. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software, Gleneden Beach, Oregon, USA.

Natural Resources Conservation Service. 2010. Field Indicators of Hydric Soils in the United States, Version 7.0.*in* L. M. Vasilas, G. W. Hurt, and C. V. Noble, editors.

Plue, J., M. Hermy, K. Verheyen, P. Thuillier, R. Saguez, and G. Decocq. 2008. Persistent changes in forest vegetation and seed bank 1,600 years after human occupation. Landscape Ecology **23**:673-688.

Thompson, K. and M. Fenner. 2000. The functional ecology of soil seed banks. Seeds: the ecology of regeneration in plant communities **2**:215-235.

Thompson, K. and J. P. Grime. 1979. Seasonal Variation in the Seed Banks of Herbaceous Species in Ten Contrasting Habitats. The Journal of Ecology **67**:893-921.

Tiner, R. W. 2003. Estimated extent of geographically isolated wetlands in selected areas of the United States. Wetlands **23**:636-652.

Tørresen, K. S. and R. Skuterud. 2002. Plant protection in spring cereal production with reduced tillage. IV.: Changes in the weed flora and weed seedbank. Crop Protection **21**:179-193.

Valkó, O., P. Török, B. Tóthmérész, and G. Matus. 2011. Restoration Potential in Seed Banks of Acidic Fen and Dry-Mesophilous Meadows: Can Restoration Be Based on Local Seed Banks? Restoration Ecology **19**:9-15.

Walker, J. L. 1993. Rare Vascular Plant Taxa Associated with the Longleaf Pine Ecosystem.*in* Tall Timbers Fire Ecology Conference.

Wang, N., J. Y. Jiao, Y. F. Jia, W. J. Bai, and Z. G. Zhang. 2010. Germinable soil seed banks and the restoration potential of abandoned cropland on the Chinese Hilly-gullied Loess Plateau. Environmental Management **46**:367-377.

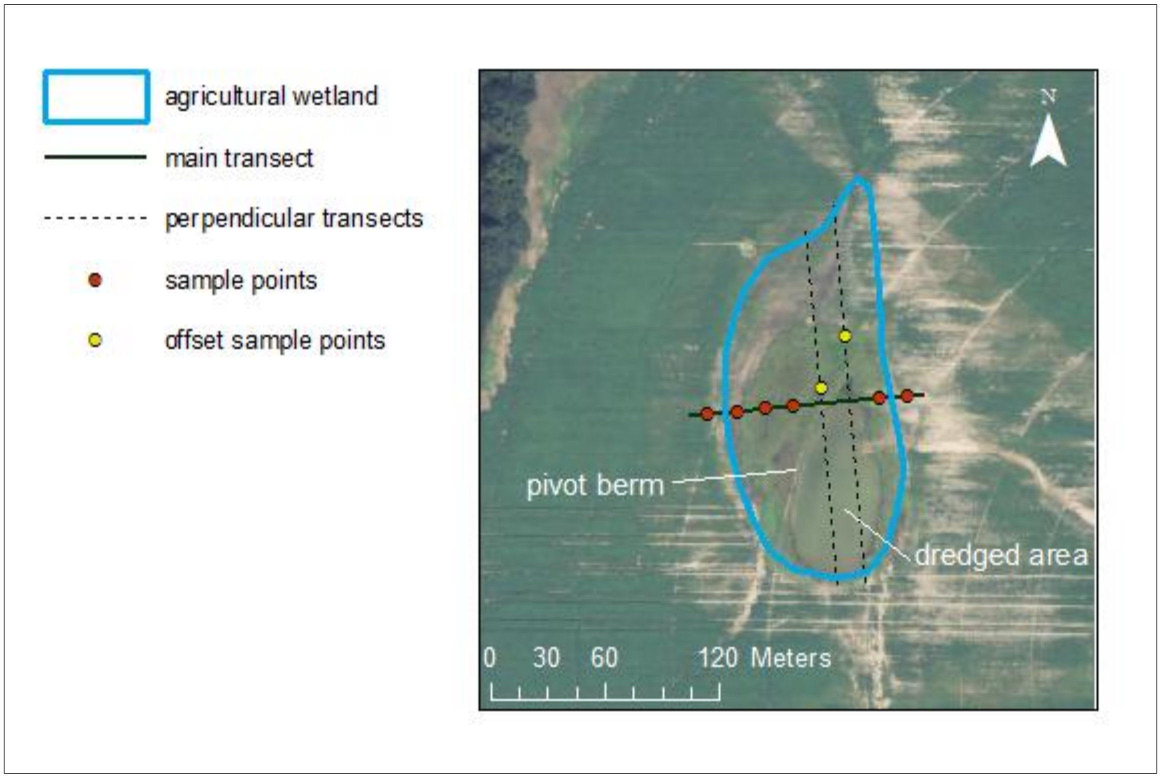

Figure 4.1 Seed bank sampling scheme in agricultural wetland with extensive topographic alteration (dredging and berms). Note that two sample points were offset to areas where topsoil was still relatively intact.

Table 4.1 (Page 1 of 3) List of species in soil seed bank and standing vegetation of agricultural wetlands (OS32, OS4, OS62, OS40, OS31, and OS44). For soil seed bank species, both density (seedlings/m^2) and proportion of seed bank is listed. N= native, E = exotic, A = annual, P = perennial. Wetland status is reported using standardized abbreviation from the USDA plants database (http://plants.usda.gov/wetland.html).

	Species Characteristics			≥ 60 Years in Cultivation						ca. 30 Years in Cultivation						Groundcover	
				OS32		OS4		OS62		OS40		OS31		OS44		OS32	OS40
Species	**Status**	**Wetland Status**	**Habit**	dens.	%	dens.	%	dens.	%	dens.	%	dens.	%	dens.	%	%	%
Acalypha gracilens	NA	---	Forb	---	---	---	---	---	---	---	---	---	---	6	---	---	---
Agrostis hyemalis	NA	FAC	Graminoid	---	---	7	< 1	---	---	---	---	---	---	65	< 1	---	---
Amaranthus blitum	EA	---	forb	---	---	---	---	---	---	---	---	30	< 1	---	---	---	---
Amaranthus palmeri	NA	FACU	forb	---	---	4	< 1	74	< 1	3181	4.6	---	---	91	< 1	---	7.0
Amaranthus spinosus	EA	FACU	Forb	13	< 1	93	< 1	---	---	---	---	---	---	---	---	---	---
Ambrosia artemisiifolia	NA	FACU	Forb	19	< 1	---	---	---	---	---	---	---	---	---	---	6.8	---
Ammania coccinea	NP	FACW+	Forb	91	< 1	408	< 1	683	4.0	2294	3.3	260	2.7	110	< 1	< 1	---
Anagallis minima	NA	FACW+	Forb	---	---	---	---	---	---	3	< 1	---	---	6	< 1	---	---
Bulbostylis barbata	EA	FAC-	Graminoid	---	---	4	< 1	---	---	55	< 1	74	< 1	---	---	---	---
Callicarpa americana	NP	FACU-	Shrub	---	---	---	---	7	< 1	---	---	---	---	---	---	---	---
Callitriche peploides	NA	OBL	Forb	---	---	---	---	171	1.0	35	< 1	---	---	273	1.2	---	---
Carex festucacea	NP	FACW	Graminoid	---	---	11	< 1	---	---	14	< 1	---	---	71	< 1	---	3.1
Cerastium glomeratum	EA	FACU-	Forb	32	< 1	---	---	---	---	---	---	---	---	---	---	---	---
Chamaesyce maculata	NA	FACU	Forb	---	---	---	---	---	---	3	< 1	7	< 1	---	---	---	---
Chenopodium album	EA	FAC-	Forb	6	< 1	11	< 1	---	---	---	---	---	---	---	---	---	---
Chenopodium ambrosioides	EA	FACU	Forb	---	---	11	< 1	---	---	3	< 1	---	---	---	---	---	---
Commelina benghalensis	EP	---	forb	---	---	---	---	---	---	---	---	---	---	---	---	< 1	---
Conyza canadensis	NA	FACU	Forb	6	< 1	41	< 1	---	---	---	---	---	---	---	---	< 1	---
Coronopus didymus	EA	---	forb	71	< 1	7	< 1	15	< 1	14	< 1	---	---	---	---	< 1	---
Crassula aquatica	NA	OBL	Forb	169	< 1	---	---	2198	12.7	---	---	---	---	961	4.1	---	---
Croton glandulosus	NA	---	Forb	52	< 1	56	< 1	22	< 1	267	< 1	7	< 1	6	< 1	---	---
Cynodon dactylon	EP	FACU	Graminoid	26	< 1	15	< 1	---	---	14	< 1	119	1.2	---	---	---	---
Cyperus	---	---	Graminoid	---	---	7	< 1	---	---	3	< 1	---	---	---	---	---	---
Cyperus compressus	NA	FACW	Graminoid	110	< 1	928	2.0	780	4.5	142	< 1	393	4.1	19	< 1	---	---
Cyperus erythrorhizos	NA	OBL	Graminoid	---	---	22	< 1	---	---	---	---	---	---	6	< 1	---	---
Cyperus iria	EA	FACW	Graminoid	84	< 1	126	< 1	483	2.8	156	< 1	134	1.4	3086	13.2	---	< 1
Cyperus polystachyos	NA	FACW	Graminoid	---	---	---	---	---	---	---	---	---	---	52	< 1	---	---
Cyperus rotundus	EP	FAC-	Graminoid	---	---	---	---	---	---	---	---	---	---	---	---	5.7	3.8
Dactyloctenium aegyptium	EA	---	Graminoid	6	< 1	4	< 1	---	---	3	< 1	37	< 1	6	< 1	---	4.1
Desmodium tortuosum	NP	---	Subshrub	---	---	---	---	---	---	3	< 1	---	---	---	---	---	---
Dicot	---	---	0	26	< 1	197	< 1	30	< 1	28	< 1	15	< 1	104	< 1	---	---
Dicot	---	---	0	---	---	---	---	---	---	---	---	---	---	---	---	---	< 1
Dicot	---	---	0	---	---	---	---	---	---	---	---	---	---	---	---	< 1	---
Digitaria ciliaris	EA	---	Graminoid	520	2.1	7	< 1	---	---	818	1.2	97	1.0	71	< 1	< 1	10.8
Diodia virginiana	NP	FACW	Forb	---	---	---	---	---	---	24	< 1	---	---	---	---	---	2.0
Diospyros virginiana	NP	FAC	Tree	---	---	---	---	---	---	---	---	---	---	---	---	---	< 1
Echinochloa colona	EA	FACW	Graminoid	---	---	---	---	---	---	---	---	---	---	---	---	< 1	< 1

