2013

Wetland Diversity In A Disturbance-maintained Landscape: Effects Of Fire And A Fire Surrogate On Aquatic Amphibian Survival And Species Depauperateness.

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WETLAND DIVERSITY IN A DISTURBANCE-MAINTAINED LANDSCAPE:
EFFECTS OF FIRE AND FIRE SURROGATE ON AQUATIC AMPHIBIAN SURVIVAL
AND SPECIES DEPAUPERATENESS

by

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A dissertation submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy
in the Department of Biology
in the College of Sciences
at the University of Central Florida
Orlando, Florida

Fall Term
2013

Major Professor: Reed F. Noss

ABSTRACT

Disturbance is one of the central concepts explaining how diversity arises and is perpetuated in ecological time. A good model system for testing hypotheses related to disturbance is the longleaf pine ecosystem in the southeastern U.S. because in this ecosystem frequent, low-severity fires acts as a disturbance that maintains a unique vegetation structure and high species richness. Vegetation structure influences animal distributions; in fire-dependent ecosystems many animals rely on open-structured, fire-maintained vegetation but shrubs and trees encroach into fire-dependent ecosystems where fire has been excluded. Prescribed burning and mechanical removal are commonly used as restoration tools to control encroachment. To better assess and compare the restoration potential of these tools, a more thorough understanding of how they change vegetation structure and habitat suitability for animals is necessary.

The southeastern U.S. is a diversity hot-spot for amphibians, many of which require ephemeral wetlands embedded in longleaf pine uplands for the aquatic phase of their life cycle. Amphibian diversity has been declining in recent decades and habitat loss/degradation has been cited as one of the leading causes. Although often overlooked in studies of fire ecology, the ephemeral wetlands required by many amphibians are also fire-dependent habitats that have been negatively impacted by lack of fire. To understand how disturbance interacts with wetland vegetation and aquatic-phase amphibians, three disturbance treatments meant to mimic the effects of natural disturbance on vegetation structure were applied randomly to 28 dry ephemeral

wetlands in the Lower Coastal Plain of South Carolina, U.S. The treatments consisted of early growing-season prescribed fire, mechanical vegetation removal (a proposed fire surrogate), and a combination of mechanical removal plus fire; some sites were left untreated for reference. Vegetation structure was quantified and amphibian assemblages were monitored before and after treatments. In addition, one species of amphibian was used in a tadpole survival experiment to examine differences in performance among treatments. Other factors that could be affected by treatments and in turn influence amphibians were measured, including water chemistry, wetland depth, quantity and quality of epilithon, and leaf litter composition.

Amphibian survival was lowest, and species depauperateness highest in untreated wetlands. Depauperateness of species whose range was restricted to the range of longleaf pine was lowest in sites that had mechanical treatment plus fire. The mechanical plus fire treatment created the most open vegetation structure with lowest leaf litter accumulation, especially of hardwood litter, conditions correlated with high amphibian survival and diversity. When data from this study was combined with data from a previous study of similar nearby wetlands, a pattern emerged in which one suite of species was absent from recently burned sites, while an entirely different suite of species was absent from long-unburned sites. This evidence suggests that disturbance is related to a shift in amphibian assemblage possibly due to changes in vegetation structure and perhaps wetland ecology in general, from an algal-based system maintained by frequent fire to a detrital-based system that develops in the absence of fire.

This is dedicated to my husband, best friend and mentor, Nathan Klaus. Thank you for your patience, advice, encouragement and shoulder to cry on. You never stopped believing in me, even when I had little faith in myself. You are one of the most dedicated, passionate, and knowledgeable conservationists I know, and an example I will strive towards always.

This is also dedicated to my parents, Everett and Lee Brown. Your truly unconditional love has gotten me through the best and worst that life had to offer, you gave me the foundation to become the person I am, and supported me through all my crazy endeavors.

Last but not least, this is dedicated to my dog, Hayduke. You followed me faithfully through hell and high water; ticks, chiggers, yellow flies and mosquitoes; cold, heat, rain, and ice. You would never leave my side and only hoped for my attention in return. Whoever said diamonds are a girl's best friend never had a dog who did field work with them.

ACKNOWLEDGMENTS

Barbara Calhoon and Patricia Webster took care of my mental health throughout the dissertation process and I owe much to them for helping me reach my goal. The writings of Thich Nhatt Hanh, Krishnamurti and Edward Abbey also helped me through the process. Regular viewing of "The Big Lebowski" kept my spirits up as well.

One big acknowledgement to all of the amazing folks I've forgotten or don't have room to mention, who are working hard for the conservation of this precious Earth's beauty.

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CHAPTER ONE: DISTURBANCE AND DIVERSITY

How is biological diversity created and maintained? This question has intrigued and challenged evolutionary biologists and ecologists dating back to Jean-Baptist Lamarck (1809) and Charles Darwin (1859). Competition, predation, productivity and disturbance are the central concepts explaining how diversity arises and is perpetuated in ecological time. Grime (1973), Horn (1975) and Connell's (1978) 'intermediate disturbance hypothesis' was a seminal ecological theory that included competition and disturbance in explaining some observed patterns of diversity. Since then a variety of exceptions, extensions and alternatives have been proposed and tested (e.g. Petraitis, Latham and Niesenbaum 1989; Kondoh 2001; Mackey and Currie 2001; Cordonnier, Courbaud and Franc 2006) including Platt and Connell's (2003) model of the effects of catastrophic and non-catastrophic disturbances on directional species replacement. In one of their modeled scenarios, directional species replacement is repeatedly interrupted by non-catastrophic disturbance, and a community of early successional species persists. They predicted that if disturbances are spatially heterogeneous but relatively consistent through time, early and late successional species may coexist across an environmental/geographic gradient. A good model system for testing hypotheses related to this proposed scenario is the longleaf pine ecosystem in the southeastern U.S. because this ecosystem is maintained by frequent, low-severity fires (Frost 1998), and a mosaic of fire histories/regimes have been created by site factors and land use/management.

The longleaf pine ecosystem is one of the most threatened ecosystems in North America (Noss et al. 1995) due to turpentine and timber extraction, open range grazing and, more recently, development and fire suppression (Blakey 1940, Croker 1987, Landers et al. 1995, Van Lear et al. 2005, Frost 2006). Fire acts as a heterogeneous, non-catastrophic disturbance in this system, but in contrast to what Platt and Connell (2003) predicted, many species associated with frequently burned habitats are not what is traditionally thought of as early successional species (i.e. short-lived, high reproductive output, high dispersal ability, poor competitor). Some longleaf-endemic plants are long-lived species with poor dispersal but have traits allowing them to take advantage of an environment associated with frequent fire (Myers 2010). These 'disturbance specialists' typically do not compete well with species that invade in the absence of fire so without fire their abundance is reduced while other species increase (Walker and Peet 1984, Peet and Allard 1993, Olson and Platt 1995, Walker and Silletti 2006). When fire is excluded from a fire-dependent system, habitat structure shifts from relatively open canopy with sparse midstory and dense or diverse groundcover, to dense canopy with thick midstory and reduced groundcover (Abrams 1992, Waldrop et al. 1992, Gilliam and Platt 1999, Metlen and Fiedler 2006, Collins et al. 2007, Nowacki and Abrams 2008, Kane et al. 2010, Outcalt and Brockway 2010).

Although often overlooked, many ephemeral wetlands embedded within longleaf pine uplands are fire-dependent habitats. They are shallow topographical depressions that dry periodically and are fed by rainwater or groundwater with no obvious surface connections to other water bodies. Historically, fires were common during the driest part of the year, a time

when ephemeral wetlands were also frequently dry (De Steven and Toner 2004). Fire suppression in recent decades has affected embedded wetlands just as it has affected longleaf pine uplands; shrubs, vines and trees invade and reduce or replace a diverse groundcover of graminoids and forbs (Olson and Platt 1995; Kirkman *et al.* 2000; Drewa, Platt and Moser 2002). One would expect concomitant changes in the entire food web (Menge and Sutherland 1987; Jenkins, Kitching and Pimm 1992; Wardle 1995; Wootton, Parker and Power 1996), but this has not been explicitly tested in this system. In addition to other factors such as upland site characteristics, wetland hyrdoperiod, bathymetry, and soil type, fire determines leaf litter depth and composition, influences plant communities that donate litter and affects the availability of nutrients from leaf litter (Maclean *et al.* 1983; Wilbur and Christensen 1983; Debano, Neary and Ffolliott 1998). Growth and nutrient quality of algae and other components of epilithon depend on available light and nutrients (Gregory 1980, Urabe and Sterner 1996, Greenwood 2005, Hill et al. 2010), so fire may influence the extent to which a wetland is an algal-based or detritus-based system by determining plant and litter structure and composition. In addition to water chemistry, hydroperiod, predator load,competition and degree of isolation (Eason and Fauth 2001), vegetation structure, litter accumulation and litter composition also influence distributions, growth and survival of larval amphibians (a primary consumer)(Skelly, Werner and Cortwright 1999; Rubbo and Kiesecker 2004; Skelly *et al.* 2005), possibly by affecting epilithon food sources (Hessen, Ferovig and Andersen 2002; Stelzer and Lamberti 2002; Schiesari 2006; Williams, Rittenhouse and Semlitsch 2008; Maerz, Cohen and Blossey 2010; Cohen, Ng and Blossey 2012).

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The southeastern U.S. is a diversity hot-spot for amphibians, many of which require ephemeral wetlands for the aquatic phase of their life cycle, but this diversity has been declining in recent decades (e.g. local extirpations or range-wide decline of *Ambystoma tigrinum* (Hammerson *et al.* 2004)*, Ambystoma cingulatum* (Palis and Hammerson 2008) and *Lithobates capito* (Hammerson and Jensen 2004)). The effects of fire on amphibians in the southeastern U.S. are not clear (Pilliod *et al.* 2003; Perry, Craig Rudolph and Thill 2012); fire affects different amphibian guilds in different ways (e.g., Greenberg and Waldrop 2008; Steen *et al.* 2010). Although Schurbon and Fauth (Schurbon 2000; Schurbon and Fauth 2003) found that amphibian species richness increased with time since burn, their results may have been confounded with habitat type (Robertson and Ostertag 2004) and they did not distinguish guilds that may respond differently to fire. In addition, the effects of fire specifically on the aquatic stage of amphibians are unknown. I hypothesized that amphibian diversity in the longleaf pine ecosystem is influenced by disturbance, and that disturbance acts directly on vegetation and leaf litter, and indirectly on other components of the food web to ultimately cause amphibian response. I tested four specific main hypotheses: 1) survival of a larval amphibian was related to a wetland environmental gradient that included vegetation structure, leaf litter composition, wetland chemistry and epilithon 2) survival of a larval amphibian species varies with disturbance treatment (fire and a fire surrogate) 3) amphibian species depauperateness is related to a wetland environmental gradient that includes wetland vegetation structure, water chemistry and water depth, and 4) amphibian species depauperateness varies with disturbance treatment.

To test my hypotheses, I selected for study a set of 28 ephemeral depression wetlands in Francis Marion National Forest, South Carolina, U.S. in close proximity to the set of wetlands used for Schurbon's previously mentioned study. The sites used in the present study were located on a relatively high ridge (6-15 m elevation), parallel to and approximately 16 km distant from the Atlantic shoreline, and surrounded by longleaf pine woodland on well-drained, sandy soil. This area had a historic fire return interval of 2-4 years (Frost 1998), and is a diversity hotspot for amphibians in the U.S. (Young *et al.* 2004). At the onset of the study, the forest stands encompassing study wetlands were burned with prescribed dormant season burns on rotations ranging from 4-15 years. Sometimes the embedded wetlands burned during prescribed burns (as evidenced by fire scars on trees), but often times they did not due to inundation or because fire was actively excluded from them. This history resulted in a range of vegetation conditions from relatively herbaceous and open-canopied to shrub-dominated and closed-canopied. Included in the set of sites were several wetlands historically occupied by threatened *Ambystoma cingulatum* (Frosted flatwoods salamander) and *Lithobates capito* (Carolina gopher frog).

Three disturbance treatments meant to mimic the effects of natural disturbance on vegetation structure were applied randomly to the 28 study-wetlands; a total of five were burned with early growing-season prescribed fire, five had mechanical midstory removal (mulched), seven were mulched and burned, and 11 were left untreated. Mulching treatments were of interest because managers faced with the challenges of using prescribed fire near developed areas or in areas with very high fuel loads are often interested in using this tool as a fire surrogate

or to enhance the restoration potential of prescribed fire (Kennedy and Fontaine 2009; McIver *et al.* 2012).

My research consists of two main components. In the first study, I selected a subset of 16 of the 28 study sites and examined survival of a larval amphibian as a response to treatments because survival has important implications for diversity. I also estimated canopy density (including midstory), relative types and amounts of leaf litter, and amount and nutrient content of epilithon after treatment in an effort to elucidate potential pathways in the food web through which disturbance might influence larval amphibian survival. In the second study I selected another subset of 24 of the 28 study sites, and examined species richness of two larval amphibian guilds, species closely associated with the longleaf pine ecosystem (> 80% of range overlapping with longleaf pine range) and species coincidental occurring with the longleaf pine ecosystem (< 80% of range overlapping with longleaf pine range), in response to treatments. For that subset of sites, I estimated canopy, midstory and groundcover vegetation density, and leaf litter depth before and after treatments, to determine which aspects of vegetation structure responded to treatment, and which aspects were correlated with amphibian diversity. I also combined amphibian data from my study and Schurbon's study to look for patterns in assemblages related to my predefined guilds.

In the concluding chapter of this dissertation I relate the results of the two main components of my research and compare my results to other related research. Because amphibian diversity is declining in the system I studied and others, it is useful to suggest how these results

can be applied toward conservation. I address three areas of specific interest to land managers whose conservation goal is to maintain or increase amphibian diversity in the longleaf pine ecosystem: 1) is mulching an effective surrogate for fire, 2) can fire alone restore degraded wetland habitat and 3) what aspects of wetland habitat are most important in relation to amphibian diversity. I also address three areas of interest to theoretical ecologists and to the broader conservation community: 1) how is disturbance related to diversity in a system with frequent, non-catastrophic disturbance, 2) suggest multiple pathways through which disturbance affects wetland food webs and 3) make suggestions for future research that would improve our understanding of ephemeral wetland and amphibian ecology.

