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RESPONSES OF UPLAND HERPETOFAUNA TO THE RESTORATION OF CAROLINA BAYS AND THINNING OF FORESTED BAY MARGINS

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Forest Resources

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by
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Accepted by:
Dr. David C. Guynn, Jr., Committee Chair
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ABSTRACT

Research on the effects of wetland restoration on reptiles and amphibians is becoming more common, but almost all of these studies have observed the colonization of recently disturbed habitats that were completely dry at the time of restoration. In a similar manner, investigations herpetofaunal responses to forest management have focused on clearcuts, and less intensive stand manipulations are not as well studied. To evaluate community and population responses of reptiles and amphibians to hydrology restoration and canopy removal in the interior of previously degraded Carolina bays, I monitored herpetofauna in the uplands adjacent to six historically degraded Carolina bays in the at the Savannah River Site (SRS) in South Carolina for four years after restoration. To evaluate the effects of forest thinning on upland herpetofauna, forests were thinned in the margins of three of these bays. I used repeated measures ANOVA to compare species richness and diversity and the abundance of selected species and guilds between these bays and with those at three reference bays that were not historically drained and three control bays that remained degraded. I also used Non-metric Multidimensional Scaling (NMDS) to look for community-level patterns based treatments

I did not detect any differences in diversity or overall abundance of reptiles or amphibians between the four treatments, and NMDS did not indicate any patterns of community structure based on treatment. I captured eleven South Carolina species of conservation concern at the twelve bays, including juvenile Carolina gopher frogs (*Rana capito*) at two restored bays. Adult gopher frogs have only rarely been documented on the

SRS despite intensive, long-term sampling at several wetlands, and successful recruitment is even rarer.

Southern toads (*Bufo terrestris*) responded quickly to bay restoration, and gopher frog recruitment can be considered an indication of habitat quality. Because many of these species are highly philopatric and have limited dispersal ability, four years may be too soon to see changes in the herpetofaunal community, especially since restoration improved existing habitat rather than restoring uninhabitable sites. Pre-restoration sampling and long-term monitoring would allow more firm conclusions to be made.

Forest thinning reduced the most common reptile, the green anole (*Anolis carolinensis*), a generalist lizard not especially sensitive to an open canopy or to harvest operations. Increased red imported fire ant (*Solenopsis invicta*) populations in disturbed areas and open canopies could be a factor, though more research is needed on the effects of fire ants on herpetofauna.

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INTRODUCTION

Imperiled Isolated Wetlands

In the southeastern United States, wetlands or former wetlands cover approximately 15% of the landscape. Approximately 84% of the wetlands that existed in 1954 were converted for agriculture or development by 1983 (Hefner and Brown 1988). Although net wetland losses declined from 117,000 ha per year to 26,700 ha after the institution of the policy of "no net loss" of wetlands, losses of wetlands with emergent vegetation continue (Dahl 2000). Until 2002, U.S. Army Corps of Engineers regulations allowed "fast-track" permits for projects that would impact isolated wetlands less than 1.2 ha in area and proposed as recently as 1998 to increase that threshold to 3 ha (Kaiser 1998). Recent Supreme Court decisions have interpreted the Clean Water Act to include only wetlands directly connected with or adjacent to major waterways, leaving isolated depression wetlands unprotected by the act (Christie and Hausmann 2003, Tiner 2003, Zedler 2003). This distinction is not based on differences in ecological functions but is related to the jurisdiction of the federal government and states' rights. Even without predictable surface connections to larger aquatic systems, isolated wetlands perform ecological services that impact the broader landscape. Some isolated depression wetlands retain and slowly release rainwater pulses, either through surface connections at periods of maximum rainfall or through slow release into groundwater. Others can retain and remove contaminants from surface runoff (Zedler 2003). Small isolated wetlands are very important for sustaining diversity of plants, vertebrates, and invertebrates, including many endemic species.

Evaluating Wetland Restoration Success Using Herpetofauna

Reptiles and amphibians are an important component of the faunas of isolated wetlands. Ironically, the factors most responsible for the herpetofaunal diversity at these wetlands are the same factors that make their protection difficult. Because they are never connected to source populations or they dry completely in at least some years, many isolated wetlands lack predatory fish. Although some terrestrial amphibians like the green frog (*Rana clamitans*) and southern cricket frog (*Acris gryllus*) will breed in wetlands containing fish (Gibbons and Semlitsch 1991), others breed exclusively in fish-free sites, often only available in small isolated wetlands. The small size of many of these wetlands and their hydrological variability make precise delineations difficult, yet hydroperiods that vary across years and across wetlands allow a larger suite of amphibian species to coexist, as some species can breed successfully at the same wetland in separate years (Semlitsch et al. 1996, Snodgrass et al. 2000) or at different wetlands in the same year. In a very wet year, even the smallest and most ephemeral of wetlands can offer breeding habitat.

The permeable skin and biphasic life histories of amphibians make them particularly sensitive to habitat disturbances, and wetland use by amphibians can be an indication of water quality (Vitt et al. 1990). Amphibians have been shown to be remarkably productive in some ecosystems, accounting for more biomass than all other vertebrates combined in some southern Appalachian forests (Hairston 1987). One Carolina bay can produce several hundred thousand of dispersing juveniles in a single year (Gibbons et al. 2006). Organic and inorganic nutrients are flushed into wetland basins by heavy rains, but eutrophication is ameliorated by this dispersal, one of the few mechanisms to transport nutrients out of wetlands into the uplands (Wassersug 1975).

Some species of snakes are highly aquatic, using uplands only for migration, dispersal, or aestivation. Some aquatic snakes, including the black swamp snake (*Seminatrix pygaea*) are almost exclusively found in seasonal wetlands. Many turtle species use temporary wetlands in addition to permanent water bodies, and some species (*Kinosternon spp.*, *Deirochelys reticularia*) prefer shallow, seasonal wetlands to deeper, more permanent habitats.

Since the majority of the amphibians and reptiles of isolated wetlands are also terrestrial for at least a portion of their life-cycles, the uplands surrounding these wetlands are also crucial herpetofaunal habitats. The distance traveled into the uplands depends on the species; salamanders are generally less vagile than frogs, and long-ranging species like the Carolina gopher frog travel up to two km (Franz et al. 1988). By synthesizing thirteen radio-telemetry and radioactive tagging studies, Rittenhouse and Semlitsch (2007) estimated that 50% of amphibians remain within a 93 m radius of wetlands, but the radius must be extended to 664 m to include 95% of individuals. In an earlier, more comprehensive review of distances traveled into the uplands, Semlitsch and Bodie (2003) proposed “core habitat” zones of 142–189 m around wetlands for both reptiles and amphibians. Most amphibians have limited home ranges once in the uplands, making only small movements between microhabitats. Some aquatic snakes move into the uplands for aestivation, and turtles travel into the uplands for nesting. While comparatively fewer reptile species are as dependent on wetlands, others reside in upland habitats and use wetlands opportunistically.

Habitat loss is considered the largest factor in the current well-documented worldwide amphibian declines (Blaustein and Wake 1990), with wetland loss and degradation of particular concern in the United States (Delis et al. 1996). Concern over reptile declines is also rising (Gibbons et al. 2000). Though there are notable physiological differences between the two classes, their similarities make them vulnerable to some of the same threats and also make them easily studied together, as they are often sympatric and susceptible to similar trapping methods.

Objectives

This research was designed to test the responses of reptile and amphibian assemblages to Carolina bay restoration and to thinning in the upland margins of restored bays. I hypothesized that the buffers surrounding undisturbed bays would harbor the highest richness, diversity, and abundance of both reptiles and amphibians, and that restored bays would support more richness, diversity, and abundance than unrestored disturbed bays, but less than reference bays. Assemblages in bay buffers that had been thinned were expected to include a different suite of species than those living in mixed pine hardwood buffers, because species adapted to higher levels of insolation could be expected to be more common under the more open canopies of the pine savannah buffers, and species known to be sensitive to forestry operations could be expected to be reduced.

BACKGROUND

Carolina Bays on the Savannah River Site

Carolina bays are elliptical depression wetlands in the Atlantic Coastal Plain of the southeastern United States, from New Jersey to Florida. The long axis of each bay is oriented from northwest to southeast, and there is raised sand rim along the southeastern edge. They range in size from 50 m to 8 km in diameter. Though a few bays have connections with groundwater (Shields et al. 1982), even these have no permanent natural connections with surface flows, and rainfall and evapotranspiration are almost always the primary sources of changes in water levels (Lide et al. 1995). A 1980 study used infrared aerial photos and assigned a minimum area of 0.12 ha to identify 189 Carolina bays on the Savannah River Site (SRS) (Shields et al. 1982), but current estimates are just above 300. The exact number depends not only on size and hydrological requirements, but also on the presence of the structural qualities described above. Regardless of the strictness of the definition, the Carolina bays on the SRS are all isolated depression wetlands (Sharitz 2003). Only 10% of known Carolina bays in South Carolina are “relatively intact” (Bennett and Nelson 1991).

Herpetofaunal Responses to Wetland Restoration

Previous efforts to evaluate wetland restoration success for amphibians have generally been limited to previously uninhabitable sites, allowing the assumption that all amphibian captures are colonists. Often, studies examine restoration of a single wetland or of several sites in a limited area and nearby source populations are known or are monitored concurrently, with reference sites also providing source populations (Bowers et al. 2000, Petranka et al. 2003a, Brodman et al. 2006).

Pechmann et al. (2001) documented amphibian colonization of small ponds that were created before a large Carolina bay, Sun Bay, was drained and covered by a parking lot. The inserted clay layers drained more quickly than those of natural bays, so plastic liners were installed after 17 months, but the liners caused the ponds to hold water permanently. Despite these and other differences between the constructed ponds and the original wetland, some individual amphibians which had been marked at Sun Bay in the years before it was drained subsequently colonized the constructed wetlands. While communities at the constructed wetlands did not match those present at Sun Bay in the last four years of its existence, in the aggregate they represented a subset of the former amphibian assemblage, with the most common species being the most successful colonizers.

In northwestern Indiana, a 3,000 ha site had been drained and converted to farmland, with seven wetlands in existence in 1998, just prior to restoration (Brodman et al. 2006). In 2003, amphibians used 44 wetlands on the site, and average amphibian species richness per wetland had increased from 2.0 to 3.9. Each of the seven species that had already been endnotedetected in 1998 was captured at more sites with each passing year. Two species, including the eastern tiger salamander (*Ambystoma tigrinum*), were not detected until 2003, and were considered slower colonizers from a nearby slough.

Seven restored wetlands in Minnesota were surveyed for amphibians for just one year, with the age of restored bays ranging from 5 to 20 months (Lehtinen and

Galatowitsch 2001). Species richness was inversely related to distance to nearest source wetlands, and 8 of the 12 species found at five reference wetlands were also found at the restored wetlands. Most of these species were all considered strong dispersers, and therefore likely early colonizers.

Bowers et al. (2000) sampled the herpetofauna within Pen Branch, a stream on the SRS in which all of the vegetation had been destroyed and several braided channels created by over 30 years of high-temperature, high-volume inputs from a nuclear reactor. Restoration did not include hydrological manipulation, only planting of bottomland vegetation, with some portions receiving site preparation and some getting applications of herbicide to reduce weedy vegetation. Seven years after hot water flows had ceased and three years after re-vegetation, several species had successfully colonized the interior floodplain of the stream. Most were species known to colonize disturbed wetlands, but species composition was similar at likely source habitat, the adjacent undamaged riparian zones (Bowers et al. 2000). The stream restoration study at Pen Branch netted 72 species in just 21 months (Bowers et al. 2000).

Amphibian populations were monitored at a restored floodplain wetland complex in the Southern Appalachians for thirteen years (Petranka et al. 2003a, Petranka et al. 2007). Four of the created wetlands previously contained small pools and breeding populations, and the other six were within 100 m of known source populations. Created ponds were colonized by seven species during the first year, and no new species arrived after the second year. Yet after monitoring for seven years post-restoration, the researchers could not be certain that wetland creation would ultimately result in an increase in the number of breeding populations (Petranka et al. 2003b). With the exception of the relatively stable populations of spotted salamanders (*Ambystoma maculatum*), extrapolation from a four-year subset of their data could lead to drastically different predictions, depending on which four years were chosen.

A wetland restoration in Maine demonstrated that increases in hydroperiod that cause ponds to become permanent may allow predators other than fish to become established and affect the successful reproduction of focal species (Vasconcelos and Calhoun 2006). Of four restored wetlands, one became permanent, and overwintering green frog (*Rana clamitans*) tadpoles preyed upon wood frog (*Rana sylvatica*) eggs and embryos.

METHODS

Study Area and Project Description

The Savannah River Site (SRS), a 750 square-km National Environmental Research Park (Figure 1), is bordered on its southwestern edge by the Savannah River, which also forms the border of South Carolina. It was acquired by the US Atomic Energy Commission in 1951, and is now under jurisdiction of the US Department of Energy (DOE). Intensive sampling of herpetofauna, including several long-term monitoring programs, has documented 99 species of reptiles and amphibians on the property (Gibbons et al. 1997).

Prior to 2001, twenty Carolina bays on the SRS were selected by the DOE and the US Forest Service (USFS) for restoration of wetland hydrology and interior vegetation. Four of these were randomly assigned to a control group, which would not be restored until 2006. The sixteen bays to be restored had been assigned to one of two blocks: eight bays with recent forestry operations in the 100-meter upland margin, and eight minimally disturbed bays. Because there were more minimally disturbed than recently disturbed bays, two of the minimally disturbed bays received additional buffer harvesting in order to create equal blocks of experimental units. Within each disturbance block, bays to be restored were randomly assigned to one of the two upland buffer treatments which are described in more detail below. Of the sixteen restored bays, I selected three bays from each of the buffer treatments for herpetofaunal monitoring; each set of three included two with minimally disturbed buffers and one with a recently disturbed buffer (Table 1).

Interior and exterior vegetation descriptions from 1951 are based on aerial photographs taken during that year, prior to the acquisition of the SRS by the DOE. Those photographs also show that all drainage systems were in place at that time. Estimates of original wetland area impacted by the drainage systems are based on topographic surveys comparing the elevations of the rim of the bay and the lowest point in the ditch with the elevation profile of the bay interior.

