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Importance of small isolated wetlands for herpetofaunal diversity in managed, young growth forests in the Coastal Plain of South Carolina

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Abstract

Freshwater wetlands support diverse and unique species assemblages, but the contribution of the smallest of these habitats to regional biodiversity continues to be underestimated, particularly within managed forests. We assessed and compared the richness, abundance, and diversity of herpetofauna at five small isolated wetlands (0.38–1.06 ha) imbedded within a commercial forest landscape in the South Carolina Coastal Plain. Continuous drift fences with pitfall traps that completely encircled the wetlands were used to sample entering and exiting herpetofauna. We also deployed coverboards to sample herpetofauna in the adjacent uplands. We captured 9186 individuals of 56 species (20 amphibians, 36 reptiles) from the five wetlands combined between 1996 and 1998. Although species richness and community composition were similar at the five sites, we found significant differences in herpetofaunal abundance and diversity among wetlands. These differences did not vary with wetland size but were related to environmental and habitat attributes of the surrounding upland stands. Amphibian abundance was positively correlated with basal area of upland conifers but negatively correlated with presence and size of hardwoods, relationships that appeared to be partially influenced by previous stand management. Amphibian diversity (H') increased with conifer diameter but decreased with increasing distance to nearest wetland. Reptile diversity was negatively correlated with upland canopy closure. Our data indicate that small isolated wetlands are focal points of herpetofaunal richness and abundance in managed coastal plain forests and contribute more to regional biodiversity than is implied by their small size or ephemeral hydrology. By incorporating small wetland values and functions into planning objectives, forest managers can significantly enhance the contribution of extensive young-growth forests to regional conservation of biodiversity.

Keywords: Amphibians; Forest management; Herpetofauna; Reptiles; Small isolated wetlands; South Carolina coastal plain

1. Introduction

Abundant rainfall and favorable topography have resulted in extensive wetlands formation in the southeastern United States (Hefner and Brown, 1985; Stanturf and Schoenholtz, 1998). Almost 50% of the 40 million hectares of wetlands in the conterminous United States are found in this region (Hefner and Brown, 1985). The Southeast also has experienced disproportionate losses of wetland habitat. Hefner and Brown (1985) estimate a 28% loss of wetland acreage in the region since colonial settlement, and within the last 30 years 84% of United

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States wetland losses have occurred in the Southeast (Hefner and Brown, 1985), primarily from agricultural conversion and urban development (Cubbage and Flather, 1993; Shepard et al., 1998).

The southeastern Coastal Plain supports the highest diversity of freshwater wetlands in North America (Sutter and Kral, 1994). Isolated wetlands are the primary natural lentic systems within this region. Supporting at least 18 distinct natural communities (Allard, 1990), these diverse habitats are defined as non-alluvial wetlands with variable hydroperiods occurring in basins or depressions with no permanent connections to above-ground stream or river systems (Sutter and Kral, 1994; Sharitz and Gresham, 1998). Water levels are controlled by rainfall, surface run-off, fluctuating water tables, and evapotranspiration. Thus, many isolated wetlands are ephemeral aquatic habitats that dry during periods of low precipitation (Sharitz and Gresham, 1998). Although the original extent of many isolated wetland communities in the Southeast is unknown, Sutter and Kral (1994) suggest these habitats are disappearing at a rate equal to or greater than that of either riverine or coastal wetlands.

The smallest isolated wetlands (e.g. $\leq$4 ha) are among the most challenging freshwater aquatic habitats from both jurisdictional and management perspectives (Gibbs, 1993; Dodd and Cade, 1998; Semlitsch and Bodie, 1998). Current and proposed federal thresholds on wetland development do not apply to areas below 4.0 and 1.2 ha, respectively (Kaiser, 1998; Semlitsch and Bodie, 1998). Additionally, small size, ephemeral hydrology, and complex wetland-upland mosaics often obscure locations and boundaries of small wetlands (Gibbs, 1993; Stout and Marion, 1993; Kirkman et al., 1998). Large numbers of small isolated wetlands in the southeastern United States are imbedded within industrial forest landscapes managed for fiber on short rotations (Marion and O'Meara, 1982; Stout and Marion, 1993; T.B. Wigley, unpublished data), presenting both challenges and opportunities for wetland conservation.