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CHAPTER TWO: FIRE AND FIRE-SURROGATE TREATMENTS ALTER WETLAND VEGETATION AND INFLUENCE AMPHIBIAN SURVIVAL

Abstract

Vegetation structure influences animal distributions, and in fire-dependent ecosystems many animals rely on fire-maintained vegetation. Shrubs and trees encroach into fire-dependent ecosystems where fire has been excluded. Prescribed burning and mechanical removal are used as restoration tools to control encroachment. To assess and compare the restoration potential of these tools, a more thorough understanding of how they change vegetation structure and habitat suitability for animals is necessary. Mechanical midstory removal, prescribed burning, and a combination of mechanical and burning treatments were applied to 12 ephemeral wetlands in South Carolina (USA) embedded in a fire-dependent ecosystem and in varying stages of encroachment; four wetlands were monitored but left untreated. After treatments were applied, I measured canopy closure; leaf litter mass and composition; water pH, dissolved oxygen, temperature and turbidity; and nutrient content and mass of epilithon (algae and other benthic microorganisms). In the same wetlands I conducted a survival experiment of larval anurans (primary consumers). Several wetland variables were interrelated, and when ordinated, ordination score differed by treatment. Tadpole survival was negatively correlated with canopy closure and hardwood litter, and positively correlated with graminoid litter, temperature, dissolved oxygen, pH and percent carbon in epilithon, conditions associated with the mulch-and-burn treatment. The effects of the burn treatment were similar to mulch-and-burn, but not as pronounced. The effects of the mulch treatment were significantly less than mulch-and-burn, but

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not statistically different from burned or untreated sites. No tadpoles survived past week one in untreated wetlands. Although canopy was one important element correlated with larval amphibian survival, leaf litter, pond chemistry and epilithon may have more direct effects on survival. By understanding key ecological elements associated with habitat suitability for animals, and how alternative management tools affect those elements, more precise and effective recommendations can be made for habitat restoration.

Introduction

A foundational concept of ecology is that vegetation structure and composition influence animal distributions (Shelford 1913; Elton 1927). In many ecosystems, and prominently in the southeastern U.S., vegetation structure and composition are determined by fire regime (e.g. Harper 1911, Fisher *et al.* 2009; Scheintaub *et al.* 2009; Louzada *et al.* 2010; Smit *et al.* 2010). Research in fire dependent ecosystems demonstrates that fire exclusion affects habitat structure and composition, favoring woody vegetation to the detriment of graminoids and forbs (Gilliam and Platt 1999; Kirkman *et al.* 2000; Van Auken 2000; Archer, Boutton and Hibbard 2001; Arkle and Pilliod 2010). These changes decrease habitat suitability for animals that evolved in fire-maintained conditions.

Survival rate of young is one metric for assessing habitat suitability. Vegetation structure and composition may affect animal survival through a variety of mechanisms including shading, determining availability and quality of food, and altering soil or water chemistry. Management

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that mimics natural fire (such as prescribed burning and mechanical vegetation removal, a proposed fire surrogate), alters vegetation structure and can affect survival rate of young animals, but effects vary with method. It is necessary to understand which habitat elements are critical to animal survival, and how management changes those elements, to select the best management practices for conserving animals dependent on fire-maintained ecosystems.

Ephemeral wetlands embedded within the longleaf pine ecosystem of the Lower Coastal Plain of South Carolina, US, are fire-maintained communities altered by canopy closure, shrub encroachment and leaf litter accumulation as a result of fire exclusion (Dr. Julian Harrison, personal communication; aerial photographs circa 1934-present). These wetlands are essential breeding and larval habitat for amphibians dependent on fire-maintained conditions. Canopy closure, litter accumulation and litter composition influence distributions, growth and survival of larval amphibians (Skelly, Werner and Cortwright 1999; Rubbo and Kiesecker 2004; Skelly *et al.* 2005). Canopy closure lowers water temperature and dissolved oxygen necessary for optimizing larval amphibian growth and development (Travis and Trexler 1986; Moore and Townsend 1998). Changes in leaf litter accumulation and composition associated with woody encroachment influence amphibians by altering detritus and epilithon (algae and other benthic microorganisms) food sources (Hessen, Ferovig and Andersen 2002; Stelzer and Lamberti 2002; Schiesari 2006; Williams, Rittenhouse and Semlitsch 2008; Maerz, Cohen and Blossey 2010; Cohen, Ng and Blossey 2012). The ratios of nitrogen, phosphorus and carbon in epilithon are indicators of food quality and influence primary consumer performance (Urabe and Sterner

1996; Sterner 1997; Frost *et al.* 2002); food quantity and quality affect larval anuran growth and metamorphosis (Steinwascher and Travis 1983; Kupferberg 1997).

I hypothesized that canopy closure (mid- and overstory combined) and related wetland attributes affect the survival of larval amphibians, and that restoration treatments would improve conditions for survival. To test this, I examined the effects of prescribed burning, mechanical treatment (mulching), and mechanical plus burning on larval amphibian survival in enclosures *in situ*. I quantified habitat responses to treatments including canopy, litter accumulation and composition, water chemistry, and epilithon quantity and nutrient content, and used these variables to explain larval amphibian survival.

Methods

Sites

I selected 16 wetlands in various stages of encroachment, in Francis Marion National Forest, Berkeley County, South Carolina, with various combinations of *Nyssa biflora* (Walter), *Taxodium ascendens* (Brongniart), *Pinus serotina* (Michaux), *Pinus palustris* (Miller), and *Liquidamar styraciflua* (Linnaeus) overstory. Wetland sizes ranged from 0.2–8 .0 ha, duration of inundation varied from a few weeks to two years and maximum depth was 25–95 cm. Wetlands were located on similar soils (poorly drained loamy fine sand) at similar elevation (< 6 m) (Long 1980) and formed in shallow topographical depressions. Hydrology was driven by

evapotranspiration with no obvious surface water connections, and wetlands were typically inundated between January and April, drying down during summer (De Steven and Toner 2004). Uplands surrounding study sites were historically dominated by *Pinus palustris* woodland with pre-settlement fire regime of low-severity fire every two to four years (Frost 1998). Uplands are currently *Pinus palustris* woodland. Prescribed fire management records were unavailable prior to 1989, after which fire return intervals ranged from 3-10 years and fire frequency was one to two fires from 1989-2006.

Experimental Design and Sampling

Three restoration treatments were applied to 12 wetlands; four were untreated, four wetlands were mulched (mechanical midstory removal in the ecotone from normal high water mark to ~10 m beyond that mark), four burned, and four mulched and burned. Mulching occurred between 2006-2007 and consisted of removal of woody vegetation < 16 cm diameter at breast height (DBH), using hand-tools and a Gyro-Trac© (Charleston, SC, USA) low-impact mulching machine, leaving cut material on site. In early spring 2008 USDA Forest Service conducted a prescribed burn through dry wetland basins in burn treatments. Due to drought, wetlands did not hold water from 2006-2008.

Adult, breeding *Hyla chrysoscelis* (Cope) were available 03 June 2009; I collected ten clutches of on eggs from two wetlands ~12 km from study sites. I chose *Hyla chrysoscelis* because it is a common, spring/summer-breeding treefrog species with a range encompassing most of the longleaf pine ecosystem (Platt, 1999; Jensen *et al.* 2008). In a separate study of

overlapping wetlands, *Hyla chrysoscelis* was detected at 13 of 24 sites surveyed over five years (J.M. Klaus, unpublished data). I maintained egg masses in separate 1-L plastic containers, in water from collection sites, at approximately 24°C. I fed thawed frozen spinach to tadpoles after hatching *ad libitum* for four weeks. Tadpole enclosures were constructed of rigid 10 mm mesh lined with fiberglass window screen to allow microorganisms, seston and light to pass through, but to exclude predators. The cone-shaped enclosures were 122 cm long and 40 cm diameter at the wide end, with a total volume of approximately 50 L; three enclosures were placed at 20 cm depth in each wetland. Ten tadpoles, stratified by clutch, were randomly assigned to each enclosure. Each enclosure held approximately 25 L of water and 10 tadpoles, well below the density threshold for poor performance (Wilbur 1982). I checked enclosures in random order to evaluate survival of tadpoles and environmental variables weekly for four weeks. Metamorphosing individuals (hind limbs and at least one front limb emerged) were removed from the enclosure. Dissolved oxygen (DO), pH, and maximum temperature were measured in each wetland in water immediately adjacent to one of the enclosures.

To determine treatment effects on litter accumulation and composition, in July 2009 I removed all accumulated litter from within three randomly positioned 30 cm diameter circular plots per wetland. Samples were dried for 24 hours in a forced-air oven and weighed. I estimated, to the nearest 5%, area of the sample taken up by hardwood and graminoid litter.

To sample epilithon abundance and quality I placed five unglazed ceramic tiles (95 mm^2) in each wetland in June 2009. Tiles remained submerged for 21 days then were retrieved and

each was brushed in 1 L deionized water to remove epilithon from the surface. I filtered water containing epilithon samples through a 0.7 nm glass fiber filter, placed each filter in a plastic tube and froze it. I used half of each sample for mass analsysis, and the other half for nutrient analysis. I used standard methods to analyze dry mass, ash-free dry mass (carbon, C), nitrogen (N) and phosphorus (P) content (Clesceri, Greenberg and Trussel 1989; Crumpton, Isenhart and Mitchell 1992).

To quantify canopy cover in each wetland, I obtained hemispherical color photographs of the canopy in June 2010 using a Nikon Coolpix © camera with fish-eye (180°) lens, leveled on a tripod 0.5 m above the ground. I took photos at eight random points at the normal high water mark of each wetland. To estimate percent canopy openness measures from each image I used Gap Light Analyzer (GLA) software (Frazer, Canham and Lertzman 1999) with the color plane set to blue and the threshold set to capture as much vegetation as possible without selecting background pixels. Percent canopy closure was calculated by taking the inverse of percent canopy openness.

Data Analysis

I calculated *H. chrysoscelis* mortality rate and survival time as measures of performance. First, I used the Turnbull method (for right-, left- and interval- censored data) to estimate the survival function of tadpoles by treatment and interval (week), then fitted a smooth exponential model to the interval estimates to produce an estimate of constant mortality rate over the entire experimental period using the JMP© (SAS Institute 2008) survival function with exponential fit

and exponential plot. The results were estimates of mean survival time and mortality rate, by treatment. To examine differences in tadpole survival among groups, I examined the confidence limits for the estimated mean survival times to determine if they overlapped.

To examine relationships among wetland environmental variables I performed pair-wise comparisons using Spearman's rho. To test for differences in environmental variables among treatments, I used analysis of variance (ANOVA) (SAS Institute 2008) where appropriate and Monte Carlo permutation F-tests with 1000 iterations (R Development Core Team 2011) for data that could not be transformed to meet ANOVA assumptions. If ANOVA or Monte Carlo procedures detected a significant difference among treatments, I used a Tukey's HSD test, or a permutation version of Tukey's test with 1000 iterations (R Development Core Team 2011) to determine which groups were different. I used Spearman correlation (Conover and Iman 1981; SAS Institute 2008) to test the strength of associations among canopy, litter, water chemistry, and epilithon variables.

To determine if tadpole survival was associated with wetland variables, I assessed correlations among variables in a correlation matrix and used non-metric multidimensional scaling (NMS) to ordinate variables (McCune and Mefford 1999). I relativized the data across columns (variables) so that they were on a similar scale, and then used Sorensen distance to ordinate data, reducing it to two axes. Only one of those axes showed a strong relationship between ordination distances and distances in the original n-dimensional space, so only this axis was used for further analysis. I used ANOVA to determine if the ordination scores of this axis

varied significantly by treatment (SAS Institute 2008). I constructed four models using treatment and ordination score as factors to explain tadpole mortality, and used Bayesian Information Criterion (BIC) (SAS Institute 2008) to select the most informative model.

<u>Results</u>

<u>Tadpole survival</u>

Tadpole mortality was high but differed among treatments; within one week of placement in experimental enclosures, all tadpoles in untreated wetlands were dead while only partial mortality occurred in other treatments (Fig. 2). Estimated mean survival time averaged over the entire experimental period was significantly lower (i.e. mortality rate higher) in the untreated group than any of the treatment groups (Fig. 3). Estimated mean survival days were 3.81 for the untreated group (lower CL = 3.06, upper CL = 4.77), 10.32 for burn treatment (lower CL = 8.53, upper CL = 12.62), 13.34 for the mulch treatment (lower CL = 11.02, upper CL = 16.33) and 10.61 for the mulch-and-burn treatment (lower CL = 8.85, upper CL = 12.86). Estimated mean mortality rates were 0.26/day (26 % of the 'population' dying/day) in untreated, 0.10/day in burn, 0.70/day in mulch and 0.90/day in mulch-and-burn.

<u>Effects of treatments on canopy cover</u>

Percent canopy cover by wetland ranged from 47.31-90.56 % and strongly differed in response to treatment (Table 1). The mean percent canopy closure by treatment varied from 52-

89 % and was lowest in mulch-and-burn and significantly higher in all other treatments; untreated wetlands had the highest percent canopy closure (Fig. 4).

Effects of treatments on litter mass and composition

Mean total litter mass differed significantly by treatment (Table 1); mulch had more litter than any of the other treatments. Percent hardwood litter and percent graminoid litter varied by treatment (Table 1). Mean hardwood litter ranged from 7 % in mulch-and-burn to 59 % in untreated. Mean hardwood-litter in mulch-and-burn was significantly lower than in mulch, and significantly higher in untreated than any treatment. Mean graminoid litter was higher in mulch-and-burn (77 %) than any other treatment (17-19%) (Fig. 4).

Effects of treatments on epilithon

I failed to reject the null hypothesis of no difference among treatments for epilithon biomass and for most of the epilithon nutrient ratios. Although there was evidence to reject the null of no difference in percent P in epilithon by treatment (df = 3, Monte Carlo F-observed = 4.85, P = 0.026), I failed to reject the null of no difference between the largest mean (no treatment = 0.12 % P) and the smallest mean (mulch = 0.08 % P) using a permutation Tukey test (df = 3, T-observed = 10.70, P = 0.064), probably because the effect size was small ($\square^2 = 0.27$).

Effects of treatments on water chemistry

Mean maximum water temperature by treatment ranged from 28-36 °C, was highest in the mulch-and-burn treatment, followed by burn, then mulch, and lowest in the untreated group

(Fig. 4). Mean DO by treatment ranged from 21-64 % and followed the same pattern as temperature. I failed to reject the null hypothesis of no difference in pH or turbidity among treatments.

Relationship between wetland biotic and abiotic responses

Several wetland variables were correlated (Table 2). Canopy closure was positively correlated with hardwood litter and negatively correlated with graminoid litter, temperature, DO, pH and percent C in epilithon (Figs 5 and 6). DO was positively correlated with water temperature because high light level increases algal photosynthetic activity, which in turn increases DO, while high light level coincidentally increases temperature (Schiesari 2006; Williams, Rittenhouse and Semlitsch 2008). Other litter and water chemistry variables were not significantly correlated with each other.

