
HABITAT ASSOCIATIONS OF REPTILE AND AMPHIBIAN COMMUNITIES IN LONGLEAF PINE HABITATS OF SOUTH MISSISSIPPI

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Abstract.—Land managers and biologists do not yet thoroughly understand the habitat associations of herpetofauna native to longleaf pine forests in southern Mississippi. From 2004 to 2006, we surveyed the herpetofauna of 24 longleaf pine communities in 12 counties in south Mississippi. We quantified herpetofaunal diversity, relative abundance, and a suite of habitat variables for each site to address the following objectives: (1) determine what levels of habitat heterogeneity exist in longleaf pine forests in south Mississippi; (2) determine if reptile and amphibian community composition differs among these sites; and (3) if habitat-faunal differences exist among sites, identify what habitat variables are driving these community differences. Multivariate analysis identified three distinct longleaf pine habitat types, differing primarily in soil composition and percentage canopy cover of trees. Canonical correspondence analysis indicated that canopy cover, basal area, percentage grass in the understory, and soil composition (percentage sand, silt, and clay) were the predominant variables explaining community composition at these sites. Many species exhibited associations with some or all of these habitat variables. The significant influence of these habitat variables, especially basal area and canopy cover, upon herpetofaunal communities in south Mississippi indicates the importance of incorporating decreased stand density into management practices for longleaf pine habitat.

Key Words.—amphibian; canopy cover; community; habitat associations; herpetofauna; longleaf pine; Mississippi; reptile

INTRODUCTION

The longleaf pine ecosystem, a landscape that once almost entirely characterized the southeastern coastal plain of the United States (Stout and Marion 1993), has been severely diminished (Ware et al. 1993). The reduction of longleaf pine forest to less than five percent of its historic range is largely due to fire suppression and the conversion of longleaf pine forests to agricultural, silvicultural, or human use areas (Noss 1989; Frost 1993; Outcalt 1997; Varner and Kush 2004). Due to the elusive, fossorial, and often cryptic nature of many reptile and amphibian species, the community assemblages and habitat associations of herpetofauna native to longleaf pine forests in Mississippi are poorly known. Guyer and Bailey (1993) described the unusually diverse herpetofauna of longleaf forests and estimated that about 72 reptile and amphibian species are associated with this habitat, while one third of these species are endemics of the historic Longleaf Pine (*Pinus palustris*) range. Although studies describing reptile and amphibian communities in upland longleaf pine habitats are relatively common (Tuberville et al. 2005; Smith et al. 2006), most studies addressing habitat-faunal relationships within the longleaf pine ecosystem occurred in Florida and South Carolina (Dodd and Franz 1995; Yale et al. 1999; Litt et al. 2001).

Southern Mississippi contains a relatively understudied sector of longleaf pine forest and, to our knowledge, there is only one published study concerning herpetofaunal communities within this area (Langford et

al. 2007). To better define the faunal-habitat relationships of these communities, we addressed three objectives: (1) determine what levels of habitat heterogeneity exist in longleaf pine forests in south Mississippi; (2) determine if there are differences in reptile and amphibian community composition among these sites; and (3) if habitat-faunal differences exist among sites, identify what habitat variables are driving these differences.

MATERIALS AND METHODS

Study sites.—We primarily restricted the search for suitable longleaf pine habitat to the southern, coastal plain region of Mississippi. The habitat in this study consisted of sandy soils, with an over story of Longleaf Pine (*Pinus palustris*), a fire-maintained, herbaceous, grassy understory, and a fire-suppressed mid-story. We identified and surveyed 24 sites with suitable habitat in 12 counties (Fig. 1). Of these sites, 22 were on public land and two were on private land. Of the public sites, 17 were within the DeSoto National Forest (six within the Chickasawhay District and 11 within the DeSoto District). We surveyed one site on the Mississippi Sandhill Crane National Wildlife Refuge, three sites within the Marion County Wildlife Management Area, and one site owned by the Hancock County School Board. Additionally, several private landowners in both Hancock County and George County allowed us to survey their lands.