Perhaps because of their size and ephemeral hydrology, the biological importance of small isolated wetlands continues to be neglected (Moler and Franz, 1987; Dodd, 1992; Semlitsch and Bodie, 1998). This is despite the fact that small wetlands support diverse assemblages of vertebrate, invertebrate, and plant species (Moler and Franz, 1987; Mahoney et al., 1989; Hart and Newman, 1995; Semlitsch and Bodie, 1998), and are numerically dominant within many landscapes (Gibbs, 1993; Semlitsch and Bodie, 1998). Small ephemeral wetlands are particularly important habitats for herpetofauna adapted to seasonal hydroperiods and the absence of predatory fish (Morin, 1983; Semlitsch et al., 1996). For example, over a 5-year period 16,155 individuals of 42 species of amphibians and reptiles were captured from an ephemeral pond only 0.16 ha in size (Dodd, 1992). Because several endemic and rare species of herpetofauna are associated with isolated wetlands (Dodd, 1995), loss of these habitats may significantly alter regional biodiversity (Dodd, 1992; Semlitsch and Bodie, 1998).

If we seek to maintain diversity in managed landscapes, we must learn more about protecting species diversity in our young, even-aged forests (Sharitz et al., 1992; Moore and Allen, 1999). We are aware of only one study, however, that documents the abundance and diversity of herpetofauna at small isolated wetlands within a commercial forest setting (O'Neill, 1995). Additionally, most studies of isolated wetland herpetofauna have focused on single wetlands (Dodd, 1992; Semlitsch and Bodie, 1998), and direct comparisons of herpetofaunal abundance and diversity across a range of small isolated wetland sizes are lacking. The objectives of our study were to (1) assess the contribution of small isolated wetlands surrounded by managed, young growth forests to amphibian and reptile diversity in the South Carolina Coastal Plain; (2) compare herpetofaunal, environmental, and upland habitat attributes across a range of small wetland sizes; and (3) establish a baseline from which to monitor responses of isolated wetland herpetofaunal communities to changes in the surrounding upland stands.

2. Methods

2.1. Study area

We conducted our study on the Woodbury Tract, an 8000 ha peninsula of industrial forest at the confluence of the Pee Dee and Little Pee Dee rivers in Marion County, South Carolina (33°45′51″N, 79°14′50″W) on the Lower Atlantic Coastal Plain (Fig. 1). The portion of the tract between the two river floodplains consists