Potential pathway for treatment effects on tadpole survival

Because several variables that could explain tadpole survival co-varied (were interrelated) I ordinated wetland variables with NMS; a two-dimensional solution was best with a final stress of 8.75. The first axis explained only 3.6 % of the variation in the original ordination space, while the second axis explained 89.6 % of the variation. The first axis most strongly correlated with C in epilithon ($r^2 = 0.400$), followed by graminoid litter ($r^2 = 0.323$), DO ($r^2 = 0.094$), canopy closure ($r^2 = 0.050$), hardwood litter ($r^2 = 0.043$), pH ($r^2 = 0.014$) and temperature ($r^2 = 0.003$). The second axis most strongly correlated with canopy closure ($r^2 = 0.794$), followed by hardwood litter ($r^2 = 0.767$), graminoid litter ($r^2 = 0.571$), temperature ($r^2 =$

0.537), DO ($r^2 = 0.450$), pH ($r^2 = 0.320$) and C in epilithon ($r^2 = 0.317$) (Figs 5 and 6). I did not

use the first ordination axis in further analysis because it explained little of the variation in the

original ordination space.

The second ordination axis score differed significantly by treatment (DF = 3, F =

12.1988, $P = 0.0006$, $r^2 = 0.6913$) (Fig. 5). Mulch-and-burn had the highest ordination score

(lowest canopy closure and hardwood litter, and highest graminoid litter, temperature, DO, pH

and C in epilithon), and was significantly higher than mulch and untreated ($P = 0.0270$ and $P =$

0.0004 respectively). Burn also had a significantly higher score than untreated ($P = 0.0070$).

Using treatment and ordination score I constructed a set of models to explain tadpole

mortality rate. One consisted of treatment alone, another consisted of the wetland environmental

ordination axis alone, another included treatment plus ordination axis plus treatment-ordination

axis interaction, and one was treatment plus ordination axis without an interaction term. Using

Bayesian Information Criterion (BIC) (SAS Institute 2008) I determined treatment plus

ordination axis plus treatment-axis interaction to be the most informative model explaining 65.43

% ($\omega^2 = 0.64$) of the variation in tadpole mortality (Table 3). Of the variables included in that

model, environmental ordination axis had a significant effect on mortality (df = 1, F = 5.4121, P

= 0.0484), and although treatment alone did not have a significant effect (df = 3, F = 3.46, $P =$

0.0712), there was a significant effect of the interaction of treatment and environmental

ordination axis (df = 3, F = 4.5351, $P = 0.0388$) (SAS Institute 2008). For burn, mulch-and-burn

and untreated sites, tadpole mortality rate decreased as ordination score increased. In mulch,

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tadpole mortality rate increased with increasing ordination score, although the pattern was largely influenced by a single site (Fig. 6). That site had higher tadpole mortality rate than any of the other mulch sites and had the lowest pH (3.34) of any site in the study. Although it did not correlate strongly ($r^2 = 0.320$) with the ordination axis used in the models, pH had a strong correlation with *Hyla chrysoscelis* tadpole mortality rate (df = 1, F = 13.82, *P* = 0.0023. $\omega^2 = 0.44$).

Discussion

Differences in amphibian performance and survival among wetlands were explained in this study and others by canopy cover (Werner and Glennemeier 1999; Skelly *et al.* 2005; Hocking and Semlitsch 2007), water temperature and dissolved oxygen (Werner and Glennemeier 1999; Schiesari 2006; Williams, Rittenhouse and Semlitsch 2008), and litter amount or type (Skelly, Freidenburg and Kiesecker 2002; Rubbo, Belden and Kiesecker 2008; Williams, Rittenhouse and Semlitsch 2008), but the mechanism that results in the effect is elusive. In this study, closed-canopy wetlands had high hardwood litter. A closed canopy prevents light needed by shade-intolerant graminoids from reaching the ground (Warren *et al.* 2007; Martin and Kirkman 2009), and shade may slow decomposition of hardwood litter (Henry, Brizgys and Field 2008) while the accumulating hardwood litter inhibits graminoid germination and sprout emergence (Facelli and Pickett 1991); many amphibians endemic to longleaf pine ecosystems are associated with 'grassy' open wetlands (Jensen *et al.* 2008). In this study, percent

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N, percent C and C:P ratio of epilithon, a tadpole food source, were correlated with relative amount of hardwood litter, and percent C in epilithon was positively associated with tadpole survival. Other studies found that food quantity or quality affected amphibian performance (Steinwascher and Travis 1983; Schiesari 2006) and open-canopy food was better assimilated than closed-canopy food (Skelly and Golon 2003). One hypothesis is that closed-canopy ponds are more detritus-based systems and open-canopy ponds are more autotroph-based systems (Skelly, Werner and Cortwright 1999), with different species performing better in different systems. Despite the potential importance for conservation, we have barely begun to understand the feeding ecology and trophic interactions of larval amphibians (Altig, Whiles and Taylor 2007). In addition, many amphibians call from and attach egg masses to emergent vegetation (Jensen *et al.* 2008) or use it for cover to escape some types of predators (Sredl and Collins 1992; Kopp, Wachlevski and Eterovick 2006; Hartel *et al.* 2007). It is likely that a single factor, like graminaceous cover or litter composition, affects amphibians through several pathways.

A single site with low pH and high mortality largely influenced the relationship between vegetation structure and tadpole mortality in the mulch treatment. pH is a strong predictor of larval amphibian species distribution (Eason and Fauth 2001). Warner and Dunson (1998) discovered that at least 50 % of *Hyla chrysoscelis* tadpoles failed to hatch in the lab at pH = 3.99, and 4.61 was the lowest pH recorded in a pond occupied by *H. chrysoscelis* in north Florida. In my study, pH was a significant predictor of tadpole mortality rate, explaining 46 % of the variation in mortality. Nine of ten wetlands with pH < 3.7 had mortality rates > 15 % of the population/day. Hardwood litter was negatively correlated with pH and graminoid litter was

positively correlated with pH, so one could expect that reducing hardwood canopy and hardwood litter would produce concomitant increases in graminoids and pH, and potentially increase survival of some amphibian species. However, even though the correlations between pH and hardwood litter and graminoid litter were significant, they only explained 27 % and 40 % (respectively) of the variation in pH, meaning that other factors may play an equal or more important role.

Treatments affected both vegetation structure and tadpole survival. Although I could not detect differences among the three treatment types, mean survival was significantly lower in untreated sites than any of the treated sites. This result at first seems to contradict the results of Williams and others (2008), who found that *H. chrysoscelis* survival was higher in leaf litter than grass litter mesocosms; in my study the untreated wetlands with high leaf litter and low grass litter had low survival. However, Williams and others also detected an interaction between shade and litter; *H. chrysoscelis* performed better in grass litter with low shade, a result consistent with the results of this study where all high-grass-litter wetlands also had low shade. Reproduction and larval survival of *H. chrysoscelis*, as well as other species, benefit from open-canopy conditions created by management (Hocking and Semlitsch 2007; Semlitsch *et al.* 2009).

The National Fire and Fire Surrogate study and other studies were conducted in response to concerns about the effects of wildfire fuel management activities on forests and wildlife (Kennedy and Fontaine 2009). Although upland mechanical thin plus prescribed-burn had a negative effect on amphibian species richness in the southern Appalachians (Matthews *et al.*

2010) it had a positive effect on species richness of longleaf pine woodland associated amphibians in the Gulf Coastal Plain (Steen *et al.* 2010). This difference can be explained by differences in the suite of species studied and ecology of the sites; the coastal plain longleaf pine sites had ongoing fire and timber management starting in the 1980s (*Solon Dixon Forestry Education Center* 2012) and contained amphibian species that require open or fire-maintained habitat (e.g. *Ambystoma tigrinum* (Green), *Hyla femoralis* (Bosc), *Hyla gratiosa* (LeConte), *Pseudacris ornata* (Holbrook)), whereas the Appalachian sites had no fire for at least 50 years, were composed of many mesic tree and shrub species, and contained amphibian species not expected in fire-maintained habitat (e.g. *Lithobates sylvaticus* (LeConte), *Plethodon metcalfi* (Brimley), *Desmognathus monticola* (Dunn)*, Pseudotriton ruber*(Latreille)). If the restoration goal were to change plant composition from mesic, fire-intolerant species to fire-adapted, shade-intolerant species, one would expect co-occurring animals to experience a similar shift in community composition. Although the *H. chrysoscelis* used in my study is a widespread species, larvae perform better in open habitats (Hocking and Semlitsch 2007; Semlitsch *et al.* 2009). Although it is likely that overall mortality was too high and replicates too few in this study to detect differences among treatments, there are still important distinctions to be made between fire and fire-surrogate treatments; effects on vegetation were not equal, and vegetation structure was a strong predictor of tadpole survival.

The mulch-and-burn treatment had the lowest hardwood litter, highest graminoid litter and lowest canopy closure, conditions correlated with high amphibian survival, while the mulch treatment had the highest hardwood litter and canopy closure of the three treatments, and burn

was intermediate. These results are similar to those of studies conducted in other geographic regions and across multiple habitats. Research in northern Sierra Nevada, northern Arizona, Gulf Coastal Plain, southern Appalachia and Ohio Hills Country demonstrated that mechanical plus burn treatments are most effective at decreasing over- or midstory and increasing graminoid abundance or diversity (Griffis *et al.* 2001; Phillips, Brudnak and Waldrop 2007; Kane *et al.* 2010; Outcalt and Brockway 2010). In every case mulching or thinning alone had no effect or was a detriment to understory vegetation; hypotheses explaining the effect include shade or root competition from resprouting woody plants, slash or chipped material preventing germination or sprouting of understory plants and lack of exposure of mineral soil. In other studies, graminoid abundance or diversity was not affected by treatment even when mechanical treatments reduced woody plants (Metlen, Fiedler and Youngblood 2004; Metlen and Fiedler 2006; Collins, Moghaddas and Stephens 2007). the effects of treatments on forest floor development can explain this result (Hiers *et al.* 2007); as demonstrated in my study and others, litter has a critical role in ecosystem function and is affected differently by various management tools. Although fire has the most direct effect on litter of the treatments discussed here, fire alone may not be sufficient to push a degraded system onto a trajectory that would sustain desired future conditions (Suding, Gross and Houseman 2004; Martin and Kirkman 2009). Fire effects are highly variable and depend on starting conditions; in the absence of fire, some systems pass an ecological threshold that is resistant to change by fire (Olson and Platt 1995; Drewa, Platt and Moser 2002; Nowacki and Abrams 2008).

Considering all research on fire and fire surrogates, a picture is emerging that shows mechanical treatments are not a precise fire surrogate. Prescribed burning is useful and preferable for maintenance, but in the initial stages of restoration or fuel reduction, mechanical treatments plus fire may be more efficient or effective. Midstory mulching followed by prescribed fire created conditions most conducive to survival of a larval amphibian in my study wetlands, but for amphibians, as with any taxon, different species will have different responses depending on their particular ecology; there are no silver bullets in restoration. Careful consideration of site characteristics, ecological relationships and conservation goals should be given before management activities are implemented.

Table 1. Test results comparing variables among treatments. F-values are reported for parametric ANOVA and Monte Carlo permutation (1000 iterations) F-tests. * = significant difference among treatments. DF = 3 and α = 0.05.

Variable	**Test**	**F-value**	*P*-value
Canopy	ANOVA	15.77	0.0002*
Litter dry mass	ANOVA	8.90	0.0022*
% Hardwood litter	Monte Carlo	13.48	0.0030*
% Graminoid litter	Monte Carlo	7.26	0.0050*
Epilithon dry mass	Monte Carlo	1.84	0.1220
Epilithon % C	Monte Carlo	1.66	0.1800
Epilithon % N	Monte Carlo	1.52	0.1820
Epilithon % P	Monte Carlo	4.85	0.0260*
Epilithon C:N	Monte Carlo	0.65	0.6890
Epilithon C:P	Monte Carlo	1.66	0.2220
Water pH	ANOVA	1.61	0.2434
Water DO	Monte Carlo	3.58	0.0500*
Water turbidity	ANOVA	0.50	0.6930
Water max temp	ANOVA	15.59	0.0004*

Table 2. Correlation coefficients for canopy, litter and epilithon variables. Can = % canopy closure, Hdwd = % hardwood litter, Gram = % graminoid litter, MaxT = maximum temperature, DM = epilithon dry mass, %C = epilithon percent carbon, %N = epilithon percent nitrogen, %P = epilithon percent phosphorus, C:N = epilithon carbon/nitrogen ratio, C:P = epilithon carbon/phosphorus ratio. Significant correlations determined by Spearman's rho test are indicated in bold.

	Can	Hdwd	Gram	pH	DO	MaxT	DM	%C	%N	%P	C:N
Can											
Hdwd	**0.69**										
Gram	**-0.75**	**-0.57**									
pH	-0.43	**-0.56**	**0.66**								
DO	**-0.74**	-0.43	**0.49**	0.13							
MaxT	**-0.81**	**-0.64**	0.47	0.38	**0.72**						
DM	-0.28	**-0.38**	-0.02	0.11	0.10	0.21					
%C	-0.36	**-0.47**	0.09	0.22	0.15	0.28	**0.97**				
%N	-0.30	**-0.35**	-0.02	0.08	0.11	0.21	**0.98**	**0.97**			
%P	0.46	0.48	-0.32	-0.21	-0.39	-0.22	-0.16	**-0.26**	**-0.14**		
C:N	0.01	-0.13	-0.05	-0.11	0.22	0.23	**-0.29**	-0.26	**-0.24**	-0.05	
C:P	-0.41	**-0.55**	0.22	0.30	0.28	0.30	**0.86**	**0.93**	**0.85**	**-0.42**	**-0.30**

Table 3. Models explaining tadpole mortality rate, ranked from best to worst. Variables include: Rx = treatment type, Axis2 = second ordination axis of environmental variables, and RxAxis2 = interaction between treatment and ordination score.