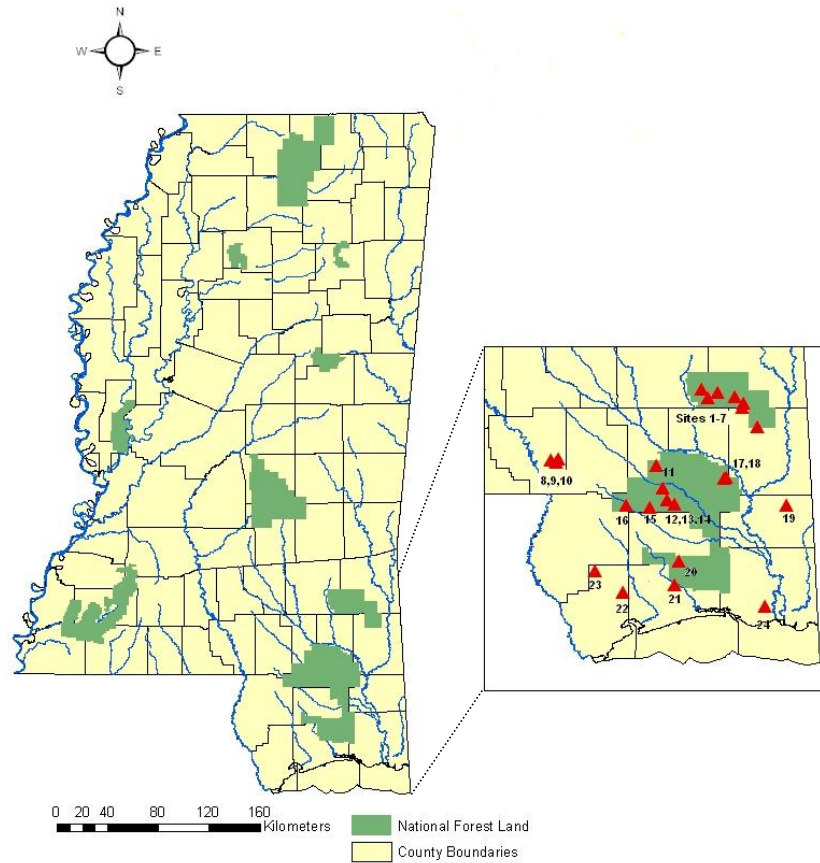


FIGURE 1. Sites surveyed (red triangles) for reptiles and amphibians in Mississippi, USA from 2004–2006. Shaded areas represent public land (national forests or wildlife management areas).

Survey techniques.—To address habitat variation as well as habitat/community associations of reptiles and amphibians in Mississippi, we divided our project into two parts. In 2004, we surveyed all identified sites with standard herpetological sampling techniques including a combination of drift fences with pitfall and funnel traps (Gibbons and Semlitsch 1981; Campbell and Christman 1982; Fitch 1987), search and hand catch (Crump and Scott 1994), cover boards (Grant et al. 1992; Olson and Warner 2003), and road surveys (Dodd et al. 1989). Due to time and budget constraints, we selected a subset of the sites surveyed in 2004 for further surveys in 2005 and 2006 (six sites), and we surveyed three sites in 2005 only (see Table 1 for number of survey years for each site). In 2004, each 30.5 m drift fence contained four funnel traps and four pitfall traps (Fig. 2). To sample multiple sites within a local region simultaneously, we continuously deployed 12 or more drift fence/trap arrays. Cover boards and pit-fall use had low capture rates for species of interest in 2004, so we did not employ these techniques in 2005 or 2006. The number of drift fences erected at each site was proportional to the area of suitable habitat present. Each year, we surveyed sites for ≥ 14 consecutive days in the spring (15 March – 27

May) and 14 consecutive days in the summer (28 May – 29 July).

We checked all arrays at least once per day, and, when temperatures exceeded 32° C, we checked traps twice per day. We removed all captured animals from traps and released them at the site of capture during each visit.

For each animal captured, we recorded the location, date, and species. We collected habitat data at each sampling site during the first week of July 2004, 2005, and 2006. We then quantified and recorded the following habitat information: soil composition, dominant vegetation species, percent canopy cover of trees, percent mid-story coverage, percent shrub coverage, basal area of trees, percentage cover of grasses, forbs, and shrubs in understory, ground-cover

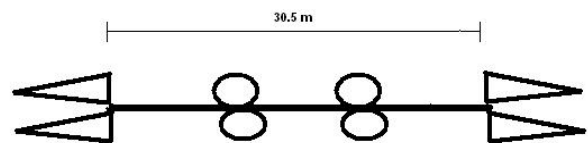


FIGURE 2. Drift fence array indicating the length and approximate placement of pitfall traps (circles) and placement of funnel traps (triangles) at sites surveyed for herpetofauna in Mississippi, USA.

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TABLE 1. Sites surveyed for reptiles and amphibians in Mississippi, USA. Site numbers corresponding to map (Figure 1), property type, number of years surveyed, species richness, and habitat type for sites included in the PCA habitat analysis (O = open canopied group, M = moderate canopy closure group, and C = closed canopy group).

Site	County	Property Type	Years Surveyed	Species Richness	Habitat Type
1	Jones	Desoto National Forest	3	20	C
2	Wayne	Desoto National Forest	2	16	-
3	Wayne	Desoto National Forest	3	20	C
4	Wayne	Desoto National Forest	3	24	C
5	Wayne	Desoto National Forest	3	29	C
6	Wayne	Desoto National Forest	1	8	O
7	Greene	Desoto National Forest	1	17	M
8	Marion	Marion Co. Wildlife Management Area	1	10	-
9	Marion	Marion Co. Wildlife Management Area	1	21	-
10	Marion	Marion Co. Wildlife Management Area	1	15	-
11	Forrest	Desoto National Forest	1	11	C
12	Forrest	Desoto National Forest	1	14	M
13	Forrest	Desoto National Forest	1	15	O
14	Perry	Desoto National Forest	3	32	M
15	Forrest	Desoto National Forest	1	7	C
16	Pearl River	Desoto National Forest	1	10	C
17	Perry	Desoto National Forest	1	13	M
18	Perry	Desoto National Forest	1	15	O
19	George	Private	1	11	M
20	Harrison	Desoto National Forest	1	17	M
21	Harrison	Desoto National Forest	1	8	M
22	Hancock	Private	1	19	O
23	Hancock	Private	1	16	M
24	Jackson	Sandhill Crane National Wildlife Refuge	1	21	O