Table 4.1 Continued (pg. 2 of 3)

	Species Characteristics			≥ 60 Years in Cultivation						ca. 30 Years in Cultivation						Groundcover	
				OS32		**OS4**		**OS62**		**OS40**		**OS31**		**OS44**		**OS32**	**OS40**
Species	**Status**	**Wetland Status**	**Habit**	dens.	%	dens.	%	dens.	%	dens.	%	dens.	%	dens.	%	%	%
Echinochloa crusgalli	EA	FACW-	Graminoid	182	< 1	353	< 1	5123	29.6	6829	9.8	2064	21.5	39	< 1	---	---
Eclipta prostrata	NP	FACW-	Forb	1760	7.1	1626	3.6	549	3.2	610	< 1	408	4.3	1338	5.7	3.0	< 1
Eleocharis microcarpa	NA	OBL	Graminoid	169	< 1	156	< 1	30	< 1	52	< 1	---	---	793	3.4	---	---
Eleusine indica	EA	FACU	Graminoid	6	< 1	22	< 1	7	< 1	2089	3.0	7	< 1	546	2.3	---	---
Eryngium prostratum	NP	FACW	Forb	---	---	---	---	45	< 1	---	---	---	---	---	---	---	---
Eupatorium capillifolium	NA	FACU	Forb	591	2.4	---	---	7	< 1	---	---	---	---	32	< 1	---	---
Fimbristylis autumnalis	NA	OBL	Graminoid	---	---	33	< 1	15	< 1	14	< 1	---	---	227	< 1	---	---
Gamochaeta falcata	NA	---	Forb	585	2.3	846	1.9	52	< 1	28	< 1	104	1.1	175	< 1	---	---
Gamochaeta pensilvanica	NA	FACU-	Forb	565	2.3	290	< 1	67	< 1	35	< 1	59	< 1	149	< 1	---	---
Geranium carolinianum	NA	---	Forb	---	---	---	---	---	---	---	---	---	---	6	< 1	< 1	---
Gossypium hirsutum	NA	---	subshrub	---	---	---	---	---	---	---	---	---	---	---	---	1.9	---
Gratiola virginiana	NA	OBL	Forb	---	---	---	---	---	---	---	---	---	---	6	< 1	---	---
Ipomoea hederifolia	NA	FACW	Vine	---	---	48	< 1	---	---	---	---	---	---	---	---	---	---
Ipomoea quamoclit	EA	FACU+	Vine	---	---	7	< 1	---	---	---	---	---	---	---	---	---	---
Ipomoea triloba	EP	---	vine	26	< 1	7	< 1	---	---	7	< 1	---	---	---	---	7.0	< 1
Isolepis carinata	NA	FACW+	Graminoid	---	---	---	---	---	---	---	---	---	---	461	2.0	---	---
Jacquemontia tamnifolia	NA	FACU-	Vine	---	---	15	< 1	---	---	10	< 1	52	< 1	39	< 1	---	---
Juncus acuminatus	NP	OBL	Graminoid	---	---	---	---	---	---	---	---	---	---	13	< 1	---	---
Juncus bufonius	NA	FACW	Graminoid	201	< 1	---	---	---	---	10	< 1	---	---	169	< 1	---	---
Juncus dichotomus	NP	FACW	Graminoid	32	< 1	---	---	---	---	132	< 1	---	---	201	< 1	---	---
Juncus marginatus	NP	FACW	Graminoid	---	---	---	---	7	< 1	7	< 1	---	---	65	< 1	---	---
Juncus repens	NP	OBL	Graminoid	6	< 1	4	< 1	---	---	3	< 1	---	---	357	1.5	---	---
Lamium amplexicaule	EA	---	Forb	13	< 1	11	< 1	22	< 1	---	---	---	---	---	---	---	---
Lindernia dubia	NP	OBL	Forb	1195	4.8	10939	24.1	2740	15.9	11960	17.2	2658	27.7	6308	27.1	---	---
Ludwigia	---	---	0	---	---	---	---	---	---	---	---	---	---	---	---	---	< 1
Ludwigia decurrens	NP	OBL	Forb	117	< 1	59	< 1	15	< 1	14	< 1	557	5.8	669	2.9	---	---
Ludwigia octovalvis	NP	OBL	Forb	19	< 1	22	< 1	---	---	14	< 1	1128	11.8	741	3.2	---	---
Ludwigia palustris	NP	OBL	Forb	91	< 1	30	< 1	---	---	239	< 1	---	---	312	1.3	---	---
Lygodium japonicum	EP	FAC	Vine	---	---	---	---	7	< 1	7	< 1	---	---	---	---	---	---
Melochia corchorifolia	NP	FAC	Subshrub	104	< 1	63	< 1	104	< 1	170	< 1	7	< 1	208	< 1	1.0	---
Mollugo verticillata	EA	FAC	Forb	591	2.4	917	2.0	646	3.7	634	< 1	616	6.4	500	2.1	1.3	< 1
Oenothera laciniata	NP	FACU	Forb	19	< 1	4	< 1	---	---	---	---	---	---	---	---	< 1	---
Oldenlandia boscii	NP	FACW-	Forb	6	< 1	1982	4.4	1678	9.7	142	< 1	---	---	149	< 1	---	< 1
Oldenlandia corymbosa	EA	FAC+	Forb	2696	10.8	48	< 1	15	< 1	7	< 1	---	---	26	< 1	---	---
Oldenlandia uniflora	NA	FACW-	Forb	---	---	---	---	---	---	---	---	---	---	13	< 1	---	---
Oxalis	---	---	0	---	---	---	---	---	---	---	---	---	---	---	---	< 1	---
Oxalis corniculata	NP	FACU	Forb	39	< 1	74	< 1	30	< 1	7	< 1	---	---	45	< 1	---	---

Table 4.1 Continued (pg. 3 of 3)