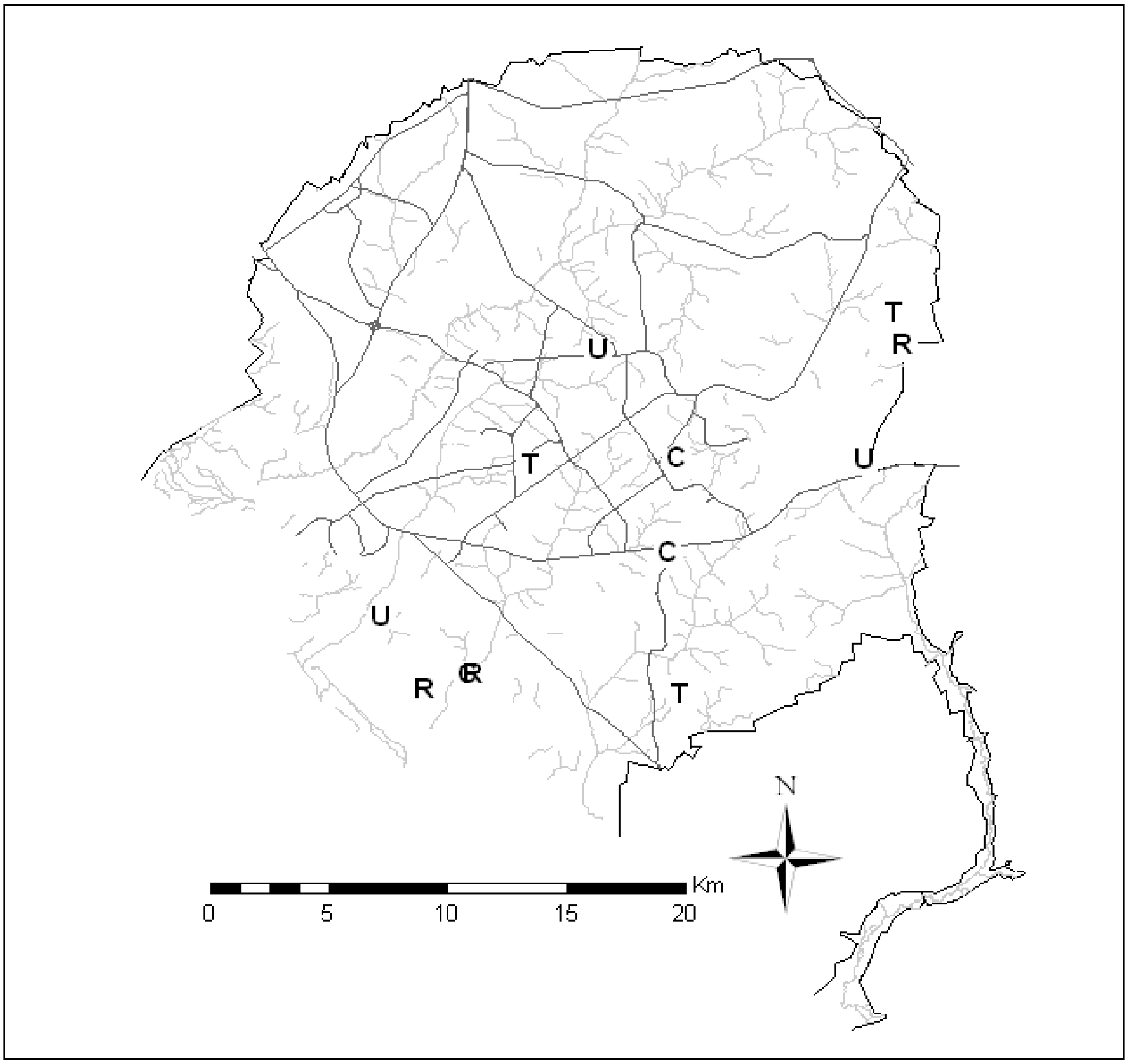

Figure 1. Map of the Savannah River Site (SRS). Letters indicate the locations of study bays, with letters indicating treatments. C = control; R = Reference; T = Restored bays with thinned buffers; U = Restored bays with un-thinned buffers.

Restored Carolina Bays

Restoration activity began in November of 2000, when trees were harvested from the interiors of all bays that were to be restored. Along with interior logging operations, overstory trees were thinned and all hardwoods were removed in the 100-meter upland buffers of the bays in the fire-maintained, open-canopy pine savanna treatment group (pine bays). The buffers of the other restored bays were not manipulated beyond necessary disturbance related to the interior logging (skid trails and logging decks). Logging operations were completed at all bays by February of 2001. Clay plugs were not installed in drainage ditches until January of 2002, due to delays in obtaining permits. Nevertheless, ditches were effectively plugged during 2001 when harvest operations filled them with compacted local soil. In September of 2001, a foliar herbicide (Garlon 4) was directly applied to stumps in the bay interiors to prevent re-sprouting.

Un-thinned Buffer Bays (Mixed Bays)

Three of the restored bays received interior harvest but no harvest in the 100-meter upland buffer. The ultimate goal is a mixed pine-hardwood buffer, though only one of the bays (5204) currently has a substantial hardwood overstory component in the buffer. The buffers of the other two bays in this treatment are dominated by pines, and may eventually be thinned to encourage hardwood development.

Bay 5071 is a 0.85 hectare bay in the center of the SRS. Its drainage system affected nearly 100% of the historic wetland area. In 1951, aerial photographs show that both the interior and exterior were cultivated for agriculture. At the time of restoration, both the interior and exterior were dominated by loblolly pine (*Pinus taeda*).

Bay 5128 covers 0.77 hectares near the eastern edge of the SRS. The drainage ditch drained roughly 92% of the historic wetland area. In 1951, the interior of this bay was forested, while the surrounding land was cultivated for agriculture. At the time of restoration, the interior and roughly half of the buffer had been planted with longleaf pine (*Pinus palustris*). The other half of the buffer is dominated by slash pine (*Pinus elliottii*).

Bay 5204 is a 0.66 hectare bay near the southwestern edge of the SRS. Its two drainage ditches drained about 75% of the historic wetland area. In 1951, the interior of Bay 5204 was forested, and surrounding land was cultivated for agriculture. Prior to restoration, the bay's interior was primarily upland hardwoods, while the buffer vegetation was a mixture of open-canopy pines and upland hardwoods.

Thinned Buffer Bays (Pine Bays)

Prescribed burns of the thinned buffers were scheduled for the winter and spring of 2001 and 2002, but were delayed until February of 2003 by several factors, including a severe drought, a moratorium on burning following the September 11, 2001 terrorist attacks, and unsafe conditions for prescribed burns. This delay probably allowed hardwood sprouts, especially sweetgum (*Liquidambar styraciflua*), to become established in many of the thinned buffers.

Bay 126 is a 1.53 hectare bay near the center of the SRS. Its drainage ditches affected roughly 59% of the historic wetland area. In 1951, the interior and parts of the buffer had a mixture of shrubs and trees, while other areas of the buffer were cultivated for agriculture. Prior to restoration, the interior was predominantly bottomland hardwoods, and the buffer was open-canopy pine, especially slash pine (*Pinus elliottii*).

Bay 5092 is near the southern edge of the SRS, and covers 1.36 hectares. The drainage ditch affected approximately 54% of the historic wetland area. The interior in 1951 was composed of both forested and herbaceous areas, and the buffer was cultivated for agriculture. Prior to restoration, the interior was dominated by sweetgum (*Liquidambar styraciflua*), and the buffer was a mixture of pines and hardwoods.

Bay 5135 is a 0.28 hectare bay along the eastern edge of the SRS. The drainage ditch drained nearly 100% of the historic wetland area. The aerial photographs show that the area may have been used as a pasture in 1951, while cultivation for agriculture was evident nearby. Prior to restoration, the interior of Bay 5135 was open-canopy longleaf pine (*Pinus palustris*), and the buffer was also open-canopy longleaf pine and upland hardwoods. In addition to thinning, an area roughly 40% of the size of the buffer of 5135 was clearcut at the time of interior harvest, in order to cause a disturbance comparable to those at the other bays in the "recently disturbed" block.

Table 1. Treatment assignments and pre-restoration status of the 100-meter upland margins of monitored Carolina bays.

Bay	**Buffer Treatment**	**Pre-restoration Buffer**	**Note**
Block One (Minimal Disturbance)			
5071	pine/hardwood	70% pine;20% p/h; 10% road	*
5204	pine/hardwood	70% p/h; 30% pine	
126	Pine	85% pine; 15% p/h	
5092	Pine	85% pine; 15% p/h	
Block Two (Recently Disturbed))			
5128	pine/hardwood	50% pine; 50% cc	*
5135	Pine	100% pine	†
Not Restored			
108	Control	70% p/h; 30% pine	
118	Control	100% cc	
5055	Control	65% p/h; 30% cc; 5% pine	
79	Reference	not assessed	
153	Reference	not assessed	
5048	Reference	not assessed	

* Mature hardwoods were absent in the buffers of these bays assigned to the pine/hardwood buffer treatment.

† The buffer of Bay 5135 underwent additional harvest at restoration to create openings similar to those at other recently disturbed bays.

p/h = mixed pine-hardwood; cc = clearcut.

Control Bays

Of the four bays that would not be restored until after 2005, I selected three at random for monitoring. Bay 108 covers 1.05 hectares near the center of the SRS. The drainage ditch drained approximately 90% of the historic wetland area. Arial photographs show that Bay 108 was primarily pasture with some hardwoods in 1951, before the creation of the SRS. During the study, the interior vegetation was dominated by a combination of pines and hardwoods, while the buffer is dominated by slash pine (*Pinus elliottii*) with a relatively dense canopy.

Bay 118 covers 1.04 hectares slightly south and east of the center of the SRS. The drainage system drained approximately 91% of the historic wetland area. The interior of Bay 118 was covered in herbaceous vegetation in 1951, while the surrounding area was cultivated for agriculture. The interior is now dominated by hardwoods, mostly sweetgum (*Liquidambar styraciflua*), and pines. An area encompassing the entire buffer was clearcut in 1998 and planted with longleaf pine (*Pinus palustris*).

Bay 5055, covering 0.30 hectares, is located near the southwestern edge of the SRS. The drainage system affected nearly 100% of the historic wetland area. In 1951, the interior was dominated by herbaceous vegetation, and the buffer was predominantly old fields. During this study, upland hardwoods and loblolly pine (*Pinus taeda*) dominated both the interior and the buffer of Bay 5055.

Reference Bays

I chose three reference bays based on placement in the landscape from a list of candidate reference bays compiled by the USFS. None of these bays had drainage systems at the time of restoration, nor did they have forested interiors.

Bay 79 lies along the eastern edge of the site, very near Craig's pond, the largest Carolina bay on the SRS, at 50.18 hectares. Bay 79 covers 0.49 hectares, and its interior is unforested, dominated primarily by herbaceous species. The buffer is dominated by loblolly pine (*Pinus taeda*). In 2001, a portion of the 100-meter buffer, including the area around one of the two drift fence arrays, was thinned due to a misunderstanding about the site use permit. This same section of the buffer was also prescribed burned in 2004.

Bay 153 covers 1.01 hectares near the southwestern edge of the SRS, within 200 meters of bay 5055. The interior is dominated by herbaceous species, and the buffer is a mixture of loblolly pine (*Pinus taeda*) and upland hardwoods.

Bay 5048 is also located along the southwestern edge of the SRS. Its interior is also predominantly herbaceous, and the buffer is dominated by upland hardwoods and loblolly pine (*Pinus taeda*).

Herpetofaunal Sampling

In the fall of 2001 I installed two herpetofaunal trapping arrays in the 100-meter buffer of each bay, 50 meters from the edge of the bay. In an effort to account for the directionality of amphibian migrations into and out of breeding sites (Dodd and Cade 1998, Rothermel 2004), I placed one array in the direction of the next-nearest neighboring wetland, and the other on the opposite side of the bay. Each drift fence was 15 meters long, constructed of aluminum flashing 1 meter in height with the lower edge buried to a depth of at least 10 centimeters. Fences were installed in a y-shaped configuration: two fences nearly parallel with the bay edge and the other perpendicular to it. An open space 5 meters in diameter occupied the center of each array. The traps at each array totaled: six funnel traps, twelve pitfall traps, three PVC tubes, and twelve coverboards - six of plywood and six of tin (Figure 2).

I created pitfall traps by burying 19-liter plastic buckets up to their rims on either side of both ends of each fence (Gibbons and Bennett 1974, Gibbons and Semlitsch 1981), four buckets per fence. The bottoms and lower sides of buckets were punctured to facilitate drainage, but the effectiveness of this approach depended on the porosity of the underlying soil. A sponge was placed in each bucket to provide a floating platform if the trap filled with rain. On dry days I poured water into the buckets in an attempt to prevent desiccation of amphibians, and the sponges helped retain moisture.

I made funnel traps from 0.6-centimeter mesh hardware cloth and placed one on the ground on either side of each fence, roughly in the middle, the openings flush with both the fence and the ground. To attract treefrogs I erected a 1.5-meter length of PVC tubing vertically (Phelps and Lancia 1995, Boughton et al. 2000), with the base at ground level within 5 meters of the outer end of each fence. These were originally inserted into holes in the ground, but I adjusted them in early 2004 to rest at ground level supported by rebar spikes after I discovered that some treefrogs escaped census by dropping into the hole as the tube was uprooted. Finally, four rectangular coverboards (0.61 X 1.22 meters), two of plywood and two of galvanized tin, were laid down beyond each PVC pipe within 10 meters of the end of each drift fence (Grant et al. 1992). Snakes, salamanders, and lizards sought cover under these boards; reptiles are attracted to cover objects made of tin which allow them to raise their body temperatures while remaining concealed.

I visited the bays to retrieve captures every second day from January through July, beginning in 2002 and ending in 2005. To prevent desiccation and red imported fire ant (*Solenopsis invicta*) predation, I began as early as available light allowed sufficient visibility. I divided the bays into two groups based on their locations, visiting each group on alternate days, and I devised three different routes for each group to avoid bias due to the timing of visits. Sampling effort was equal across the bays, since each had the same number of traps and I visited them an equal number of times in a given year.

I gave snakes individual marks by clipping a triangular section from a single ventral scale (Brown and Parker 1976). In addition, snakes larger than 1 centimeter in diameter were injected with 14-mm Passive Integrated Transponder (PIT) tags (Camper and Dixon 1988). Turtles were marked with PIT tags and shell notching (Cagle 1939) by staff at the Savannah River Ecology Laboratory (SREL). Turtles were held at SREL for

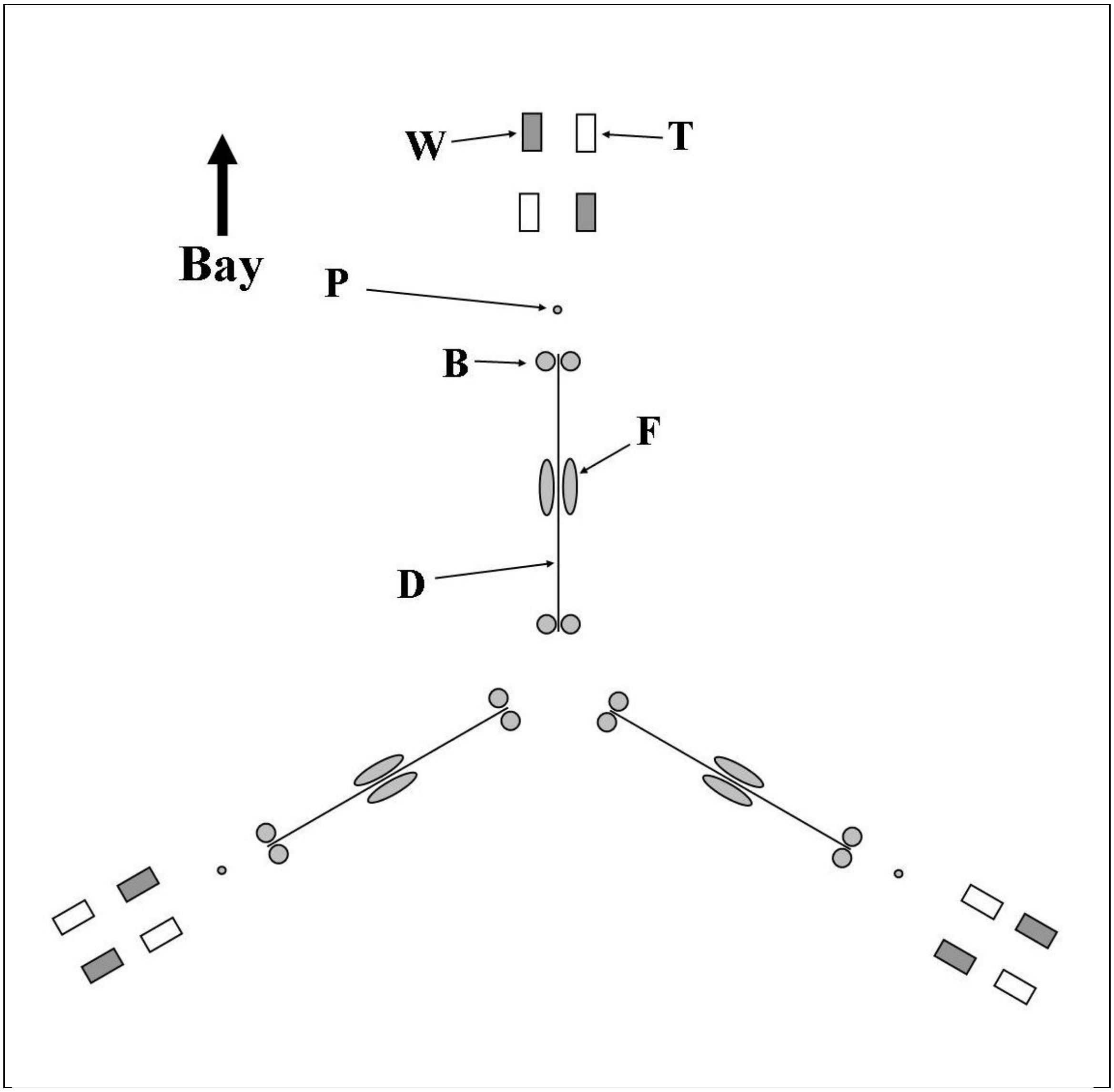

Figure 2. Overhead diagram of a herpetofaunal sampling array. Features are not drawn to scale. W= wood coverboard; T= tin coverboard; P= PVC tubing; B= pitfall trap; F= funnel trap; D= drift fence.

two nights (until the morning of the next visit to the bay of capture). I did not give lizards, frogs, and salamanders individual marks, but I marked them to year of capture by removing a single digit from a single limb (Ferner 1979) and released them immediately. I released animals back into the cover object when they were captured under a coverboard or inside PVC pipes. I released pitfall trap, funnel trap, and hand captures on the opposite side of the drift fence from the point of capture, at least 5 meters from the fence. I measured snout-vent-length (SVL) with handheld rulers, identified animals to species, classified them in adult, juvenile, or recent metamorph age classes, and recorded the sex of adults when possible.