percentage of litter and bare soil, and recency of fire. We used a spherical densiometer (Forest Densimeters model-C, City, State, Country) to measure canopy cover (Dealy 1960). At each drift fence array, we took four densiometer readings to estimate percentage canopy cover facing north, south, east, and west of the array; we then took an average of these readings to estimate overall cover. We used a Cruz-All basiometer (model 59793, City, State, Country) to measure factor-10 basal area (Dean 2004). We took measurements for both canopy cover and basal area from the middle of each 30.5 m drift fence array. We used a one-meter quadrat (four replicates per drift fence) to estimate average percentage of grasses, forbs, shrubs, litter and bare soil comprising the groundcover, and we visually estimated the percentage of mid-story coverage and percentage of shrubs in the mid-story (Dethier 1993). To increase measurement consistency, one individual (D.B.) measured all habitat parameters. Lastly, we used the soil hydrometer method (Sheldrick and Wang 1993) to determine percentage content of sand, silt, and clay for soil samples collected from each drift fence site (four samples per site).

Data analysis.—When analyzing the results of this study, we assumed that any given species present in upland habitat in south Mississippi has an equal capture probability across sites; therefore, the likelihood of capturing this species over a standardized amount of trap days should be equal for any given site. To assess

degree of habitat heterogeneity among survey sites, we used principal components analysis (PCA) coupled with analysis of similarity (ANOSIM) using the Bray Curtis similarity index (Bray and Curtis 1957). For this analysis, we included all sites surveyed in 2004 (20 sites). To explicitly assess habitat associations of reptiles and amphibians, we employed canonical correspondence analysis (CCA) using all sites (and all years) surveyed. For the CCA, P = proportion of randomized runs with eigenvalues greater than or equal to the observed eigenvalue. Because habitat parameters for each site did not remain constant across years (substantial changes in habitat resulted from prescribed fire and Hurricane Katrina; post-hurricane, canopy coverage decreased at many sites), we considered each survey year for a given site a different replicate. We standardized all community data to adjust for small disparities in number of trap days for each site (resulting from differences in suitable habitat and number of drift fence arrays per site). We considered one drift fence array open for one 24-hour period equal to one trap day. We did not include arboreal snakes (*Opheodrys aestivus* and *Pantherophis obsoleta*), frogs of the genus *Hyla*, or extremely rare reptiles and amphibians (total number of captures less than five individuals) in our community analyses. We excluded arboreal snakes and tree frogs from our analysis because these groups cannot be effectively sampled using drift fences with funnel and pitfall traps (Dodd 1991), and we sought to minimize sampling bias to the greatest extent possible. Scaling

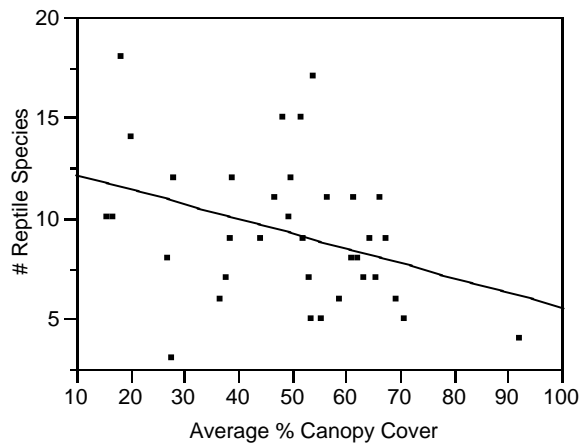


FIGURE 3. Regression of reptile diversity and canopy cover for all sites surveyed in Mississippi from 2004–2006.

options for CCA were as follows: axis scores centered and standardized to unit variance, axes scaled to optimize representation of sites. We chose to use Monte Carlo permutation tests (Manly 1991) with 9,999 iterations to test two null hypotheses: that there is no relationship between the species and habitat matrices, and that there are no species-environment correlations.

To test the null hypothesis that slope of reptile diversity plotted against percentage canopy cover is equal to zero, we conducted a one-way ANOVA using JMP (Version 6. SAS Institute., Cary, NC, 1989–2005); alpha was 0.05 for all tests. For all multivariate analyses, we used PRIMER 5.2.9 (Primer-E Ltd, Roborough, Plymouth, United Kingdom) and PcOrd 5 (MJM Software Design, Gleneden Beach, Oregon, United States).

