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Amphibian Distributions within Three Types of Isolated Wetlands in Southwest Georgia

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Abstract.—Conservation of isolated wetlands is critical for maintaining regional biodiversity within the southeastern U.S. However, relatively little is known about the ecological communities of these wetland systems, particularly within the karst wetlands of the southeastern Coastal Plain. In southwestern Georgia seasonal isolated wetlands include marshes, cypress savannas and cypress/gum swamps, which have fundamental differences in vegetation and soils, hydrology, water chemistry and invertebrate abundance and diversity. We examined the relationship between wetland type and the distribution of amphibians in 28 relatively undisturbed, seasonally flooded isolated wetlands in southwestern Georgia, USA. We sampled wetlands for amphibians in the winter, spring and summer using aquatic traps, dipnetting, PVC pipe refugia and automated frog call recording devices (frogloggers). Mean amphibian species richness among study wetlands was 12.7 ± 0.5 species (range 7–18). Both species richness and composition varied among wetland types, with different wetland types supporting different amphibian assemblages. Our results highlight the importance of wetland diversity in promoting regional amphibian diversity.

Introduction

Seasonally flooded, hydrologically isolated wetlands are of primary importance for maintenance of biological diversity within the southeastern Coastal Plain (Sutter and Kral, 1994; Semlitsch *et al.*, 1996; Sharitz, 2003). Within the region, these wetlands provide breeding or primary habitat for 36 amphibian species (Moler and Franz, 1987; Petranka, 1998). Southeastern isolated wetlands are highly threatened habitats, receiving little legal protection and high levels of development pressure (Christie and Hausmann, 2003; Tiner, 2003). A solid understanding of the relationships between wetland habitat variables and wildlife communities is essential if realistic wetland conservation and restoration strategies are to be formed for the region.

Isolated wetlands in southwestern Georgia consist of limesink depressional wetlands formed by the subsidence of underlying limestone deposits (Sutter and Kral, 1994). Kirkman *et al.* (2000) identified three primary wetland types in southwestern Georgia based on soil and vegetation characteristics. These wetlands vary widely in canopy cover from open grass-sedge marshes to sparsely forested cypress savannas to densely forested cypress/gum swamps. The three wetland types also are characterized by distinct differences in size, depth, water chemistry, water temperature and hydroperiod (Battle and Golladay, 2001; Kirkman *et*

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al., 2000). While plant and invertebrate communities also differ with wetland type (Kirkman *et al.*, 2000; Battle and Golladay, 2001), little is known regarding the amphibians within these wetland habitats.

Given the fundamental differences in physical and biological characteristics among the three wetland types, we hypothesized that they would be used by different amphibian species. In this study, we examine the relationship between wetland type and the amphibian community composition in a relatively undisturbed longleaf-pine dominated landscape.

STUDY AREA

We conducted this study on Ichauway (31°13′16.88″N and 84°28′37.81″W), an 11,800 ha private reserve in Baker County, Georgia, USA. The site primarily consists of 70–90-y-old longleaf pine forest with numerous limesink wetlands ranging from 0.2–76.5 ha in size. Limesink wetlands in the region include: (1) marshes with coarse sandy soils, an open overstory and an understory of dense panic grasses (*Panicum* spp.) and cutgrass (*Leersia hexandra*); (2) cypress savannas with fine sandy soil underlain by a layer of clay, with a relatively open pond cypress (*Taxodium ascendens*) canopy and an understory of panic grasses and broomsedge (*Andropogon virginicus*); and (3) cypress/gum swamps with thick organic soils and a dense overstory of pond cypress and swamp tupelo (*Nyssa biflora*) with virtually no understory or midstory vegetation (Kirkman *et al.*, 2000; Battle and Golladay, 2001). Wetlands on Ichauway vary considerably in hydroperiod, which is dependent upon annual patterns in inputs from precipitation and shallow subsurface runoff, as well as morphological characteristics of individual wetlands (Battle and Golladay, 2001). Amphibian breeding activity within the wetlands occurs year-round, but involves different species at different times of the year.

FIELD METHODS

We selected 28 wetlands for study including 10 marshes, 7 cypress savannas and 11 cypress/gum swamps (Fig. 1). Wetlands were selected because they have been designated as long-term reference wetlands at Ichauway. As a group, they have minimal impact from human land-use (traditional agricultural and forestry practices) both within their boundaries and in adjacent uplands. Collectively, they represent the least impacted isolated wetlands available for study within the region. Study wetlands ranged in size from 0.35–19.6 ha. We sampled all study wetlands in three sampling periods, summer (23 Jun.–20 Aug. 2004), winter (17 Dec. 2004–9 Feb. 2005) and spring (15 Mar.–21 May 2005) using five methods (dip net surveys, anuran call surveys, crayfish and funnel traps and PVC pipes).