Capture and handling of animals was conducted in accordance with Animal Use Protocol #50029, as approved by the Clemson University Animal Research Committee.

Environmental Sampling

I retrieved daily rainfall totals, maximum and minimum air temperature, and maximum and minimum humidity (%) from a National Oceanic and Atmospheric Administration (NOAA) weather station on the SRS for all years of the study. In 2004 and 2005, rainfall since previous visit was collected by Tru-Check Direct Reading Rain Gauges (Forestry Suppliers Inc., Jackson, MS) and recorded during each visit to each bay. I also recorded the current and two-day maximum and minimum air temperatures at every visit during 2004 and 2005, along with estimates of wind speed (based on the standard Beaufort scale) and cloud cover to the nearest five percent.

Depth of ponding was recorded at six-hour intervals by WL 40 loggers (Global Water Instrumentation, Inc., Gold River, CA) at each control and restored bay, beginning in 2000. Recordings were supplemented with manual readings of staff gauges when the instruments failed. Loggers were installed in each reference bay during the spring of 2005, and fluctuations during that period allowed inferences to be made about the depths during the previous four years. Monthly pH readings were acquired at each of the control and restored bays, but the pH was never tested at reference bays.

Vegetation Sampling

I surveyed vegetation of the buffer sites during July of 2004 and again in 2005, using a whole-plot survey method. I delineated the vegetative survey plots as 0.2-hectare circles, centered at the center of the array. Within this circle, I randomly placed eight 1-m^2 subplots and estimated the percentage of the plot occupied by groundcover types (woody species name, herbaceous, or bare ground). I measured leaf litter depth at the center and the lower-left and upper-right corners of each of these subplots. I identified all overstory and midstory trees (greater than 5 centimeters dbh) to species and recorded their diameters into size classes. I measured the length and diameter of all coarse woody debris (CWD), and assigned each piece to one of five decay classes. I used a spherical crown densiometer (Forestry Suppliers, Inc., Jackson, MS) to estimate canopy coverage at the center of each plot and also on the perimeter (25 meters from the center) at each of the four cardinal directions. Ocular estimations of the percent cover of understory vegetation in each quadrant of the plot were made from each of these same five vantage points, for a total of three estimates to be averaged per quadrant. To maintain consistency across sites and years, all estimates (canopy cover, overall understory cover, and all subplot estimates) were made by the same researcher in both 2004 and 2005.

Statistical Analysis

Because captures of dispersing juveniles are subject to greater annual variation than those of breeding adults, I separated captures into these two age classes. I calculated the diversity of breeding adults separately for reptiles and for amphibians. I used the total number of species observed at each site (S_{obs}) as an estimate of the actual species richness (S). I visually inspected species accumulation curves, which plotted the cumulative number of species against date of sampling, to determine whether they appeared to reach an asymptote, indicating a relatively complete census of true species richness. As an indicator of diversity, species richness is heavily influenced by rare species, because each species carries equal weight. I therefore chose Simpson's index (D) (Simpson 1949), which emphasizes the more common species, as a complementary diversity statistic. Simpson's index is a measure of the probability that two individuals selected at random from a sample will belong to the same species. It is calculated, with corrections for a finite population, as:

$$D = \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{N(N - 1)}$$

where n_i = the number of individuals in the sample that belong to the i^{th} species, N = the total number of individuals in the sample, and S = the total number of species in the sample. Simpson's D is also known as species dominance, since a value of one represents the lowest possible diversity (when a single species is completely dominant) and a zero represents the highest. The complement of dominance (1 – *D*) was used as the diversity index, which maintains the range from zero to one while allowing the higher values to indicate more diverse assemblages.

As an indication of diversity, evenness depends only on the relative proportions of species, and therefore represents one end of a continuum, with species richness at the other extreme. Simpson’s evenness measure was calculated from Simpson's dominance (*D*) and the observed species richness (*S*) by:

$$E_{1/D} = \frac{(1/D)}{S}$$

Examining richness and evenness along with the intermediate diversity index can allow assessment of whether differences in diversity are attributable to differences in evenness or species richness or both.

I used PROC MIXED (SAS Institute 2003) to perform repeated-measures mixed-model ANOVAs to test for differences in species richness, total number of captures, Simpson’s Diversity (1-*D*) and evenness (*E*). The evenness values were inverted to meet the assumption of normally distributed residuals. PROC MIXED allows for different covariance structures to account for the lack of independence from repeated testing. I tested four different covariance structures: autoregressive, compound symmetry, heterogeneous compound symmetry, and unstructured, and chose the best one based on Akaike’s Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002).

If an ANOVA indicated a significant F-statistic for the treatment effect, appropriate linear contrasts were estimated. The number of possible orthogonal contrasts is one less than the total number of treatments, so I examined the following three *a priori* contrasts:

1. Control bays versus all restored bays
2. Reference bays versus all restored bays
3. Restored bays with thinned buffers versus those with un-thinned buffers

When an ANOVA indicated a significant year by treatment interaction, contrasts tested for significant treatment effects within each year separately, and contrasts were then made within the years that showed a significant overall treatment effect.

I sorted species into ecological guilds based on taxonomic group and habitat association (Guyer and Bailey 1993, Conant and Collins 1998, Means 2006). Although I recaptured several thousand individuals during the course of the study, I rarely had enough recaptures of a given species to model using capture-recapture techniques, and those species with numerous recaptures violated model assumptions of constant catchability. I therefore used the total number of unmarked individuals captured as an estimate of abundance. When I captured adults of a given species consistently enough to model, I removed those captures from the guild total and analyzed the species separately. I tested these adult species and guild captures for effects of treatment and year, again using PROC MIXED for repeated-measures ANOVA tests. Although I captured dispersing juveniles of several species, only the juvenile recruitment of a few anuran species was substantial enough for the repeated-measures analysis. When a test produced a significant treatment F-statistic, the same orthogonal linear contrasts were examined as for the diversity measures above.

I used Pearson rank correlations to test for relationships between daily reptile and amphibian activity (total captures) and environmental variables.

I used the NMDS procedure of the PC-ORD software package (McCune and Mefford 2006) to produce Non-Metric Multidimensional Scaling plots using adult capture totals. NMDS is a graphical technique that reduces the dimensionality of multivariate data after ranking the dissimilarity between observations. I removed species which contributed negligible information by only appearing in a single sample, then log-transformed capture totals to reduce the influence of the most abundant species. I used the Bray-Curtis dissimilarity measure, being the ratio of the number of unshared species over the number of shared species, computed for bays *i* and *j* as:

$$D_{ij} = \frac{\sum_{k=1}^{n} \left| a_{ik} - a_{jk} \right|}{\sum_{k=1}^{n} \left(a_{ik} + a_{jk} \right)}$$

where n = the total number of species in bays *i* and *j*. I repeated the analysis using only presence/absence of species at each bay during the four-year course of the study.

RESULTS

Capture Success

From 1 January 2002 to 31 July 2005, I captured 67 different species of reptiles and amphibians, roughly two-thirds of the herpetofaunal species known to occur on the Savannah River Site (Gibbons et al. 1997), a total of 47,414 individuals including 30,005 young-of-the-year amphibians. I also recaptured marked animals 4,944 times. Amphibians comprised 97.0% of total captures. There were 19 species of frogs and toads (n=42,655; 90.0% of individuals) and 8 species of salamanders (n=3,304; 6.98% of individuals). The eastern spadefoot, *Scaphiopus holbrookii,* was the most commonly encountered anuran (n=20,677; 43.7% of individuals), and the mole salamander, *Ambystoma talpoideum*, was the salamander captured most often (n=2,442; 5.2% of individuals). Forty-one species of reptiles comprised only 3.0% of the total number of captures (n=1,455). Seven species of lizards (n=1,037) accounted for 70.7% of reptile captures (2.1% of individuals). The green anole, *Anolis carolinensis*, was the most common reptile (n=265), followed by the eastern fence lizard, *Sceloporus undulatus* (n=228). Capture totals by treatment of marked adults are summarized in Tables 2 & 3, and totals of young-of-the-year are presented in Table 4.

In addition to the above commonly-encountered species, I documented thirteen South Carolina Species of Conservation Concern (Kohlsaat et al. 2005), and each of the twelve bays supported at least one of these rare and imperiled species. I captured four species of concern at control bays, six at mixed bays, five at pine bays and eight at reference bays. An ANOVA test on the average observed richness of species of concern indicates no significant differences between treatments (F=2.00; p=0.1927).

Amphibian Activity by Month

Adult amphibian activity was highest during the month of March, due in no small part to the sizable eastern spadefoot toad breeding event during March of 2003. Except for that peak, adult amphibian captures showed a slight increase from February through June, but then dropped off sharply in July (Figure 3). The mole salamander was captured frequently in late winter and activity gradually declined into the summer, while eastern narrowmouth toad (*Gastrophryne carolinensis*) adult activity increased beginning in April and remained relatively high through July. While reptile activity was less variable, captures were relatively low during the warmest and coldest months and highest in April and May.

Juvenile dispersal was generally minimal before April, the month during which large eastern spadefoot dispersal events occurred in 2003. Juvenile activity tended to be even higher in May, then diminished in June before decreasing greatly in July (Figure 4).

Table 2. Captures of individual adult amphibians by guild and species at twelve Carolina bays on the SRS from January 2002 through July 2005. Each treatment group included three bays. The second number, when present, represents the number of recaptures.

Guild	Species	Control	Mixed	Pine	Reference	Total	Note
Upland Frogs							
	Bufo terrestris	411/33	1832/177	1905/237	1420/140	5568/587	a b
	Scaphiopus holbrookii	931/122	997/196	604/108	681/89	3213/515	a b
	Gastrophryne carolinensis	527/14	381/6	1120/24	994/18	3022/62	a b
	Pseudacris ornata	19/9	21/1	57/16	180/7	277/33	a
	Bufo quercicus		2	2	18/2	22/2	a
	Pseudacris nigrita			4/2	17	21/2	
	Rana capito		1	2	3	6	a ***
	Pseudacris ocularis			1	1	2	
	Pseudacris feriarum		1		1	2	**
Aquatic Frogs							
	Rana sphenocephala	41/2	98/2	18	190/9	347/13	a b
	Acris gryllus	11/2	25/1	6	45	87/3	
	Rana clamitans	17/1	16/1	6	17/1	56/3	a
	Rana catesbeiana	1	2		2	5	a
	Acris crepitans		1			1	*
Treefrogs							
	Hyla squirella	15/234	184/1299	29/102	18/145	246/1780	a b
	Hyla femoralis	8/52	12/26	11/32	23/137	54/247	
	Hyla cinerea	2/4	13/54	8/8	10	33/66	a
	Pseudacris crucifer	6	3	3	8/2	20/2	a
	Hyla chrysoscelis	3	5/1	1	8/22	17/23	
Aquatic-breeding Salamanders							
	Ambystoma talpoideum	444/115	487/32	299/38	1089/138	2319/323	a b
	Ambystoma opacum	51/9	54/2	60/15	68/13	233/39	a
	Ambystoma maculatum	21	43/5	37/5	28	129/10	a
	Notophthalmus viridescens	2	1	2/1	3	8/1	a
	Ambystoma tigrinum	1			4	5	a ***
	Pseudotriton ruber		1	1		2	
	Eurycea quadridigitata		1			1	
Plethodon							
	Plethodon glutinosus complex	50/17	88/14	29/3	54/21	221/55	a b
	Amphibian Totals	2561/611	4269/1813	4205/590	4882/739	15917/3753	

a Reproduction was documented by captures of metamorphs or juveniles.

b Species was captured consistently enough to analyze separately from the rest of its guild.

Asterisks denote South Carolina DNR Species of Special Concern (Kohlsaat et al. 2005):

* = Moderate priority ** = High Priority *** = Highest Priority

Table 3. Captures of individual reptiles by guild and species at twelve Carolina bays on the SRS from January 2002 through July 2005. Each treatment group included three bays. The second number, when present, represents the number of recaptures.

Guild	Species	Control	Mixed	Pine	Reference	Total	Note
Mesic Lizards							
	Anolis carolinensis	60/2	77/7	32/7	93/14	262/30	a b
	Eumeces laticeps	21/9	20/3	15/1	38/7	94/20	a
	Eumeces fasciatus	15/1	20/1	10/1	36/1	81/5	a
Open-canopy Lizards							
	Sceloporous undulatus	43/2	20	86/39	70/10	219/51	a
	Eumeces inexpectatus	17/4	10/1	25/18	22/29	74/52	a
	Cnemidoporous sexlineatus	15	2	17/2	14/4	48/6	
Scincella							
	Scincella lateralis	58/5	49/5	71/8	39/2	217/20	a b
Semi-fossorial Snakes							
	Tantilla coronata	20	19/1	20	32/2	91/3	a
	Diadophis punctatus	11	17/12	8/9	9	45/21	
	Storeria occipitomaculata	2	9	5	14/1	30/1	
	Cemophora coccinea	4	4/1	2	10/1	20/2	a
	Thamnophis sirtalis	2	4	8	5/2	19/2	
	Virginia valeriae	6	7	1	2	16	
	Heterodon platyrhinos	3	3	4	3	13	
	Lampropeltis triangulum	1	7/14	2	2	12/14	
	Storeria dekayi		1	1	1	3	
	Carphophis amoenus				3/1	3/1	
	Heterodon simus			1		1	***
	Thamnophis sauritus				1	1	
	Virginia striatula	1				1	

a Reproduction was documented by captures of juveniles.

b Species was captured consistently enough to analyze separately from the rest of its guild.