	Species Characteristics			≥ 60 Years in Cultivation						ca. 30 Years in Cultivation						Groundcover	
				OS32		**OS4**		**OS62**		**OS40**		**OS31**		**OS44**		**OS32**	**OS40**
Species	**Status**	**Wetland Status**	**Habit**	dens.	**%**	dens.	**%**	dens.	**%**	dens.	**%**	dens.	**%**	dens.	**%**	**%**	**%**
Panicum dichotomiflorum	NA	FACW	Graminoid	169	< 1	6173	13.6	30	< 1	24	< 1	22	< 1	760	3.3	---	---
Panicum repens	EP	FACW-	Graminoid	---	---	4	< 1	---	---	3	< 1	---	---	130	< 1	---	---
Paspalum dissectum	NP	OBL	Graminoid	---	---	---	---	---	---	3	< 1	---	---	---	---	---	---
Paspalum urvillei	NP	FAC	Graminoid	---	---	---	---	---	---	---	---	---	---	---	---	---	< 1
Physalis angulata	NA	FAC	Forb	---	---	---	---	---	---	547	< 1	---	---	32	< 1	< 1	< 1
Plantago virginica	NA	FACU-	Forb	---	---	---	---	---	---	---	---	---	---	13	< 1	---	---
Poa annua	EA	FAC	Graminoid	---	---	4	< 1	---	---	---	---	---	---	6	< 1	---	---
Poa sylvestris	NP	FAC+	Graminoid	208	< 1	89	< 1	171	1.0	---	---	---	---	71	< 1	---	---
Polygonum hydropiperoides	NP	OBL	Forb	---	---	---	---	---	---	---	---	---	---	---	---	---	< 1
Polygonum lapathifolium	NA	FACW	Forb	8913	35.7	16318	35.9	22	< 1	28846	41.4	37	< 1	331	1.4	< 1	43.3
Polypremum procumbens	NP	FACU-	Forb	721	2.9	587	1.3	572	3.3	828	1.2	423	4.4	702	3.0	---	---
Portulaca amilis	EA	---	forb	32	< 1	4	< 1	52	< 1	3	< 1	---	---	13	< 1	---	---
Portulaca oleracea	EA	FACU	forb	---	---	4	< 1	7	< 1	315	< 1	7	< 1	---	---	---	< 1
Ranunculus platensis	EA	FAC+	Forb	6	< 1	---	---	---	---	---	---	7	< 1	6	< 1	---	---
Ranunculus pusillus	NA	FACW+	Forb	6	< 1	---	---	---	---	---	---	---	---	6	< 1	---	---
Rhexia mariana	NP	FACW+	Forb	---	---	---	---	---	---	---	---	---	---	13	< 1	---	---
Richardia brasiliensis	NP	---	Forb	---	---	---	---	---	---	---	---	15	< 1	---	---	---	---
Rorippa teres	NA	FACW	Forb	13	< 1	987	2.2	186	1.1	3284	4.7	15	< 1	52	< 1	---	---
Rotala ramosior	NA	OBL	Forb	19	< 1	52	< 1	7	< 1	152	< 1	52	< 1	6	< 1	---	---
Rumex	---	---	Forb	---	---	19	< 1	---	---	97	< 1	---	---	175	< 1	---	---
Senna obtusifolia	EA	---	Forb	19	< 1	7	< 1	---	---	---	---	---	---	130	< 1	7.6	< 1
Senna occidentalis	EA	---	Forb	---	---	---	---	---	---	---	---	---	---	---	---	< 1	---
Sesbania herbacea	NP	FACW-	Forb	6	< 1	4	< 1	312	1.8	---	---	---	---	156	< 1	---	---
Setaria parviflora	NP	FAC	Graminoid	---	---	---	---	---	---	---	---	---	---	---	---	---	< 1
Sibara virginica	NA	FAC	Forb	78	< 1	---	---	---	---	---	---	---	---	---	---	---	---
Sida rhombifolia	NA	FACU	Subshrub	175	< 1	33	< 1	7	< 1	3	< 1	7	< 1	1039	4.5	< 1	< 1
Solidago canadensis	NP	FACU	Forb	---	---	---	---	7	< 1	---	---	---	---	6	< 1	---	---
Stellaria media	EA	FACU	Forb	26	< 1	11	< 1	15	< 1	---	---	---	---	---	---	---	---
Symphyotrichum simmondsii	NP	---	forb	---	---	---	---	---	---	---	---	---	---	---	---	< 1	---
Triodanis biflora	NA	---	Forb	331	1.3	67	< 1	---	---	3	< 1	---	---	39	< 1	---	---
Urochloa platyphylla	NP	FAC+	Graminoid	279	1.1	45	< 1	7	< 1	3641	5.2	97	1.0	110	< 1	---	1.3
Verbena bonariensis	EP	FAC+	Subshrub	13	< 1	56	< 1	---	---	---	---	---	---	19	< 1	---	---
Verbena brasiliensis	EP	FAC-	Subshrub	---	---	---	---	---	---	---	---	---	---	---	---	---	< 1
Veronica peregrina	NA	FAC+	Forb	3612	14.5	1448	3.2	267	1.5	1809	2.6	67	< 1	968	4.2	---	---
Wahlenbergia marginata	EP	---	Forb	26	< 1	4	< 1	---	---	---	---	7	< 1	---	---	---	---
Xanthium strumarium	EA	FAC	Forb	39	< 1	---	---	---	---	---	---	---	---	---	---	9.8	---

Table 4.2 A comparison of seed bank and standing vegetation community metrics among wetlands.

Community Metrics[a]	≥ 60 years cultivated			ca. 30 years cultivated			Average seed bank metrics (± SE)	Standing Vegetation[c]	
	OS32[b]	OS4	OS62	OS40	OS31	OS44		OS32	OS40
Seedling Density (per m^2)	24945	45432	17283	69642	9592	23315	31,702 (± 9,020)	n/a	n/a
Richness	57	62	43	58	34	66	53 (± 5)	27	27
Annual/Perennial ratio	4.2	1.8	1.5	2.5	0.7	1	1.9 (± 0.5)	1.4	5.6
% Exotic	17.8	3.8	37.0	15.7	33.3	19.6	21.2 (± 5.0)	68.5	25.7
% Herbaceous	98.6	99.1	99.1	99.7	99.1	94.0	98.3 (± 0.9)	76.7	97.0
% Hydrophytes	53.6	88.7	87.2	79.0	80.6	76.8	77.6 (± 5.2)	6.8	61.0
% Native Perennial Hydrophytes	13.3	33.2	34.9	22.2	52.2	45.1	33.5 (± 5.8)	3.1	5.7

[a] All metrics except richness were calculated based on proportion of total seedling density or relative vegetative cover for each wetland.
[b]The six wetlands sampled were labeled accordingly: OS32, OS4, OS62, OS40, OS31, and OS44
[c] Standing vegetation metrics were calculated based on relative cover.

CHAPTER 5

CONCLUSIONS

Geographically isolated wetlands are a prominent feature of the landscape across the Dougherty Plain, a physiographic region of southwestern Georgia characterized by karst topography (Beck and Arden 1983). The underlying limestone bedrock distinguishing the region drives the formation of these isolated wetlands from limestone sinkholes which occur at densities of approximately 1.7 isolated wetlands per km^2 (Martin et al. 2012). One of the most important functions of the isolated wetlands in this region is the provision of habitat for a highly diverse suite of flora and fauna adapted to the natural seasonal fluctuations in wetland inundation and dry-down (Kirkman et al. 1999, Battle and Golladay 2002, Smith et al. 2006). However, isolated wetlands are unprotected at the federal level and in Georgia at the state level due to lack of an obvious surficial hydrologic connection to jurisdictional "waters of the United States" (*Rapanos v United States* 2006), thus they are particularly vulnerable to modification.

Throughout much of the Dougherty Plain, isolated wetland condition and function is severely compromised as a result of anthropogenic alteration (Martin 2010), namely via draining, filling, ditching, and dredging associated with the agricultural and silvicultural land use that dominates the region. In this study, I examined the relationship between land use and the ecological integrity of wetlands at multiple spatial and temporal scales to identify: 1) how historic and current anthropogenic land use has impacted the provision of isolated wetland habitat across the region, 2) how land use influences biotic and environmental variables associated with wetland condition, and 3) whether historic land use influences the restoration potential of agricultural isolated wetlands.

My results indicate that the widespread agricultural and silvicultural land use across the Dougherty Plain has had a marked impact on the provision of isolated wetland habitat throughout the region, particularly with respect to water quality and macrophyte community composition. The intensification of land use and increasing fragmentation within the Dougherty Plain over the past six decades documented by Martin et al. (2013) was associated with a concurrent intensification of land use within isolated wetlands and a decrease in connectivity among wetlands through contiguous forested habitat. Ultimately, fewer than half of the predicted isolated wetlands in the region could be considered potential habitat suitable for isolated wetland-dependent flora and fauna. Small wetlands (< 1 ha) in particular were disproportionately affected by conversion to anthropogenic land use. Of the specific land use classes focused on in this study, wetlands embedded in agricultural landscapes (Irrigated Row-crop and Pecan Orchard) differed most from wetlands in Reference condition, and were generally characterized by higher cover of non-native macrophytes and increased nutrient loads. Interestingly, the macrophyte community of wetlands in natural forested landscapes also differed significantly from Reference wetlands, presumably due to historical exclusion of fire. Finally, agricultural isolated wetlands, often considered prime candidates for federal restoration programs such as the Wetlands Reserve Program (WRP), had seed banks characterized by a dominance of herbaceous species, many of which were native species or wetland-associated species. The lengths of time in cultivation examined in this study (ca. 30 versus > 60 years) were not related to seed bank composition.

The estimated loss of isolated wetland habitat in this study has implications for the continued survival of the flora and fauna associated with the isolated wetlands, particularly the rare, threatened, and endangered species (Kirkman et al. 1999, Battle and Golladay 2002, Smith et al. 2006). My findings suggest that most isolated wetlands within the Dougherty Plain are incapable of supporting the suite of flora and fauna characteristic of minimally disturbed wetlands, either through direct, physical conversion of wetland habitat to agriculture or pasture land, or indirectly, through the fragmentation of upland forest which connects wetland habitat, thereby limiting or eliminating potential dispersal of species to and from the wetlands.

In fact, the map I produced in Chapter 2 of predicted wetlands which potentially provide suitable habitat is likely an overestimation. Results from this study demonstrate that wetland condition can also be significantly impacted by adjacent agricultural land use (see Chapter 3). However, because the research presented in this thesis was conducted concurrently, the map does not explicitly exclude wetlands degraded due to the influence of adjacent agricultural land use. Likewise, some of the mapped wetlands surrounded largely by forest may be characterized as hardwood depressions, which are recognized as alternate community states incapable of supporting the diversity characteristic of depressional marshes and swamps (Martin and Kirkman 2009). Thus, to generate a more accurate estimate of suitable isolated wetland habitat in the Dougherty Plain, additional work is needed. Specifically, the removal of all wetlands embedded in uplands dominated by agriculture, and the removal of wetlands with canopies dominated by oak species would greatly improve the map.

It should be noted, however, that highly degraded wetlands may still perform some limited wetland functions, such as floodwater retention and nutrient sequestration (Rogers et al. 2009). Likewise, they do provide habitat for more generalist, disturbance-tolerant flora and fauna, though the diversity of species is much-reduced relative to reference sites. Some of the macrophytes strongly associated with agricultural wetlands in this study were annual native wetland species (e.g. *Paspalum boscianum* Fluegge and *Polygonum lapathifolium* L.). Herpetofauna such as *Ambystoma tigrinum* (tiger salamander) and *Rana catesbeianus* (bullfrog) have been observed in agricultural wetlands, likely due to the relatively high dispersal ability of these species (Smith and Howze 2011). Battle et al. (2001) found that oligochaetes, snails, and leeches were generally more prevalent in agriculturally disturbed wetlands relative to reference sites. Over the course of this study, I observed numerous species of birds utilizing agricultural wetlands, including heron species, black-bellied whistling ducks (*Dendrocygna autumnalis*), and the endangered wood stork (*Mycteria americana*). Such wetlands offer food and habitat, especially during times of drought when many wetlands are dry, but agricultural wetlands are inundated due to irrigation inputs.