We used a square-frame dip net (36 × 38 cm, 5 mm mesh) to conduct dipnet surveys. Dipnet surveys included one visit to each wetland per season. The number of 1 m sweeps was scaled by wetland perimeter as follows: small wetlands (<500 m perimeter) 50 sweeps, medium wetlands (500–1500 m) 100 sweeps and large wetlands (>1500 m) 200 sweeps. Sweeps were distributed equally around the wetland perimeter and among all shallow (<0.5 m) microhabitats. We used automated recording devices (frogloggers; Dodd, 2003) to record anuran calls at study wetlands. Frogloggers were placed at the wetland edge and programmed to record 1 min/h between 2000 and 0700 h for three consecutive nights per sampling period.

We set two types of aquatic traps, crayfish traps (Johnson and Barichivich, 2004) and funnel traps, for six consecutive nights per sampling period. Crayfish traps had a plastic-coated chicken-wire mesh (2.5 × 1.25 cm). Five crayfish traps were distributed evenly

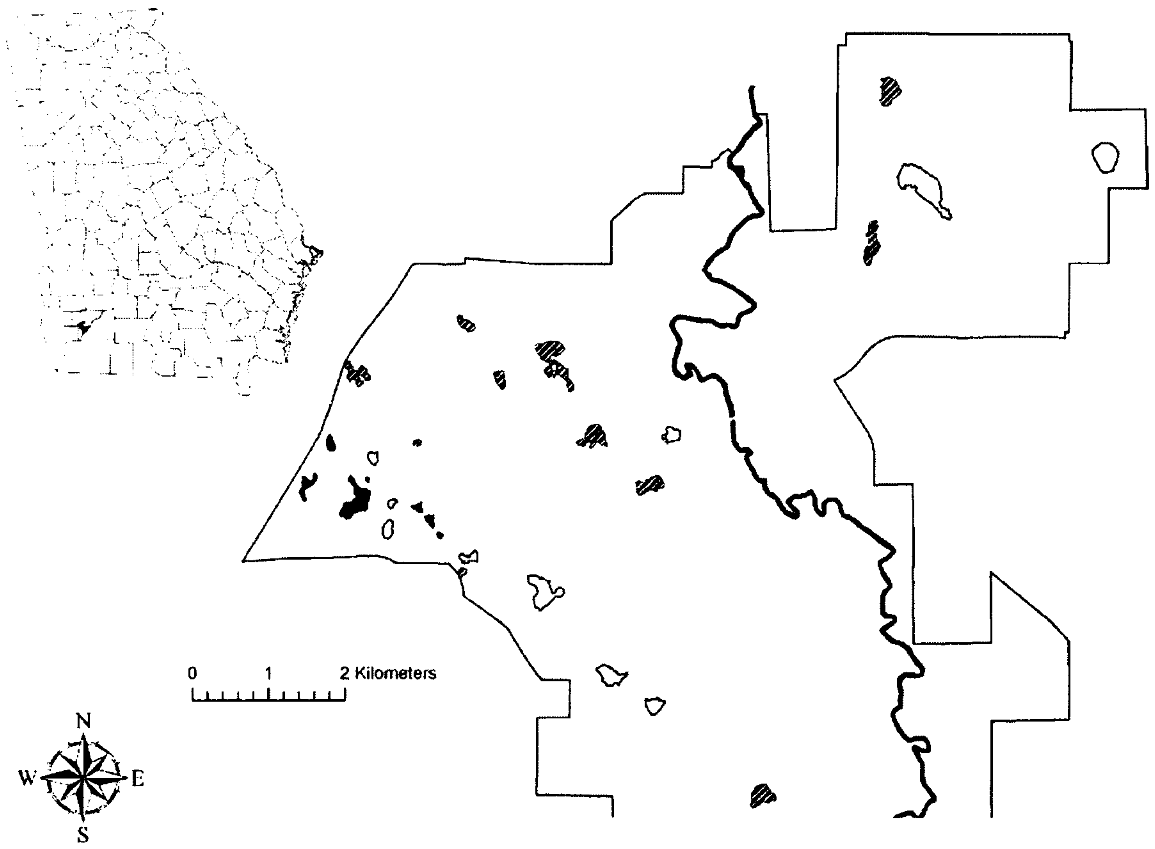

FIG. 1.—Location of wetland sites on Ichauway Preseve (31°13′16.88″N and 84°28′37.81″W) used in an investigation of the influence of wetland type on amphibian distributions from Jun. 2004 to May 2005. Wetlands are displayed by wetland type (unshaded = marshes, black = cypress savannas, vertical bars = cypress/gum swamps)

around the wetland perimeter at a depth of ca. 20 cm. Double-ended funnel traps were constructed from aluminum window screen (Heyer *et al.*, 1994) and contained a styrofoam float that kept the funnels submerged just below the surface. Funnel traps were placed every 50 m at a water depth of ca. 25 cm. Wetlands were randomly sorted into "trapping weeks" within a sampling period to avoid a temporal bias in sampling.