Rank	Model Description	log(£)	BIC	adjusted r²	ω
1	Rx + Axis2 + RxAxis2	2.93	-30.33	0.65	0.9113
2	Axis2	3.75	-24.86	0.21	0.0592
3	Rx + Axis2	3.48	-22.75	0.32	0.0206
4	Rx	3.67	-21.06	0.18	0.0089

Figure 1. Map of US showing location of (A) South Carolina and (B) Francis Marion National Forest.
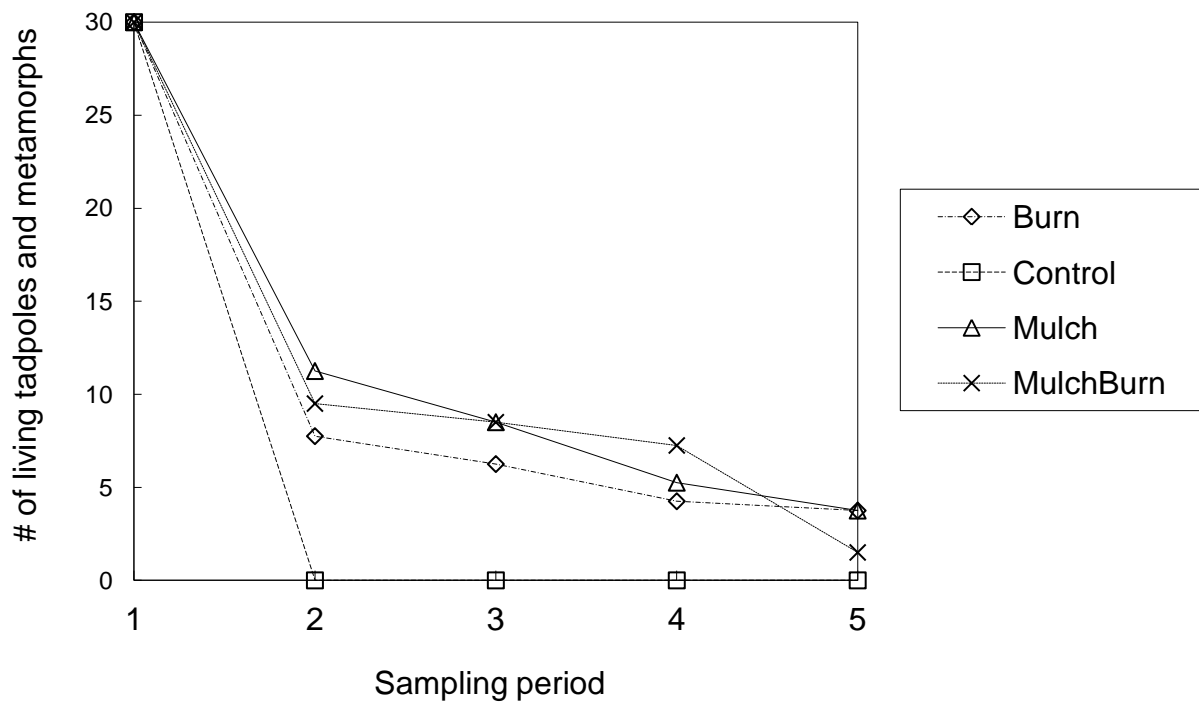
Figure 2. Mean number of surviving tadpoles plus metamorphs by treatment over weeks.
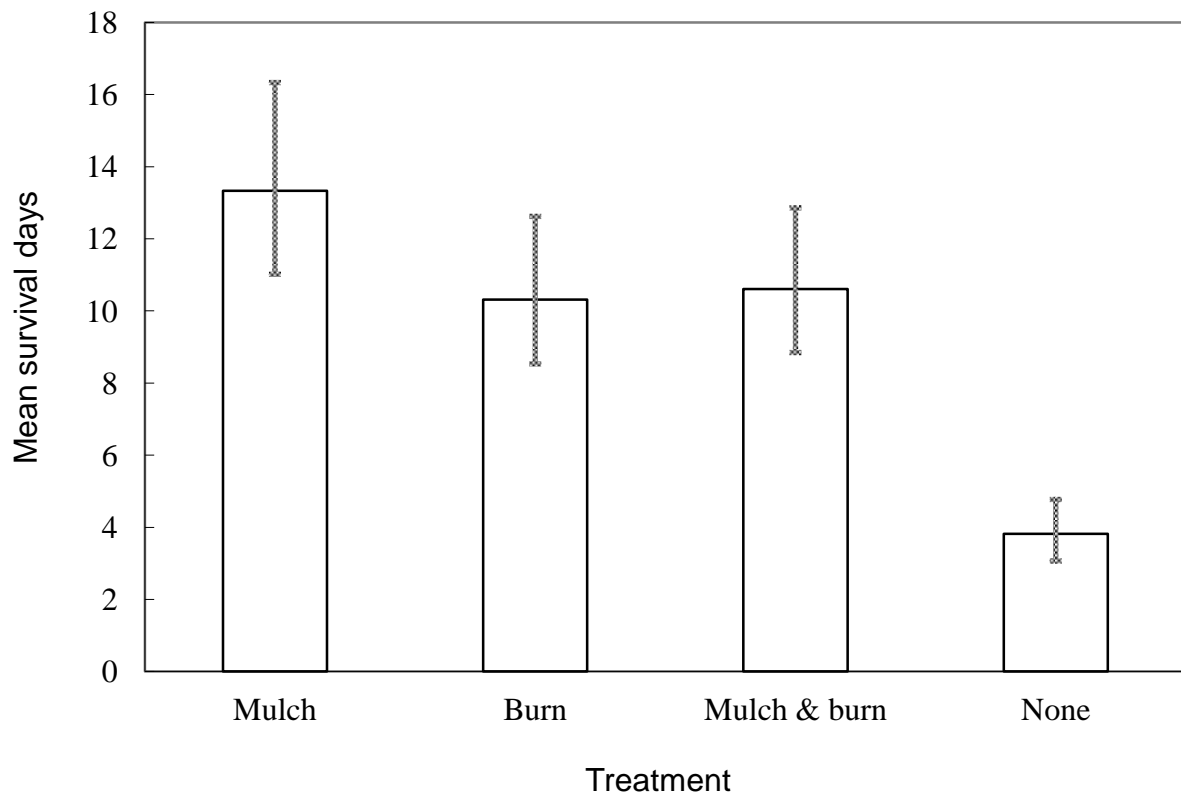
Figure 3. Mean tadpole survival time by treatment with confidence limits.
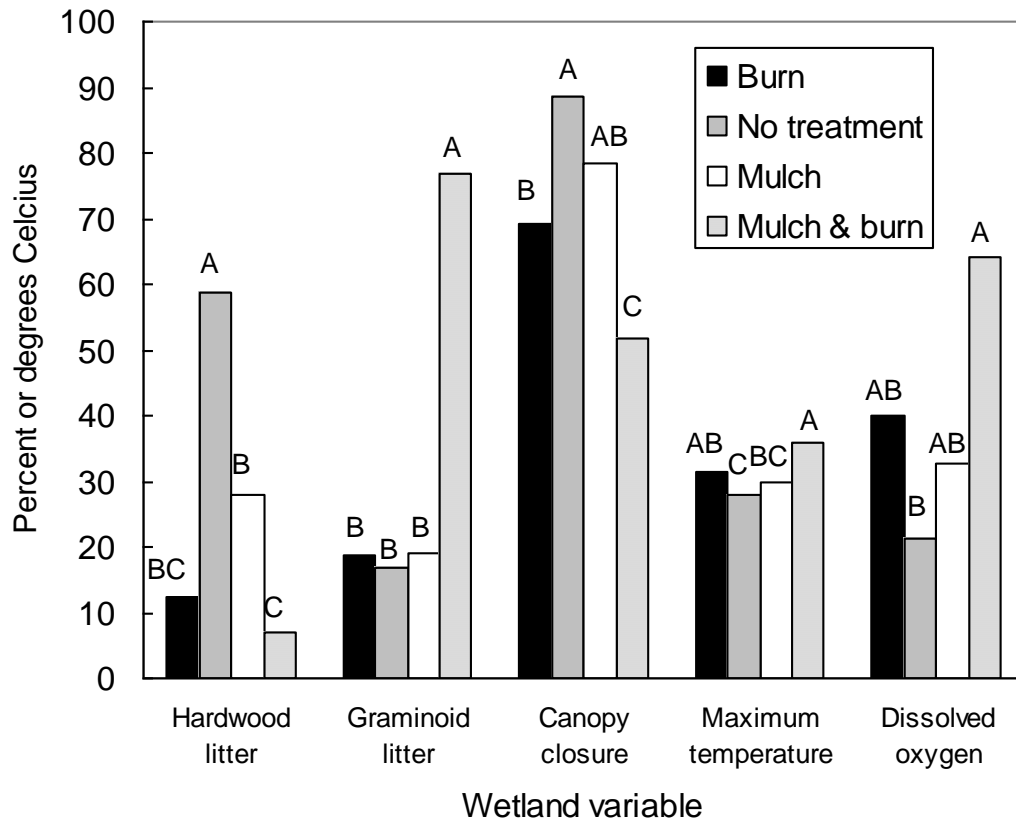
Figure 4. Comparison of correlated variables that also differed by treatment. Letters show significant differences in a variable by treatment; treatments with the same letter are not significantly different.
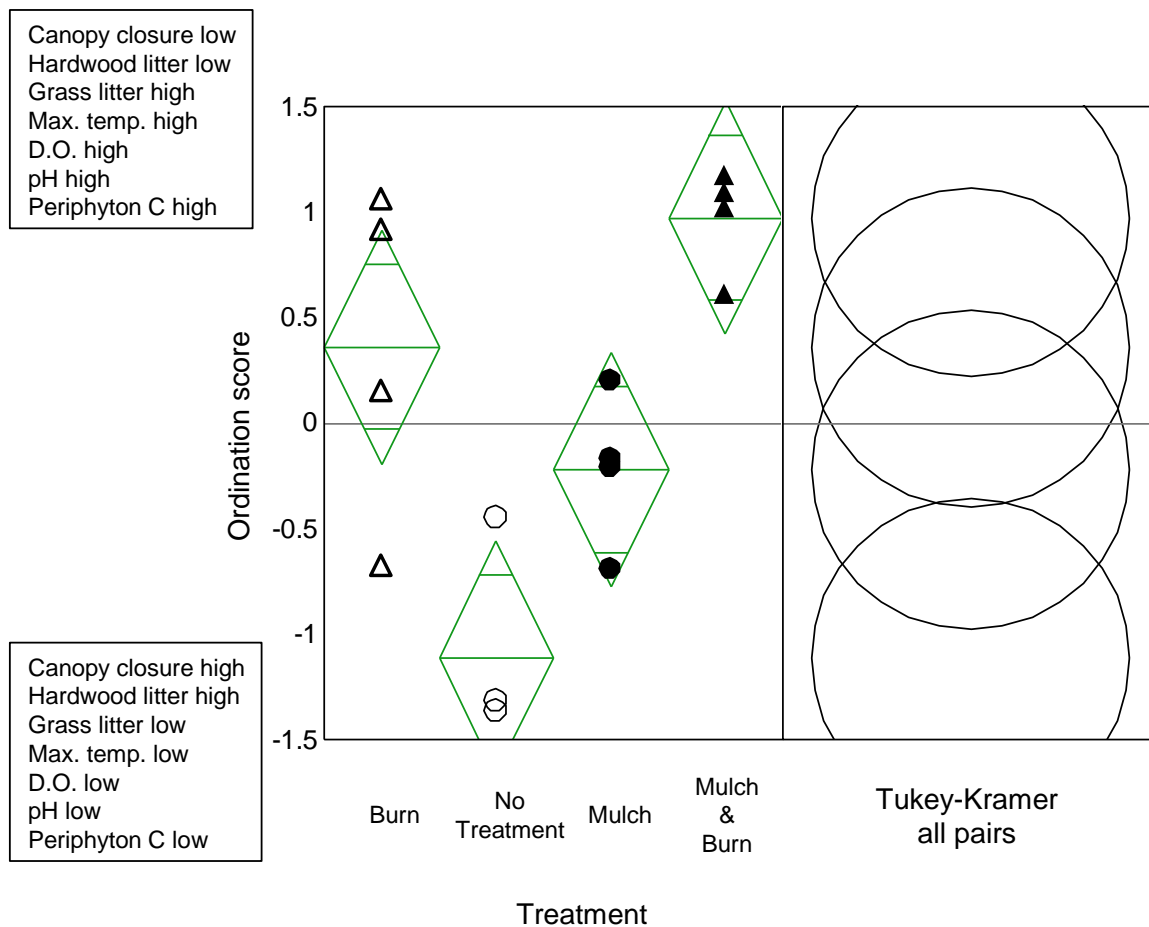
Figure 5. Oneway ANOVA of wetland environmental ordination score by treatment. Diamonds represent group means with 95 % confidence intervals. Circles are a visual representation of the comparisons among group means; circles for means that are significantly different either do not intersect, or intersect so that the outside angle of intersection is less than 90°. Boxes to the left of the graph describe ordination components.
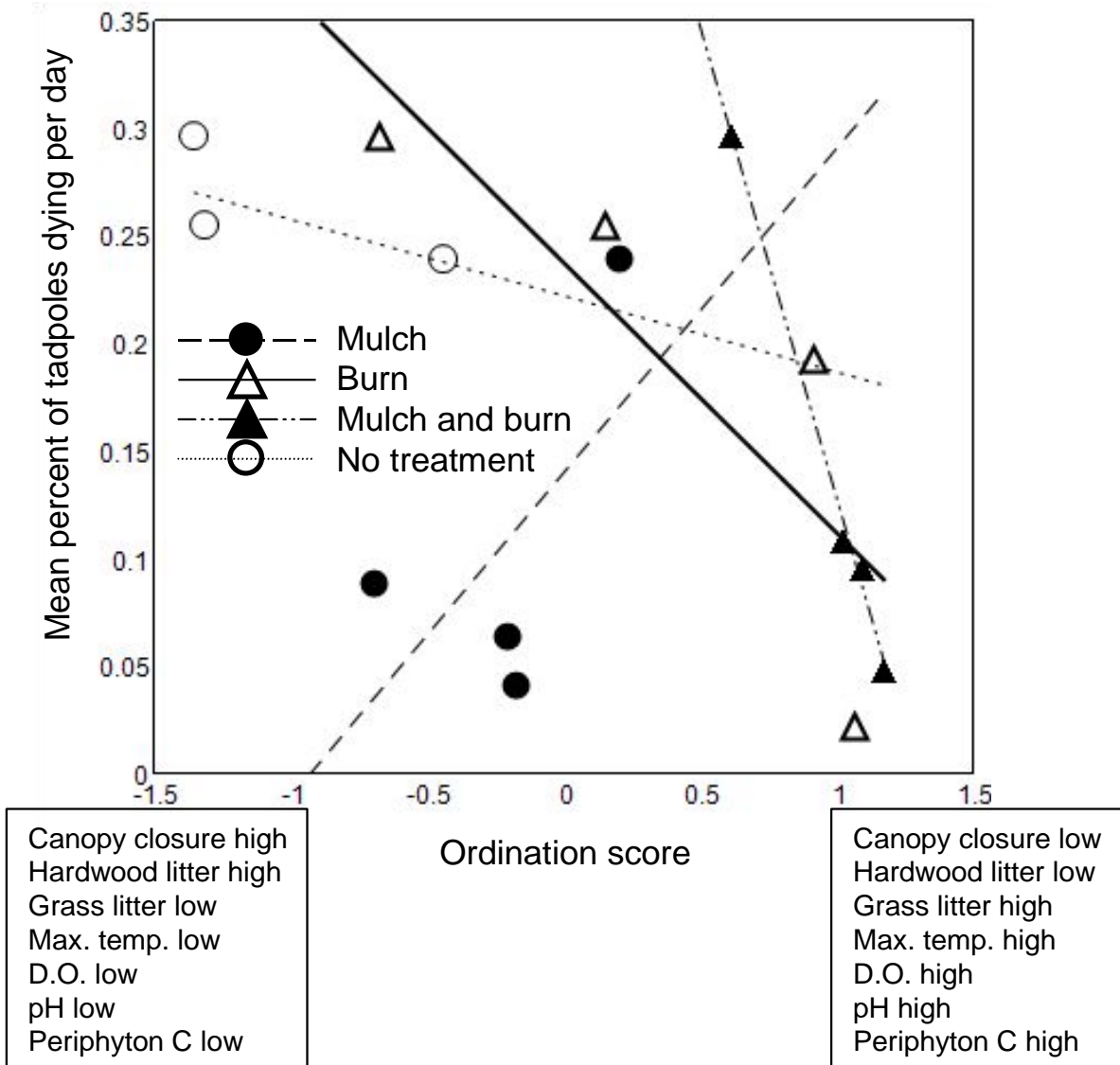
Figure 6. Tadpole mortality rate by wetland environmental ordination score with treatment interaction. Boxes below x-axis describe ordination components.
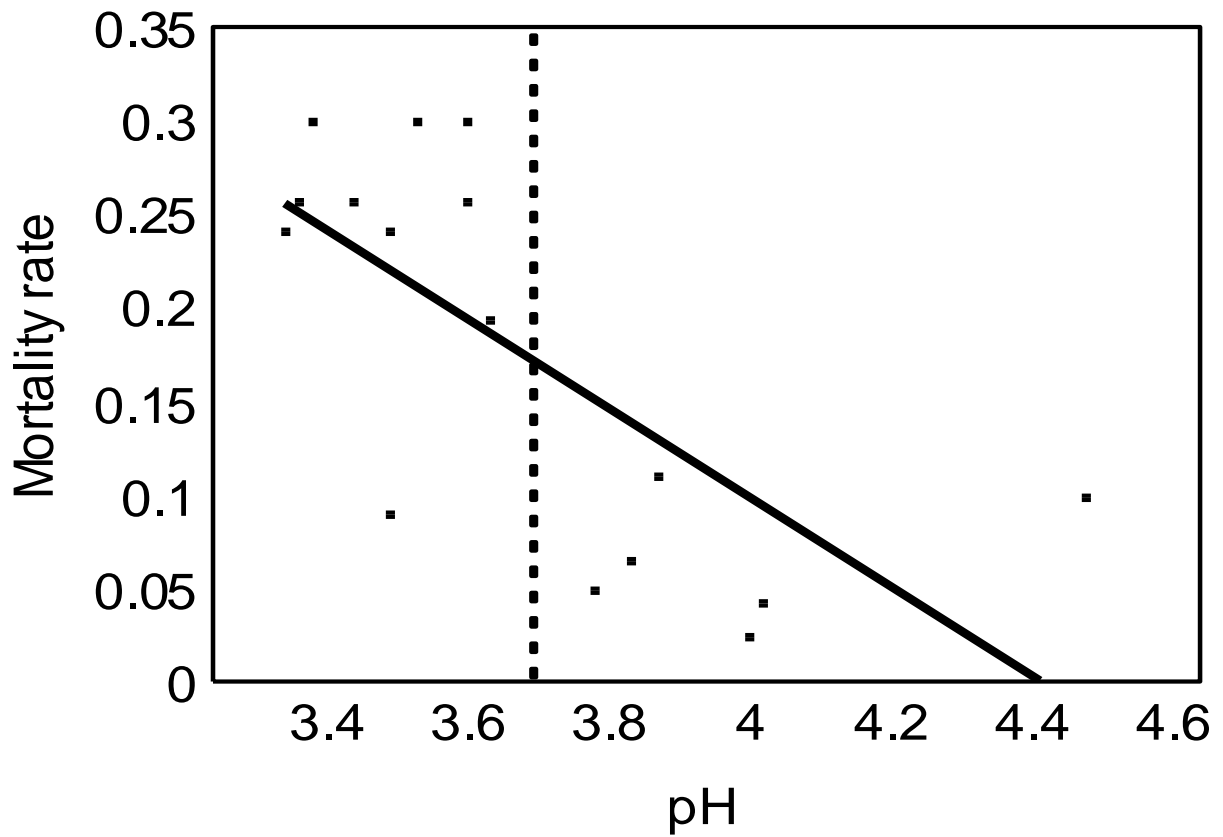
Figure 7. *Hyla chrysoscelis* tadpole mortality rate regressed against pH. The solid line is the regression line (df= 1, F = 13.82, *P* = 0.0023, r^2 = 0.46). The dashed line represents the threshold below