From this study, a mixed picture emerges of the isolated wetlands across the Dougherty Plain. Due to the intensive agricultural land use in the region, most wetlands are degraded and only offer habitat to a limited suite of disturbance-tolerant species; however, this study has also highlighted the areas of the region where high-quality isolated wetland habitat may be present. Natural forests and pine plantations, prevalent in an otherwise intensively agricultural landscape, represent potential refuges of low-intensity land use in which wetlands with macrophyte communities and water quality similar to those of reference wetlands are likely to persist. In other agricultural regions populated with high densities of isolated wetlands (e.g. Carolina bays of South Carolina (Bennett and Nelson 1991), prairie potholes of Iowa (van der Valk pers. comm. as cited in Leibowitz 2003) and Illinois (McCauley and Jenkins 2005), and vernal pools of southern California (Bauder and Wier 1990 as cited in King 1998) estimates of wetland loss range upwards of 90%. In contrast, the Dougherty Plain may still contain a relatively high proportion of wetlands that retain considerable wetland function.

The development of conservation policies that effectively safeguard these unique isolated wetland habitats and the species associated with them is contingent upon increasing our knowledge of the condition and function of these wetlands within the regional landscape. More research is needed to describe and quantify explicit ecological functions and ecosystem services provided by these isolated wetlands at the individual wetland level, as well as interactions between wetlands and other surface waters and between wetlands and uplands. Specifically with regard to habitat provision and connectivity, a more complete understanding of regional amphibian population dynamics is required to clarify the relative importance of wetland complexes (Smith and Green 2005, McKee 2012). Further research might also entail identifying species-specific thresholds of connectivity (e.g. inter-wetland distance and related habitat parameters) for habitat assessments targeted towards rare or threatened species in particular.

Concurrent with research into wetland function, the most ecologically intact and most highly-connected isolated wetlands that persist within the Dougherty Plain should be selected as conservation targets from the wetlands identified as potential habitat in this study. A visual survey of the largest clusters of these least-impacted, highly-connected wetlands projected over recent aerial photography (2010) suggests that most of these clusters occur on large tracts of privately held land, including natural and planted stands of pine, and quail hunting plantations. A few clusters also occur within publicly owned and managed properties, such as Georgia Wildlife Management Areas (WMA’s).

To identify the most valuable clusters of remaining isolated wetland habitat, I suggest focusing on wetland complexes that meet a threshold of desired habitat connectivity (e.g., at least

5 wetlands), and further excluding wetlands classified as hardwood depressions as well as wetlands degraded by adjacent upland land use (e.g. with a Landscape Development Intensity index score > 2; see Martin 2010 and Lane et al. 2012).

When considering policy development and creation of incentives, property owners should be identified for each wetland complex of interest, as well as the predominant purpose of the land (e.g. silviculture or quail hunting). The most effective conservation policies will target these specific types of landholders, and introduce regulations and incentives that prevent direct alteration/conversion of the most valuable isolated wetland conservation areas, as well as promote ecological stewardship of these sites (e.g. the regular application of fire) to ensure their persistence in the future.

Additionally, this research can be used by wetland restoration programs such as the Wetlands Reserve Program (WRP) as a starting-point for identifying those wetlands most valuable for habitat restoration. It may also provide a helpful database with which to begin answering landscape-scale ecological questions regarding the role of wetland connectivity in wildlife health and disease transmission.

Literature Cited

Battle, J. and S. W. Golladay. 2002. Aquatic invertebrates in hardwood depressions of southwest Georgia. Southeastern Naturalist **1**:149-158.

Battle, J., S. W. Golladay, and B. Clayton. 2001. Aquatic macroinvertebrates and water quality characteristics in five wetland types: Preliminary results on biomonitoring.*in* Proceedings of the Georgia Water Resources Conference. Institute of Ecology, The University of Georgia, Athens, Georgia, University of Georgia.

Beck, B. F. and D. D. Arden. 1983. Hydrology and geomorphology of the Dougherty Plain, southwest Georgia. Southeastern Geological Society, Tallahassee, FL.

Bennett, S. H. and J. B. Nelson. 1991. Distribution and status of Carolina bays in South Carolina. South Carolina Wildlife and Marine Resources Department, Nongame and Heritage Trust Section, Columbia, SC.

King, J. L. 1998. Loss of diversity as a consequence of habitat destruction in California vernal pools. Pages 119-123 *in* Ecology, conservation and management of vernal pool ecosystems-proceedings from a 1996 conference. California Native Plant Society, Sacramento, California.

Kirkman, L. K., S. W. Golladay, L. LaClaire, and R. Sutter. 1999. Biodiversity in southeastern seasonally ponded, isolated wetlands: management and policy perspectives for research and conservation. Journal of the North American Benthological Society **18**:553-562.

Lane, C., E. D'Amico, and B. Autrey. 2012. Isolated Wetlands of the Southeastern United States: Abundance and Expected Condition. Wetlands **32**:753-767.

Leibowitz, S. G. 2003. Isolated wetlands and their functions: An ecological perspective. Wetlands **23**:517-531.

Martin, G. I. 2010. Evaluating the location, extent, and condition of isolated wetlands in the Dougherty Plain, Georgia, USA [electronic resource] / by Glenn I. Martin. 2010.

Martin, G. I., J. A. Hepinstall, and L. K. Kirkman. 2013. Six decades (1948 - 2007) of landscape change in the Dougherty Plain of Southwest Georgia, USA. Southeastern Geographer **53**.

Martin, G. I., L. K. Kirkman, and J. Hepinstall-Cymerman. 2012. Mapping geographically isolated wetlands in the Dougherty Plain, Georgia, USA. Wetlands **32**:149-160.

Martin, K. L. and L. K. Kirkman. 2009. Management of ecological thresholds to re-establish disturbance-maintained herbaceous wetlands of the south-eastern USA. Journal of Applied Ecology **46**:906-914.

McCauley, L. A. and D. G. Jenkins. 2005. GIS-based estimates of former and current depressional wetlands in an agricultural landscape. Ecological Applications **15**:1199-1208.

McKee, A. M. 2012. Correlations between community diversity and within-species genetic diversity in an amphibian assemblage: Potential processes and implications for conservation management. University of Georgia, Athens, GA.

Rapanos v United States. 2006. 547 U.S. 715.

Rogers, J. S., K. W. Potter, A. R. Hoffman, J. A. Hoopes, C. H. Wu, and D. E. Armstrong. 2009. Hydrologic and Water Quality Functions of a Disturbed Wetland in an Agricultural Setting. Journal of the American Water Resources Association **45**:628-640.

Smith, L. L. and J. M. Howze. 2011. Amphibian Persistence in Isolated Wetlands in an Agricultural Landscape. Ecological Society of America Annual Meeting, Austin, TX.

Smith, L. L., D. A. Steen, J. M. Stober, M. C. Freeman, S. W. Golladay, L. M. Conner, and J. Cochrane. 2006. The vertebrate fauna of Ichauway, Baker County, GA. Southeastern Naturalist **5**:599-620.

Smith, M. A. and D. M. Green. 2005. Dispersal and the Metapopulation Paradigm in Amphibian Ecology and Conservation: Are All Amphibian Populations Metapopulations? Ecography:110.

APPENDIX A

PROTOCOL FOR HABITAT CONNECTIVITY ANALYSIS

Appendix A contains a detailed step-by-step protocol for assessing wetland connectivity via contiguous forest, as discussed in Chapter 2.

Analysis Objectives

Examine potential influence of the fragmented landscape of the Dougherty Plain on isolated wetlands via assessment of structural connectivity through forested matrix. For each wetland, calculate 1) the number of isolated wetlands to which it is connected via contiguous forest, and 2) the total area (ha) of wetlands to which it is connected via contiguous forest. Present these indices of connectivity at two spatial scales, where the extent of data permits:

A) 500 meters: representative of the lower end of amphibian dispersal distance. Empirical movement data supports this, as well as local studies of genetic diversity (McKee 2012, Smith and Green 2005, Veysey et al 2011)

B) 2.5 kilometers: representative of long distance dispersal of amphibians with higher vagility, as well as the scale at which rare long distance migration events may occur for species with typically low vagility (McKee 2012)

Data Requirements

1. Glenn Martin's model of predicted isolated wetlands in the Dougherty Plain (hereafter referred to as "Combined Model"), with an imposed minimum size limit of 0.05 ha.