RESULTS

Over three field seasons, 3,464 trap days resulted in 2,192 captures (Table 2), representing 54 species (20 amphibians and 34 reptiles). Average trap mortality was 3.3% and Red Imported Fire Ants (*Solenopsis invicta*) were present in 71% of these mortality events. There were significant yearly differences in reptile and amphibian communities sampled (ANOSIM *Global r* = 0.316, *P* = 0.008); we sampled lowest numbers of both species and individuals in the severe drought year of 2006, though yearly differences were not significant (relative abundance $\chi^2 = 4.82$, *df* = 2, *P* = 0.089; diversity (S) $\chi^2 = 4.07$, *df* = 2, *P* = 0.13). There was a significant negative linear relationship between percentage canopy cover and reptile diversity (*F* = 4.92, *df* = 1,33, *P* = 0.03; Fig. 3; Table 2). We deposited

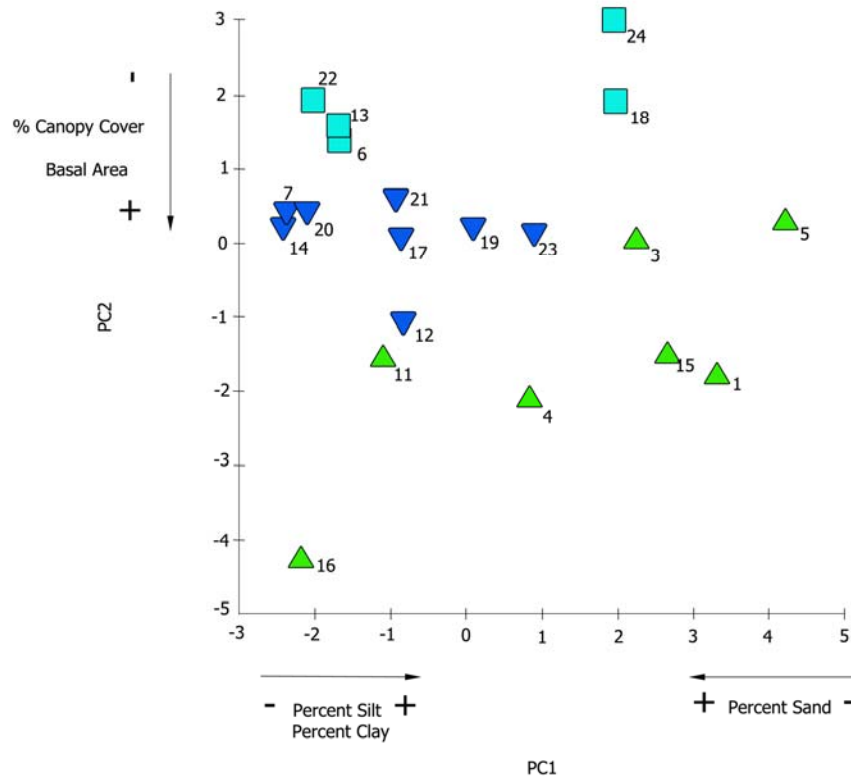


FIGURE 4. Principal components analysis (PCA) of habitat variables for all of the sites we surveyed in 2004. Triangles represent closed canopied sites, inverse triangles represent sites with moderate canopy coverage, and squares represent sites with relatively open canopies. Numbers correspond to site numbers used in both Fig. 1 and Table 1.

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TABLE 2. Reptiles and amphibians found using drift fences and active searching and the percentage of sites where each species was found from 2004–2006.