Polyvinylchloride (PVC) pipes were used to detect hylid frogs (Moulton *et al.*, 1996). One m segments of open-ended opaque, schedule 40 white PVC pipe (5 cm inside diameter) were inserted upright into the ground at 50 m intervals around the perimeter of each wetland. Pipes were deployed ca. 1 mo before the first sampling period to give frogs time to colonize them. Pipes were checked at the beginning and end of each sampling period. Frogs were identified to species and released back into the pipes.

Amphibians captured in aquatic traps and dipnet surveys were identified in the field and released. Representative amphibian larvae that could not be identified in the field were identified from appropriate keys (Altig, 1970; Altig *et al.*, 1998) or raised in the lab to metamorphosis. Larvae of the spring peeper (*Pseudacris crucifer*), southern chorus frog, (*Pseudacris nigrita*) and southeastern chorus frog (*Pseudacris feriarum*) are similar in appearance and there are currently no adequate keys to distinguish among them.

Therefore, we report only data for locations from which larvae of these species were successfully reared and identified or where adults were observed.

STATISTICAL ANALYSES

We used Detrended Correspondence Analysis (DCA) with amphibian presence/absence data to determine if distinct patterns in species composition existed among wetland types. Separate DCA analyses were conducted for both adult (all amphibian observations combined) and larval (only wetlands with larval observations) distributions. For both ordinations, only axes that significantly contributed to the percentage of variance explained were considered. Differences in larval and adult anuran and caudate species richness among wetland types were examined using Kruskal-Wallis rank sum tests. We used this nonparametric alternative to ANOVA because our data did not meet assumptions of normality and equality of variances among groups. Posthoc Wilcoxon rank sum tests were used to identify differences between anuran and caudate species richness among individual wetland types. All DCA analyses were conducted using PC-ORD for Windows Version 4.01 (MjM Software Design, Gleneden Beach, Oregon). All other analyses were performed in SAS Version 8.2 (SAS Institute, Cary, North Carolina).

RESULTS

We recorded 17,748 captures of 25 amphibian species over the study period (Table 1). Larvae or metamorphs were detected for 21 of the 25 species. Mean species richness was 12.7 ± 0.5 (SE) species (range 7–18) across all wetlands. Mean adult caudate species richness significantly differed among wetland types ($\chi^2 = 7.02$, df = 2, $P = 0.03$), but adult anuran richness did not ($\chi^2 = 1.02$, df = 2, $P = 0.61$) (Fig. 2). More adult caudate species were found in cypress/gum swamps than in cypress savannas ($P = 0.02$). Both larval anuran ($\chi^2 = 14.47$, df = 2, $P < 0.001$) and larval caudate ($\chi^2 = 7.15$, df = 2, $P = 0.025$) species richness differed among wetland types (Fig. 3). More larval anurans were found in marshes than in cypress savannas ($P = 0.005$) or cypress/gum swamps ($P < 0.001$). Conversely, more larval caudates were observed in cypress/gum swamps than in cypress savannas ($P = 0.024$).

The DCA ordinations of adult and larval amphibian distributions revealed similar patterns. In both ordinations the wetland types clustered in groups that formed a gradient from marshes to cypress savannas to cypress/gum swamps along axis 1. In each ordination some overlap existed among the wetland types, although more overlap existed between the species compositions of marshes and cypress savannas than between cypress/gum swamps and these wetland types. Axes one and two of the adult DCA explained 52.8% of the variation in adult amphibian species composition among wetlands (Fig. 4). Axes one and three of the DCA of larval species composition explained 45.7% of the variation in the composition of breeding amphibian species among sites (Fig. 5).

Extensive overlap in the amphibian composition occurred among sites, but several species appeared to display breeding preferences for particular wetland types (Table 1). Larval mole salamanders (*Ambystoma talpoideum*) and eastern newts (*Notophthalmus viridescens*), were only observed in cypress/gum swamps, whereas larvae of the eastern tiger salamanders (*A. tigrinum*) were never observed in this wetland type. Similarly, the green treefrog (*Hyla cinerea*) and gopher frog (*Rana capito*) larvae were only found in marshes, whereas southeastern chorus frogs were not observed breeding in this wetland type. The larvae of several species (N = 11) that were found in marshes and cypress/gum swamps were absent

TABLE 1.—Number of wetlands in which adult (and larval) amphibians were observed in a study of 28 isolated wetlands in southwestern Georgia from Jun. 2004 to May 2005. Numbers for larval *Ambystoma talpoideum* include both terrestrial and gilled morphs (TA = terrestrial adult, GA = gilled adult)