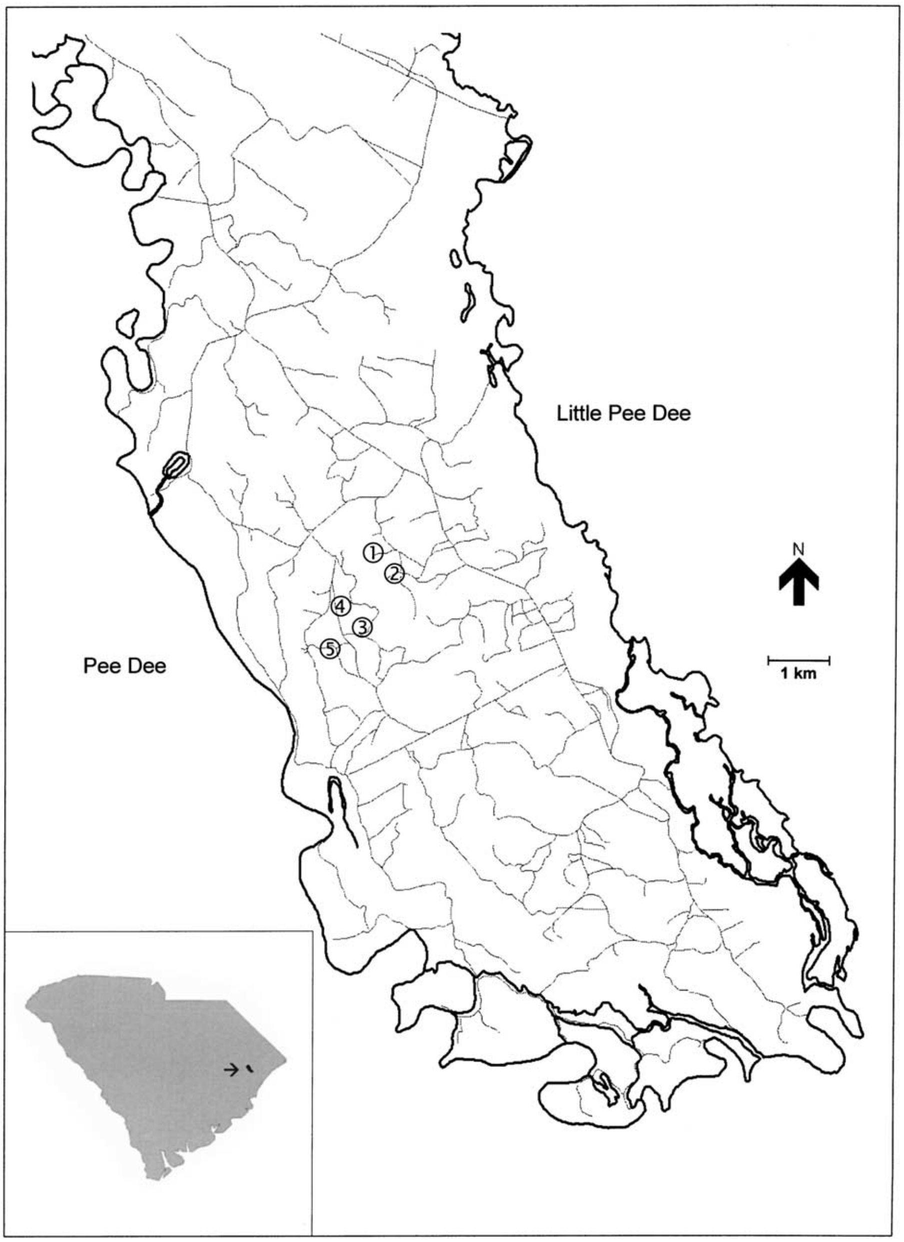

Fig. 1. Map of the Woodbury Tract study area in Marion County, South Carolina Coastal Plain with locations of wetland study sites: (1) 0.38 ha; (2) 0.47 ha; (3) 0.72 ha; (4) 1.06 ha; and (5) 0.59 ha.

of sandhill ridges dominated by stands of loblolly (*Pinus taeda*) and longleaf (*P. palustris*) pine ranging from recent clearcuts to mature trees over 50 years in age. The tract is heavily influenced by water, with numerous isolated wetlands interspersed among the sandhill ridges and seasonal flooding of rivers, creeks, and sloughs in lowland areas (Leiden et al., 1999). The resulting landscape is a complex mosaic of upland and aquatic habitats. Long-term daily mean temperatures and monthly mean precipitation in the area range from

6.7 °C and 90.4 mm in January to 26.9 °C and 140.5 mm in July (National Oceanic and Atmospheric Administration, 1992).