Scientific Name	Common Name	# Surveyed	% of Sites
Turtles			
<i>Gopherus polyphemus</i>	Gopher Tortoise	68	66.7
<i>Terrapene carolina</i>	Eastern Box Turtle	13	33.3
Lizards			
<i>Anolis carolinensis</i>	Green Anole	37	66.7
<i>Aspidoscelis sexlineatus</i>	Six-lined Racerunner	31	37.5
<i>Eumeces fasciatus</i>	Common Five-lined Skink	11	33.3
<i>Eumeces inexpectatus</i>	Southeastern Five-lined Skink	53	66.7
<i>Eumeces laticeps</i>	Broad-headed Skink	2	8.3
<i>Ophisaurus attenuatus</i>	Slender Glass Lizard	1	4.2
<i>Ophisaurus ventralis</i>	Eastern Glass Lizard	2	8.3
<i>Sceloporus undulatus</i>	Eastern Fence Lizard	160	88
<i>Scincella lateralis</i>	Ground Skink	362	92
Snakes			
<i>Agkistrodon contortrix</i>	Copperhead	7	29.2
<i>Agkistrodon piscivorus</i>	Cottonmouth	5	20.8
<i>Cemophora coccinea</i>	Scarlet Snake	63	58.3
<i>Coluber c. priapus</i>	Black Racer	158	87.5
<i>Crotalus adamanteus</i>	Eastern Diamondback Rattlesnake	6	25.0
<i>Diadophis punctatus</i>	Ring-necked Snake	3	12.5
<i>Pantherophis guttata</i>	Corn Snake	9	25
<i>Pantherophis obsoleta</i>	Gray Rat Snake	10	16.6
<i>Heterodon platirhinos</i>	Eastern Hog-nosed Snake	19	37.5
<i>Lampropeltis getula</i>	Eastern King Snake	18	33.3
<i>Lampropeltis triangulum</i>	Scarlet King Snake	24	33.3
<i>Masticophis flagellum</i>	Eastern Coachwhip	52	45.8
<i>Micrurus fulvius</i>	Coral Snake	3	8.3
<i>Nerodia erythrogaster flavigaster</i>	Yellow-bellied Water Snake	2	8.3
<i>Ophedrys aestivus</i>	Rough Green Snake	3	12.5
<i>Pituophis melanoleucus</i>	Pine Snake	10	20.8
<i>Regina rigida</i>	Crayfish Snake	3	12.5
<i>Sistrurus miliarius</i>	Pygmy Rattlesnake	8	29.2
<i>Storeria dekayi</i>	Dekay's Brownsnake	8	16.7
<i>Storeria occipitomaculata</i>	Red-bellied Snake	1	4.2
<i>Tantilla coronata</i>	Southeastern Crowned Snake	13	54.2
<i>Thamnophis sauritus</i>	Eastern Ribbon Snake	16	33.3
<i>Thamnophis sirtalis</i>	Common Garter Snake	79.2	
		19	
Salamanders			
<i>Eurycea guttolineata</i>	Three-Lined Salamander	8	25.0
<i>Eurycea quadridigitata</i>	Dwarf Salamander	2	8.3
<i>Notophthalmus viridescens</i>	Eastern Newt	1	4.2
<i>Plethodon mississippi</i>	Mississippi Slimy Salamander	22	37.5
Frogs			
<i>Acris gryllus</i>	Southern Cricket Frog	22	37.5
<i>Bufo terrestris</i>	Southern Toad	244	87.5
<i>Bufo quercicus</i>	Oak Toad	16	4.2
<i>Gastrophryne carolinensis</i>	Eastern Narrow-mouthed Toad	557	91.7
<i>Hyla chrysoscelis/versicolor</i>	Gray Treefrog	2	8.3
<i>Hyla cinerea</i>	Green Treefrog	2	8.3
<i>Hyla femoralis</i>	Pinewoods Treefrog	20	29.2
<i>Hyla gratiosa</i>	Barking Treefrog	8	12.5
<i>Hyla squirella</i>	Squirrel Treefrog	2	8.3
<i>Pseudacris crucifer</i>	Spring Peeper	2	8.3
<i>Rana catesbeiana</i>	American Bullfrog	6	20.8
<i>Rana c. clamitans</i>	Green Frog	51	41.7
<i>Rana grylio</i>	Pig Frog	1	4.2
<i>Rana palustris</i>	Pickerel Frog	1	4.2
<i>Rana sphenoccephala</i>	Southern Leopard Frog	7	29.2
<i>Scaphiopus holbrooki</i>	Eastern Spadefoot Toad	154	25.0

specific locality data and further survey data for sites

surveyed in 2004 and 2005 in the Mississippi Museum of Natural Science.

The first three PCA axes explained 71.5% of the habitat variation between sites. Percentage canopy coverage and soil composition (percentage sand, silt and clay in the soil) were the factors with highest loadings on the first two axes, and explained most of the variation in the model. Basal area, percentage of shrub growth, and bare soil in the understory explained most of the variation on the third axis (Table 2). We visually identified three habitat-group clusters from our PCA (Fig. 4), and subsequently defined each group as separate factors within ANOSIM. Monte Carlo tests indicated that these three groups represent significantly different site types (*Global r* = 0.452, *P* = 0.001; Table 3).

The first three axes of the CCA explained 22.9% of the variance within the site and species matrices (Fig. 5 and Table 4). Soil composition (percentage sand, silt and clay in the soil) accounted for most of the variation explained on the first axis. Percentage grass in the understory and percentage sand accounted for most of the species-habitat variation explained by axis two. Finally, canopy cover and basal area explained most of the variation on the third axis. Monte Carlo permutation tests revealed significant structure in the habitat and community data for the second and third axes, but not for axis one (axis one *P* = 0.12, axis two *P* = 0.02, axis three *P* = 0.0006).

Although species-environment correlations were statistically significant only for axis three (axis one *P* = 0.22, axis two *P* = 0.49, and axis three *P* = 0.002), these correlations were extremely high for both observed (real data mean correlation = 0.90) and simulated data (Monte Carlo mean correlation = 0.85). When we plotted sites

in ordination space according to habitat parameters, the majority of sites cluster near the middle of the habitat ordination; however, several sites are outliers characterized by unique habitat compared to other sites.