2. NLCD 2006 LULC data layer, converted to vector for the full extent of the Dougherty Plain.

3. Screen-digitized historical LULC for the years:
    a. 1948
    b. 1968
    c. 1993
    d. 2007

4. Subunit extent

Protocol

1. Select and extract all Forested habitat from NLCD 2006 vector layer (this includes Deciduous, Evergreen, Mixed, and Woody Wetland) [nlcd06_dp_ForHab]. Generate a 1cm buffer around each polygon. This will have a negligible effect on area, overlap, etc, but will simulate the 8-neighbor connectivity.
2. Select and export only wetlands which intersect with this forested matrix [CombMod_w.For]. Union these with the forested habitat layer. [CombMod_ForHab_Union]. For reference purposes, the identifying field for all combined model wetlands and their associated buffers in all analyses is "CM_ID" , a numerical field which assigned a unique id to each of the 11620 wetlands in Glenn Martin's original Combined Model. In that original attribute table, both the "FID" field and the "Id" field are equivalent. In other layers, refer to "CM_ID" only.
3. Dissolve all forested and isolated wetland habitat into discrete polygons of "preferred" matrix. Uncheck the "create multipart polygons" option in Dissolve tool dialogue box [CombMod_ForHab_dslv]. This creates discrete patches of forested/isolated wetland habitat, each with a unique identifying label. (May need to dissolve twice; the first dissolve may produce split patches due to limited computer memory.)
4. Use the spatial join tool to assign the patch ID # to each isolated wetland. I also included the patch size, in case it's useful in the future. [CombMod_w.For]
5. Create an internal buffer within the Dougherty Plain Outline at 2500 m. Export all wetlands which do NOT intersect this buffer to create a separate shapefile [CombMod_w.For2500]. Removing wetlands that intersect the 2500m buffer will eliminate edge effects at both the 500m and 2500m scales.

6. Using the set of wetlands you just created, generate buffers (outside only), allowing overlap, for two spatial scales (500 m and 2.5 km) [CombMod_wForBuff500 and CombModwForBuff2500].
7. Intersect buffer layers with the set of wetlands you've created for analysis [CombMod_w.For]. This should create a layer where each buffer polygon that overlaps a wetland has a forest patch ID associated with the original focal wetland, and a forest patch id associated with the wetland the buffer is intersecting [CombMod_wForBuff2500Intersect].
8. To obtain the indices of connectedness for each wetlands, you will need to count the number of wetlands which intersect each focal wetland's buffer (by design, intersect will not include the wetland of origin) <u>and</u> which share the same patch of forest. To accomplish this:
    a. Using "select by attributes", select all intersected buffer polygons where the forest patch ID associated with the focal wetland and the forest patch ID associated with the intersected wetland are equal. Export these to a new shapefile [CombMod_wForBuff2500_SelectSame].
    b. Use the Frequency tool to generate a frequency table of all the polygons associated with a unique Combined Model ID [CombMod_wForBuff2500_SelectS.dbf]. Check both CM_ID and CM_ID_1 in the "Frequency Fields" box. This will generate frequencies for all other wetlands connected to each focal wetland.

c. Join the area (in hectares) associated with each intersected wetland to the frequency table. Base the join on the Combined Model ID (CM_ID_1) of each intersected wetland.

d. Run a second frequency analysis on the original frequency table to count the number of times each buffer ID occurs (this effectively tallies the total number of wetlands the focal wetland buffer intersects with), and check the box for a summary of "hectares". This will sum the area of all wetlands within same forest patch as the focal wetland that are intersected by each buffer.

9. Repeat steps 1-6, this time using the historical data (1948, 1968, 1993, 2007) digitized by Glenn Martin. Step 5 should exclude all wetlands which intersect with a 500m internal buffer within each subunit, thus reducing edge effects in this spatially restricted analysis. Keep in mind a unique set of wetland/forest patches and patch IDs will need to be created for each year.

10. Perform the same analysis for NLCD 06 data within the subunits. This allows for crosswalking of results.

**Notes: Due to an anomaly in the spatial join processes, 5 wetland IDs (1535, 8294, 8342, 10274, and 10873) were duplicated and assigned to two geographically adjacent wetlands which share a border. This duplication resulted in the elimination of five wetlands from the final results. Since this is a very small error in a sample of about 9,500 wetlands assessed for connectivity, and because wetlands that share a border are likely functionally the same wetland, I proceeded with the analysis despite the anomaly.

APPENDIX B

WETLAND DATA: AREA, VEGETATION, WATER QUALITY, AND SEED BANK SPECIES

Appendix B contains tables of the data collected and summarized from each wetland sampled in 2011 and 2012 in Chapters 3 and 4. Data collected from wetlands sampled in 2009 and 2010 by Glenn Martin can be found in his thesis (Martin 2010).

Literature Cited

Martin, G. I. 2010. Evaluating the location, extent, and condition of isolated wetlands in the Dougherty Plain, Georgia, USA [electronic resource] / by Glenn I. Martin. 2010.

Table A.1. Summary table of wetland descriptions and data collection for each wetland sampled for Chapters 3 and 4 (1 of 2).

Wetland ID	Surrounding Land Use	Canopy	Area (ha)	Vegetation Sampled	Seed Bank Sampled	Water Sampled
OS04	Irrigated Row-crop	Open	2.26	2009	2011	2010
OS06	Irrigated Row-crop	Open	2.27	2009	---	2010
OS07	Irrigated Row-crop	Open	2.48	2009	---	2010
OS08	Irrigated Row-crop	Open	2.05	2009	---	2010
OS09	Dryland Row-crop	Open	0.29	2009	---	2010
OS10	Planted Pine	Open	1.61	2009	---	2010
OS11	Dryland Row-crop	Open	1.57	2009	---	2010
OS13	Planted Pine	Open	0.37	2009	---	2010
OS16	Planted Pine	Closed	3.37	2009	---	2010
OS17	Planted Pine	Closed	1.16	2009	---	2010
OS18	Planted Pine	Closed	2.69	2009	---	2010
OS19	Pecan Orchard	Open	1.02	2009	---	2010
OS20	Pecan Orchard	Open	1.07	2009	---	2010
OS22	Forest	Open	0.63	2009	---	2010
OS23	Planted Pine	Open	3.63	2009	---	2010
OS24	Pecan Orchard	Open	0.45	2009	---	2010
OS25	Pecan Orchard	Open	1.37	2009	---	2010
OS27	Forest	Closed	1.22	2009	---	2010
OS28	Forest	Closed	1.00	2009	---	2010
OS31	Irrigated Row-crop	Open	0.43	---	2011	---
OS32	Irrigated Row-crop	Open	1.39	2011	2011	2012
OS38	Pecan Orchard	Open	0.05	2011	---	2012
OS39	Forest	Closed	0.19	2011	---	2012
OS40	Irrigated Row-crop	Open	1.47	2011	2011	2012
OS41	Irrigated Row-crop	Open	1.10	2011	---	2012
OS42	Pecan Orchard	Open	6.87	2011	---	2012
OS43	Irrigated Row-crop	Open	0.27	2011	---	2012
OS44	Irrigated Row-crop	Open	0.56	---	2011	---
OS45	Irrigated Row-crop	Closed	1.64	2011	---	2012
OS46	Pecan Orchard	Closed	4.42	2011	---	2012
OS47	Pecan Orchard	Open	0.94	2011	---	2012
OS48	Pecan Orchard	Open	0.43	2011	---	2012
OS49	Pecan Orchard	Open	4.32	2011	---	2012
OS50	Forest	Open	2.39	2011	---	2012
OS51	Forest	Open	2.95	2011	---	2012

Table A.1. Summary table of wetland descriptions and data collection, continued (2 of 2).

Wetland ID	Surrounding Land Use	Canopy	Area (ha)	Vegetation Sampled	Seed Bank Sampled	Water Sampled
OS52	Planted Pine	Closed	3.05	2011	---	2012
OS53	Planted Pine	Closed	4.45	2011	---	2012
OS54	Dryland Row-crop	Closed	0.95	2011	---	2012
OS55	Forest	Closed	0.62	2011	---	2012
OS56	Pecan Orchard	Closed	0.97	2011	---	2012
OS57	Planted Pine	Closed	0.89	2011	---	2012
OS58	Dryland Row-crop	Closed	1.39	2011	---	2012
OS59	Forest	Closed	2.73	2011	---	---
OS60	Dryland Row-crop	Open	2.35	2011	---	2012
OS61	Dryland Row-crop	Open	0.22	2011	---	2012
OS62	Irrigated Row-crop	Open	0.41	---	2011	---
OS63	Planted Pine	Closed	0.10	2011	---	2012
OS64	Planted Pine	Closed	0.77	2011	---	2012
OS65	Dryland Row-crop	Closed	0.28	2011	---	2012
OS67	Forest	Closed	2.78	2011	---	2012
OS68	Forest	Closed	0.70	2011	---	2012
OS69	Forest	Open	0.89	2011	---	2012
OS70	Forest	Closed	0.09	2011	---	2012
OS71	Planted Pine	Open	0.23	2011	---	2012
OS72	Planted Pine	Closed	0.92	2011	---	2012
P02	Reference	Closed	4.06	2009	---	2010, 2012
P03	Reference	Closed	3.41	2009	---	2010, 2012
P21	Reference	Open	5.81	2009	---	2010, 2012
P32	Reference	Closed	2.85	2009	---	2010
P35	Reference	Open	0.68	2009	---	2010
P41	Reference	Closed	0.67	2009	---	2010
P50	Reference	Open	6.22	2009	---	2010
P53	Reference	Open	3.81	2009	---	2010, 2012
GM29	Reference	Open	1.67	2009	---	2010

Table A.2. List of macrophyte species and associated characteristics encountered in sample wetlands (1 of 8).