We used aerial photography and ground searches to select five small isolated wetlands, 0.38, 0.47, 0.59, 0.72, and 1.06 ha in size, from within the upland sandhills as study sites (Fig. 1). We chose to focus our sampling at these sites rather than invest less effort at more wetlands because brief or infrequent surveys underestimate both the richness and abundance of ephemeral wetland herpetofauna (Dodd, 1992). Although the wetlands are roughly circular, they do not exhibit the distinctive characteristics of Carolina bays (Sharitz and Gresham, 1998) and are best categorized as coastal plain small depression ponds (Sutter and Kral, 1994). Water inputs are limited to precipitation, runoff, and groundwater recharge. Wetland vegetation is similar among sites, with overstories dominated by pond cypress (*Taxodium distichum*), pond pine (*Pinus serotina*), black gum (*Nyssa sylvatica*), sweetgum (*Liquidambar styraciflua*), and red maple (*Acer rubrum*). Wetland basins support no submerged, emergent, or floating vegetation but contain a thick layer of decomposing leaves. Wetland margins support brushy plants, including blueberries (*Vaccinium* spp.), hollies (*Ilex* sp.), sweet bay (*Magnolia virginica*), common wax myrtle (*Myrica cerifera*), greenbrier (*Smilax* spp.), and fetterbush (*Lyonia lucida*). The surrounding uplands are dominated by 18–25-year-old stands of loblolly pine with turkey oak (*Quercus laevis*), southern red oak (*Quercus falcata*), and post oak (*Quercus stellata*) in the midstory. Distances between the five wetlands range from 402 to 1509 m.

2.2. Herpetofaunal sampling

We completely encircled each wetland with a continuous drift fence (Gibbons and Semlitsch, 1981; Dodd, 1992) to capture herpetofauna as they entered and exited the wetlands. Fences were constructed of 60 cm high aluminum flashing or silt fencing buried 10–15 cm in the ground (192, 226, 271, 302, and 366 m circumference). Paired pitfall traps (19 l plastic buckets) were buried on each side of the fences at 10 m intervals. We positioned drift fences just above the anticipated high water mark in the ecotone between wetland depressions and the upland stands. To sample the adjacent uplands, we arranged individually numbered plywood coverboards (0.61 m × 1.22 m; Grant et al., 1992) in linear arrays of 20 boards each, with three arrays equally spaced around each wetland. We placed the first board in each array at the wetland periphery and subsequent boards extended into the upland stand at 10 m intervals.

We checked pitfall traps and coverboards daily between 07.00 and 10.00 h, depending on season, from September 1996–August 1998 (0.38, 0.47, and 0.72 ha wetlands) or April 1997–August 1998 (0.59 and 1.06 ha wetlands). We identified the species, sex (when possible), and age-class (e.g. larvae, recent metamorph, juvenile, sub-adult, adult) of each capture. Salamanders, anurans (frogs and toads), and lizards were marked by toe-clipping (Ferner, 1979), but not for individual recognition. Snakes and turtles were transported to a field station at the study area and individually marked with 14 mm PIT tags (Russell and Hanlin, 1999) and shell notching (Cagle, 1939), respectively. We released marked individuals at least 5 m from the point of capture and on the opposite side of drift fences to minimize the probability of immediate recapture. All capture, handling, and marking protocols were approved by the Clemson University Animal Research Committee (ARC Protocol # 97-009).

2.3. Environmental and habitat attributes

We recorded daily precipitation and air temperatures (maximum/minimum) 1.5 m above ground level from plastic rain gauges and Taylor maximum/minimum thermometers, respectively, located at the periphery of each wetland. We measured water depth daily from a permanently fixed gauge in the deepest part of each wetland. In March and again in June 1998, we measured pH at four randomly located points in each wetland with an Oakton portable pH meter with automatic temperature compensation. Canopy closure was measured at five randomly selected points within each wetland with a spherical densiometer.

We characterized habitat characteristics of the upland stands surrounding each wetland by quantifying 17 variables. We recorded diameter at breast height (dbh) of all conifer and hardwood trees ≥12.5 cm. We sampled trees from 15 plots of

0.04 ha, randomly located within each stand. The number of trees per hectare, percent hardwood composition, and basal area of conifers and hardwoods were calculated for each plot. To characterize ground cover, we established 10 $1 m^2$ plots that were placed at 10 m intervals along three randomly located line transects (Mueller-Dombois and Ellenberg, 1974) in each stand (30 plots per stand). Ocular estimates of percent cover woody debris, bare soil, conifer and deciduous litter, moss, herbaceous plants, and shrubs ($\leq$1.5 m) were made for each plot. Canopy closure was measured at alternating plots along each transect. We measured leaf litter depth at the center of each plot with a ruler. Soil pH was measured at the first, fifth, and tenth plots along each transect with a Kelway portable meter. We calculated distance to nearest wetland using measurements taken from aerial photographs.