When we plotted species in ordination space according to habitat parameters, several species correlate positively or negatively with one or more habitat parameters (See Table 5 for loadings). For example, Oak Toad (*Bufo quercicus*) numbers/presence correlate positively with high percentages of grass in the understory and extremely low percentages of canopy cover. Several species, such as the Six-lined Racerunner (*Aspidoscelis sexlineatus*), Spadefoot Toad (*Scaphiopus holbrooki*), and Eastern Coachwhip (*Masticophis flagellum*), associated positively with sandy soils and open canopies. Conversely, several species are associated with sites characterized by more closed canopies and less sand in the soil: Eastern Ribbon Snake (*Thamnophis sauritus*), Copperhead (*Agkistrodon contortrix*), Scarlet Kingsnake (*Lampropeltis triangulum*), Garter Snake (*Thamnophis sirtalis*), and Dekay's Brownsnake (*Storeria dekayi*). As expected, many common/generalist species plot near the center of the ordination, and do not correlate either positively or negatively with specific habitat parameters: Southern Toad (*Bufo terrestris*), Fence Lizard (*Sceloporus undulatus*), Narrowmouth Toad (*Gastrophryne carolinensis*), Black Racer (*Coluber constrictor priapus*), Southern Cricket Frog (*Acris gryllus*), and Green Frog (*Rana clamitans clamitans*).

DISCUSSION

As proposed by Dodd and Franz (1993), we sought to add to the base of information concerning entire herpetofaunal communities, including common species,

TABLE 3. Summary of habitat variables quantified (mean ± standard deviation) at 20 sites surveyed for reptiles and amphibians in south Mississippi. Groups represent different site types identified by PCA and ANOSIM (see Fig. 3). CC = Canopy Cover, BRM = burn recency in months, MSC = midstory coverage, SIM = shrubs in midstory.

Habitat Variable	Group 1 Closed Canopy	Group 2 Moderate Canopy	Group 3 Open Canopy
% Sand	61.7 ± 11.9	83.3 ± 12.6	80.2 ± 11.6
% Clay	6.2 ± 2.2	3.4 ± 2.2	3.9 ± 2.4
% Silt	32.1 ± 10.9	13.2 ± 10.5	15.9 ± 9.8
% Forb	3.9 ± 3.9	1.8 ± 1.1	3.8 ± 4.3
% Shrub	22.3 ± 14.0	33.1 ± 15.3	25.8 ± 25.8
% Litter	66.7 ± 26.7	78.2 ± 16.3	57.0 ± 15.5
% Bare Ground	16.4 ± 17.1	12.1 ± 12.9	17.9 ± 14.9
Basal area (m ²)	110 ± 27.7	69.0 ± 9.9	24.0 ± 8.9
% CC	67.1 ± 12.1	45.0 ± 5.9	23.6 ± 8.8
BRM	17.6 ± 18.0	28.0 ± 8.8	28.8 ± 15.5
% Grass	15.9 ± 11.0	11.7 ± 12.8	21.7 ± 15.6
% MSC	17.0 ± 30.0	18.0 ± 12.2	28.2 ± 25.8
% SIM	48.2 ± 22.1	68.0 ± 16.2	48.9 ± 27.1

Table 4. PCA loadings of habitat variables from 20 sites surveyed in 2004. The first three axes of the PCA explain 71.5% of habitat variance. The major axis loading for each habitat variable is in bold.

Habitat Variable	PC1	PC2	PC3
% Midstory	-0.25	-0.20	-0.12
% Shrubs in midstory	-0.14	0.15	0.46
% Sand	-0.41	0.25	-0.09
% Clay	0.40	-0.12	0.07
% Silt	0.40	-0.27	0.08
Average Forb	0.28	0.16	0.34
Average Leaf Litter	0.30	-0.33	0.21
Average Bare Soil	0.12	-0.26	0.58
Average Shrub	-0.10	0.02	0.59
Basal Area	0.12	0.22	-0.49
% Canopy Cover	0.02	-0.54	-0.07
Burn Recency	-0.34	-0.08	0.01
Average Grass	0.36	0.17	0.09