Species	Wetland Status[a]	Native[b]	Duration	Habit
Acalypha gracilens	---	Native	Annual	Forb
Acalypha setosa	---	Native	Annual	Forb
Acer rubrum	FAC	Native	Perennial	Tree
Agalinis fasciculata	FAC	Native	Annual	Forb
Amaranthus spp.	---	---	---	Forb
Amaranthus blitum	---	Exotic	Annual	Forb
Amaranthus palmeri	FACU	Native	Annual	Forb
Amaranthus viridis	---	Native	Annual	Forb
Ambrosia artemisiifolia	FACU	Native	Annual	Forb
Ammania coccinea	FACW+	Native	Perennial	Forb
Amphicarpum muhlenbergianum	FACW	Native	Perennial	Graminoid
Amsonia tabernaemontana	FACW	Native	Perennial	Forb
Andropogon virginicus	FAC-	Native	Perennial	Graminoid
Apios americana	FACW	Native	Perennial	Vine
Arachis hypogaea	---	Exotic	Annual	Forb
Aristida purpurascens	FAC	Native	Perennial	Graminoid
Aristida stricta	FAC-	Native	Perennial	Graminoid
Asplenium platyneuron	FACU	Native	Perennial	Forb
Axonopus fissifolius	---	Native	Perennial	Graminoid
Axonopus furcatus	OBL	Native	Perennial	Graminoid
Baccharis halimifolia	FAC	Native	Perennial	Shrub
Berchemia scandens	FACW	Native	Perennial	Vine
Bidens bipinnata	---	Native	Annual	Forb
Bidens discoidea	FACW	Native	Annual	Forb
Boehmeria cylindrica	FACW+	Native	Perennial	Forb
Callicarpa americana	FACU-	Native	Perennial	Shrub
Campsis radicans	FAC	Native	Perennial	Vine
Carex festucacea	FACW	Native	Perennial	Graminoid
Carex glaucescens	OBL	Native	Perennial	Graminoid
Carex joorii	OBL	Native	Perennial	Graminoid
Carex longii	OBL	Native	Perennial	Graminoid
Carex spp. (x 7)[c]	---	---	---	Graminoid
Carex verrucosa	OBL	Native	Perennial	Graminoid
Carex, Ovales group	---	Native	Perennial	Graminoid
Carya cordiformis	FAC	Native	Perennial	Tree
Carya illinoensis	FAC+	Exotic	Perennial	Tree
Celtis laevigata	FACW	Native	Perennial	Tree
Celtis occidentalis	---	Native	Perennial	Shrub
Centella asiatica	FACW	Native	Perennial	Forb

Table A.2. List of macrophyte species and associated characteristics, continued (2 of 8).

Species	Wetland Status	Native	Duration	Habit
Cephalanthus occidentalis	OBL	Native	Perennial	Shrub
Chamaesyce hyssopifolia	FAC	Native	Annual	Forb
Chamaesyce maculata	FACU	Native	Annual	Forb
Chasmanthium laxum	FACW-	Native	Perennial	Graminoid
Chasmanthium nitidum	FACW+	Native	Perennial	Graminoid
Clematis crispa	FACW+	Native	Perennial	Vine
Clethra alnifolia	FACW	Native	Perennial	Shrub
Coelorachis rugosa	OBL	Native	Perennial	Graminoid
Commelina benghalensis	---	Exotic	Perennial	Forb
Commelina communis	FAC	Exotic	Annual	Forb
Commelina erecta	---	Native	Perennial	Forb
Conyza canadensis	FACU	Native	Annual	Forb
Coronopus didymus	---	Exotic	Biennial	Forb
Crataegus aestivalis	OBL	Native	Perennial	Shrub
Crataegus viridis	FACW	Native	Perennial	Tree
Croton capitatus	---	Native	Perennial	Forb
Croton elliottii	FACW+	Native	Perennial	Forb
Cuphea carthagenensis	FACW	Exotic	Annual	Forb
Cynodon dactylon	FACU	Exotic	Perennial	Graminoid
Cyperus compressus	FACW	Native	Annual	Graminoid
Cyperus croceus	FAC	Native	Perennial	Graminoid
Cyperus esculentus	FAC	Exotic	Perennial	Graminoid
Cyperus filiculmis	---	Native	Perennial	Graminoid
Cyperus iria	FACW	Exotic	Annual	Graminoid
Cyperus polystachyos	FACW	Native	Annual	Graminoid
Cyperus pseudovegetus	FACW	Native	Perennial	Graminoid
Cyperus retrorsus	FACU+	Native	Perennial	Graminoid
Cyperus rotundus	FAC-	Exotic	Perennial	Graminoid
Cyperus spp. (x 15)	---	---	---	Graminoid
Cyperus virens	FACW	Native	Perennial	Graminoid
Cyrilla racemiflora	FACW	Native	Perennial	Shrub
Dactyloctenium aegyptium	---	Exotic	Annual	Graminoid
Desmodium glabellum	---	Native	Perennial	Forb
Desmodium tortuosum	---	Native	Perennial	Subshrub
Dichanthelium aciculare	FACU	Native	Perennial	Graminoid
Dichanthelium acuminatum	FAC	Native	Perennial	Graminoid
Dichanthelium clandestinum	FACW	Native	Perennial	Graminoid
Dichanthelium commutatum	FAC	Native	Perennial	Graminoid
Dichanthelium dichotomum	FAC	Native	Perennial	Graminoid

Table A.2. List of macrophyte species and associated characteristics, continued (3 of 8).

Species	Wetland Status	Native	Duration	Habit
Dichanthelium erectifolium	OBL	Native	Perennial	Graminoid
Dichanthelium Leucothrix	---	Native	Perennial	Graminoid
Dichanthelium scoparium	FACW	Native	Perennial	Graminoid
Dichanthelium sphaerocarpon	FACU	Native	Perennial	Graminoid
Dichanthelium spp. (x 2)	---	Native	Perennial	Graminoid
Dichanthelium strigosum	FAC	Native	Perennial	Graminoid
Dichondra carolinensis	FACW-	Native	Perennial	Forb
Digitaria ciliaris	---	Exotic	Annual	Graminoid
Diodia teres	FACU-	Native	Annual	Forb
Diodia virginiana	FACW	Native	Perennial	Forb
Diospyros virginiana	FAC	Native	Perennial	Tree
Echinochloa colona	FACW	Exotic	Annual	Graminoid
Echinochloa crusgalli	FACW-	Exotic	Annual	Graminoid
Echinodorus cordifolius	OBL	Native	Perennial	Forb
Eclipta prostrata	FACW-	Native	Perennial	Forb
Eleocharis microcarpa	OBL	Native	Annual	Graminoid
Eleocharis spp. (x 2)	---	---	---	Graminoid
Eleocharis vivipara	OBL	Native	Annual	Graminoid
Eupatorium capillifolium	FACU	Native	Annual	Forb
Eupatorium hyssopifolium	---	Native	Perennial	Forb
Eupatorium leptophyllum	FAC+	Native	Perennial	Forb
Eupatorium rotundifolium	FAC	Native	Perennial	Forb
Eupatorium semiserratum	FACW-	Native	Perennial	Forb
Eupatorium serotinum	FAC	Native	Perennial	Forb
Euthamia caroliniana	FAC	Native	Perennial	Forb
Euthamia graminifolia	FACW-	Native	Perennial	Forb
Fimbristylis autumnalis	OBL	Native	Annual	Graminoid
Forestiera acuminata	OBL	Native	Perennial	Shrub
Galactia regularis	---	Native	Perennial	Vine
Galium hispidulum	---	Native	Perennial	Forb
Galium pilosum	---	Native	Perennial	Forb
Gamochaeta pensilvanica	FACU-	Native	Annual	Forb
Gamochaeta purpurea	UPL	Native	Annual	Forb
Gelsemium sempervirens	FAC	Native	Perennial	Vine
Geranium carolinianum	---	Native	Annual	Forb
Gossypium hirsutum	---	Native	Perennial	Subshrub
Gratiola ramosa	FACW	Native	Perennial	Forb
Helianthus angustifolius	FAC+	Native	Perennial	Forb
Heterotheca subaxillaris	FACU-	Native	Biennial	Forb

Table A.2. List of macrophyte species and associated characteristics, continued (4 of 8).

Species	Wetland Status	Native	Duration	Habit
Hibiscus moscheutos	OBL	Native	Perennial	Subshrub
Hydrocotyle ranunculoides	OBL	Native	Perennial	Forb
Hypericum brachyphyllum	FACW	Native	Perennial	Shrub
Hypericum crux-andreae	FACW-	Native	Perennial	Subshrub
Hypericum gentianoides	FACU	Native	Annual	Forb
Hypericum gymnanthum	FACW	Native	Annual	Forb
Hypericum harperi	---	Native	Perennial	Forb
Hypericum hypericoides	FAC	Native	Perennial	Shrub
Hypericum mutilum	FACW	Native	Perennial	Forb
Hypericum spp. (x 3)	---	Native	---	---
Hypericum suffruticosum	---	Native	Biennial	Subshrub
Hyptis alata	OBL	Native	Perennial	Forb
Ilex cassine	---	Native	Perennial	Shrub
Ilex glabra	FACW	Native	Perennial	Shrub
Ipomoea purpurea	FACU	Exotic	Annual	Vine
Ipomoea quamoclit	FACU+	Exotic	Annual	Vine
Ipomoea triloba	---	Exotic	Perennial	Vine
Iva microcephala	FACW	Native	Annual	Forb
Jacquemontia tamnifolia	FACU-	Native	Annual	Vine
Juncus effusus	FACW+	Native	Perennial	Graminoid
Juncus repens	OBL	Native	Perennial	Graminoid
Juncus spp.	---	---	---	Graminoid
Juncus tenuis	FAC	Native	Perennial	Graminoid
Justicia ovata	OBL	Native	Perennial	Forb
Kyllinga brevifolia	FACW	Native	Perennial	Graminoid
Kyllinga pumila	FACW	Native	Perennial	Graminoid
Lechea minor	---	Native	Perennial	Forb
Leersia hexandra	OBL	Native	Perennial	Graminoid
Leersia virginica	FACW	Native	Perennial	Graminoid
Leucothoe racemosa	FACW	Native	Perennial	Shrub
Ligustrum sinense	FAC	Exotic	Perennial	Shrub
Lindernia dubia	OBL	Native	Perennial	Forb
Liquidambar styraciflua	FAC+	Native	Perennial	Tree
Lonicera japonica	FAC-	Exotic	Perennial	Vine
Ludwigia decurrens	OBL	Native	Perennial	Forb
Ludwigia erecta	OBL	Native	Perennial	Forb
Ludwigia glandulosa	OBL	Native	Perennial	Forb
Ludwigia leptocarpa	OBL	Native	Perennial	Subshrub
Ludwigia linearis	OBL	Native	Perennial	Forb

Table A.2. List of macrophyte species and associated characteristics, continued (5 of 8).