Asterisks denote South Carolina DNR Species of Special Concern (Kohlsaat et al. 2005):

* = Moderate priority ** = High Priority *** = Highest Priority

Table 3 (continued).

Guild	Species	Control	Mixed	Pine	Reference	Total	Note
Terrestrial Snakes							†
	Coluber constrictor	14/3	14/2	14	12	54/5	a
	Elaphe guttata	3/1	5	1	1	10/1	
	Agkistrodon contortrix	1	4	1		6	
	Lampropeltis getula		1	3	1	5	
	Elaphe alleghaniensis			2	2/1	4/1	
	Masticophis flagellum		1			1	
	Pituophis melanoleucus	1				1	**
Aquatic Snakes							†
	Nerodia fasciata	1	1	4	4	10	a
	Farancia abacura	1			3	4	
	Seminatrix pygaea	3			1	4	**
	Nerodia erythrogaster	1	1	1		3	
	Agkistrodon piscivorus		1		1	2	
	Farancia erytrogramma	1				1	
Turtles							†
	Kinosternon subrubrum	1	9	4	15	29	a
	Chelydra serpentina	1			3	4	*
	Deirochelys reticularia			2	1	3	**
	Kinosternon baurii		2		1	3	**
	Pseudemys floridana				3	3	a **
	Trachemys scripta		1	1		2	**
	Terrapene carolina				1	1	
Crocodilians							†
	Alligator mississippiensis		1			1	*
	Reptile Totals	307/27	310/47	341/85	440/76	1398/235	

a Reproduction was documented by captures of juveniles.

b Species was captured consistently enough to analyze separately from the rest of its guild.

Asterisks denote South Carolina DNR Species of Special Concern (Kohlsaat et al. 2005):

* = Moderate priority ** = High Priority *** = Highest Priority

† There were too few captures in this guild to test for treatment effects with repeated-measures ANOVA.

Table 4. Captures of individual young-of-the-year amphibians in the buffers of twelve Carolina bays on the SRS from January through July, 2002 to 2005. The number of bays at which juveniles were documented is also presented. There were three bays in each treatment.

Treatment	**Control**		**Mixed**		**Pine**		**Reference**		**Total**	**Total**
Species	**Captures**	**Bays**	**Captures**	**Bays**	**Captures**	**Bays**	**Captures**	**Bays**	**Captures**	**Bays**
Frogs										
Scaphiopus holbrookii	1328	3	5599	3	3665	3	6872	3	17464	12
Bufo terrestris	337	3	2820	3	2420	3	2275	3	7852	12
Rana sphenocephala	1519	3	679	3	254	3	1079	3	3531	12
Pseudacris ornata	16	2	13	2	13	1	414	3	456	8
Rana clamitans	68	3	71	3	32	3	40	3	211	12
Gastrophryne carolinensis	6	3	11	3	23	3	17	3	57	12
Pseudacris crucifer	0	0	42	2	3	2	8	2	53	6
**Rana capito*	0	0	0	0	12	2	29	1	41	3
Rana catesbeiana	5	1	0	0	1	1	2	2	8	4
Salamanders										
Ambystoma opacum	1	1	4	1	7	1	223	2	235	5
†Ambystoma talpoideum	19	2	20	2	37	3	47	3	123	10
Ambystoma maculatum	14	1	7	1	0	0	3	1	24	3
Plethodon glutinosus complex	3	2	4	3	0	0	7	2	14	7
**Ambystoma tigrinum*	3	1	0	0	1	1	0	0	4	2
Number of Species	**12**		**11**		**12**		**13**		**14**	

* Species designated as highest conservation priority by South Carolina Department of Natural Resources (2005).

† Many bays did not dry during 2003, and I captured large numbers of dispersing paedormorphic A. talpoideum adults in 2004. Recruitment of this species was therefore underestimated, since these adults would have been included in the previous year's cohort had they not remained in the bays.

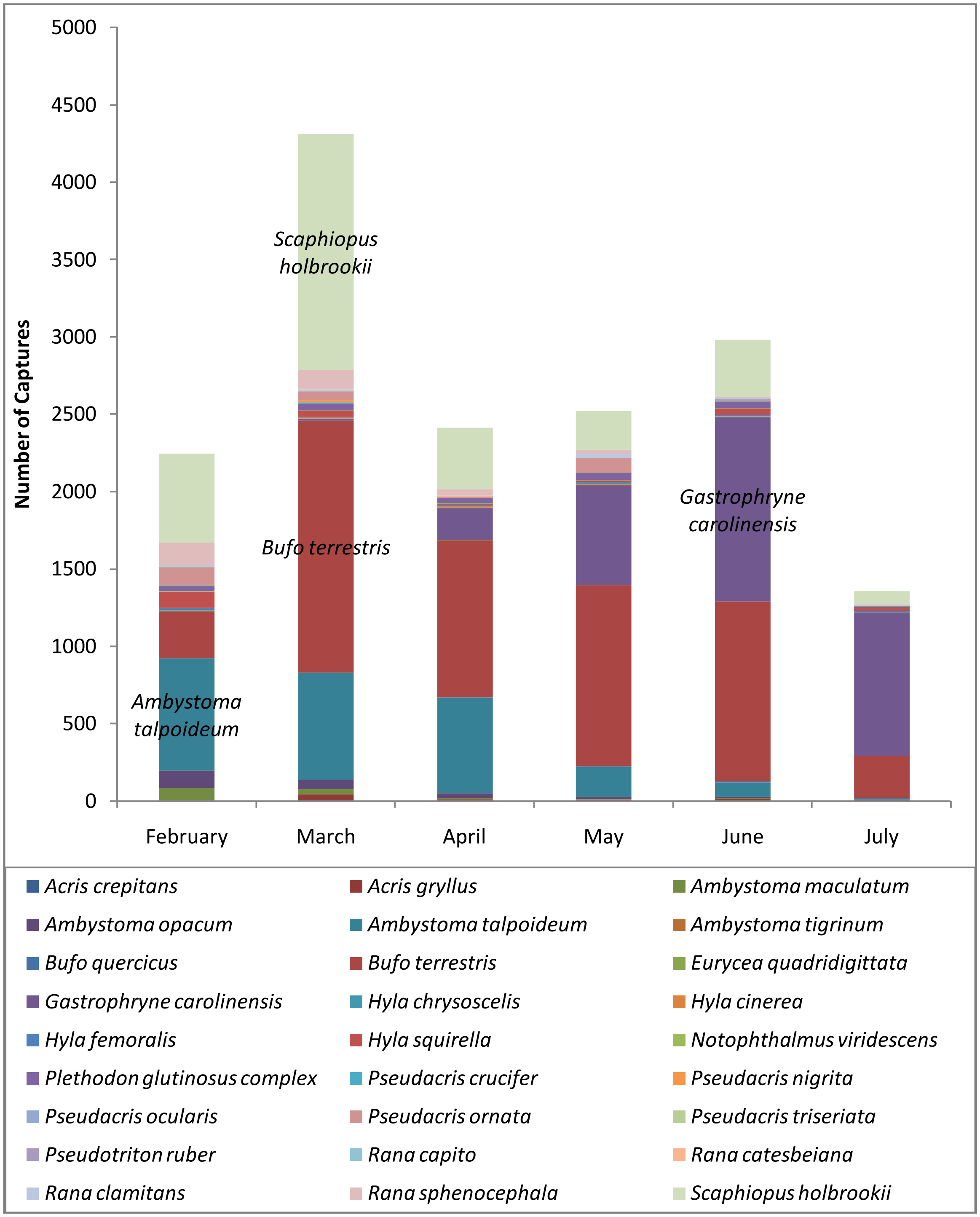

Figure 3. Total captures of adult amphibians by month at twelve Carolina bays on the SRS, 2002 – 2005.

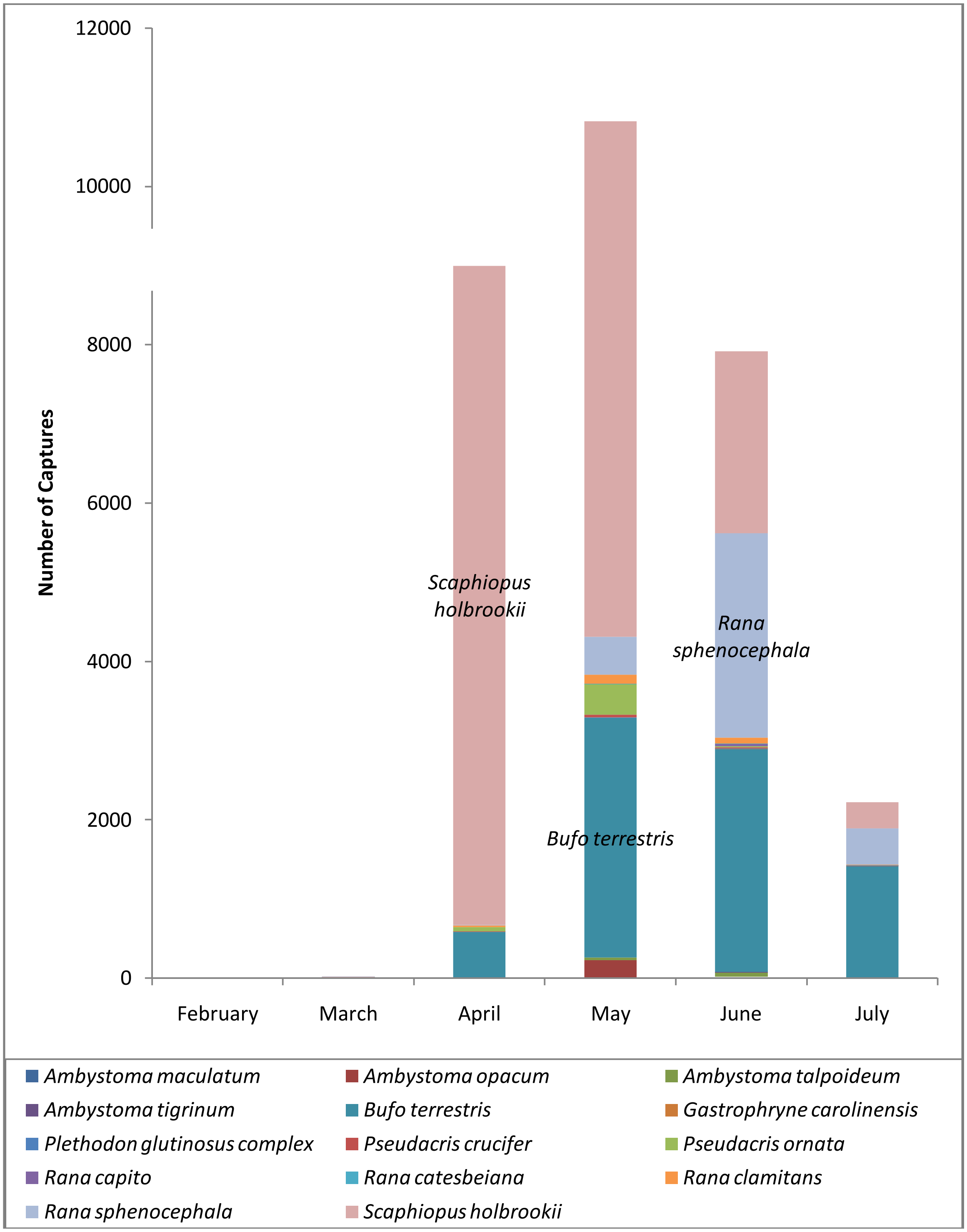

Figure 4. Total captures of recently metamorphosed amphibians by month at twelve Carolina bays on the SRS, 2002 – 2005.

Weather

Daily amphibian captures were positively correlated with rainfall (r_s=0.431; p<0.0001), cloud cover (r_s=0.217; p<0.0001), minimum daily temperature (r_s=0.275; p,0.0001), and minimum relative humidity (r_s=0.351; p<0.0001). Reptile captures were negatively correlated with rainfall (r_s= -0.102; p<0.0001), minimum relative humidity (r_s= -0.197; p<0.0001), and maximum relative humidity (r_s= -0.179; p<0.0001), and positively correlated with maximum daily temperature (r_s=0.116; p<0.0001) (Table 5).

Table 5. Pearson correlations between weather variables and reptile and amphibian captures, with corresponding p-values, at twelve Carolina bays on the SRS, 2004 – 2005.

Weather Variable	**Amphibians**		**Reptiles**	
	r_s	p	r_s	p
Cloudcover (%)	0.217	<.0001	-0.042	0.057
Air temperature During Visit (ºC)	0.100	<.0001	0.092	<.0001
Hour of visit (600 - 1900)	0.064	0.004	0.040	0.067
Maximum air temperature (ºC)	0.115	<.0001	0.120	<.0001
Minimum air temperature (ºC)	0.208	<.0001	0.000	0.988
Rainfall (mm)	0.431	<.0001	-0.102	<.0001
Wind speed (Beaufort scale)	-0.082	0.0002	0.023	0.304

Diversity

The average of Simpson's diversity by treatment of adult amphibians did not vary by year (F=1.32, p=0.293), being one of only two response variables for which I did not find differences between years. Average estimates of amphibian diversity at control and restored bays were very similar, at 0.62, 0.62, and 0.63 for control, mixed, and pine bays, respectively. The average at reference bays was slightly higher at 0.73, but not significantly so (F=1.1, p=0.401) (Figure 5). On the other hand, Simpson's diversity of adult reptiles was different both across years and across treatments (Year: F=21.16, p<0.0001; Treatment: F=11.02, p=0.0003). The linear contrasts indicated that reptile captures exhibited higher diversity at restored bays (at 0.82 and 0.76 at mixed and pine bays, respectively) compared to control bays (0.75) (F=5.51, p=0.0465), higher at reference bays (0.83) than at restored bays (F=8.89, p=0.0187), and higher at mixed bays compared to pine bays (F=14.40, p=0.0058). Tests for treatment effects within each year only revealed significant differences between treatments in 2003, the extremely wet year that yielded less than 10% of the reptile captures (Figure 6).

Reptiles tended to be captured less frequently than amphibians, due to differences in either abundance, catchability, or both, so that fewer reptile species were captured in multiple years at a given bay. Therefore, average annual observed richness (S_{obs}) tended to be higher for amphibians, even though cumulative richness of reptiles was higher. Both reptile and amphibian richness varied across years (Amphibians: F=27.9, p<0.0001; Reptiles: F= 37.9, p<0.0001), but did not vary across treatments (Amphibians: F=2.24, p=0.161. Reptiles: F= 1.72, p=0.240). Average annual S_{obs} ranged from 9.75 at control bays to 12.75 at reference bays for amphibians, and 8.17 at control bays to 11.08 at reference bays for reptiles (Figures 7 & 8).

The three most common amphibian species accounted for 74% of the total number of individual amphibians captured, while the three most common reptiles represented just 49% of reptiles. This difference in dominance is a major reason for the difference in evenness between the two groups. Amphibian evenness estimates ranged from 0.23 at mixed bays to 0.32 at control bays, while reptile estimates ranged from 0.51

at pine bays to 0.66 at control bays. Both varied significantly across years (Amphibians: F=4.19, p=0.0172; Reptiles: F=8.65, p=0.0005), but did not vary by treatment (Amphibians: F=2.35, p=0.1307; Reptiles: F=1.61, p=0.2614) (Figures 9 & 10).