	Wetland type		
Species	Marsh (N = 10)	Cypress savanna (N = 7)	Cypress/Gum (N = 11)
Acris gryllus	10 (8)	6 (0)	8 (1)
Ambystoma talpoideum – GA	0 (0)	0 (0)	6 (7)
Ambystoma talpoideum – TA	2 (0)	0 (0)	2 (0)
Ambystoma tigrinum	4 (3)	1 (1)	0 (0)
Amphiuma means	2 (0)	1 (0)	8 (0)
Bufo terrestris	7 (7)	4 (3)	2 (1)
Eurycea quadridigitata	1 (1)	0 (0)	2 (2)
Gastrophryne carolinensis	10 (5)	5 (0)	7 (1)
Hyla chrysoscelis	2 (1)	4 (3)	9 (2)
Hyla cinerea	9 (5)	6 (0)	11 (0)
Hyla femoralis	10 (9)	7 (4)	11 (2)
Hyla gratiosa	10 (10)	6 (6)	4 (2)
Hyla squirella	10 (5)	7 (0)	11 (1)
Notophthalmus viridescens	1 (0)	0 (0)	4 (3)
Pseudacris crucifer	2 (1)	0 (0)	2 (1)
Pseudacris feriarum	4 (0)	3 (2)	8 (3)
Pseudacris nigrita	9 (9)	6 (5)	10 (4)
Pseudacris ocularis	4 (3)	5 (1)	9 (2)
Pseudacris ornata	10 (10)	6 (6)	5 (5)
Pseudobranchus striatus	4 (0)	2 (0)	1 (0)
Rana capito	1 (1)	0 (0)	0 (0)
Rana catesbeiana	8 (1)	4 (0)	10 (9)
Rana grylio	0 (0)	0 (0)	1 (0)
Rana sphenocephala	10 (10)	7 (7)	11 (10)
Scaphiopus holbrookii	2 (2)	0 (0)	2 (2)
Siren lacertina	0 (0)	0 (0)	3 (0)

from cypress savannas (Table 1). Greater sirens (*Siren lacertina*) were only observed in cypress/gum swamps, although no eggs or larvae were ever detected for this species.

For some species, larval occupancy patterns within wetland types differed from adult occupancy patterns (Table 1). For instance, adult American bullfrogs (*Rana catesbeiana*) were common in marshes and cypress savannas, but larvae were found primarily in cypress/gum swamps. Adult treefrogs (*Hyla* spp.) were present in PVC pipes at all wetland types, but treefrog larvae were found primarily in marshes and cypress savannas. A similar pattern was also observed in southern cricket frogs (*Acris gryllus*) and eastern narrow-mouthed toads (*Gastrophryne carolinensis*).

DISCUSSION

In this study, we observed that seasonal isolated wetlands in southwestern Georgia supported a large number of amphibian species. We detected the presence of 25 species within our study wetlands, a number comparable with some of the most biodiverse wetland habitats within the Southeast and the nation (Gibbons *et al.*, 2006). Our results add to a growing body of literature that supports the need for increased local and federal regulatory