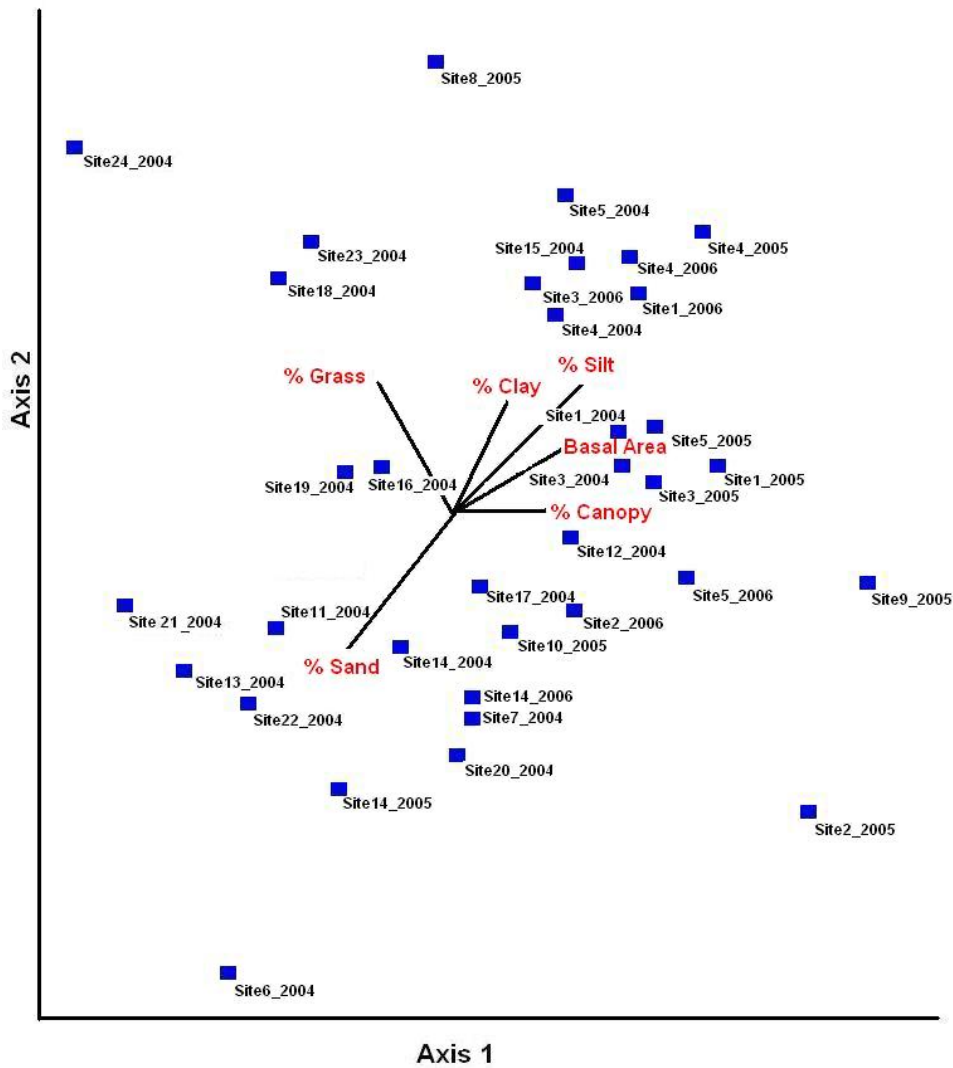


FIGURE 5. Canonical correspondence analysis (CCA) output of all sites surveyed. Sites are plotted in ordination space based on habitat parameters. Each of the six habitat parameters in the figure has an un-plotted vector extending in the opposite direction from the labeled vector.

such that monitoring protocols may ultimately be developed and implemented in South Mississippi. The first objective towards these goals was to determine levels of habitat heterogeneity within historical upland longleaf pine habitat in south Mississippi. It is apparent from our ANOSIM that substantial variation exists. In contrast to the densely planted silvicultural forests typifying much of the Gulf Coast Plain, old-growth longleaf pine forests are savannah habitats with relatively open canopies and low basal areas (Bartram 1791). This frequently burned; open-canopied longleaf habitat has high percentages of grasses and forbs in the groundcover, constituting some of the richest plant biodiversity in North America: up to 30 species per

square meter (Frost et al. 1986). As most forest stands in south Mississippi are in some stage of forest regeneration, it follows that basal area and percentage canopy cover are two factors explaining much of the variation between surveyed stands.

Our second objective sought to correlate reptile and amphibian community differences with differences in longleaf pine habitat. Although we saw significant structure in our CCA, the CCA model did not explain most of the community variation among sites. The missing variation in our model is likely due to both historical and landscape-level effects (habitat fragmentation, proximity to roads, previous forestry practices such as intensive site preparation, etc.).

Although 54 species of amphibians and reptiles made up the sampled communities, it is of note that we surveyed few true longleaf pine specialists; furthermore, we failed to detect Southern Hognose Snake (*Heterodon simus*), Eastern Indigo Snake (*Drymarchon corais couperi*), Mississippi Gopher Frog (*Rana sevosia*), or Ornate Chorus Frog (*Pseudacris ornata*).

The highly significant structure and species-environment correlation on axis three of the CCA indicate that percentage canopy cover and basal area are two factors contributing greatly to faunal diversity in longleaf pine forests of South Mississippi. Canopy cover is widely recognized as a key factor for assessing forest biomes (Jennings et al. 1999), and fire is the driving force that maintains the open canopies of longleaf pine savannahs in the southeast (Komarek 1965). Without fire, hardwood encroaches on the pine savannah, leading to a canopy closure followed by the loss of herbaceous groundcover (Waldrop et al. 1992). This herbaceous groundcover is essential for growth, development, and reproduction of the gopher tortoise (*Gopherus polyphemus*; Mushinsky and McCoy 1994), a species often portrayed as an ecosystem engineer (Jones et al. 1994) of the longleaf pine ecosystem. Although

recommended percentage canopy cover for gopher tortoises is between 30–50% (Wilson et al 1997), our CCA did not positively associate Gopher Tortoises with open canopied forests. This anomaly is likely because we encountered most active burrows within our study sites along roads or power lines (pers. obs.). These edge areas contain more canopies that are open and grassier understories than the interior areas containing our drift fences, where we collected habitat parameters. Open-canopied forests are extremely important to Gopher Tortoises. Aresco and Guyer (1999) demonstrated that Gopher Tortoises abandon their burrows primarily in association with changes in overstory structure (increased canopy cover), which result in shading of active burrows.