2.4. Statistical analysis

We determined amphibian and reptile richness, evenness (J'), and species abundance for each wetland, pooling captures from drift fences and coverboards (the latter accounted for only 2% of captures). We also calculated the Shannon diversity index (H') for amphibian and reptile communities at each wetland and used Student's *t*-test to determine significant differences in community diversity among sites (Brower et al., 1998). We used chi-square (χ^2) goodness-of-fit tests with Bonferroni simultaneous confidence intervals (Neu et al., 1974) to test the hypothesis that amphibians and reptiles were captured in proportion to wetland size. Expected values for the χ^2 analyses were based on proportional trapping effort among wetlands (i.e. the percentage of total effort made at a wetland $\times$ total captures for all wetlands) and observed values were the actual numbers of captures from each wetland. To assess the degree of species overlap among wetlands we calculated Sorenson Coefficients of Community Similarity (C_{C_S}; Brower et al., 1998) for all possible pairs. Because of the shorter sampling period at the 0.59 and 1.06 ha wetlands, captures were converted to standardized catch-per-unit effort measurements ((animals/trapweek) $\times$ 100). Juveniles were included (Dodd, 1992) and recaptures excluded from the data set for the above analyses.

We compared environmental and habitat attributes among wetlands and adjacent upland stands with analysis of variance (ANOVA). When an ANOVA yielded a significant *F*-statistic, we used Tukey's honestly significant difference (HSD) to identify significant differences among means. All variables were tested for normality (Shapiro–Wilk's *W*; SYSTAT, 1999) and log or square-root transformed when required (Sokal and Rohlf, 1981). We converted pH measurements to hydrogen ion concentrations before analysis. All data reported are nontransformed values.

We used Spearman rank correlations to examine patterns of herpetofaunal abundance and diversity in relation to differences in environmental and habitat attributes among sites. Weekly mean values, pooled across sites, were used to calculate correlations between environmental variables and herpetofaunal abundance. All other correlations were calculated using total numbers of captures or values of H' and site averages for each variable. We present means $\pm$ 1 S.E. and significance levels were set at $\alpha = 0.05$. Statistical analyses were performed with SYSTAT 8.0 (SYSTAT, 1999).

3. Results

3.1. Species richness, evenness, and diversity

We captured 56 species of herpetofauna (20 amphibians, 36 reptiles) from the five wetlands combined (Table 1). Four species (*Rana palustris*, *Clemmys guttata*, *Kinosternon baurii*, *Seminatrix pygaea*) are classified by the South Carolina Department of Natural Resources as Species of Special Concern (Table 1). We documented use of the wetlands or adjacent terrestrial stands for reproduction, as determined by the presence of larvae, recent metamorphs, hatchlings, or juveniles, for 15 amphibian species and 23 reptile species (68% of the total species assemblage; Table 1).

There were no consistent trends in the richness, evenness, or diversity of herpetofauna with respect to wetland size. Amphibian species richness ranged from a low of 16 at the 0.59 and 0.72 ha wetlands to a high of 19 at the 0.47 ha wetland (Table 2). Evenness (J') of amphibians, or the relative distribution of

Table 1
The species and total number of amphibians and reptiles captured at five small isolated wetlands from September 1996–August 1998, Woodbury Tract, South Carolina Coastal Plain[a]