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CHAPTER THREE: AQUATIC AMPHIBIAN DEPAUPERATENESS VARIES IN RESPONSE TO FIRE AND A FIRE-SURROGATE IN A LONGLEAF PINE WOODLAND

Abstract

Specialist species with an evolutionary history closely tied to a limited habitat type may be more vulnerable to extinction than generalist species that tend to be successful in a broad range of habitats. If conservation priority is given to specialist species, we must understand specialist's habitat requirements, and determine responses to habitat degradation and restoration efforts as distinct from generalist species. I examined the relationship between aquatic amphibian species depauperateness and wetland vegetation structure, and determined response to two commonly used habitat restoration tools, prescribed fire and mechanical vegetation removal (a fire surrogate), plus a combination of mulching and burning. I trapped aquatic amphibians and measured vegetation structure in wetland basins and ecotones in 24 ephemeral wetlands embedded in imperiled, fire-dependent, longleaf pine upland before and after prescribed fire and mechanical treatments were applied. Amphibians were categorized as longleaf associates (specialists) or longleaf coincidentals (generalists) based on range overlap with longleaf pine, and depauperateness was regressed onto vegetation structure ordination axes. I quantified changes in amphibian species depauperateness and vegetation structure in response to treatments. Data from this study and a previous study were combined to elucidate patterns in amphibian assemblage composition in relation to fire history. Wetlands that were mulched and burned had the lowest species depauperateness of associates, and wetlands that were untreated had the highest species depauperateness of coincidentals. Coincidental depauperateness was not

correlated with vegetation structure, but associate depauperateness was negatively correlated with groundcover and graminoid mass, and canopy openness, and positively correlated with leaf litter depth. The combination of mulching and burning significantly increased canopy openness and decreased leaf litter depth. There was a suite of species not detected in wetlands embedded within uplands with >8 years since fire, and a distinct suite of species not detected in wetlands with 0-1 years since fire, indicating that as wetlands succeed with time since fire, there is a related shift in amphibian assemblages. Important patterns in species distributions can be overlooked if relationships to environment and responses to change are too generalized. Appropriate management action should be based on carefully selected conservation priorities and consideration of site characteristics.

Introduction

Endemic or specialist taxa that evolved in the context of a limited habitat may be more vulnerable to extinction than widespread generalist species, especially where declines are caused by habitat loss and degradation related to anthropogenic disturbance (Futuyma and Moreno 1988, Foufopoulos and Ives 1999, Owens and Bennett 2000, Davies et al. 2004, Munday 2004, Devictor et al. 2008, Clavel et al. 2010). Habitat specialists tend to be less resilient to habitat change (e.g. unable to utilize alternative food resources or unable to tolerate changes in temperature) or more limited in dispersal abilities (i.e. ability to move to another suitable and available area) than generalists. These differences have been noted in taxa ranging from plants (Witt 2004) to fish (Feary 2007), lizards (Gilchrist 1995), birds (Klaus and Keyes 2007) and primates (Harcourt et al. 2002), although it may not hold true for all taxa in all situations (Jonsen

and Fahrig 1997, Attum et al. 2006, Ali and Agrawal 2012). Studies that focus on species richness without regard to such potential differences may overlook important patterns in species distribution or make imprecise recommendations for habitat restoration and maintenance (Schurbon and Fauth 2003, Means et al. 2004, Robertson and Ostertag 2004, Schurbon and Fauth 2004, Steen et al. 2010). To restore degraded habitat to benefit vulnerable specialist taxa we need to understand species habitat requirements, how different suites of species respond to degradation and restoration efforts, and how restoration efforts affect habitat elements crucial to persistence (Palmer, Falk and Zedler 2006). This study was designed to examine the relationship between wetland vegetation structure and specialist and generalist species of amphibians, and to determine if the responses to habitat restoration efforts differed between these groups for the purpose of informing management decisions intended to benefit amphibians in a highly threatened ecosystem.

The longleaf pine ecosystem is one of the most endangered ecosystems in North America (Noss, LaRoe and Scott 1995; Frost 2006), making its numerous endemic taxa (Sorrie and Weakley 2001) equally vulnerable. Several longleaf-endemic species of amphibians have been locally extirpated or are in serious decline throughout their range (e.g. *Ambystoma cingulatum* and *Lithobates capito,* IUCN 2012). These species require terrestrial and ephemeral aquatic breeding habitat maintained by fire, but fire regimes have been disrupted since European colonization (Croker 1987; Nowacki and Abrams 2008). Although prescribed fire is utilized in many fire-dependent systems for restoration and maintenance, it can be difficult to apply, especially with increasing encroachment of human development and disturbance around and into

natural systems. In response to the challenges of managing fire-dependent systems in the wildland-urban interface, recent research examined alternatives to fire that are intended to mimic the effects of fire mainly on vegetation structure (Schwilk et al. 2009, Stephens et al. 2012, McIver et al. 2013). Fire surrogates used in these studies are frequently some type of mechanical vegetation removal such as thinning of overstory trees or 'mulching' of woody midstory plants. Although the number of fire and fire surrogate studies have increased in the last decade, few studies have examined the effects of fire and fire surrogates in wetland habitat embedded within the fire-dependent landscape.

Ephemeral wetlands embedded within the longleaf pine ecosystem of the Lower Coastal Plain of South Carolina, US, are fire-maintained communities altered by canopy closure, shrub encroachment and leaf litter accumulation as a result of fire exclusion (Kirkman *et al.* 2000; Hester 2001; Dr. Julian Harrison, personal communication; aerial photographs circa 1934-present). These wetlands are essential breeding and larval habitat for many amphibians, and provide habitat for all life-stages of obligate aquatic species like *Siren spp.* and *Amphiuma spp.* Canopy closure, litter accumulation and litter composition influence distributions, growth and survival of larval amphibians (Skelly, Werner and Cortwright 1999; Rubbo and Kiesecker 2004; Skelly *et al.* 2005). Canopy closure lowers water temperature and dissolved oxygen necessary for optimizing larval amphibian growth and development (Travis and Trexler 1986; Moore and Townsend 1998). Changes in leaf litter accumulation and composition associated with woody encroachment influence amphibians by altering detrital and epilithonal food sources (algae and other benthic microorganisms)(Hessen, Ferovig and Andersen 2002; Stelzer and Lamberti 2002;

Schiesari 2006; Williams, Rittenhouse and Semlitsch 2008; Maerz, Cohen and Blossey 2010; Cohen, Ng and Blossey 2012) and increasing or decreasing water pH beyond the tolerance of some species ((Warner and Dunson 1998, Eason and Fauth 2001), J.M. Klaus unpublished data). Amphibian distributions among wetlands may be influenced by some amphibians avoiding reproduction in some wetlands or by poor larval survival, growth or recruitment into the adult population from some wetlands.

I assumed that amphibian species whose range overlaps > 80% with that of longleaf pine habitat were restricted to that range by some elements of the habitat (i.e. were specialists on longleaf pine habitat). I predicted that amphibian species 'restricted' to longleaf pine habitat would be negatively correlated with canopy closure, shrub density and litter accumulation in ephemeral breeding wetlands embedded within longleaf pine uplands, while generalist species (i.e. range overlapping < 80% with habitat of interest) would have varying relationships with those variables. Historically, periodic fire would have kept canopy closure, shrub density and litter accumulation low, and I would expect many animals restricted to fire-maintained longleaf pine habitat to have evolved mechanisms for taking advantage of those conditions. Because habitat specialists are frequently less resilient or resistant to habitat changes (i.e. increased canopy closure, shrub density and litter accumulation) than generalists, I would expect generalists to be less negatively affected by habitat changes than longleaf habitat specialists. For the same reasons, I also predicted that these guilds would respond differently to restoration treatments.

Methods

Sites

Within dispersal distance of known records of two imperiled amphibian species (*Ambystoma cingulatum* and *Lithobates capito*), I randomly selected 24 geographically isolated wetlands in a range of stages of woody encroachment, in Francis Marion National Forest, Berkeley County, South Carolina, with various combinations of *Nyssa biflora*, *Nyssa sylvatica*, *Taxodium ascendens*, *Pinus serotina*, *Pinus palustris*, and *Liquidamar styraciflua* overstory. Wetland sizes ranged from 0.2–8.0 ha, duration of inundation varied from a few weeks to two years and maximum depth was 25–95 cm. Wetlands were located on similar soils (poorly drained loamy fine sand) at similar elevation (6-15 m above sea level) (Long 1980) and formed in shallow topographical depressions. Hydrology was driven by evapotranspiration with no obvious surface water connections, and wetlands were typically inundated between January and April, drying down during summer (De Steven and Toner 2004). Uplands surrounding study sites were historically dominated by *Pinus palustris* woodland with a pre-settlement fire regime of low-severity surface fire every two to four years (Frost 1998), and continue to be dominated by *Pinus palustris* woodland. Fire management records were unavailable prior to 1989, after which prescribed fire frequency was one to three fires from 1989-2007 and time since fire was 4-15 years (Table 4). There is no record of fire effects prior to this study, so whether or not fires burned through wetlands is unknown.

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Three restoration treatments were applied to 17 wetlands and seven were untreated; six

wetlands were mulched as a fire surrogate treatment (mechanical midstory removal in the

ecotone from normal high water mark to ~10 m beyond that mark), four burned with prescribed

fire and seven mulched and burned (Table 4). Mulching occurred between 2006-2007 and

consisted of removal of trees, shrubs, vines < 16 cm DBH, using hand tools and a Gyro-Trac©

low-impact mulching machine, leaving cut material on site. In early spring 2008 USDA Forest

Service conducted a prescribed fire that burned through dry wetland basins in burn treatments.

Due to drought wetlands did not hold water from 2006-2008.

To determine amphibian species present in the wetlands prior to treatment application, I

sampled aquatic-phase amphibians (larvae of all species and adult obligate aquatic species) ten

times between May 2005 and November 2006, and I sampled amphibians seven times from

September 2008 to February 2010 after treatments were applied. In each wetland I placed 16

plastic double-ended funnel-type minnow traps in sets of four positioned in cardinal directions.

The traps were aligned parallel to wetland edge and deployed in enough water to cover funnel

openings but allow enough air space at the top so that animals would not drown (~15-20 cm

water). Traps were left in wetlands for 24 hours then all animals were removed, identified,

counted and returned to the wetland.