Our research supports the findings of several previous studies regarding the importance of canopy cover to herpetofaunal community structure in the southeast. For example, Meshaka and Layne (2002) described openings with sparse or no shrub cover as critical factors allowing the persistence of xeric specialists on a long unburned site in Florida. In addition, a study of herpetological diversity within young growth forests of South Carolina also found a negative correlation between reptile

TABLE 5. Canonical correspondence analysis (CCA) final scores for 34 reptile and amphibian species. See Ter Braak (1986) for detailed explanation of CCA output. The major axis loading for each species is displayed in bold.

Species	Axis 1	Axis 2	Axis 3
<i>Acris gryllus</i>	0.14	0.62	-0.94
<i>Agkistrodon contortrix</i>	2.47	-0.10	0.29
<i>Agkistrodon piscivorus</i>	-1.36	2.23	1.93
<i>Anolis carolinensis</i>	0.83	0.45	-0.52
<i>Aspidocelis sexlineatus</i>	-2.63	-1.08	0.23
<i>Bufo terrestris</i>	-0.39	0.04	-0.12
<i>Bufo quercicus</i>	-5.23	5.35	6.80
<i>Cemophora coccinea</i>	0.50	-0.31	0.75
<i>Coluber c. priapus</i>	-0.03	0.56	-0.01
<i>Crotalus adamanteus</i>	1.32	0.53	0.84
<i>Pantherophis guttata</i>	-0.92	0.88	0.98
<i>Eumeces fasciatus</i>	-0.98	1.99	0.28
<i>Eumeces inexpectatus</i>	0.08	-0.10	0.97
<i>Eurycea guttolineata</i>	0.12	-1.00	-1.96
<i>Gastrophryne carolinensis</i>	-0.60	0.29	-0.28
<i>Gopherus polyphemus</i>	0.18	-2.33	0.42
<i>Heterodon platirhinos</i>	0.61	-0.26	-1.17
<i>Lampropeltis getula</i>	-1.00	-1.82	-0.24
<i>Lampropeltis triangulum</i>	1.88	0.01	0.13
<i>Masticophis flagellum</i>	-0.27	-2.18	1.04
<i>Pituophis melanoleucus</i>	0.95	-1.54	0.63
<i>Plethodon mississippi</i>	-0.92	1.03	-2.98
<i>Rana catesbeiana</i>	-0.77	1.58	-0.92
<i>Rana c. clamitans</i>	-0.28	0.53	-1.90
<i>Rana sphenoccephala</i>	-1.12	0.21	0.30
<i>Scaphiopus holbrooki</i>	-2.60	-1.78	-1.27
<i>Sceloporus undulatus</i>	-0.10	0.32	0.47
<i>Scincella lateralis</i>	0.96	0.40	-0.50
<i>Sistrurus miliarius</i>	-0.68	-0.02	0.44
<i>Storeria dekayi</i>	1.34	-0.53	3.98
<i>Tantilla coronata</i>	0.48	1.44	-0.25
<i>Terrapene carolina</i>	1.69	-0.16	2.16
<i>Thamnophis sirtalis</i>	1.35	-0.06	0.65
<i>Thamnophis sauritus</i>	2.11	1.05	0.01

diversity and upland canopy closure (Russell et al. 2002). Lastly, Dodd and Franz (1995) found snake communities of high pine habitats in north-central Florida to be more diverse and evenly distributed than snake communities sampled in closed xeric hammock habitat.

Many previous habitat association studies targeting herpetofaunal communities specifically address community differences in response to management practices. For example, Litt et al. (2001) captured more *Aspidoscelis sexlineatus*, and *Sceloporus undulatus* in burned habitat plots than in control or herbicide treated plots. Although we did not find notable habitat associations for either of these species when examining recency of prescribed burn, we did find that *Aspidoscelis sexlineatus* often occurred in open habitats. This is not surprising given that teiid lizards have the highest metabolic rates among reptiles (Asplund 1974), and may require open basking sites, which are more common in open canopies, to maintain high body temperatures.

The significant influence of basal area and canopy cover upon longleaf pine communities has important management and conservation implications. Longleaf pine residents and specialists are subject to evolutionary pressures within this ecosystem; consequently, lowering stand densities and basal areas may benefit species characteristic of this imperiled community. The aftermath of Hurricane Katrina has increased development pressures in coastal Mississippi. As remaining tracts of longleaf pine forests become more fragmented and subdividing and development of forested land continues, the lifespan of native longleaf pine communities certainly will become more endangered. This warrants careful public lands management to avoid the collapse of these important North American ecosystems. To conserve the biodiversity of the longleaf pine ecosystem, we must recognize the marked effect that management decisions have on community structure.

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