Species	Wetland Status	Native	Duration	Habit
Ludwigia maritima	FACW	Native	Perennial	Forb
Ludwigia palustris	OBL	Native	Perennial	Forb
Ludwigia pilosa	OBL	Native	Perennial	Forb
Ludwigia repens	OBL	Native	Perennial	Forb
Ludwigia spathulata	OBL	Native	Perennial	Forb
Ludwigia spp. (x 2)	---	---	---	Forb
Lycopus amplectens	OBL	Native	Perennial	Forb
Lycopus rubellus	OBL	Native	Perennial	Forb
Lygodium japonicum	FAC	Exotic	Perennial	Vine
Mecardonia acuminata	FACW	Native	Perennial	Subshrub
Melia azedarach	---	Exotic	Perennial	Tree
Melochia corchorifolia	FAC	Native	Perennial	Subshrub
Menispermum canadense	---	Native	Perennial	Vine
Microstegium vimineum	FAC+	Exotic	Annual	Graminoid
Mikania scandens	FACW+	Native	Perennial	Vine
Modiola caroliniana	FACU+	Native	Perennial	Forb
Mollugo verticillata	FAC	Exotic	Annual	Forb
Myrica cerifera	FAC	Native	Perennial	Tree
Nothoscordum bivalve	FAC	Native	Perennial	Forb
Nyssa sylvatica	FAC	Native	Perennial	Tree
Oenothera laciniata	FACU	Native	Perennial	Forb
Oldenlandia boscii	FACW-	Native	Perennial	Forb
Oldenlandia uniflora	FACW-	Native	Annual	Forb
Oxalis spp.	---	Native	Perennial	Forb
Packera glabella	FACW+	Native	Annual	Forb
Panicum anceps	FAC-	Native	Perennial	Graminoid
Panicum dichotomiflorum	FACW	Native	Annual	Graminoid
Panicum hemitomon	OBL	Native	Perennial	Graminoid
Panicum hians	OBL	Native	Perennial	Graminoid
Panicum longifolium	FACW	Native	Perennial	Graminoid
Panicum rigidulum	FACW	Native	Perennial	Graminoid
Panicum verrucosum	FACW	Native	Annual	Graminoid
Parthenocissus quinquefolia	FAC	Native	Perennial	Vine
Paspalum dissectum	OBL	Native	Perennial	Graminoid
Paspalum laeve	FACW-	Native	Perennial	Graminoid
Paspalum notatum	FACU+	Exotic	Perennial	Graminoid
Paspalum urvillei	FAC	Native	Perennial	Graminoid
Passiflora incarnata	---	Native	Perennial	Vine
Phyllanthus tenellus	---	Exotic	Annual	Forb

Table A.2. List of macrophyte species and associated characteristics, continued (6 of 8).

Species	Wetland Status	Native	Duration	Habit
Physalis angulata	FAC	Native	Annual	Forb
Phytolacca americana	FACU+	Native	Perennial	Forb
Pinus echinata	---	Native	Perennial	Tree
Pinus elliottii	FACW	Native	Perennial	Tree
Pirequeta cistoides	---	Native	Perennial	Forb
Pityopsis graminifolia	UPL	Native	Perennial	Forb
Pluchea rosea	FACW	Native	Perennial	Forb
Polygonella polygama	---	Native	Perennial	Forb
Polygonum aviculare	FAC-	Exotic	Perennial	Forb
Polygonum caespitosum	---	Exotic	Annual	Forb
Polygonum hydropiperoides	OBL	Native	Perennial	Forb
Polygonum lapathifolium	FACW	Native	Annual	Forb
Polygonum pensylvanicum	FACW	Native	Annual	Forb
Polygonum punctatum	FACW+	Native	Perennial	Forb
Polypremum procumbens	FACU-	Native	Perennial	Forb
Portulaca amilis	---	Exotic	Annual	Forb
Portulaca oleracea	FACU	Exotic	Annual	Forb
Portulaca pilosa	FACU	Native	Perennial	Forb
Proserpinaca pectinata	OBL	Native	Perennial	Forb
Prunus serotina	FACU	Native	Perennial	Tree
Pseudognaphalium obtusifolium	---	Native	Annual	Forb
Quercus falcata	FACU-	Native	Perennial	Tree
Quercus laurifolia	FACW	Native	Perennial	Tree
Quercus nigra	FAC	Native	Perennial	Tree
Quercus virginiana	FACU+	Native	Perennial	Tree
Rhexia mariana	FACW+	Native	Perennial	Forb
Rhexia nashii	FACW+	Native	Perennial	Forb
Rhexia virginica	FACW+	Native	Perennial	Forb
Rhus copallinum	---	Native	Perennial	Shrub
Rhynchospora filifolia	FACW-	Native	Perennial	Graminoid
Rhynchospora globularis	FACW	Native	Perennial	Graminoid
Rhynchospora microcarpa	FACW+	Native	Perennial	Graminoid
Rhynchospora perplexa	OBL	Native	Perennial	Graminoid
Rhynchospora spp. (x 2)	---	---	---	Graminoid
Rotala ramosior	OBL	Native	Annual	Forb
Rubus argutus	---	Native	Perennial	Forb
Rubus cuneifolius	FACU	Native	Perennial	Forb
Rubus flagellaris	UPL	Native	Biennial	Vine
Rubus trivialis	FAC	Native	Perennial	Vine

Table A.2. List of macrophyte species and associated characteristics, continued (7 of 8).

Species	Wetland Status	Native	Duration	Habit
Rudbeckia mohrii	FACW+	Native	Perennial	Forb
Ruellia spp.	---	---	---	Forb
Rumex verticillatus	FACW+	Native	Perennial	Forb
Sabatia stellaris	OBL	Native	Annual	Forb
Saccharum coarctatum	---	Native	Perennial	Graminoid
Saccharum giganteum	FACW	Native	Perennial	Graminoid
Saccharum spp.	---	Native	Perennial	Graminoid
Salix nigra	OBL	Native	Perennial	Tree
Sassafras albidum	FACU	Native	Perennial	Tree
Saururus cernuus	OBL	Native	Perennial	Forb
Scirpus cyperinus	OBL	Native	Perennial	Graminoid
Scleranthus annuus	FACU	Exotic	Annual	Forb
Scutellaria racemosa	OBL	Exotic	Perennial	Forb
Senna obtusifolia	---	Exotic	Annual	Forb
Senna occidentalis	---	Exotic	Annual	Forb
Sesbania herbacea	FACW-	Native	Perennial	Forb
Setaria parviflora	FAC	Native	Perennial	Graminoid
Sida rhombifolia	FACU	Native	Annual	Subshrub
Silphium asteriscus	---	Native	Perennial	Forb
Sisyrinchium spp.	---	Native	Perennial	Graminoid
Smilax auriculata	FACU	Native	Perennial	Vine
Smilax bona-nox	FAC	Native	Perennial	Vine
Smilax glauca	FAC	Native	Perennial	Vine
Smilax lasioneuron	---	Native	Perennial	Vine
Smilax rotundifolia	FAC	Native	Perennial	Vine
Solanum carolinense	FACU	Native	Perennial	Subshrub
Solidago canadensis	FACU	Native	Perennial	Forb
Solidago leavenworthii	FAC+	Native	Perennial	Forb
Solidago nemoralis	---	Native	Perennial	Forb
Solidago spp. (x 2)	---	---	---	Forb
Solidago stricta	OBL	Native	Perennial	Forb
Solidago tortifolia	---	Native	Perennial	Forb
Spirodela punctata	OBL	Native	Perennial	Forb
Stylisma aquatica	FACW+	Native	Perennial	Vine
Symphyotrichum dumosum	FAC	Native	Perennial	Forb
Symphyotrichum lanceolatum	---	Native	Perennial	Forb
Symphyotrichum simmondsii	---	Native	Perennial	Forb
Symphyotrichum spp. (x 2)	---	---	---	Forb
Taxodium ascendens	---	Native	Perennial	Tree

Table A.2. List of macrophyte species and associated characteristics, continued (8 of 8).