Vegetation was sampled after leaf-out was complete in June 2006 prior to treatment

application and again in June 2008 post-treatment. To quantify basin shrub cover, line-transects

were established in eight directions (N, NE, E, SE, S, SW, W, NW) radiating from the center

(deepest point) of each wetland basin and terminating at the normal high-water mark; I measured the length of transect intersected by any part of a midstory plant (trees < 16 cm diameter at breast-height, shrubs, and vines) and calculated percent cover. To measure canopy closure, at each of the eight transect termini I took hemispherical color photographs of the canopy using a Nikon Coolpix © camera fitted with a fish-eye (180°) lens, leveled on a tripod 0.5 m above the ground. To calculate percent canopy openness from each image I used Gap Light Analyzer (GLA) software (Frazer, Canham and Lertzman 1999) with the color plane set to blue and the threshold set to capture as much vegetation as possible without selecting background pixels. To sample ecotone shrub-layer density, at the same eight points previously described I took pictures of a 1.0-m x 0.75-m, orange target 5 m outside the high water line and parallel to it. I analyzed photos using Adobe Photoshop to select non-orange pixels and calculate percent target covered by vegetation. To sample groundcover, I placed sixteen 0.25-m^2 quadrats in each wetland, eight at the termini and eight at the half-way points of each previously described transect. I clipped all herbaceous vegetation within two centimeters of the ground and dried samples in a forced-air oven. Dried plant material was sorted into categories: grass/sedge, redroot/iris, fern, or other and weighed. I measured leaf litter depth from the duff/peat layer (organic particles too small to identify with the naked eye) to the litter surface within each ground cover sampling quadrat.

Data analysis

To examine differences in aquatic amphibian assemblages before and after treatments, I used minimum abundance (maximum abundance of each species observed during a single sampling session) of amphibians as a response variable. For this analysis, I used naïve abundance

because detection rates were very low for most species, resulting in nonsensical estimates of detection, abundance and occupancy (Steen 2010). I used multi-response permutation procedures (MRPP) with Sorensen distance measure to test the null hypothesis of no differences in amphibian assemblages among wetlands before and after treatments were applied. I followed up with an indicator species analysis to determine if any species was indicative of any particular treatment (McCune and Mefford 1999). These analyses were performed with PC-ORD.

To examine the difference in amphibian assemblages based on their range of occurrence, I categorized amphibian species as longleaf pine assoicate (> 80 % of their range overlapping the range of longleaf pine) or longleaf pine coincidental (< 80 % of their range overlapping the range of longleaf pine) (Steen *et al.* 2010). I used naïve percent species depauperateness as a response variable (number of species missing from the total species pool divided by number of species in the species pool) because treatments and environmental variables act as ecological filters, excluding some species. I did not adjust depauperateness for potential differences in detection because the sampling technique I employed has known species detection of 83-100% (Werner *et al.* 2007; Farmer *et al.* 2009; J. Fauth, unpublished data). I used ANOVA to test the null hypotheses of no difference in associate and coincidental species depauperateness among treatment groups before and after treatments were applied. I used the same method to test the null hypothesis of no difference in change in species depauperateness among treatment groups.

Because Canonical Correspondence Analysis cannot handle data with a large number of zero detections (McCune and Mefford 1999), I ordinated vegetation variables with PC-ORD (McCune and Mefford 1999) and used linear regression to examine relationships between

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vegetation gradients and associate and coincidental amphibian species depauperateness (SAS Institute 2008). I then used vegetation ordination axes that had significant correlations with species depauperateness, in conjunction with pH, maximum water temperature and maximum wetland depth to construct and compare sets of models that explained depauperateness (SAS Institute 2008).

Because direct effects of treatments on amphibian occupancy may have a lag time or be difficult to detect, I also examined treatment effects on elements of vegetation structure that were correlated with amphibian species depauperateness. I used ANOVA to test the null hypotheses of no difference in vegetation ordination scores due to treatments. I set $\alpha = 0.05$ for all tests.

<div align="center">Results</div>

Effects of treatments on amphibian assemblages

No differences among amphibian assemblages were present in ordination space prior to treatments but untreated wetlands differed in species composition from all treatment wetlands after treatments (T = -4.9898, A = 0.2038, $P < 0.0001$). Using species indicator analysis I found *Acris gryllus* (indicator value = 81.8, mean indicator value from randomized groups = 17.5, SD = 9.84, $P = 0.0004$), *Anaxyrus terrestris* (indicator value = 41.2, mean indicator value from randomized groups = 14.1, SD = 8.75, $P = 0.0222$), and *Scaphiopus holbrookii* (indicator value = 56.4, mean indicator value from randomized groups = 16.2, SD = 9.9, $P = 0.0080$) indicative of the mulch-and-burn treatment.

Of 22 amphibian species sampled, 13 were longleaf pine associates and nine were coincidentals (Table 5). Species depauperateness increased over the duration of the study for associates and coincidentals regardless of treatment, presumably due to drought. I detected no differences in species depauperateness of associate or coincidental amphibians among groups of wetlands selected for different treatment types before treatments, but found evidence that there were differences after treatments were applied (df = 3, F = 6.0550, P = 0.0042, and df = 3, F = 4.0795, P = 0.0206 for associate and coincidental species respectively) (Fig. 8). The mulched-and-burned wetlands had lower mean species depauperateness of associate amphibians (mean = 0.8878, confidence limits = 0.8568 and 0.9187) than burned (mean = 0.9583, confidence limits = 0.9174 and 0.9993) or untreated (mean = 0.9702, confidence limits = 0.9413 and 0.9992) wetlands. Untreated wetlands had higher mean species depauperateness of coincidental larval amphibians (mean = 0.9494, confidence limits = 0.8924 and 1.0064) than mulched (mean = 0.8238, confidence limits = 0.7517 and 0.8959) or mulched-and-burned wetlands (mean = 0.8333, confidence limits = 0.7724 and 0.8943). However, I failed to reject the null hypothesis of no significant difference in the *change* (after − before) in species depauperateness among treatment types for associates or coincidentals using ANOVA because confidence intervals were very large.

Relationship between vegetation structure and amphibian assemblages

Vegetation variables ordinated onto three axes: the first axis was most strongly correlated with fern mass, basin shrub cover, leaf litter depth and ecotone shrub-layer openness; the second most strongly correlated with total groundcover mass and graminoid mass; and the third with

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canopy openness and leaf litter depth. Coincidental amphibian species depauperateness was not

correlated with any of the vegetation ordination axes. Associate amphibian species

depauperateness was positively correlated with axis two (negatively correlated with groundcover

mass and graminoid mass) (F = 11.1725, P = 0.0017), which explained 18% of the variation in

depauperateness (Fig. 9). Associate species depauperateness was negatively correlated with axis

three (negatively correlated with canopy openness and positively correlated with leaf litter depth)

(F = 6.4219, P = 0.0147) which explained 10% of the variation in depauperateness (Fig. 9). I

constructed two sets of models, including plant ordination axes, pH range, DO range, and

maximum water depth, for a more comprehensive understanding of species depauperateness of

longleaf associates and coincidentals among wetland environmental gradients (Table 6). For

associates, the most informative model included plant ordination axes two (ground cover mass

and graminoid mass) and three (canopy openness and leaf litter depth), DO range, and pH range

(AIC = -155.58, ω = 0.9965, adjusted r^2 = 0.49). For coincidentals, models including pH range,

DO range and maximum depth were closely ranked with depth being the most influential factor

(Table 6).

Effects of treatments on vegetation structure

Wetlands did not differ in vegetation structure before treatments were applied but

vegetation structure ordination axis one and axis three differed after treatment application (DF =

3, F = 3.3669, P = 0.0390; and DF = 3, F = 45.5633, P <0.0001 respectively). I could not

differentiate among treatment groups for axis one using Tukey's HSD, likely owing to large

standard errors (ranging from 0.15937 to 0.23905), but for axis three, untreated wetlands had a

lower ordination score (higher leaf litter depth and lower canopy openness) than any of the treatment groups (Fig. 10). In addition, the mulch-and-burn group had a higher ordination score (lower leaf litter depth and higher canopy openness) than mulch or untreated groups, and burn was intermediate between mulch-and-burn and mulch. The *change* in axis three score (post-treatment – pre-treatment) for mulch-and-burn (0.65) was significantly different from untreated (-0.11) (F = 4.12, P = 1.0199, Fig. 11). Change in axis three score for burn and mulch were intermediate (0.22 and 0.33 respectively). The change observed in mulch-and-burn was toward more open canopy and less leaf litter, whereas the change in untreated wetlands was toward less open canopy and more leaf litter. MRPP on direction of change revealed that vegetation in mulch-and-burn and burn treatments changed in a similar direction, one that was different from the untreated group (Fig. 12) (A = 0.0991, P = 0.0169).

Discussion

As predicted, the two amphibian guilds differed in their relationship to vegetation, but contrary to predictions, they had similar responses to management treatments. Associate species depauperateness was lowest when total canopy openness was high and leaf litter was low, conditions best achieved by the mulch-and-burn treatment. Although coincidental species depauperateness was also lowest in the mulch-and-burn treatment, it does not appear to be due to any relationship with total canopy cover, but rather to fern and shrub cover. Species depauperateness was highest in untreated wetlands.

Other studies have shown that amphibian responses to fire and fire surrogates are variable because different species respond in different ways. For example, upland mechanical thin plus prescribed-burn had a negative effect on amphibian species richness in the southern Appalachians (Matthews *et al.* 2010) but had a positive effect on species richness of longleaf pine woodland associated amphibians in the Gulf Coastal Plain (Steen *et al.* 2010). This difference can be explained by initial disparities in the suite of species studied and the ecology of the sites; the coastal plain longleaf pine sites had ongoing fire and timber management starting in the 1980s (*Solon Dixon Forestry Education Center* 2012) and contained amphibian species that require open or fire-maintained habitat (e.g. *Ambystoma tigrinum*, *Hyla femoralis*, *Hyla gratiosa*, *Pseudacris ornata*), whereas the Appalachian sites had no fire for at least 50 years, were composed of many mesic tree and shrub species and contained amphibian species not expected in fire-maintained habitat (e.g. *Lithobates sylvaticus*, *Plethodon metcalfi*, *Desmognathus monticola, Pseudotriton ruber*). If the restoration goal were to change plant composition from mesic, fire-intolerant species to fire-adapted, shade-intolerant species, one would expect co-occurring animals to experience a similar shift in community composition.

In my study all sites were located in close proximity to each other at similar elevation, in longleaf pine stands, and all but two were on the same ridge; if I had included sites in hardwood stands, for example, it is likely results would be different. Schurbon and Fauth (Schurbon and Fauth 2003) found that total species richness was higher in long-unburned areas, but all of their sites in the > 8 years since fire category were located at lower elevation and on different soils from the sites in the < 1 year since burn and 1 year since burn categories potentially confounding

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these factors. The sites I used in my study were more comparable to Schurbon and Fauth's < 0

and 1 year since burn sites than to their > 8 year since burn sites.

When comparing Schurbon and Fauth's associate species richness to coincidental species

richness (using the same criterion I used for my study) for each time-since-fire category, I found

that associate species richness was higher than coincidental species richness in the < 1 year since

burn category (ANOVA, df = 1, p = 0.0022). Six coincidental species were missing from the 0-1

year categories and five longleaf associate species were missing from the > 8 years since fire

category, indicating a shift in community composition (Table 7). Three of the species missing in

Schurbon and Fauth's zero and one year categories were present in at least one of my mulch-and-

burn sites, and three species detected only in their > 8 year category were completely missing

from my study. This demonstrates how taxa-lumping can obscure important patterns in

community data (Robertson and Ostertag 2004; Steen *et al.* 2010; Fontaine and Kennedy 2012).

Of the three species identified in my study as mulch-and-burn treatment indicators, two

(*Acris gryllus* and *Anaxyrus terrestris*) are longleaf pine habitat associates that can be expected

to thrive in open-canopied, fire-maintained conditions. *Acris gryllus* prefers to breed in open

areas of vegetated wetlands (Bayless 1969; Jensen *et al.* 2008), and *Anaxyrus terrestris* has rapid

larval development and performs well in high water temperatures associated with an open

canopy (Noland and Gordon 1981). One of the three mulch-and-burn indicator species,

Scaphiopus holbrookii, is not a longleaf pine associate, but has rapid larval development, like

Anaxyrus terrestris. The mulch-and-burn treatment may have provided a high light, high

temperature environment with high primary production, resulting in abundant and high quality

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food resources necessary for rapid development (Chapter 2 this document; John Jensen, personal communication). More information about trophic interactions and tadpole feeding ecology is necessary to better understand these possibilities.

Incidentally, I documented very large (on the order of hundreds) choruses of *Lithobates capito*, a globally vulnerable species petitioned for listing under the Endangered Species Act (IUCN 2012) during a breeding event in March 2009 (J.M. Klaus, unpublished data). These choruses were heard at two mulch sites and one mulch-and-burn site. Additional smaller choruses were heard at one burn site, one mulch site and one mulch-and-burn site, but none were observed at untreated wetlands. Tadpoles were confirmed at one mulch-and-burn site (J.M. Klaus, unpublished data, Steve Bennett, personal communication).

The longleaf pine ecosystem has been greatly reduced and some of its endemic amphibians are threatened with extinction; hence, my goal was to find restoration tools to improve habitat for longleaf-associated amphibian species. Careful consideration of historical and present site factors should guide restoration goals; trying to restore fire-maintained conditions on a site that presumably never supported frequent fire in evolutionary time makes no more sense than expecting species that are not adapted to fire-maintained conditions (e.g. *Ambystoma maculatum, Ambystoma opacum,* etc.) to persist in fire-maintained habitat. Because altered fire regimes allow for invasion of fire-intolerant species (Klaus and Keyes 2007; Nowacki and Abrams 2008), land managers should not be alarmed if they observe a reduction in populations of some of those species when fire-maintained conditions are restored. My study

demonstrates that when restoration tools designed to mimic natural fire are applied at appropriate

sites, even some generalist species may benefit, while fire-dependent species prosper.

Table 4. Wetland sites with corresponding fire history and restoration treatment.

Site #	# Fires	Years-since-fire	Treatment
1	3	4	Burn
2	3	4	Burn
3	3	4	Burn
4	3	4	Burn
5	1	10	Mulch
6	1	8	Mulch
7	1	4	Mulch
8	1	15	Mulch
9	1	4	Mulch
10	3	4	Mulch and burn
11	3	4	Mulch and burn
12	3	4	Mulch and burn
13	3	4	Mulch and burn
14	3	4	Mulch and burn
15	2	4	Mulch and burn
16	3	4	Mulch and burn
17	1	10	None
18	1	10	None
19	2	4	None
20	2	4	None
21	1	15	None
22	2	4	None
23	1	10	None
24	1	8	None

Table 5. Amphibian species categorized as longleaf pine associate (>80% of range within longleaf pine range) and longleaf pine coincidental (<80% of range within longleaf pine range).

LL associate	LL coincidental
Acris gryllus	*Ambystoma talpoideum*
Ambystoma mabeei	*Gastrophryne carolinensis*
Amphiuma means	*Hyla chrysoscelis*
Anaxyrus terrestris	*Notopthalmus viridescens*
Hyla cinerea	*Lithobates catesbeianus*
Hyla femoralis	*Lithobates clamitans*
Hyla gratiosa	*Lithobates sphenocephalus*
Hyla squirella	*Scaphiopus holbrookii*
Pseudacris ocularis	*Siren intermedia*
Pseudacris ornata	
Lithobates capito	
Lithobates grylio	
Lithobates virgatipes	

Table 6. Model descriptions, ranked by model weight, for models explaining variation in longleaf associate amphibian species depauperateness and coincidental amphibian species depauperateness with Akaike Information Criterion (BIC) scores, amount of variation explained (adjusted r^2), and relative model weights (ω). Depth = mean maximum depth of wetland, axes = plant ordination axes, pH is the range of concentration of hydrogen ions in wetland water and DO is the range of percent saturation of water with oxygen.