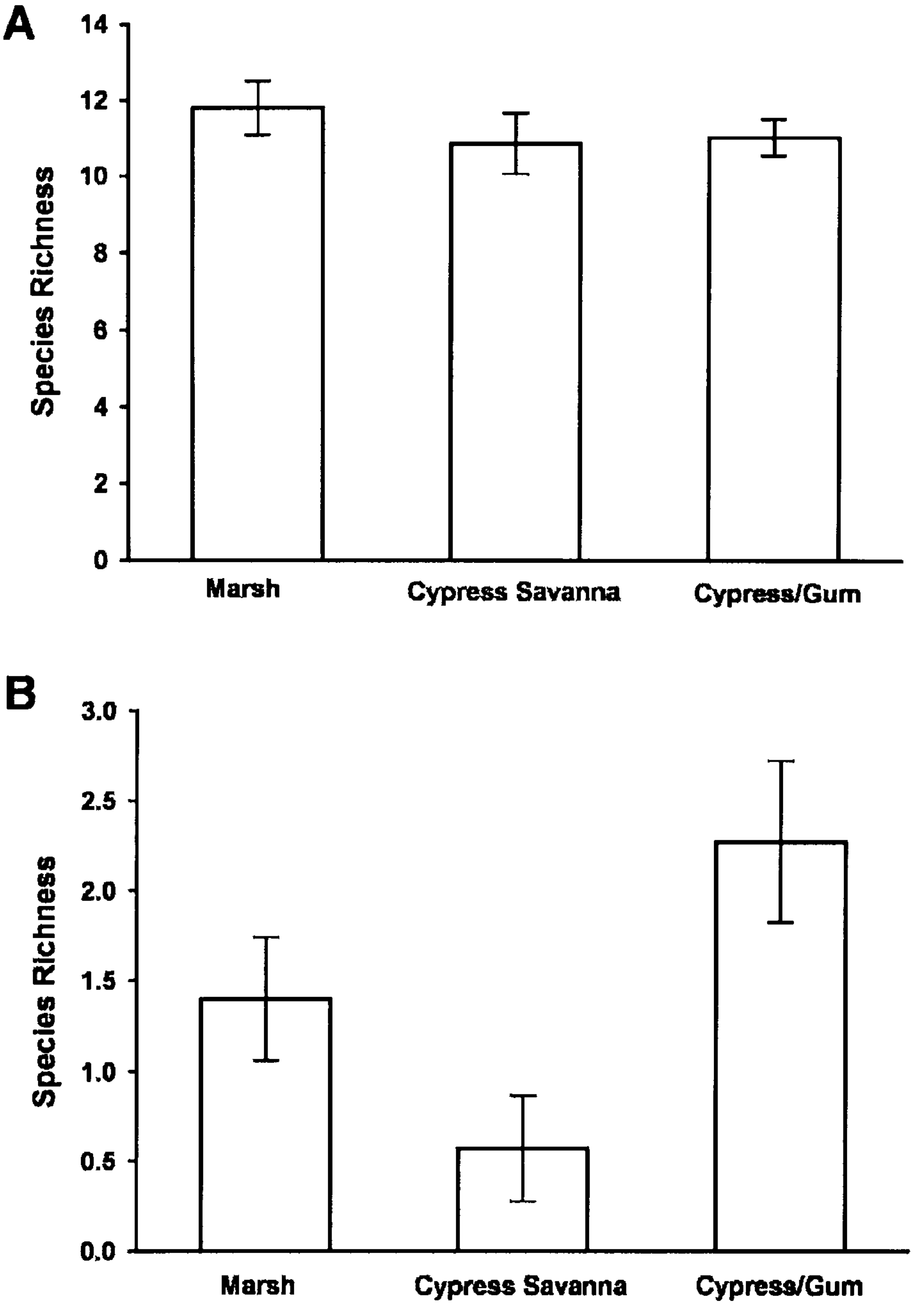

FIG. 2.—Comparison of mean (±SE) adult species richness of (a) anurans and (b) caudates captured in 28 isolated wetlands in southwestern Georgia from Jun. 2004 to May 2005 among three wetland types

protection of these water bodies to maintain regional species diversity (*e.g.*, Gibbs, 1993; Sutter and Kral, 1994; Sharitz, 2003; Gibbons *et al.*, 2006). We also observed that the three seasonal wetland types supported different amphibian communities. Cypress/gum swamps supported more caudate species than cypress savannas, while more larval anurans were found within marshes than in cypress/gum swamps and cypress savannas. The amphibian composition of cypress savannas overlapped with that of marshes and cypress/gum swamps, but supported fewer amphibian species. These results emphasize the importance of the