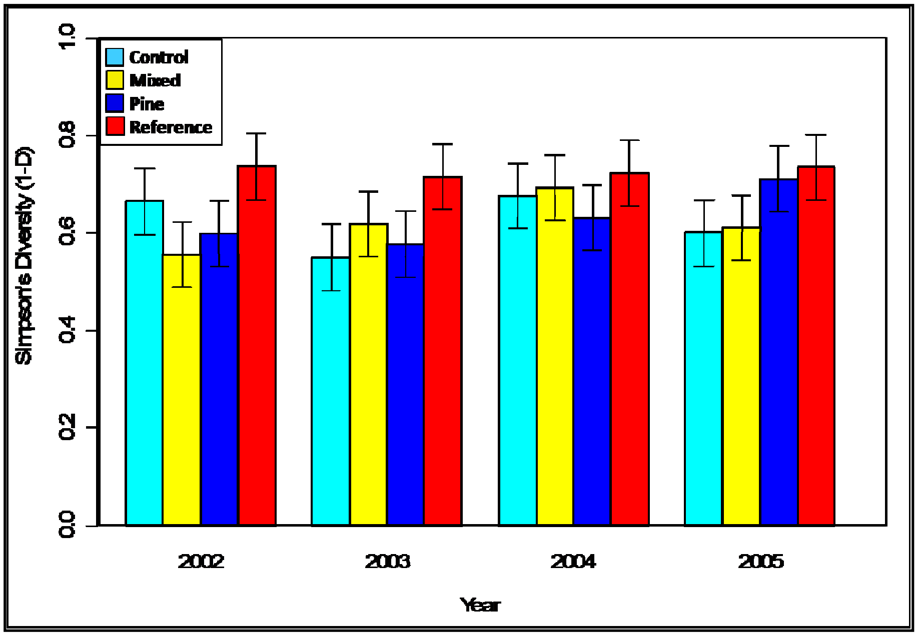

Figure 5. Average amphibian Simpson diversity by treatment and year at twelve Carolina bays on the SRS. Error bars are standard errors.

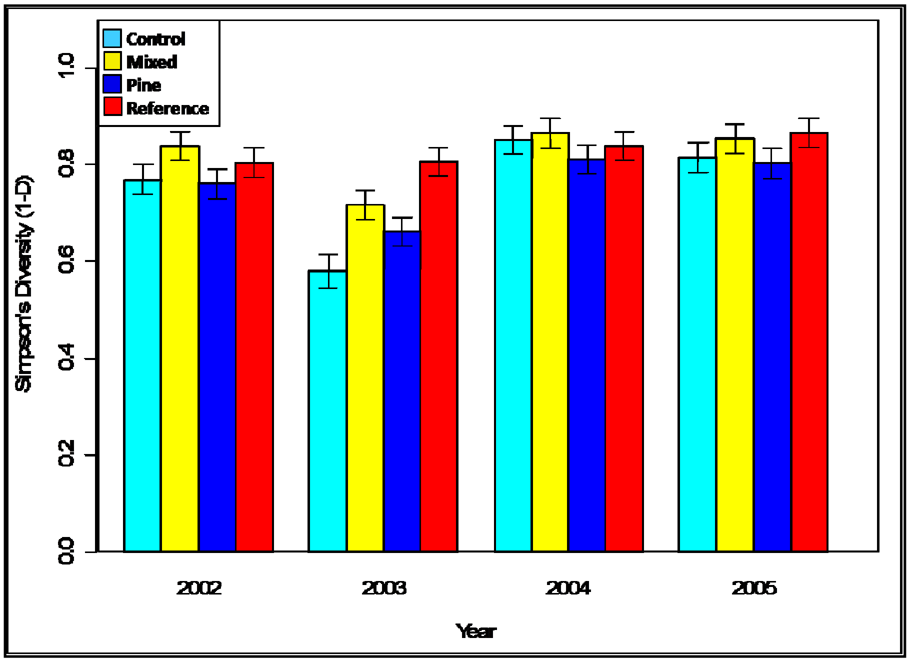

Figure 6. Average reptile Simpson diversity by treatment and year at twelve Carolina bays on the SRS. Error bars are standard errors.

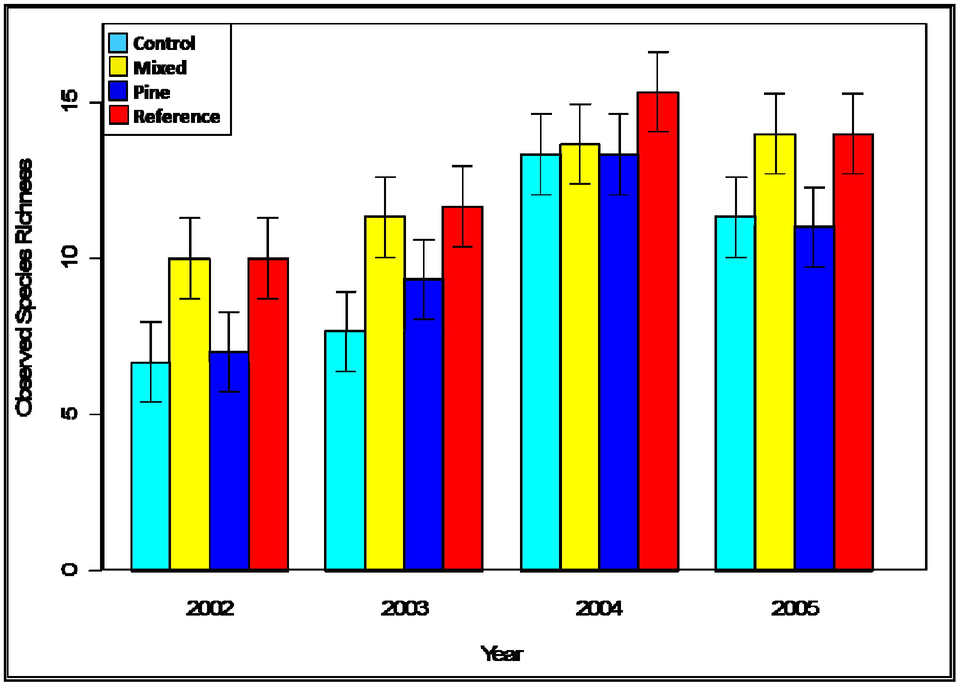

Figure 7. Average observed amphibian species richness by treatment and year at twelve Carolina bays on the SRS. Error bars are standard errors.

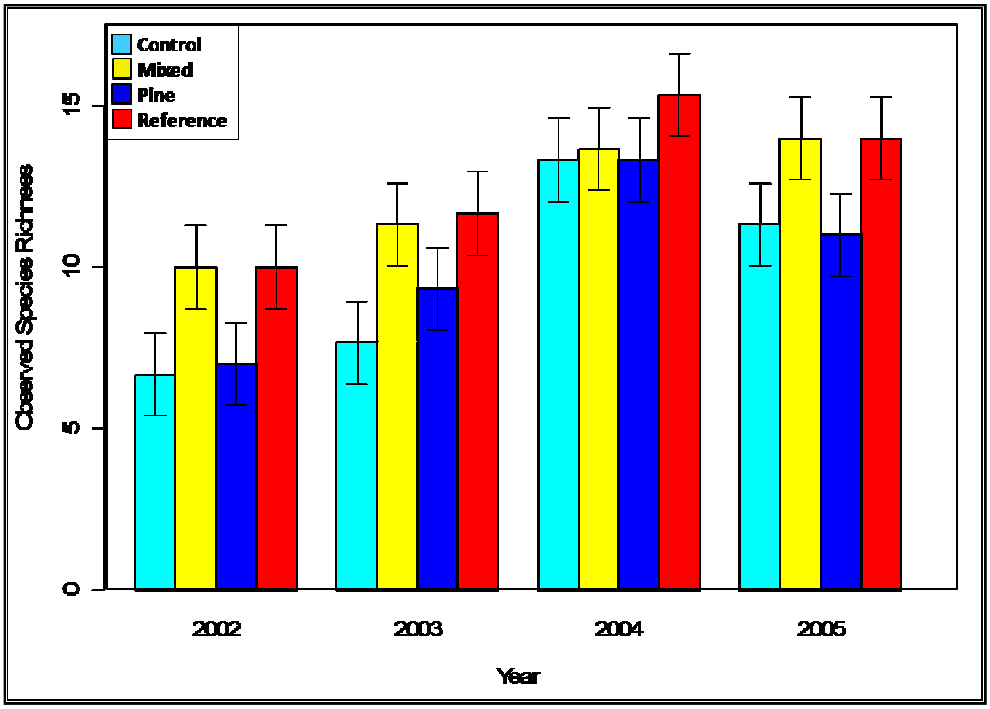

Figure 8. Average observed reptile species richness by treatment and year at twelve Carolina bays on the SRS. Error bars are standard errors.

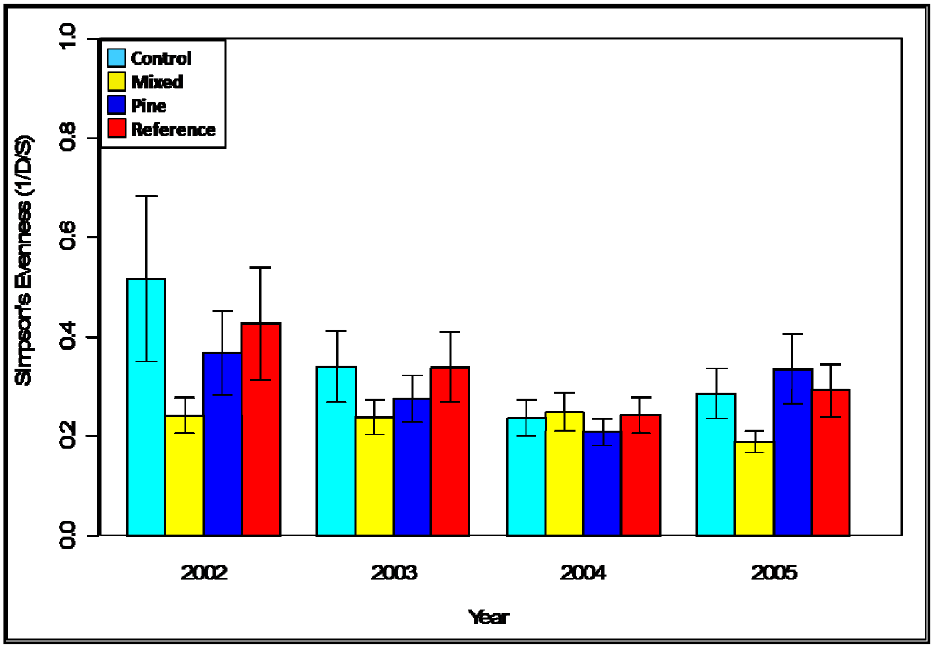

Figure 9. Average amphibian Simpson evenness by treatment and year at twelve Carolina bays on the SRS. Error bars are standard errors.

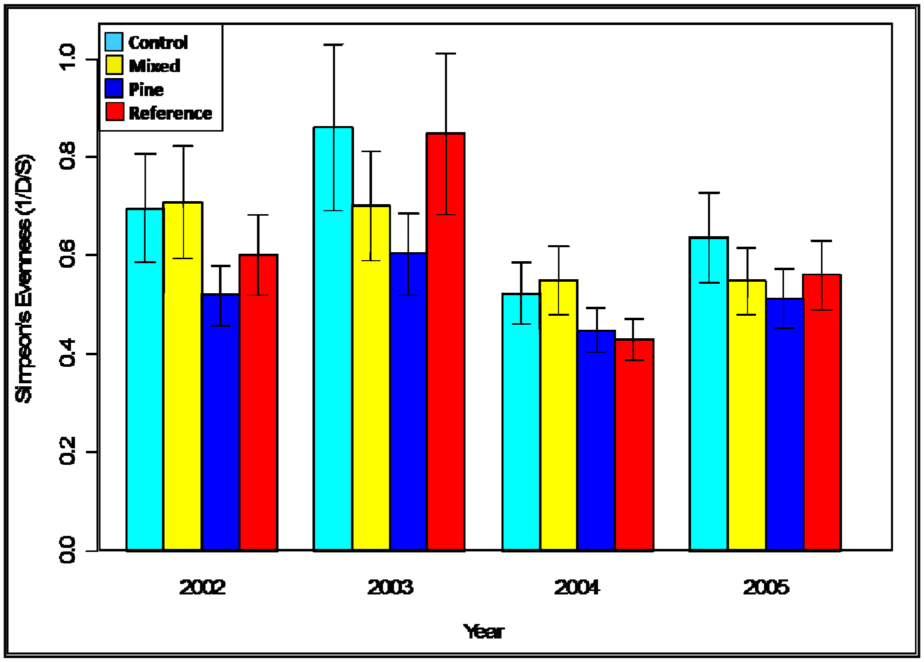

Figure 10. Average reptile Simpson evenness by treatment and year at twelve Carolina bays on the SRS. Error bars are standard errors.

Abundance Estimates

I compared capture totals using repeated measures ANOVAs for 21 species and groups of species (Table 6), and only one species, the green anole, Anolis carolinensis, showed a significant treatment effect at α=0.10 (F=3.33, p=0.0729). Anoles were more common at reference than restored bays, and more common at mixed bays than at pine bays (Figure 11). Likewise, a single species exhibited a significant year-by-treatment interaction, the southern toad, *Bufo terrestris* (F=2.27, p=0.0684), and the treatment p-value was very close to significant (F=2.92, p=0.1005). Southern toad captures were significantly higher at restored bays than at control bays (F=8.67, p=0.0186); in 2002 and 2005, more were captured in the un-thinned buffers of mixed bays, and in 2003 and 2004, the thinned buffers of pine bays produced more southern toad captures (Figure 12). The significant interaction effect likely stems from the alternation between pine and mixed bays as the treatment exhibiting the highest numbers. Conversely, only one group did not vary significantly by year at α=0.10, the slimy salamanders of the *Plethodon glutinosus* complex (F=1.09, p=0.388). Across reptile groups, captures were lowest in 2003, the year with the highest amount of spring rainfall. Most amphibians were least common in 2002, the driest year.

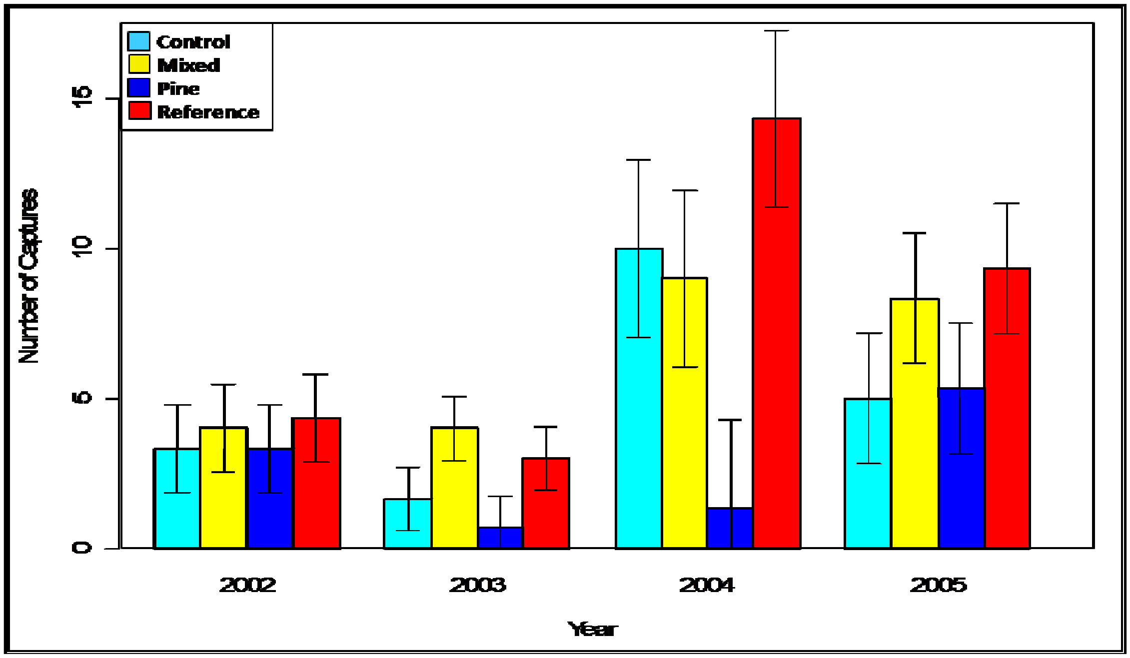

Figure 11. Captures of unique adult green anoles (*Anolis carolinensis*) at twelve Carolina bays on the SRS. Error bars show standard errors.