Associate models	AIC	adjusted r^2	ω
1. pH + DO + Axis2 + Axis3	-155.58	0.49	0.9965
2. pH + DO	-143.59	0.30	0.0025
3. pH	-140.46	0.23	0.0005
4. DO	-139.15	0.21	0.0003
5. Axis2 + Axis3	-137.84	0.21	0.0001
6. Axis2	-137.16	0.18	0.0001
7. Axis3	-132.00	0.10	0.0000
Coincidental models	**AIC**	**adjusted r^2**	ω
1. pH + Depth	-86.29	0.40	0.3449
2. DO + Depth	-85.66	0.39	0.2525
3. pH + DO + Depth	-85.24	0.38	0.2049
4. Depth	-85.12	0.34	0.1927
5. pH + DO	-76.82	0.24	0.0030
6. pH	-74.83	0.18	0.0011
7. DO	-74.25	0.17	0.0008

Table 7. Combined species list from (Schurbon 2000) and Klaus 2013. YSF = years since fire. Species NOT detected in a YSF category are marked with "X". Three species have "?" in the 8+ YSF category indicating that they were not detected in the Schurbon or the Klaus study, but would likely be absent from this category based on other literature (e.g. Jensen et al. 2008).

Species	0-1 YSF	3-5 YSF	8+ YSF
Longleaf associates			
Acris gryllus			X
Ambystoma cingulatum			?
Ambystoma maybeei			
Amphiuma means			
Anaxyrus terrestris			
Hyla cinerea			
Hyla squirella			
Lithobates virgatipes			X
Pseudacris ornata		X	X
Pseudacris ocularis			
Anaxyrus quercicus		X	X
Pseudacris nigrita			
Hyla gratiosa			?
Lithobates capito			?
Lithobates grylio			?
Longleaf coincidentals			
Ambystoma talpoideum			
Gastrophryne carolinensis			
Hyla chrysoscelis	X		
Lithobates catesbeinus			
Lithobates clamitans			
Lithobates sphenocephalus			
Notopthalmus viridecens	X		
Scaphiopus holbrookii			
Siren intermedia	X		
Ambystoma maculatum	X	X	
Ambystoma opacum	X		
Pseudacris crucifer	X		
Plethodon variolatus			
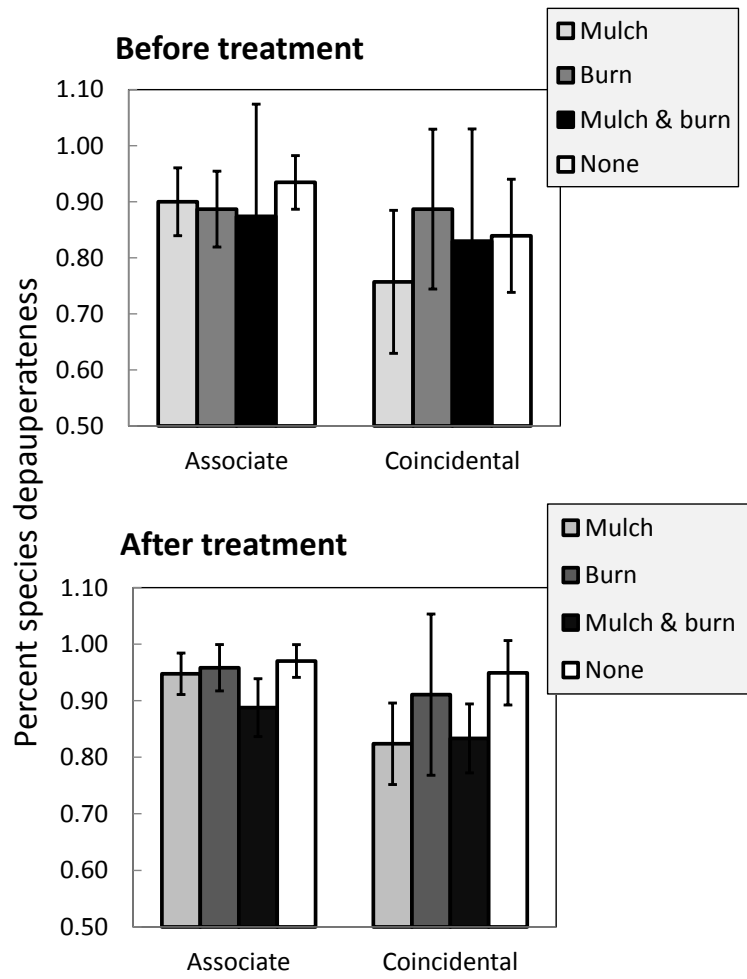
Figure 8. Mean percent species depauperateness by treatment for longleaf pine habitat associate amphibians and coincidental amphibians before and after treatment application. Error bars represent 95% confidence intervals.
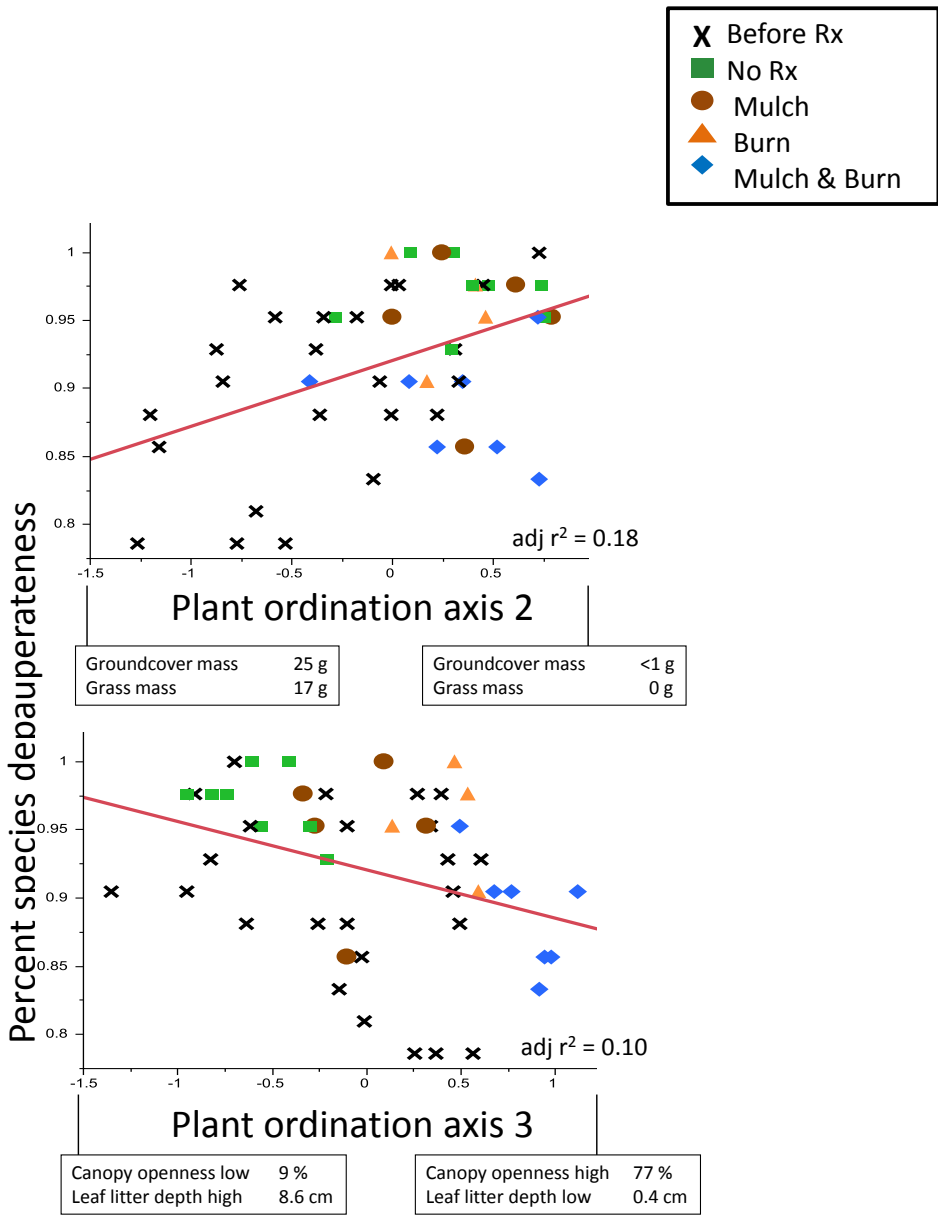
Figure 9. Longleaf associate amphibian species depauperateness correlated with plant ordination axes. Boxes below x-axes describe the components of each ordination axis with minimum and maximum site means.
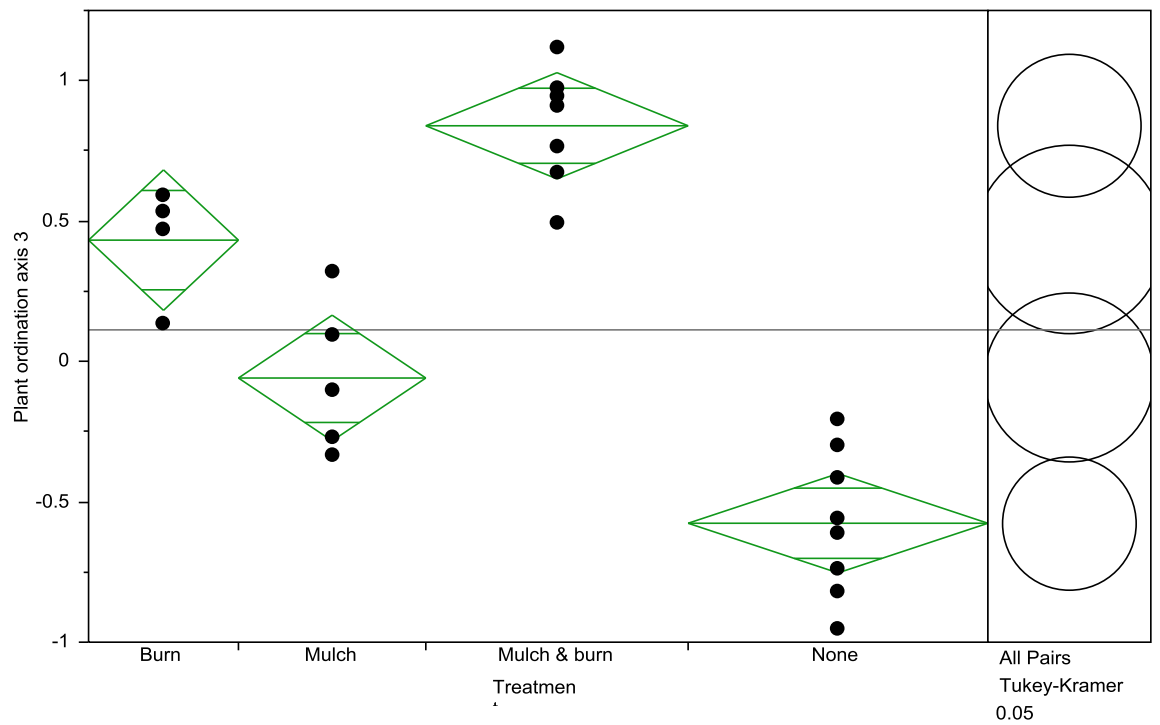
Figure 10. One-way ANOVA of plant ordination axis 3 by treatment type after treatment applications. Diamonds represent group means with 95 % confidence intervals. Circles are a visual representation of the comparisons among group means; circles for means that are significantly different either do not intersect, or intersect so that the outside angle of intersection is less than 90°.
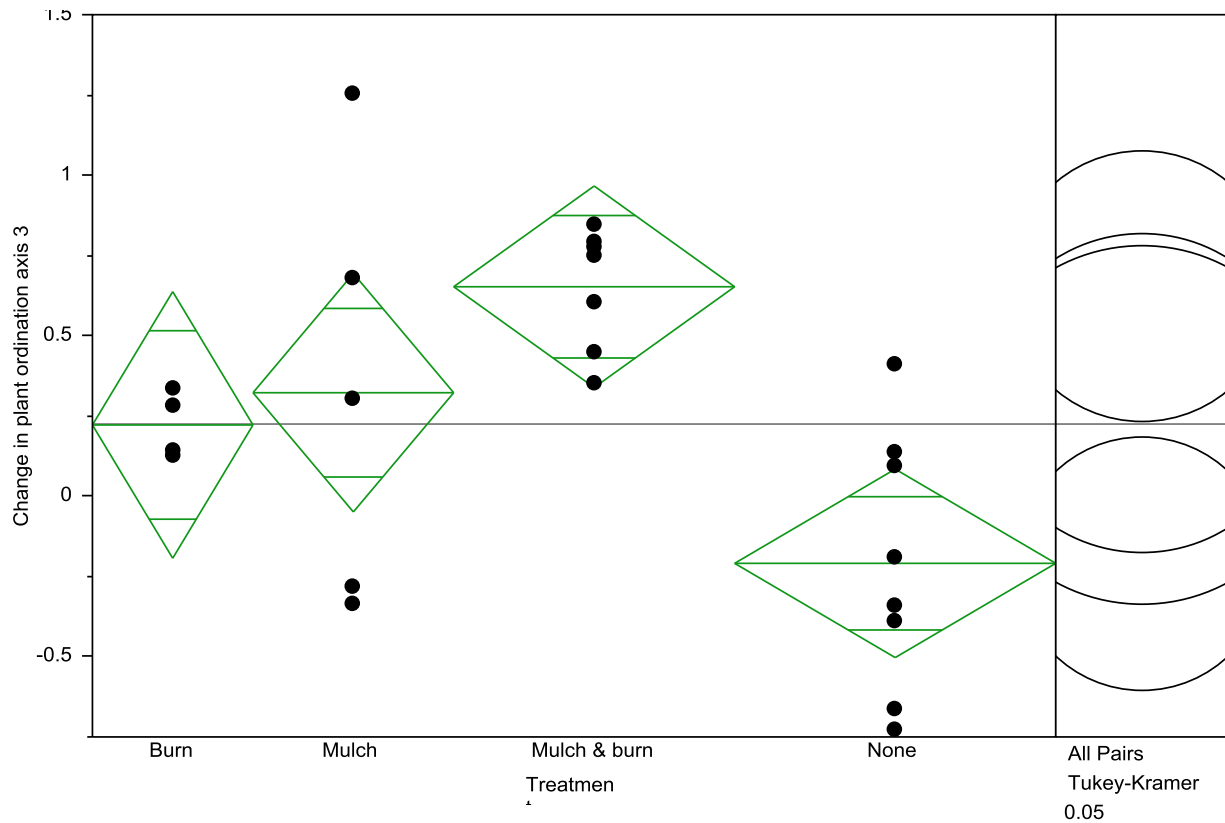
Figure 11. One-way ANOVA of change in plant ordination axis 3 from before to after by treatment type. Diamonds represent group means with 95 % confidence intervals. Circles are a visual representation of the comparisons among group means; circles for means that are significantly different either do not intersect, or intersect so that the outside angle of intersection is less than 90°.
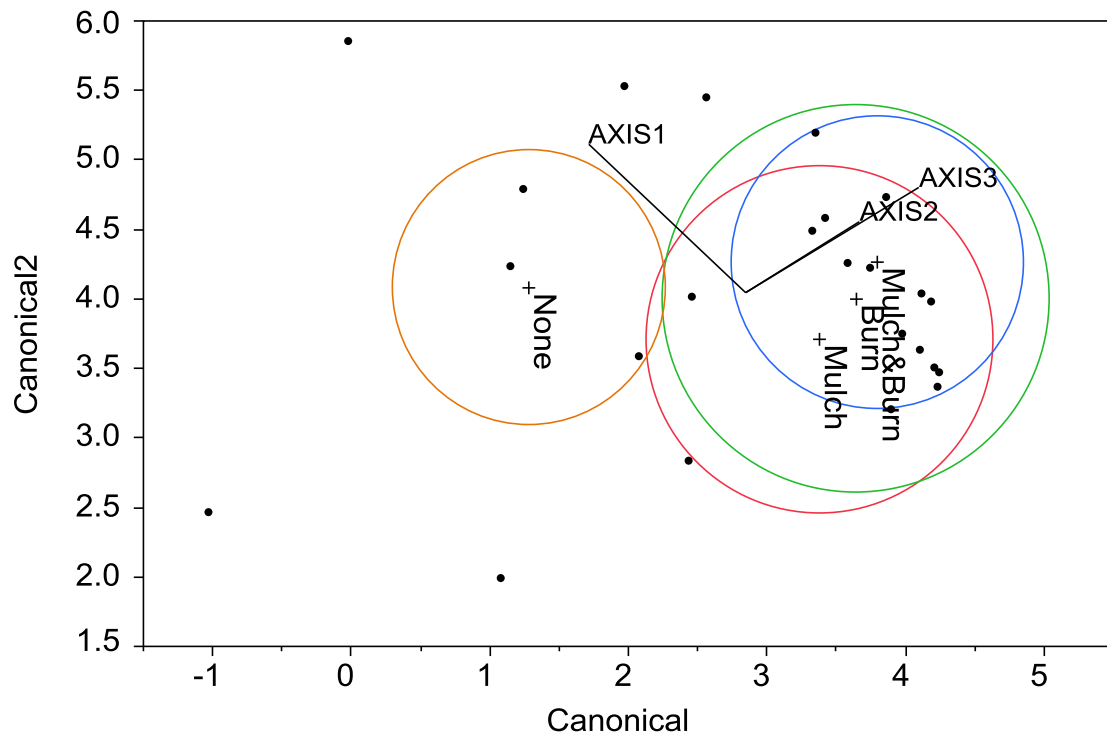
Figure 12. Discriminant analysis describing direction of change of wetland vegetation by treatment type. Axes one, two and three are plant ordination axes. The yellow circle represents 95% mean confidence limit of the untreated group, red is mulch, green is burn and blue is mulch-and-burn.