Species	Wetland Status	Native	Duration	Habit
Toxicodendron radicans	FAC	Native	Perennial	Vine
Trachelospermum difforme	FACW	Native	Perennial	Vine
Triadenum walteri	OBL	Native	Perennial	Forb
Trichostema dichotomum	---	Native	Perennial	Forb
Trifolium spp.	---	---	---	Forb
Triplasis americana	---	Native	Perennial	Graminoid
Ulmus alata	FACU+	Native	Perennial	Tree
Unknown Composite (x 5)	---	---	---	Forb
Unknown Dicot (x 21)	---	---	---	---
Unknown Grass (x 18)	---	---	---	Graminoid
Unknown Legume	---	---	---	Forb
Unknown Sedge (x 17)	---	---	---	Graminoid
Unknown Woody	---	---	---	---
Urochloa platyphylla	FAC+	Native	Perennial	Graminoid
Vaccinium corymbosum	FACW	Native	Perennial	Shrub
Vaccinium stamineum	FACU	Native	Perennial	Shrub
Verbena brasiliensis	FAC-	Exotic	Perennial	Subshrub
Viburnum obovatum	FACW+	Native	Perennial	Shrub
Vicia spp.	---	---	---	Forb
Viola lanceolata	OBL	Native	Perennial	Forb
Vitis rotundifolia	FAC	Native	Perennial	Vine
Wahlenbergia marginata	---	Exotic	Perennial	Forb
Woodwardia virginca	OBL	Native	Perennial	Forb
Xanthium strumarium	FAC	Exotic	Annual	Forb
Xyris spp.	---	---	---	Graminoid

[a] "Wetland Status" indicates the Region 2 (Southeastern U.S.) wetland indicator status of each species (OBL = obligate wetland; FACW = facultative wetland; FAC = facultative; FACU = facultative upland; UPL = obligate upland; and **---** = no available Region 2 wetland status). The + and – modifiers indicate species more frequently found in wetlands (+) and less frequently found in wetlands (**-**). (http://plants.usda.gov/wetland.html)
[b] "Native" indicates whether the species is native or exotic to the conterminous US.
[c] To indicate multiple unknown specimens collected and classified with the same descriptor (e.g. *Carex* spp.), the number of unique specimens are indicated in parentheses: "(x7)".

Table A.3. Descriptive macrophyte community metrics for each isolated wetland sampled and analyzed in 2011. Abundance metrics are based on relativized cover of species. (1 of 2)

Wetland ID	Richness	Shannnon Diveristy (*H'*)	% Native Perennials	% Wetland Species[a]	% Facultative Species[b]	% Upland Species[c]	% Exotic Species	Annual/ Perennial Ratio	% Woody Species	% Vine Species	% Herbaceous Species
OS32	27	2.28	13.5	6.8	37.4	16.5	68.5	1.4	8.1	14.6	76.7
OS38	18	1.90	72.0	73.1	0.0	12.1	19.2	0.1	0.0	0.0	95.1
OS39	35	1.87	88.5	28.4	66.5	0.2	5.6	0.1	5.8	65.4	26.8
OS40	27	1.76	9.7	61.0	7.6	10.1	25.7	5.6	1.5	0.3	97.0
OS42	53	2.92	55.0	39.0	23.3	4.3	29.0	0.7	4.5	1.9	93.5
OS43	21	1.09	87.0	1.3	85.3	12.9	1.7	0.1	6.4	78.1	15.5
OS45	27	0.92	85.8	1.3	84.4	7.0	9.8	0.1	12.6	84.8	2.4
OS46	32	2.23	89.3	15.3	71.4	6.3	0.7	0.0	47.9	28.1	23.5
OS47	21	1.42	98.1	81.6	0.0	4.0	1.3	0.0	0.1	0.5	99.3
OS48	28	2.28	41.8	58.9	12.0	11.3	33.4	0.9	0.0	0.0	99.2
OS49	64	2.42	78.0	15.6	71.6	4.4	12.7	0.1	2.3	56.5	40.3
OS50	34	2.18	61.0	75.8	9.1	5.0	0.0	0.6	5.9	0.0	91.4
OS51	68	3.12	78.6	57.7	12.8	2.9	0.1	0.0	10.8	5.9	82.8
OS52	24	2.04	99.8	32.5	58.4	7.0	0.0	0.0	38.0	34.1	28.0
OS53	18	1.79	94.8	12.9	56.0	0.0	0.1	0.0	70.2	3.1	26.7
OS54	22	1.90	94.6	73.7	21.0	2.8	0.0	0.0	19.0	14.8	64.6
OS55	12	1.75	81.1	2.4	78.0	17.3	0.0	0.2	10.2	65.4	23.6
OS56	27	2.33	97.8	16.0	67.5	7.9	0.0	0.0	5.5	58.6	35.8
OS57	9	1.54	100.0	18.3	25.6	54.2	0.0	0.0	54.2	34.6	11.3
OS58	13	1.69	99.1	28.9	39.6	0.9	0.0	0.0	44.9	25.8	28.9
OS59	56	2.64	96.4	20.8	58.3	6.6	0.0	0.0	22.2	0.8	76.7
OS60	49	2.82	56.2	45.0	9.4	2.3	0.0	0.1	4.5	6.4	89.0

Table A.3. Descriptive macrophyte community metrics, continued. (2 of 2)

Wetland ID	Richness	Shannnon Diveristy (*H'*)	% Native Perennials	% Wetland Species	% Facultative Species	% Upland Species	% Exotic Species	Annual/ Perennial Ratio	% Woody Species	% Vine Species	% Herbaceous Species
OS61	11	1.32	42.6	0.8	69.7	1.7	55.7	0.4	31.0	0.0	69.0
OS63	13	1.23	95.9	87.7	0.7	0.0	0.0	0.0	19.5	0.3	79.8
OS64	34	2.25	60.6	35.4	14.8	11.2	3.0	0.5	6.6	11.3	81.3
OS65	13	1.95	96.5	0.0	82.9	3.5	0.4	0.0	3.5	93.4	3.1
OS67	26	2.42	95.5	14.2	65.1	18.7	0.2	0.0	28.8	65.3	5.9
OS68	24	1.83	50.6	1.5	13.1	66.1	48.1	0.0	22.3	8.7	69.1
OS69	36	1.92	42.8	78.4	13.9	2.5	2.2	1.3	5.6	3.8	89.8
OS70	6	1.65	100.0	53.6	46.4	0.0	0.0	0.0	35.7	55.2	9.1
OS71	34	2.26	98.2	42.8	54.2	0.4	0.0	0.0	5.1	0.9	93.9
OS72	22	1.41	98.8	13.6	84.4	1.1	0.0	0.0	17.6	71.2	11.2

[a] "% Wetland Species" refers to the relative percent cover of all species with obligate wetland or facultative wetland status in Region 2 (Southeastern U.S.). (http://plants.usda.gov/wetland.html)
[b] "% Facultative Species" refers to the relative percent cover of all species with facultative status.
[c] "% Upland Species" refers to the relative percent cover of all species with facultative upland or obligate upland status. (http://plants.usda.gov/wetland.html)

Table A.4. Water quality variables for each isolated wetland sampled and analyzed in 2012. Values represent the average of all samples collected for each wetland.

Wetland ID	PO4-P (µg/L)	NO3-N (µg/L)	NH4-N (µg/L)	AFDM[a]	TDM[b]	pH
OS32	107.7	2927.2	203.9	40.7	274.3	6.7
OS38	2531.4	7958.6	265.3	12.8	16.4	7.0
OS39	85.7	85.2	842.0	30.1	152.4	5.8
OS40	554.1	1473.2	270.6	23.6	110.3	6.9
OS41	1446.7	627.1	10107.8	209.7	851.2	7.2
OS42	505.0	297.7	791.4	16.7	43.5	6.7
OS43	419.6	0.3	11.7	5.2	27.3	6.5
OS45	3.6	638.3	22.3	7.7	52.6	4.9
OS46	1929.3	8489.8	15962.3	93.5	178.3	5.8
OS47	218.0	130.1	55.5	5.6	12.1	7.3
OS48	555.6	92.9	4.2	5.1	7.1	6.8
OS49	93.3	131.8	14.7	13.9	40.7	7.3
OS50	dry	dry	dry	dry	dry	dry
OS51	10.0	16.1	23.1	6.3	9.4	5.5
OS52	9.1	17.3	8.0	2.8	5.9	5.1
OS53	24.3	633.2	178.4	9.0	30.8	5.2
OS54	28.2	1008.8	276.1	4.5	14.3	5.9
OS55	102.2	11.1	36.9	9.2	51.8	5.4
OS56	dry	dry	dry	dry	dry	dry
OS57	dry	dry	dry	dry	dry	dry
OS58	16.8	1278.1	710.5	5.6	9.3	5.4
OS60	10.7	4720.5	69.0	5.1	19.8	5.9
OS61	170.1	1223.8	4.6	0.5	5.0	6.5
OS63	22.6	27.9	11.6	3.8	5.5	4.4
OS64	46.7	40.3	15.8	1.4	3.3	5.8
OS65	dry	dry	dry	dry	dry	dry
OS67	dry	dry	dry	dry	dry	dry
OS68	17.6	31666.6	634.1	3.2	5.5	4.3
OS69	207.2	21.4	16.3	2.8	4.0	6.0
OS70	76.8	16.3	265.6	33.8	44.8	5.2
OS71	10.9	233.2	23.7	5.4	14.8	5.6
OS72	dry	dry	dry	dry	dry	dry
P02	42.0	8.8	64.1	10.4	7.0	4.5
P03	152.8	12.0	30.8	51.8	43.8	4.8
P21	2168.8	0.0	1176.9	5.6	11.0	6.3
P53	2.8	4.0	30.9	6.8	11.5	5.2

[a] "AFDM" = Ash-free dry mass of suspended material.
[b] "TDM" = Total dry mass of suspended material .