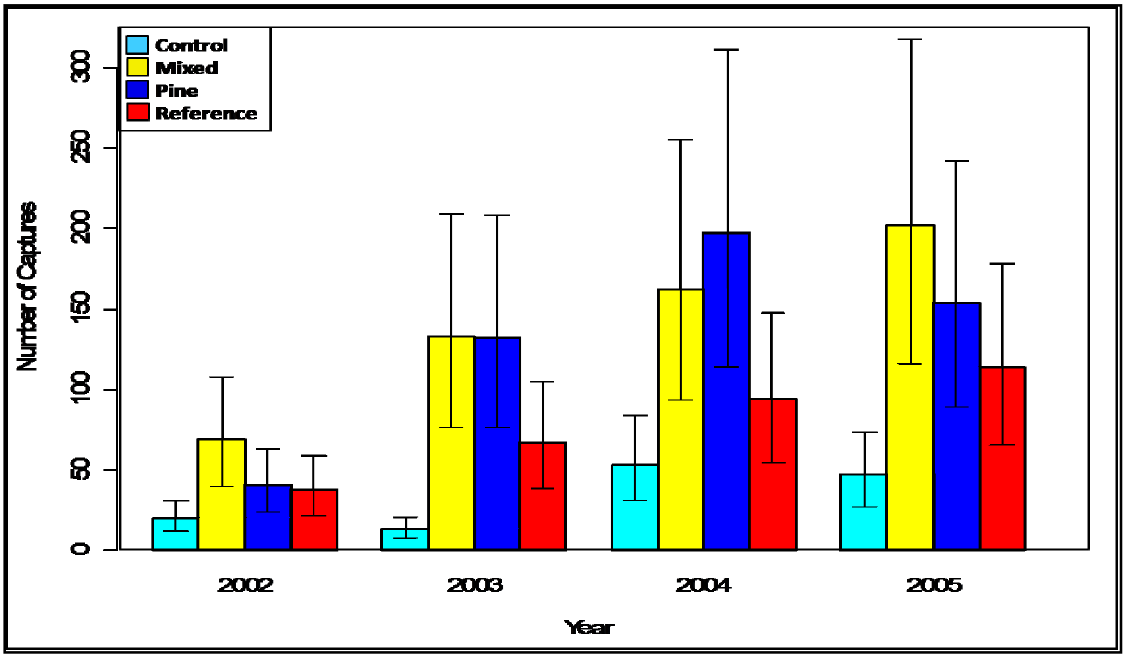

Figure 12. Captures of unique adult southern toads (*Bufo terrestris*) at twelve Carolina bays on the SRS. Error bars show standard errors.

Table 6. Repeated-measures ANOVA estimates and standard errors of captures per bay per year of ecological guilds and selected species of reptiles and amphibians at twelve Carolina bays on the SRS. Species assignments to guild are in Table 2 and Table 3.

	Control			**Mixed**			**Pine**			**Reference**			**Treatment**	
Species or Guild	**Mean**	**±**	**SE**	**Mean**	**±**	**SE**	**Mean**	**±**	**SE**	**Mean**	**±**	**SE**	**F**	**p**
Adult Amphibians														
All Amphibians	154.88	±	40.75	292.18	±	76.87	247.69	±	65.17	317.91	±	83.64	1.48	0.2925
Upland Frogs	0.70	±	0.40	1.46	±	0.84	2.69	±	1.56	4.89	±	2.83	0.86	0.5022
†Bufo terrestris	28.30	±	11.25	131.54	±	52.29	112.81	±	44.84	71.60	±	28.46	2.92	0.1005
Scaphiopus holbrookii	25.52	±	7.56	31.06	±	9.20	26.23	±	7.77	32.86	±	9.73	0.16	0.9171
Gastrophryne carolinensis	30.16	±	8.18	24.90	±	6.75	47.75	±	12.95	68.85	±	18.67	2.72	0.1085
Highly-Aquatic Frogs	1.24	±	0.38	1.87	±	0.56	0.58	±	0.17	3.18	±	0.96	1.84	0.2174
Rana sphenocephala	1.77	±	0.75	4.21	±	1.77	1.11	±	0.47	8.16	±	3.44	0.12	0.739
Treefrogs	1.53	±	0.57	8.55	±	3.19	2.09	±	0.78	4.16	±	1.55	2.53	0.1191
Aquatic Salamanders	4.48	±	2.89	3.78	±	2.44	3.61	±	2.33	5.17	±	3.33	0.04	0.9873
Ambystoma talpoideum	9.36	±	5.33	13.69	±	7.80	11.29	±	6.43	38.38	±	21.85	1.1	0.4023
‡*Plethodon glutinosus* complex	4.08	±	2.68	7.33	±	2.68	2.42	±	2.68	4.5	±	2.68	0.58	0.6443
Young-of-the-year														
Bufo terrestris	17.95	±	12.73	87.43	±	61.99	32.44	±	23.00	35.08	±	24.87	0.81	0.5247
Rana sphenocephala	6.23	±	5.27	14.96	±	12.65	5.04	±	4.26	16.10	±	13.62	0.4	0.7569
Adult Reptiles														
All Reptiles	25.33	±	4.75	25.25	±	4.75	28.42	±	4.75	36	±	4.75	1.13	0.386
Mesic Lizards	1.49	±	0.44	2.18	±	0.65	1.02	±	0.31	4.95	±	1.48	2.45	0.1318
**Anolis carolinensis*	5	±	1.19	6.33	±	1.19	2.67	±	1.19	7.75	±	1.19	3.33	0.0729
Open-canopy Lizards	1.67	±	0.40	0.70	±	0.17	2.37	±	0.56	2.15	±	0.51	1.69	0.2256
Sceloporus undulatus	3.58	±	2.42	1.67	±	2.42	7.17	±	2.42	5.83	±	2.42	1.01	0.4386
Scincella lateralis	2.32	±	0.64	2.96	±	0.82	4.61	±	1.28	2.12	±	0.59	0.9	0.4832
Fossorial Snakes	2.04	±	0.59	4.61	±	1.34	2.58	±	0.75	3.32	±	0.96	0.83	0.5151
Terrestrial & Aquatic Snakes	1.15	±	0.24	1.75	±	0.36	1.87	±	0.39	1.64	±	0.34	0.39	0.7646

* Significant treatment effect at α = 0.10

† Significant year-by-treatment interaction at α = 0.10

‡ The *Plethodon glutinosus* complex was the only species or group that did not vary significantly by year.

Non-metric Multidimensional Scaling

Although no patterns based on treatment are obvious in the Non-metric Multidimensional Scaling plots based on abundance data from all years (the upper plots in Figure 13), trends can be observed in the lower plots, in which the treatment classifications have been converted to classification by year. While there is some overlap in the amphibian plot by year, those points representing 2002 data, the year with generally the fewest captures, are somewhat clustered toward the lower right, while the 2004 and 2005 points, the years with the highest diversity and abundance, are clustered toward the upper left. The reptile plot by year exhibits more overlap between years than the amphibian plot by year, but also exhibits more structure than the plot by treatment.

The species presence and absence matrix for amphibians does not exhibit enough structure for a useful NMDS ordination. The plot in Figure 14 shows the first and third axes of the reptile presence/absence NMDS. NMDS axes are dimensionless, and are not necessarily ranked in descending order of explanatory power. In this case the second axis had little explanatory power, determined by r^2 value. Some clustering can be observed in this plot, with the mixed bays clustered near the top, although most treatments are not clearly separated.

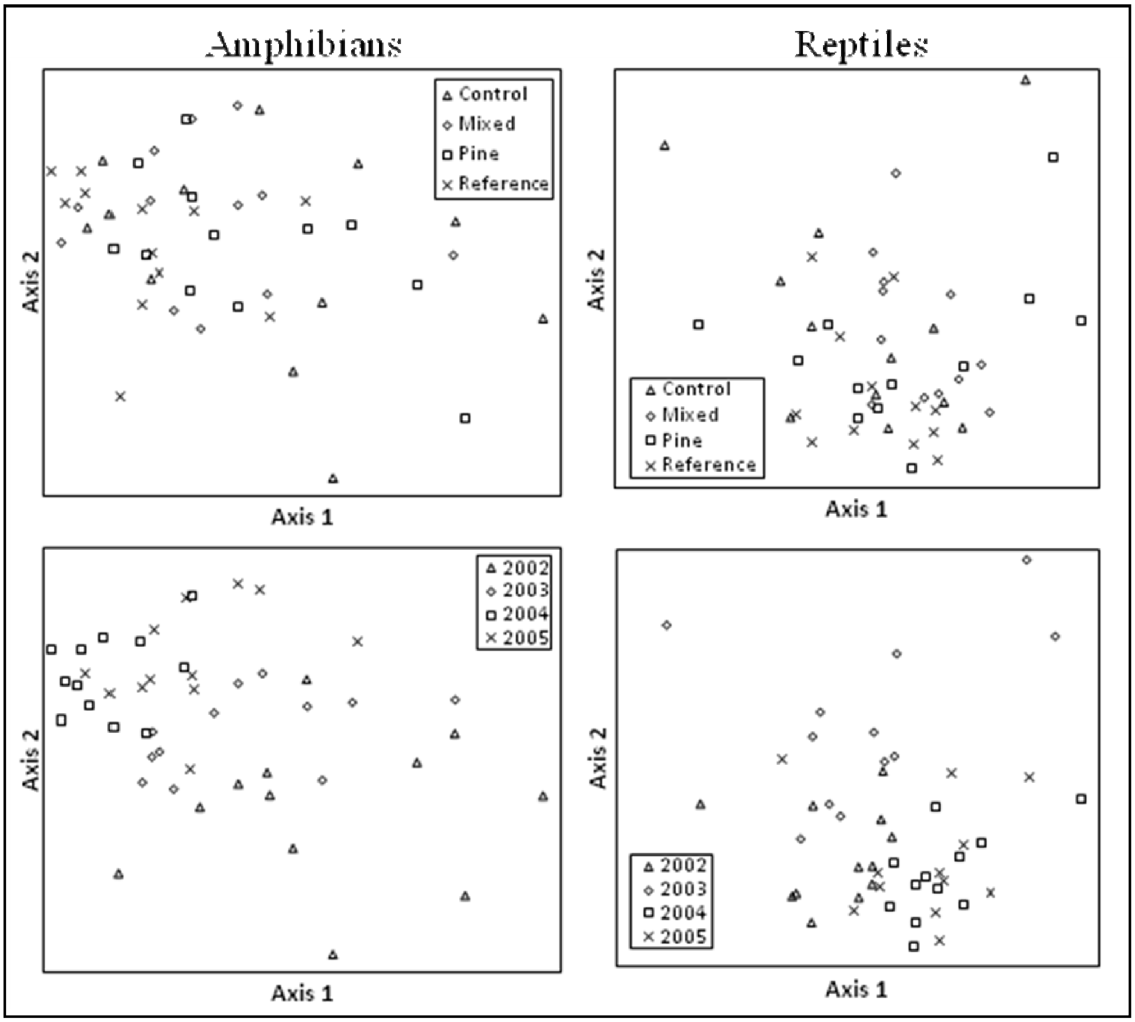

Figure 13 Non-metric Multidimensional Scaling plots of species composition of Carolina bays based on Bray-Curtis dissimilarity of log-transformed abundance estimates. The lower plots were created by assigning labels to years rather than treatments.

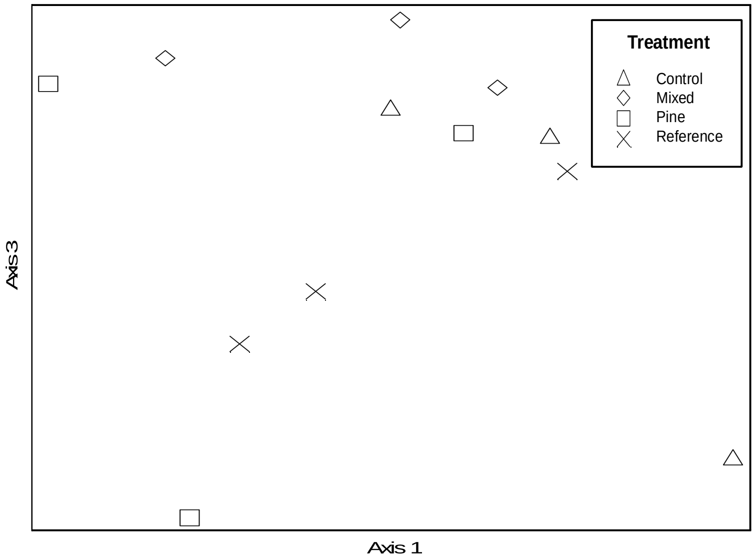

Figure 14 Non-metric Multidimensional Scaling representation of reptile species composition of Carolina bays, based on Bray-Curtis dissimilarity of four-year cumulative species presence or absence.

DISCUSSION

Reverted Wetlands

The Carolina bays chosen as restoration candidates in this study had been abandoned from use as pasture or cropland for a minimum of 50 years prior to their restoration. Kirkman et al. (1996) noted that the effectiveness of many drainage systems on the Savannah River Site had been reduced by erosion between 1951 and 1992. Several former bays on the Savannah River Site were included in high-intensity pine plantations, but most of the study bays had developed mixed pine-hardwood interiors through natural succession. Though forestry operations represented a new disturbance to bay interiors, heavy harvest equipment would also have disrupted drainage ditches more substantially than natural processes.

The bays randomly assigned to the control group had longer hydroperiods than the other candidate bays before restoration (Figure 15). Even after the other bays were restored, these three bays were ponded longer in most years, and are therefore of questionable value as reduced hydroperiod controls. Some of the restored bays also held water prior to restoration, even in the relatively dry years of 2000 and 2001. It was estimated that less than 60% of the historic wetland area was affected by the drainage systems of some of these bays. Even a bay with 90% of its area drained could serve as breeding habitat for those species with very brief larval stages like the southern toad (30–55 days), eastern spadefoot (14-60 days), and eastern narrowmouth toad (20-70 days). The topographic survey of the drainage system at Bay 118 led to the conclusion that it drained 100% of the historic wetland area, yet this bay was ponded for longer than any others in all years except 2001 and 2002.