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CHAPTER FOUR: THEORETICAL AND PRAGMATIC IMPLICATIONS: RELATING AQUATIC AMPHIBIAN SURVIVAL AND DISTRIBUTIONS TO HABITAT AND DISTURBANCE

Summary of key findings

The purpose of this study was to gain insight into the wetland habitat requirements of amphibians in a fire-dependent (disturbance-dependent) ecosystem and to assess two restoration tools (fire and a fire surrogate meant to mimic natural disturbance) in terms of their effectiveness in enhancing wetland habitat suitability for amphibians, especially those restricted to the longleaf pine ecosystem. I tested four main hypotheses: 1) survival of a larval amphibian is related to a wetland habitat gradient that includes vegetation structure, litter composition, water chemistry and epilithon quantity and quality; 2) survival of a larval amphibian varies across restoration/disturbance treatments; 3) aquatic amphibian species depauperateness is related to a wetland habitat gradient that includes vegetation structure, water chemistry and water depth; 4) aquatic amphibian species depauperateness varies across restoration/disturbance treatments. I found that species depauperateness was lowest in mulched-and-burned wetlands and highest in untreated wetlands, and survival of a larval amphibian was lowest in untreated wetlands. I studied a set of wetlands that were located on similar soils, at similar elevation, and embedded within longleaf pine uplands, and found that the entire species pool, including specialists and generalists, benefited from creating more open vegetation structure.

Untreated and degraded wetlands in a longleaf pine woodland had higher canopy closure, higher litter accumulation, more hardwood litter and less graminaceous litter than wetlands treated by mulching, burning or a combination of mulching and burning. The mulched-and-burned wetlands had the lowest canopy closure, lowest litter accumulation, least hardwood litter and most graminaceous litter. Other researchers observed similar results of fire and fire surrogates on canopy (Harrod *et al.* 2009; Schwilk *et al.* 2009; Stephens *et al.* 2009; Outcalt and Brockway 2010) but little attention has been given to the effects of fire and fire surrogates on leaf litter. Research focused on leaf litter suggests it is a critical component of energy and nutrient cycling that requires further study (Skelly and Golon 2003; Hiers *et al.* 2007; Maerz, Cohen and Blossey 2010). Fire removes leaf litter, influences plant communities that donate litter and affects the redistribution of nutrients in leaf litter (Maclean *et al.* 1983; Wilbur and Christensen 1983; Debano, Neary and Ffolliott 1998). Thus, impacts to the litter layer should be given more consideration in fire effects studies.

I found evidence to suggest several pathways through which disturbance and vegetation structure influence larval amphibian survival and aquatic amphibian species depauperateness, all of which warrant further research. This and other research documented a consistent effect of litter type and amount on consumer performance and community assembly (Skelly, Freidenburg and Kiesecker 2002; Skelly and Golon 2003; Rubbo and Kiesecker 2004; Schiesari 2006; Williams, Rittenhouse and Semlitsch 2008). Although tadpoles in my survival experiment did not have direct access to detritus they presumably accessed flocculent detritus from the water column (Seale and Wassersug 1979; Seale and Beckvar 1980; Viertel 1992; Hart and Lovvorn

2003). Leaf litter type was influential on survival, and leaf litter depth was important in determining species depauperateness. In addition to having varying nutritional quality, some litter types break down readily while other litter types are difficult for decomposers to break down (Taylor, Parkinson and Parsons 1989; Enriquez, Duarte and Sand-Jensen 1993; Ostrofsky 1997; Baker *et al.* 2001) and pass through the guts of detritivores with little of their nutrients absorbed (Skelly and Golon 2003). Canopy closure affects this process by regulating available light and influencing temperature, which in turn affects litter decomposition rates (Kadlec and Reddy 2001; Fierer *et al.* 2005) and consumer feeding and growth rates (Warkentin 1992; Álvarez and Nicieza 2002).

Canopy closure and leaf litter influence the amount and nutritional quality of epilithon, the other main tadpole food source in addition to detritus (Altig, Whiles and Taylor 2007). Canopy regulates light needed for growth of autotrophic components of epilithon (a.k.a. periphyton) (Urabe and Sterner 1996; Mosisch, Bunn and Davies 2001; Hill, Smith and Stewart 2010) and litter can enhance or diminish growth and nutritional quality of epilithon (Friberg and Winterbourn 1996). In my study, mass and percent organic matter (carbon) of epilithon were negatively correlated with relative amount of hardwood litter and percent canopy closure, and positively correlated with amphibian survival. In addition, high litter accumulation was correlated with high species depauperateness. Slow decomposition rates of leaf litter suggests nutrients are not as readily available for epilithon growth.

This study and others suggest that closed-canopied wetlands with high litter accumulation and low macrophyte abundance are detritus-based systems that support different consumer

assemblages than open-canopied, macrophyte-rich, algal-based systems (Hart and Lovvorn 2000; Engelhardt and Ritchie 2001; Rubbo and Kiesecker 2004). Fire regime plays a major role in determining depressional wetland plant community development in the southeastern U.S. (Kirkman *et al.* 2000) and I contend that fire regime can be manipulated to result in a range of conditions from detritus-based to algal-based depressional wetland systems.

Future research in wetland restoration should focus on the effects of management on entire food webs, or at least key elements of them, to better understand how a diversity of systems develop and function (Hart and Lovvorn 2000; Engelhardt and Ritchie 2001; Hart and Lovvorn 2003). Amphibian conservation would greatly benefit from further examinations of tadpole-feeding ecology, specifically ontogenetic and opportunistic niche shifts, selective feeding, and how different food resources affect growth, survival and distribution of species.

<u>Limitations of the study</u>

One of the main limitations of this study was that amphibian-sampling design and lack of appropriate models restricted the types of analysis that could be performed. Larval amphibians present a unique set of problems in estimating detection and occupancy: 1) one female anuran can produce thousands of larva at a single site, making detection of any one individual extremely low, 2) some larval periods are as short as three weeks, 3) tadpole mortality can be extremely high, 4) the population of tadpoles at a site is continuously open and several species breed year-round and 5) reproduction can be sporadic and unpredictable. Future research should focus on developing sampling protocols and models that can account for all of these factors.

Survival of larval amphibians in enclosures was extremely low in all treatment types. Some factors that could account for this include enclosure design, water pH and rapid dry-down of wetlands during the experiment. It would be helpful to test alternative enclosure designs to determine if survival could be increased. I also hoped to use several species of amphibians in the survival experiment, but only one was available. In future experiments I would also sample epilithon from both inside and outside the enclosure to determine a) if the enclosure was affecting what food was available and b) to see what effect tadpoles had on epilithon growth.

In addition, this study confounded the effects of canopy closure and leaf litter because closed-canopy wetlands tended to be composed of hardwood trees and shrubs. Wetlands with equal basal areas of hardwoods versus pines or cypress have disparate canopy densities due to variation in leaf shapes, and different tree compositions naturally donate different amounts and types of litter. It would be useful for restoration to separate these effects and better understand how they interact.

<u>Conservation implications</u>

Mulching or other mechanical treatments are not an effective surrogate for fire. There were several important distinctions between fire and mechanical treatments in this study: 1) mechanical treatments did not improve herbaceous groundcover and probably suppressed, 2) chipped material left on site effectively increased litter depth, a detriment to longleaf associated amphibian species, and 3) cut woody plants resprouted quickly and in some cases mulched habitat was indistinguishable from untreated habitat. Repeated mulching may be cost-prohibitive (Hartsough et al. 2008) and the effects of mulching versus burning on soil properties are unclear

(Boerner et al. 2009). On the other hand, fire alone may not be enough to restore degraded habitat. Research has demonstrated that in several cases habitat is degraded to a point that simply reintroducing the historical disturbance regime is not enough to reset the successional trajectory (Suding et al. 2004, Martin and Kirkman 2009).

Past research has shown that degree of isolation, wetland size and hydroperiod, presence of keystone predators, conserving amphibian diversity in ephemeral wetlands (Fauth 1999, Eason and Fauth 2001). In addition to those factors, some of which are difficult for managers to manipulate, vegetation structure influences amphibian diversity. Canopy closure, groundcover type and density, and leaf litter especially, were correlated with species depauperateness in this study, and affected growth, survival or diversity in other studies (Skelly et al. 2002, Skelly and Golon 2003, Skelly et al. 2005, Schiesari 2006, Williams et al. 2008, Maerz et al. 2010). When managers are manipulating habitat to benefit amphibians they may monitor some or all of these factors to assess effectiveness of management to better understand the outcome and make restoration an iterative process.

The contrasting results of my research and that of Schurbon and Fauth (2003) demonstrate the effect of scale on diversity. My research focused on alpha diversity (similar habitats in terms of elevation and soils) while Schurbon and Fauth's study included both alpha and beta diversity (habitats spanning a broader range of elevation and soils types). While higher-elevation, recently burned sites (0-5 years since fire) had lower alpha diversity than the low-elevation, less recently burned sites (> 8 years since fire), if one considers species richness across the entire gradient of sites, a pattern of high 'regional landscape' (Noss 1983), gamma

(Whittaker 1960) diversity emerges, one unique to the U.S. Southeastern Coastal Plain. This diversity is maintained, in part, by heterogeneous, non-catastrophic disturbance, i.e. fire that burns lower, wetter areas less frequently and intensely, and higher, drier areas more frequently and intensely. Although this effect is partially anthropogenic because fire is either suppressed or applied by managers, one could reasonably expect similar patterns of fire behavior and effects without human intervention.

To recommend a single specific disturbance regime on a landscape scale to promote species richness may be too broad a generalization to result in accurate and precise habitat management because the response depends on the scale of the observation (Walker and Peet 1984; White and Pickett 1985; Schwilk, Keeley and Bond 1997) and species richness alone does not take into account community composition (Noss 1983). Although a particular disturbance regime may produce high alpha diversity, a variety of regimes across the landscape in accordance with edaphic and other environmental gradients will create a mosaic of communities and seral stages supporting greater beta and ultimately gamma diversity (Noss 1990; Parr and Brockett 1999; Tews *et al.* 2004).

<u>Disturbance promotes persistence of specialist species</u>

My research was a snap-shot of how disturbance can create a vegetation structure that sustains a specific assembly of species. The longleaf pine ecosystem and its embedded wetlands fit the criteria for what Bond et al. (2005) describe as "fire-dependent ecosystems," i.e., they would disappear in the absence of fire; amphibian assemblages associated with fire-dependent ecosystems will cease to exist in the absence of fire. While some amphibian species have

evolved mechanisms to take advantage of closed canopy wetlands, others are better adapted to, and in fact require, open canopy conditions (Steinwascher and Travis 1983; Skelly, Werner and Cortwright 1999; Werner and Glennemeier 1999; Schiesari 2006; Williams, Rittenhouse and Semlitsch 2008). The assembly that is found in open canopied wetlands approximates what Platt and Connell (Platt and Connell 2003) describe as 'early successional species' that persist because frequent, non-catastrophic disturbance (e.g. fire) interrupts directional species replacement, except that several of the species examined in this study are long-lived, have low fecundity or low vagility. Shift in amphibian assemblies associated with disturbance regime may not be due to direct competition, but instead determined by species tolerances to environmental factors associated with different disturbance regimes and resulting habitats. To what degree competition among amphibian species influences assemblages in natural settings remains to be seen; more research on tadpole feeding ecology and physiology could help sort these factors out. More empirical research is needed to test specific hypotheses about how patterns of amphibian diversity arise and are maintained (Platt and Connell 2003).

<div align="center">References</div>

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