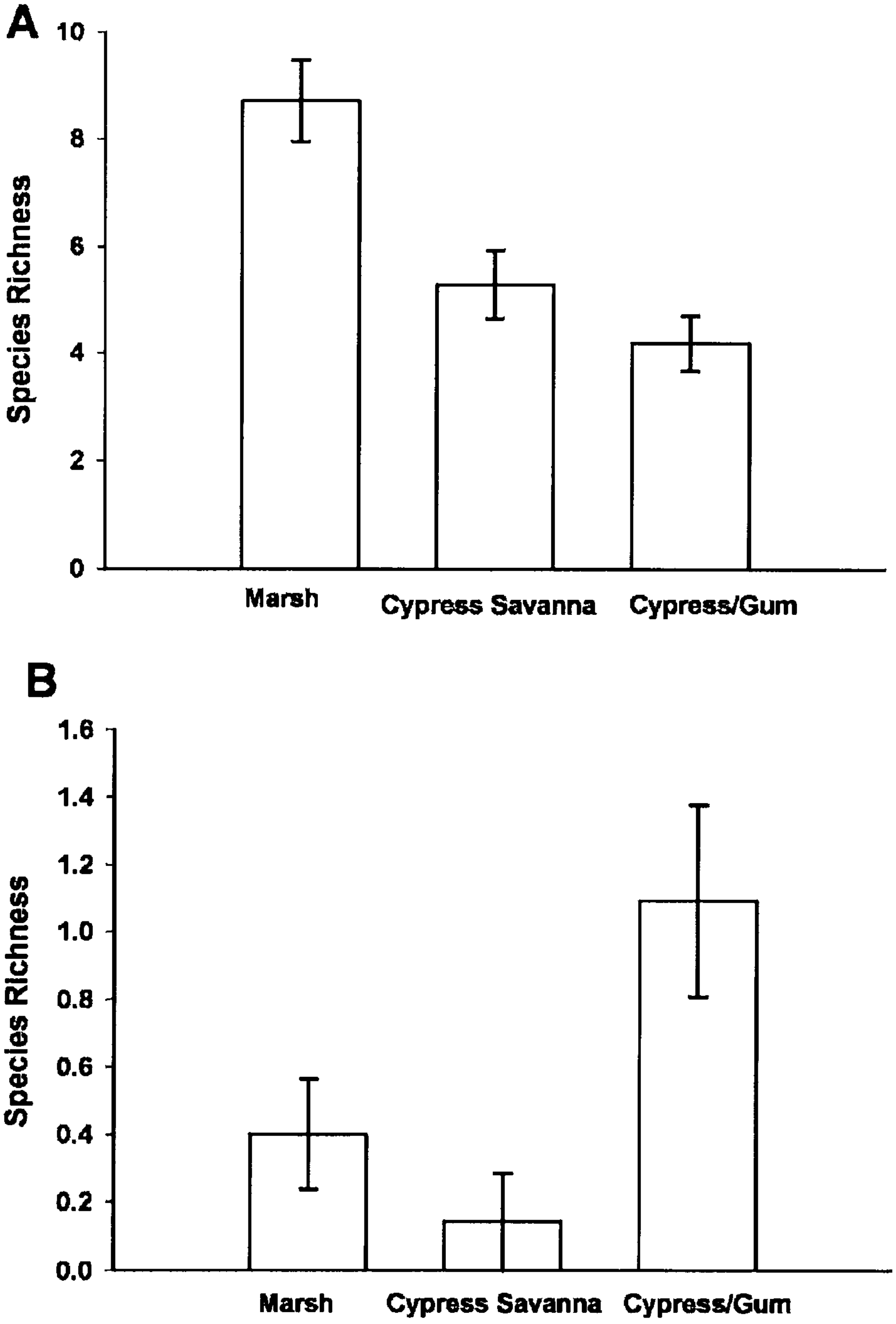

FIG. 3.—Comparison of mean (±SE) larval species richness of (a) anurans and (b) caudates captured in 28 isolated wetlands in southwestern Georgia from Jun. 2004 to May 2005 among three wetland types

variation in natural wetland systems and their role in supporting biodiversity. Past wetland mitigation and restoration efforts have often ignored or failed to maintain all of the components of functioning watersheds (National Research Council, 1995). In particular, many forested wetlands have been lost nationwide as the result of unsuccessful mitigation strategies (Sifneos *et al.*, 1992; National Research Council, 1995; Cole and Shafer, 2002). Our results suggest that, at least in terms of isolated wetlands, such practices could have

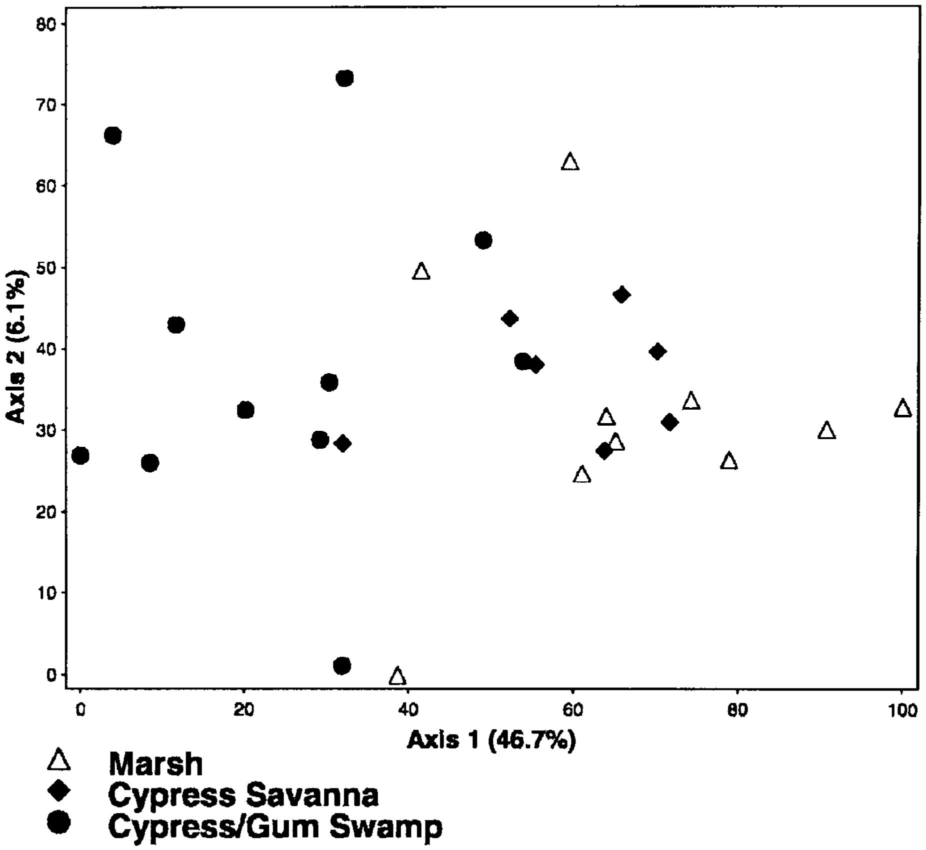

FIG. 4.—Detrended Correspondence Analysis of all amphibian species captured (represented by adults and larvae) in 28 isolated wetlands in southwestern Georgia from Jun. 2004 to May 2005 versus wetland type. Points represent individual wetlands categorized according to type