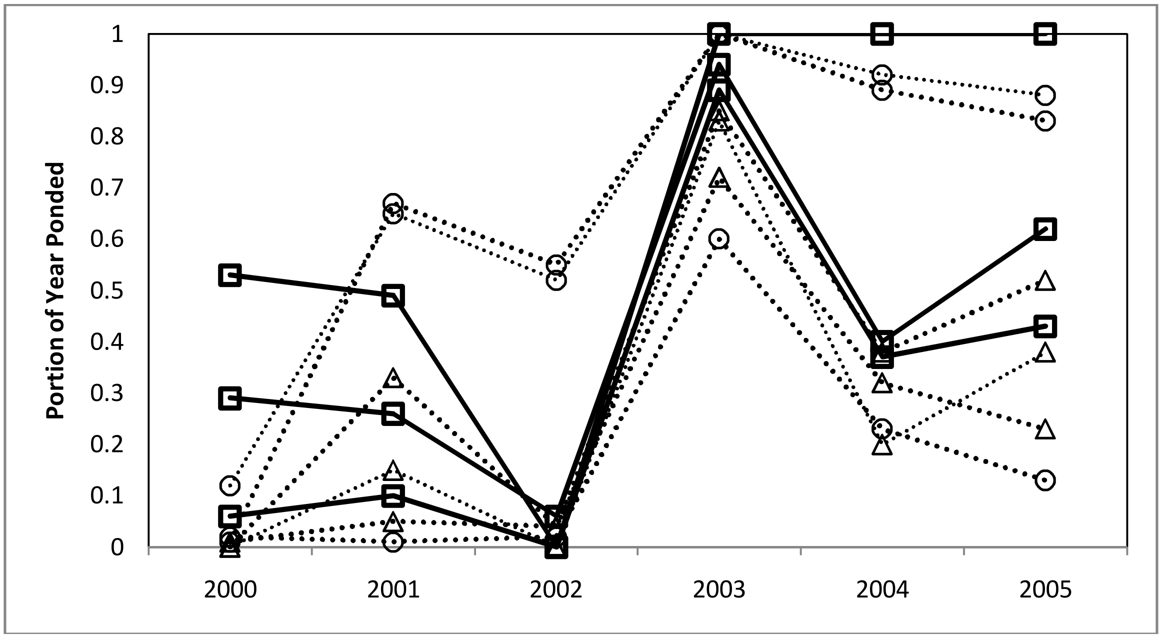

Figure 15. Portion of the year that control and restored bays contained water during one year prior to restoration (2000), one year after interior harvest but before hydrological restoration (2001), and four years post-restoration. Squares = Control Bays; Triangles = Pine Bays; Circles = Mixed Bays.

Some amphibian species prefer unforested breeding sites (Hocking and Semlitsch 2007), some may become locally extinct as ponds succeed to a full canopy (Skelly et al. 1999), and some studies have shown reduced larval success and growth rates in forested compared to unforested sites (Werner and Glennemeier 1999, Skelly et al. 2002). The forested interiors of the control bays and pre-restoration bays had minimal emergent herbaceous vegetation, which some amphibians require for breeding sites or larval habitat. Forested wetlands also have high amounts of deciduous leaf litter, which determines the structure of the substrate and can result in lower pH, and may have less dissolved oxygen (Werner and Glennemeier 1999). There is evidence that upland clearcutting reduces amphibian populations by increasing desiccation risk due to higher temperatures, reduced litter, and reduced burrow availability after soil compaction by heavy machinery (Petranka et al. 1994, Chazal and Niewiarowski 1998, Rothermel and Luhring 2005). However, the restoration activities including timber harvest in the bay interiors did not appear to have a negative effect on amphibians.

The twelve Carolina bays studied represent a continuum of isolation from other wetlands that could provide source populations for colonizing reptiles and amphibians. Some of the bays are located within 50 meters of the nearest neighboring wetland. Others are isolated, with no possible amphibian source populations for hundreds of meters. Censuses of neighboring wetlands to identify possible source populations or attempts to control for the degree of isolation are beyond the scope of this study, but it may be several years before some of the more isolated restored bays are colonized by the more philopatric species and those species that will most benefit from unforested breeding sites.

Diversity

Because southern toads, eastern spadefoots, and eastern narrowmouth toads were consistently numerically dominant at study bays, amphibian Simpson’s diversity and evenness did not vary by treatment or year. Reptile diversity tended to be higher than amphibian diversity because the most common reptiles were not nearly as dominant; that is, the reptile assemblages were more even. Reptilian Simpson’s diversity was lowest at control bays and highest at reference bays. This conclusion is not obvious from an examination of the numbers, however (Figure 6), and when examined within each year, the differences were only significant in 2003, the year with by far the fewest reptile captures in all treatments. The overall average annual diversity was actually slightly higher at control bays than pine bays. The average annual values ranged from 0.753 to 0.828, and the difference between the most and least diverse treatment was less than 0.06 in every year other than 2003. These meager differences and the lack of statistically significant differences in either richness or evenness lead me to conclude that there was no biologically significant difference in reptile diversity between treatments.

Species of Conservation Concern

I captured at least one South Carolina Species of Conservation Concern at each of the twelve study bays. While there were no obvious patterns of occurrence or species richness, I did capture more of these species at reference bays. By capturing recently metamorphosed juveniles, I also documented successful reproduction of four of these species, including the Carolina gopher frog, *Rana capito*, and the Eastern tiger salamander, *Ambystoma tigrinum*, both classified as "highest conservation priority" (South Carolina Department of Natural Resources 2005).

The Carolina gopher frog is a longleaf pine savanna specialist (Means, 2006), and is listed as an endangered species in South Carolina. It breeds in open canopy, fish-free wetlands and has been captured very infrequently on the SRS, despite extensive monitoring of several of the wetlands (Semlitsch et al, 1995). Juvenile recruitment has been documented at only three wetlands on the SRS, each in only a single year. I captured adults in the buffers of two pine bays during a short, rainfall-dependent breeding season in early 2003. In June of the same year, I captured emigrating juveniles at the third pine bay and also at a single reference bay. In 2005, I captured adults and juveniles at the same reference bay plus a single adult at a single mixed bay. Four of the five bays with gopher frogs were restored bays, of which three were pine bays.

I captured Eastern tiger salamanders at only two bays, a reference bay and a control bay, and I captured emigrating juveniles only at the control bay. The control bay in this case was Bay 118, the buffer of which had been clearcut in 1998, while the interior of the bay was the most densely forested of the study bays. This bay had the lowest observed richness and the lowest number of adult captures of both reptiles and amphibians. Such apparently marginal amphibian habitat could still be important for conserving biodiversity in the landscape.

Southern Toads

The southern toad (*Bufo terrestris*) is a habitat generalist. I captured more adult *B. terrestris* study-wide than any other species, with more captures at restored bays than at either control or reference bays in all four years. I did capture both adults and juveniles at all bays in all years, but the increased numbers of breeding adults at restored bays is likely evidence that *B. terrestris* responds more rapidly than other species to canopy removal in its breeding habitat.

Amphibian Juvenile Recruitment

I captured young-of-the-year individuals of five species of anurans at every bay, including the three amphibians most commonly captured as adults: the southern toad, eastern spadefoot, and eastern narrowmouth toad, and two ranids: the southern leopard frog (*R. sphenocephala*) and the bronze frog (*R. clamitans*). Despite catching on average less than five adults per bay and a maximum of six in a single year at any bay, I captured juvenile bronze frogs at every bay studied, almost all of them during 2004. This species does not usually migrate, preferring permanent bodies of water for both breeding and non-breeding habitat (Minton 1972). Since juveniles are known to disperse up to 4.8 km during their first year (Schroeder 1976), it is likely that most of the juveniles I captured were not dispersing from the study bays, but encountered the drift fences while dispersing from other locations.

Eastern narrowmouth toad juveniles, though detected at every bay, were captured at very low frequencies relative to adult captures. Adults began breeding migrations in April (Figure 3), and the larval period of 20 – 70 days from egg deposition to metamorphosis (Wright 1932) would have been completed in time for emergence before bays dried or sampling was discontinued. Pechmann et al. (1989) found that juveniles of this species only emerged from bays that had dried and refilled before its breeding season. They hypothesized that eastern narrowmouth toad larvae are susceptible to predation by insect larvae and the larvae of other amphibian species. An increase in hydroperiod that prevented a bay from drying and refilling in late spring or early summer could create a population sink for this species.

Population Fluctuations

It is tempting to look for trends and to try to predict future population sizes when looking at results from four years of monitoring amphibian breeding migrations and recruitment. Of the 19 species and guilds that I examined, only slimy salamander (*Plethodon glutinosus* complex) captures did not vary significantly by year. Many aquatic-breeding amphibian species may forego breeding in a given year, especially when rainfall is absent during breeding seasons (Semlitsch et al. 1996). Juvenile recruitment is even more variable than adult breeding populations, and it may be nonexistent or low in a given year at a given wetland due to early drying of the wetland before larvae are large enough to metamorphose, or because pre-breeding conditions allowed predators to become particularly well-established before eggs were deposited or larvae hatched, or because of a lack of breeding. However, Semlitsch et al. (1996) found no correlations between breeding population size and number of emigrating juveniles of several amphibian species for 16 years at a single SRS bay. The frequency of complete or nearly complete reproductive failure at that same bay over 22 years led Taylor et al. (2006) to conclude that marbled salamanders (*Ambystoma opacum*) require high terrestrial survivorship for the species to persist, based on a computer-simulated population model.

After monitoring for seven years post-restoration, Petranka et al (2003b) could not be certain that wetland creation would ultimately result in an increase in the number of breeding populations. With the exception of the relatively stable populations of spotted salamanders (*Ambystoma maculatum*), extrapolation from a four-year subset of their entire 13-year dataset could lead to drastically different predictions, depending on which four years were chosen (Petranka et al. 2007).

Responses to Forest Thinning

The green anole (*Anolis carolinensis*) was the only species to show a significant overall treatment effect. Anoles were more abundant in the buffers of reference bays than restored bays and more abundant at mixed bays than at pine bays. Anole captures by treatment and year can be seen in Figure 11. Captures were lowest at pine bays in 2003 and 2004, but increased in 2005 to levels comparable to the other treatments. Anole populations were reduced by forestry operations. While the increase in the fourth year of sampling seems to indicate that recovery is beginning, further sampling would be required to justify this conclusion.

Amphibian responses to upland clearcuts have been relatively well-studied (Phelps and Lancia 1995, Chazal and Niewiarowski 1998, Harper and Guynn Jr. 1999), but researchers have only recently begun to assess the effects of thinning or other forms of partial canopy removal. Plethodontid salamanders are absent or nearly absent from recently clearcut stands due to increased desiccation risk, but they increase rapidly after stands have regenerated for a few years (Petranka et al. 1994, Ash 1997). Brooks (1999) found no effects of thinning on populations of a plethodontid salamander in Massachusetts. Rothermel and Luhring (2005) did not find differences in mortality or water loss in juvenile *Ambystoma talpoideum* exposed to thinned stands versus control stands for 72 hours on the Savannah River Site, though both mortality and water loss were higher in clearcuts. Artificial burrows were used extensively in all habitat types when they were made available, and salamanders with burrows retained more moisture and were more likely to survive. Soil compaction by heavy logging machinery can both destroy existing burrows and prevent salamanders from digging new ones. Leaf litter and coarse woody debris can provide alternative moist microhabitats to reduce desiccation risk (Moseley et al. 2004). Patrick et al. (Patrick et al. 2006) found fewer adults and juveniles of most of the amphibian species they captured in clearcuts versus uncut stands, but few differences in the use of uncut versus partially cut stands. Knapp et al (2003) found that all plethodontid salamanders in the southern Appalachians were as reduced under four different levels of canopy removal as they were in clearcuts after one year, and all were reduced compared to controls after four years. Uniquely among the four species with enough juvenile captures to make comparisons, the proportion of slimy salamanders that were juveniles was lower in all of the cut treatments.

I captured fewer slimy salamanders (*Plethodon glutinosus* complex) in pine buffers than at the other treatments, though differences were not statistically significant. I also failed to catch any young-of-the-year slimy salamanders in those thinned buffers in any year of the study, though I did find them at seven of the other nine bays (Table 4). This species is unique among the amphibians I captured in undergoing direct development on land from eggs to terrestrial juveniles. The semi-permeable eggs and then hatchlings are guarded in the nest by the female under coarse woody debris or in an underground burrow. Plethodontid salamanders are more slender than the ambystomatid species, and the higher surface area to volume ratio may be one reason for higher rates of evaporative water loss (Spight 1967). Increased desiccation risk and the dependence of all life cycles on terrestrial habitat may mean that this species is more sensitive than others to forestry operations and changes in canopy coverage. Though more abundant in mature pine stands than recent clearcuts (Grant et al. 1994), slimy salamanders prefer moist forest with a dense canopy to even mature pine stands (Bennett et al. 1980). Abundance can therefore be expected to remain lower in the thinned stands even as they continue to develop into pine savannas.

Canopy removal can also increase the abundance of the Red Imported Fire Ant (Solenopsis invicta), which favors disturbed areas and reduced canopies and outcompetes and sustains greater densities than native fire ants (Tschinkel 1988). Predation by these ants has been documented for several species of amphibians and reptiles, especially hatchling turtles (Allen et al. 2004). Though direct population-level effects are difficult to measure, their range expansion has coincided geographically with the decline of the southern hognose snake (*Heterodon simus*) (Tuberville et al. 2000). They may also reduce the availability of arthropods as prey, as they have been shown to severely reduce both richness and abundance of native arthropods (Porter and Savignano 1990). I did not attempt to quantify fire ant abundance or activity in the thinned buffers compared to un-thinned buffers, but during 2004 and 2005 I recorded more within-trap fire ant predation at pine bay arrays and three other arrays in recent thinnings or clearcuts (average 14.6 events per array) than at arrays under intact canopies and with undisturbed soils (average 1.1 events per array). Habitat improvements for open canopy species may be more difficult to achieve and the effects more difficult to quantify in the presence of invasive fire ants. Fire ants could be a factor in the reduction of both green anoles and slimy salamander juveniles in the thinned forests, either by direct predation or through competition for invertebrate prey.

While the thinned sites were also burned in early 2003, several factors make it difficult to assess the effects of this prescribed burning effectively. First, thinning could be said to have a greater impact on the vegetation structure in the bay margins, and that impact was very recent. Second, because burning was delayed by security and safety concerns, the woody sprouts that burns are supposed to prevent became established at several sites. Further, the effectiveness of the burn to prevent hardwood re-sprouting was patchy, and varied greatly by bay, and even between the arrays at a single bay. Finally, the response to a single burn is not the same as the response to a fire regime. Though some direct effects of prescribed burns on reptiles and amphibians have been documented, these are rare, and the broad habitat modifications achieved by a fire regime are considered more important (Russell et al. 1999).

MANAGEMENT IMPLICATIONS

The species richness of both reptiles and amphibians 50 meters from the edges of these bays adds to existing evidence that isolated wetlands are sites of high herpetofaunal diversity in the landscape. The presence of at least one species of conservation concern at every bay, including the nine bays that had been drained for agriculture prior to 1951, demonstrates that even historically disturbed habitat can be important for conserving regional biodiversity. Some wetland restoration projects have seen immediate and dramatic colonization by reptiles and amphibians (Bowers et al. 2000, Petranka et al. 2003a, Brodman et al. 2006). Almost all of these sites had been uninhabitable immediately before restoration, and potential colonists were known to be nearby. The restoration of wetlands that have had time to partially revert since disturbance may be more likely to succeed, and initial changes in vegetation structure can be obvious and extensive, but functional successes will take longer to develop and may be more difficult to observe. Evaluating the success of restored wetlands that are relatively isolated from source populations is also problematic, as it may take years for some species to colonize them. Though many of these species show limited dispersal rates, dispersal across longer distances does occur regularly (Kinkead et al. 2007, Semlitsch 2008), and more isolated sites may serve as “stepping stones” to bridge gaps between distant populations.

The timing of sampling was not ideal for evaluating restoration success. When restoration candidate sites are known to be uninhabitable, pre-treatment sampling may be unnecessary because all captures post-restoration can be assumed to be colonizers. In this case, restoration candidates had partially reverted to wetlands during the preceding 50 years, and the absence of pre-restoration sampling leaves me unable to determine whether diversity and species abundances have changed since restoration. Pre-restoration sampling would also have made it easier to evaluate the utility of the controls that tended to remain ponded longer than most of the restored and reference bays, which could partially account for the lack of differences between even reference and control bays. Because of disease outbreaks and predatory fish invasions, Petranka et al. (2003b) were not confident after seven years of monitoring that created ponds would continue to support focal species. Semlitsch (2002) proposed that restoration can only be considered a success when adults continue to breed 5-10 years later. Censuses in this timeframe are therefore required to truly evaluate restoration success.

On the other hand, this early post-restoration sampling has provided some evidence that management activities aimed at restoration have minimal negative impact on herpetofauna in the short-term. Restored sites had larger southern toad populations, but not large enough to reduce evenness or diversity measures compared to reference wetlands. This seems to indicate that the southern toad, perhaps the most generalist local amphibian species, has been the first to capitalize on habitat improvements, though it remains to be seen whether other species will follow suit. Thinning in the bay margins seemed to affect only two species: the green anole and the slimy salamander. Slimy salamanders prefer closed canopy forests, so their extirpation upon conversion to pine savannas can be expected. The green anole is generalist lizard, readily adaptable to different habitats including anthropogenic ones, and may have already been recovering in the thinned buffers by 2005. As with wetland colonization, it is too early to determine whether species adapted to the open canopies and abundant herbaceous groundcover of pine savannas will be more abundant at these sites.

LITERATURE CITED

Allen, C. R., D. M. Epperson, and A. S. Garmestani. 2004. Red imported fire ant impacts on wildlife: A decade of research. American Midland Naturalist 152:88-103.

Ash, A. N. 1997. Disappearance and return of plethodontid salamanders to clearcut plots in the southern blue ridge mountains. Conservation Biology 11:983-989.

Bennett, S. H., J. W. Gibbons, and J. Glanville. 1980. Terrestrial activity, abundance and diversity of amphibians in differently managed forest types. American Midland Naturalist 103:412-416.

Bennett, S. H., and J. B. Nelson. 1991. Distribution and status of carolina bays in south carolina. South Carolina Wildlife & Marine Resources Dept, Columbia, SC.

Blaustein, A. R., and D. B. Wake. 1990. Declining amphibian populations - a global phenomenon. Trends in Ecology & Evolution 5:203-204.

Boughton, R. G., J. Staiger, and R. Franz. 2000. Use of pvc pipe refugia as a sampling technique for hylid treefrogs. American Midland Naturalist 144:168-177.

Bowers, C. F., H. G. Hanlin, D. C. Guynn, J. P. McLendon, and J. R. Davis. 2000. Herpetofaunal and vegetational characterization of a thermally-impacted stream at the beginning of restoration. Ecological Engineering 15:S101-S114.

Brodman, R., M. Parrish, H. DKraus, and S. A. Cortwright. 2006. Amphibian biodiversity recovery in a large-scale ecosystem restoration. Herpetological Conservation and Biology 1:101-108.

Brooks, R. T. 1999. Residual effects of thinning and high white-tailed deer densities on northern redback salamanders in southern new england oak forests. Journal of Wildlife Management 63:1172-1180.

Brown, W. S., and W. S. Parker. 1976. A ventral scale clipping system for permanently marking snakes (reptilia, serpentes). Journal of Herpetology 10:247-249.

Cagle, F. R. 1939. A system of marking turtles for future identification. Copeia 1939:170-173.

Camper, J. D., and J. R. Dixon. 1988. Evaluation of a microchip marking system for amphibians and reptiles. Texas Parks and Wildlife Department, Austin, TX.

Chazal, A. C., and P. H. Niewiarowski. 1998. Responses of mole salamanders to clearcutting: Using field experiments in forest management. Ecological Applications 8:1133-1143.

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

Conant, R., and J. T. Collins. 1998. A field guide to reptiles & amphibians: Eastern and central North America. Houghton Mifflin. 640 pp.

Dahl, T. E. 2000. Status and trends of wetlands in the conterminous united states 1986 to 1997. US Dept. of the Interior, Fish and Wildlife Service.

Delis, P. R., H. R. Mushinsky, and E. D. McCoy. 1996. Decline of some west-central florida anuran populations in response to habitat degradation. Biodiversity and Conservation 5:1579-1595.

Dodd, C. K., and B. S. Cade. 1998. Mover patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12:331-339.

Ferner, J. W. 1979. A review of marking techniques for amphibians and reptiles. Society for the Study of Amphibians and Reptiles Herpetofaunal Circular 9.

Franz, R., K. D. Jr, and C. Jones. 1988. Life history notes: *Rana areolata aesopus* (florida gopher frog). Movement. Herpetol. Rev 19:82.

Gibbons, J. W., and D. H. Bennett. 1974. Determination of anuran terrestrial activity patterns by a drift fence method. Copeia 1974:236-243.

Gibbons, J. W., V. J. Burke, J. E. Lovich, R. D. Semlitsch, T. D. Tuberville, J. R. Bodie, J. L. Greene, P. H. Niewiarowski, H. H. Whiteman, D. E. Scott, J. H. K. Pechmann, C. R. Harrison, S. H. Bennett, J. D. Krenz, M. S. Mills, K. A. Buhlmann, J. R. Lee, R. A. Seigel, A. D. Tucker, T. M. Mills, T. Lamb, M. E. Dorcas, J. D. Congdon, M. H. Smith, D. H. Nelson, M. B. Dietsch, H. G. Hanlin, J. A. Ott, and D. J. Karapatakis. 1997. Perceptions of species abundance, distribution, and diversity: Lessons from four decades of sampling on a government-managed reserve. Environmental Management 21:259-268.

Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, deja vu amphibians. Bioscience 50:653-666.

Gibbons, J. W., and R. D. Semlitsch. 1981. Terrestrial drift fences with pitfall traps: An effective technique for quantitative sampling of animal populations. Brimleyana 7:1-6.

_____. 1991. Guide to the reptiles and amphibians of the savannah river site. University of Georgia Press, Athens.

Gibbons, J. W., C. T. Winne, D. E. Scott, J. D. Willson, X. Glaudas, K. M. Andrews, B. D. Todd, L. A. Fedewa, L. Wilkinson, R. N. Tsaliagos, S. J. Harper, J. L. Greene, T. D. Tuberville, B. S. Metts, M. E. Dorcas, J. P. Nestor, C. A. Young, T. O. M. Akre, R. N. Reed, K. A. Buhlmann, J. Norman, D. A. Croshaw, C. Hagen, and B. B. Rothermel. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: Implications for wetland conservation. Conservation Biology 20:1457-1465.

Grant, B. W., K. L. Brown, G. W. Ferguson, and J. W. Gibbons. 1994. Changes in amphibian biodiversity associated with 25 years of pine forest regeneration: Implications for biodiversity management. Pages 354–367 *in* S. K. Majumdar, I. F. Brenner, J. E. Lovich, J. F. Schalles, andE. W. Miller, editors. Biological diversity: Problems and challenges. Pennsylvania Academy of Science,Philadelphia.

Grant, B. W., A. D. Tucker, J. E. Lovich, A. M. Mills, P. M. Dixon, and J. W. Gibbons. 1992. The use of coverboards in estimating patterns of reptile and amphibian biodiversity. Pages 379-403 *in* D. R. McCullough, andR. H. Barrett, editors. Wildlife 2001 : Populations. Elsevier Science Publishing, Inc.,London, England.

Guyer, C., and M. A. Bailey. 1993. Amphibians and reptiles of longleaf pine communities. Pages 139-158 *in* Proceedings of Tall Timbers Fire Ecology Conference. 18:139-158.

Hairston, N. G. S. 1987. Community ecology and salamander guilds. Cambridge University Press, New York, NY.

Harper, C. A., and D. C. Guynn Jr. 1999. Factors affecting salamander density and distribution within four forest types in the southern appalachian mountains. Forest Ecology and Management 114:245-252.

Hefner, J. M., and J. D. Brown. 1988. Wetland trends in the southeastern united states. Wetlands 4:1-11.

Hocking, D. J., and R. D. Semlitsch. 2007. Effects of timber harvest on breeding-site selection by gray treefrogs (*Hyla versicolor*). Biological Conservation 138:506-513.

Kaiser, J. 1998. Ecology - new wetlands proposals draws flak. Science 279:980-980.

Kinkead, K. E., A. G. Abbott, and D. L. Otis. 2007. Genetic variation among ambystoma breeding populations on the savannah river site. Conservation Genetics 8:281-292.

Kirkman, L. K., R. F. Lide, G. Wein, and R. R. Sharitz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western coastal plain of south carolina: 1951-1992. Wetlands 16:564-576.

Knapp, S. M., C. A. Haas, D. N. Harpole, and R. L. Kirkpatrick. 2003. Initial effects of clearcutting and alternative silvicultural practices on terrestrial salamander abundance. Conservation Biology 17:752-762.

Kohlsaat, T., L. Quattro, and J. Rinehart. 2005. South carolina comprehensive wildlife conservation strategy, 2005-2010. South Carolina Department of Natural Resources, Columbia, S.C.

Lehtinen, R. M., and S. M. Galatowitsch. 2001. Colonization of restored wetlands by amphibians in minnesota. American Midland Naturalist 145:388-396.

Lide, R. F., V. G. Meentemeyer, J. E. Pinder, and L. M. Beatty. 1995. Hydrology of a carolina bay located on the upper coastal-plain of western south-carolina. Wetlands 15:47-57.

McCune, B., and M. J. Mefford. 2006. PC-ORD: Multivariate analysis of ecological data. Version 5.05. Gleneden Beach, OR.

Means, D. B. 2006. Vertebrate faunal diversity in longleaf pine savannas. Pages 155-213 *in* S. Jose, E. Jokela, andD. Miller, editors. Longleaf pine ecosystems: Ecology, management, and restoration. Springer,New York, NY.

Minton, S. A. 1972. Amphibians and reptiles of indiana. Indiana Academy of Science, Indianapolis, Ind. 346 pp.

Moseley, K. R., S. B. Castleberry, and W. M. Ford. 2004. Coarse woody debris and pine litter manipulation effects on movement and microhabitat use of *Ambystoma talpoideum* in a *Pinus taeda* stand. Forest Ecology and Management 191:387-396.

Patrick, D. A., M. L. Hunter, and A. J. K. Calhoun. 2006. Effects of experimental forestry treatments on a maine amphibian community. Forest Ecology and Management 234:323-332.

Pechmann, J. H. K., R. A. Estes, D. E. Scott, and J. W. Gibbons. 2001. Amphibian colonization and use of ponds created for trial mitigation of wetland loss. Wetlands 21:93-111.

Pechmann, J. H. K., D. E. Scott, J. Whitfield Gibbons, and R. D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3-11.

Petranka, J. W., M. P. Brannon, M. E. Hopey, and C. K. Smith. 1994. Effects of timber harvesting on low elevation populations of southern appalachian salamanders. Forest Ecology and Management 67:135-147.

Petranka, J. W., E. M. Harp, C. T. Holbrook, and J. A. Hamel. 2007. Long-term persistence of amphibian populations in a restored wetland complex. Biological Conservation 138:371-380.

Petranka, J. W., C. A. Kennedy, and S. S. Murray. 2003a. Response of amphibians to restoration of a southern appalachian wetland: A long-term analysis of community dynamics. Wetlands 23:1030-1042.

Petranka, J. W., S. S. Murray, and C. A. Kennedy. 2003b. Responses of amphibians to restoration of a southern appalachian wetland: Perturbations confound post-restoration assessment. Wetlands 23:278-290.

Phelps, J. P., and R. A. Lancia. 1995. Effects of a clearcut on the herpetofauna of a south carolina bottomland swamp. Brimleyana 22:31-45.

Porter, S. D., and D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71:2095-2106.

Rittenhouse, T. A. G., and R. D. Semlitsch. 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands 27:153-161.

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 T. M. Luhring. 2005. Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested forest stands. Journal of Herpetology 39:619-626.

Russell, K. R., D. H. Van Lear, and D. C. Guynn. 1999. Prescribed fire effects on herpetofauna: Review and management implications. Wildlife Society Bulletin 27:374-384.

SAS Institute. 2003. Sas/stat software, version 9.1 of the sas system for windows. SAS Institute, Inc., Cary, NC, USA.

Schroeder, E. E. 1976. Dispersal and movement of newly transformed green frogs, *rana clamitans*. American Midland Naturalist 95:471-474.

Semlitsch, R. D. 2002. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology 16:619-629.

_____. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72:260-267.

Semlitsch, R. D., and J. R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17:1219-1228.

Semlitsch, R. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 1996. Structure and dynamics of an amphibian community: Evidence from a 16-year study of a natural pond. Pages 217–248 *in* Long-term studies of vertebrate communities. Academic press, san diego, california, USA.

Sharitz, R. R. 2003. Carolina bay wetlands: Unique habitats of the southeastern united states. Wetlands 23:550-562.

Shields, J. D., N. D. Woody, A. S. Dicks, G. J. Hollod, J. Schalles, and G. J. Leversee. 1982. Locations and areas of ponds and carolina bays at the savannah river plant. DOE, Du Pont de Nemours (EI) and Co., Savannah River Lab., Aiken, SC.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Skelly, D. K., L. K. Freidenburg, and J. M. Kiesecker. 2002. Forest canopy and the performance of larval amphibians. Ecology 83:983-992.

Skelly, D. K., E. E. Werner, and S. A. Cortwright. 1999. Long-term distributional dynamics of a michigan amphibian assemblage. Ecology 80:2326-2337.

Snodgrass, J. W., M. J. Komoroski, A. L. Bryan, and J. Burger. 2000. Relationships among isolated wetland size, hydroperiod, and amphibian species richness: Implications for wetland regulations. Conservation Biology 14:414-419.

Spight, T. 1967. The water economy of salamanders: Exchange of water with the soil. The Biological Bulletin 132:126-132.

Taylor, B. E., D. E. Scott, and J. W. Gibbons. 2006. Catastrophic reproductive failure, terrestrial survival, and persistence of the marbled salamander. Conservation Biology 20:792-801.

Tiner, R. W. 2003. Geographically isolated wetlands of the united states. Wetlands 23:494-516.

Tschinkel, W. R. 1988. Distribution of the fire ants *Solenopsis invicta* and *S. geminata* (hymenoptera: Formicidae) in northern florida in relation to habitat and disturbance. Annals of the Entomological Society of America 81:76-81.

Tuberville, T. D., J. R. Bodie, J. B. Jensen, L. Laclaire, and J. W. Gibbons. 2000. Apparent decline of the southern hog-nosed snake, heterodon simus. Journal of the Elisha Mitchell Scientific Society 116:19-40.

Vasconcelos, D., and A. J. K. Calhoun. 2006. Monitoring created seasonal pools for functional success: A six-year case study of amphibian responses, sears island, maine, USA. Wetlands 26:992-1003.

Vitt, L. J., J. P. Caldwell, H. M. Wilbur, and D. C. Smith. 1990. Amphibians as harbingers of decay. Bioscience 40:418-418.

Wassersug, R. J. 1975. The adaptive significance of the tadpole stage with comments on the maintenance of complex life cycles in anurans. American Zoologist 15:405-417.

Werner, E. E., and K. S. Glennemeier. 1999. Influence of forest canopy cover on the breeding pond distributions of several amphibian species. Copeia 1999:1-12.

Wright, A. H. 1932. Life-histories of the frogs of okefinokee swamp, georgia. Comstock Publishing Associates, Ithaca, NY.

Zedler, P. H. 2003. Vernal pools and the concept of "Isolated wetlands". Wetlands 23:597-607.