detrimental effects on regional amphibian diversity by eliminating preferred breeding and adult habitat of particular species. In addition to the protection of individual wetlands, terrestrial habitat for post-breeding adults and forested corridors which provide avenues for dispersal are also necessary to maintain functioning amphibian communities (Rothermel, 2004; Semlitsch and Bodie, 2003). Therefore, we recommend that future wetland protection and mitigation strategies within southwest Georgia seek to maintain the existence of all three wetland types within wetland complexes in order to maintain an intact amphibian community.

The amphibian community differences we observed among wetland types undoubtedly result from the large habitat differences among the types that have been reported by previous studies. In particular, canopy cover varies greatly among the wetland types from a dense canopy in cypress/gum swamps, to a relatively sparse canopy in cypress savannas, to marshes which completely lack overstory vegetation. These canopy cover differences in turn cause other habitat differences among the wetlands. Within cypress/gum swamps the dense canopy results in relatively low water temperatures, reduced growth of algal and herbaceous vegetation and low dissolved oxygen concentrations from the decomposition of leaf litter by microorganisms (Battle and Golladay, 2001). The lower numbers of anuran larvae we observed in these wetlands may be linked to the poor food quality and lower temperatures and dissolved oxygen levels of these wetlands, as development rate and size are strongly

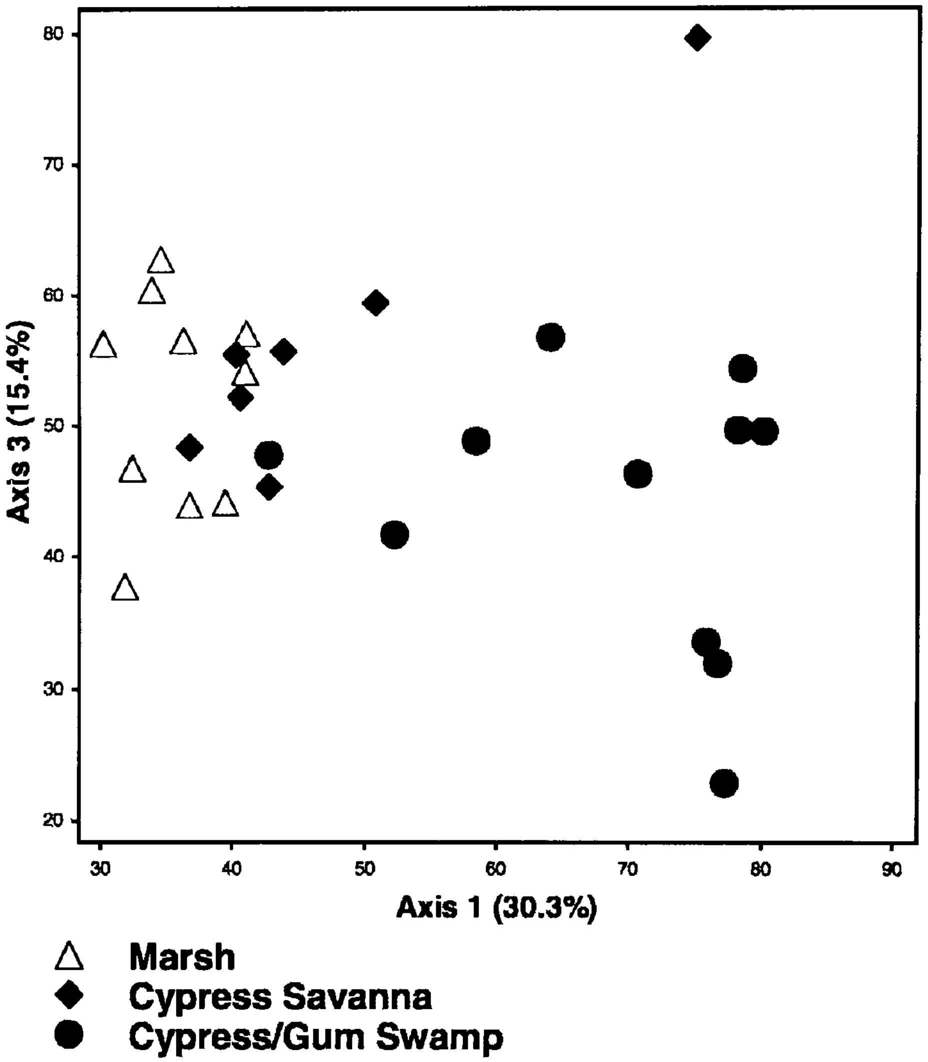

FIG. 5.—Detrended Correspondence Analysis of amphibian species (represented by larvae only) in 28 isolated wetlands in southwestern Georgia from Jun. 2004 to May 2005 versus wetland type. Points represent individual wetlands categorized according to wetland type

influenced by these factors (Smith-Gill and Berven, 1979; Mills and Barnhart, 1999; Alvarez and Nicieza, 2002; Doughty and Roberts, 2003). In addition, macroinvertebrate diversity and abundance are inversely related to canopy cover in southwest Georgia wetlands (Battle and Golladay, 2001). Amphibian community differences among wetland types also may be the result of greater abundance and diversity of invertebrate predators in marshes and savannas. Invertebrate predators play key roles in structuring larval amphibian communities, both directly through predation and indirectly by inducing costly predator-avoidance behaviors and morphological changes (*e.g.*, Relyea, 2000; Van Buskirk, 2000; Yurewicz, 2004). It is interesting to note that our observations of increased salamander diversity in cypress/gum swamps are not consistent with studies elsewhere that have found decreased amphibian species richness in forested wetlands (Skelly *et al.*, 1999; Skelly *et al.*, 2005).

In addition to canopy cover, large variations in hydroperiod also exist among the wetland types and range from short hydroperiod cypress savannas to intermediate hydroperiod marshes to cypress/gum swamps that occasionally hold water year-round (Liner, 2006). The relatively long hydroperiod of cypress/gum wetlands potentially explains why they contained more salamander species, particularly aquatic species, such as two-toed amphiuma (*Amphiuma means*) and greater siren (*Siren lacertina*) and those with long larval development periods such as the mole salamander. Aquatic salamanders can be significant predators of larval amphibians (Morin, 1981; Wilbur, 1987; Lawler, 1989), which may explain differences in anuran distributions between cypress/gum swamps and other wetland types, although additional data are needed to determine if this is indeed the case in our study wetlands. Alternatively, ovipositing females of some species avoid wetlands with predators and competitors, thus cypress/gum swamp species assemblages may differ from other wetland types because ovipositing anurans avoid breeding within them (*e.g.*, Resetarits and Wilbur, 1989, 1991). The lower amphibian species richness of cypress savannas was most likely related to the short hydroperiods of these wetlands. On average these wetlands contain standing water for only 130 d per year (Liner, 2006), making them inhospitable for aquatic salamanders and amphibians with long larval periods.

The differences we observed between larval and adult amphibian distributions were unexpected, and we suspect there are several potential explanations for this observation. These differences may be an artifact of differences in detection rates between methods biased towards detecting larvae (dipnetting, funnel traps) and methods biased towards detecting adults (frogloggers, crayfish traps, PVC pipes). Liner (2006) noted large variations in the detection rates for individual species among different methods in a subset of the study wetlands during the spring sampling period. Also, it is possible that the larvae of species with relatively short development periods (*i.e.*, *Gastrophryne carolinensis*) were not present during the sampling periods chosen for this study. It is also possible that these observations reflect real differences between non-breeding and breeding habitat. Differences between breeding and non-breeding amphibian distributions could result from differences in hydrologic condition among years. Amphibian breeding success is strongly tied to hydroperiod, which can fluctuate widely from year to year in isolated wetlands (Pechmann *et al.*, 1989). Alternatively, it is possible that some species use wetlands in which they do not breed either as dispersal corridors or as nonbreeding or foraging habitat. This is a likely explanation for our observations of American bullfrogs in marshes and cypress savannas, which typically do not hold water long enough for the larval development of this species (Liner, 2006). More information is needed about the distributions of amphibians outside of the breeding season to determine the importance of non-breeding wetlands to their persistence in the landscape.

Amphibian populations in isolated seasonal wetlands are highly variable from year to year (Pechmann *et al.*, 1991). Therefore, we recognize that a single year of study cannot provide definitive answers as to the mechanisms that drive amphibian community dynamics. Furthermore, a major limitation of using presence/absence data in wildlife studies is the difficulty in determining whether the nondetection of a species represents a true absence or merely the inability of a method to detect a species (MacKenzie, 2005). In this study, we assumed that by using multiple methods that were repeated within and across seasons, that the probability of a false absence is negligible and that the nondetection of a species represents a true absence of that species from a wetland. Despite these potential limitations, our results suggest wetlands of different types support different amphibian species. Our study emphasizes the importance of wetland diversity in supporting amphibian diversity. Southwest Georgia wetlands exist as a patchwork of wetlands of different types that collectively support a diverse amphibian fauna. If future wetland conservation efforts in this region are to succeed, they must recognize the importance all wetland types in supporting biological diversity.

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