Species	Wetland (ha)					Total
	0.38	0.47	0.59	0.72	1.06	
Amphibians						
Salamanders						
Ambystoma mabeei[b]	6/0	3/0	0/0	0/0	0/0	9/0
Ambystoma opacum[b]	0/0	1/0	0/0	1/1	0/0	2/1
Eurycea quadridigitata	0/0	2/0	0/0	0/0	0/0	2/0
Notophthalmus viridescens[b]	2/0	10/2	0/0	6/0	1/0	19/2
Pseudotriton montanus[b]	95/5	12/1	25/0	2/1	11/1	145/8
Anurans						
Acris gryllus[b]	249/6	65/0	465/15	201/4	318/12	1298/37
Bufo quercicus[b]	52/12	5/3	7/0	2/0	21/1	87/16
Bufo terrestris[b]	336/82	329/57	557/117	241/78	535/112	1998/446
Gastrophryne carolinensis[b]	29/3	53/6	67/3	26/0	172/14	347/26
Hyla chrysocelis	1/0	1/0	1/0	0/0	1/0	4/0
Hyla cinerea[b]	1/0	1/0	1/0	1/0	2/0	6/0
Hyla femoralis[b]	10/0	1/0	1/0	4/0	3/0	19/0
Hyla squirella	1/0	1/0	1/0	0/0	1/0	4/0
Pseudacris crucifer	2/0	2/0	1/0	2/0	3/0	10/0
Rana catesbeiana[b]	4/1	4/0	17/4	3/0	7/1	35/6
Rana clamitans[b]	73/15	145/15	212/20	46/5	179/26	655/81
Rana palustris[b,c]	0/0	3/1	22/12	2/0	4/5	31/18
Rana utricularia[b]	324/16	1274/65	246/21	93/3	1267/43	3204/148
Rana virgatipes[b]	30/6	20/8	194/37	29/0	34/6	307/57
Scaphiopus holbrookii	1/1	0/0	2/0	1/0	2/0	6/1
Total amphibians	1216/147	1932/158	1819/229	660/92	2561/221	8188/847
Reptiles						
Turtles						
Chelydra serpentina[b]	5/6	3/0	0/0	2/3	2/0	12/9
Clemmys guttata[b,c]	12/7	0/0	2/1	2/0	8/5	24/13
Deirochelys reticularia[b]	0/0	0/0	2/1	0/0	0/0	2/1
Kinosternon baurii[b,c]	1/0	0/0	3/0	0/0	0/0	4/0
Kinosternon subrubrum[b]	8/2	1/1	8/0	1/0	18/4	36/7
Sternotherus odoratus[b]	1/1	2/0	12/0	3/0	6/0	24/1
Terrapene carolina	0/0	9/0	3/0	5/4	2/1	19/5
Trachemys scripta[b]	12	0/0	6/0	0/0	8/8	15/10
Lizards						
Anolis carolinensis[b]	19/0	18/1	21/0	7/0	51/1	116/2
Cnemidophorus sexlineatus	0/0	6/0	2/0	27/1	1/0	36/1
Eumeces fasciatus[b]	1/0	3/0	2/0	2/0	1/0	9/0
Eumeces inexpectatus[b]	10/1	19/1	3/0	36/2	3/0	71/4
Eumeces laticeps[b]	12/1	12/1	6/0	21/1	14/0	65/3
Ophisaurus attenuatus	0/0	1/0	0/0	0/0	0/0	1/0
Ophisaurus ventralis	0/0	0/0	1/1	0/0	0/0	1/1
Scincella lateralis[b]	91/0	77/0	16/0	36/1	28/0	248/1
Snakes						
Agkistrodon contortrix	0/0	0/0	0/0	0/0	1/0	1/0
Carphophis amoenus[b]	34/3	15/0	16/1	45/4	24/0	134/8
Cemophora coccinea[b]	1/0	6/0	8/0	10/2	3/2	28/4

Table 1 (*Continued*)

Species	Wetland (ha)					Total
	0.38	0.47	0.59	0.72	1.06	
Coluber constrictor[b]	4/0	10/0	14/0	3/0	13/1	44/1
Elaphe obsoleta[b]	0/0	0/0	0/0	2/0	0/0	2/0
Farancia abacura[b]	1/0	0/0	0/0	3/0	3/1	7/1
Heterodon platyrhinos	0/0	1/0	2/0	0/0	1/0	4/0
Lampropeltis getula	1/0	1/1	0/0	1/0	0/0	3/1
Lampropeltis triangulum	0/0	0/0	0/0	1/0	2/0	3/0
Masticophis flagellum	0/0	0/0	0/0	1/0	0/0	1/0
Nerodia erythrogaster[b]	0/0	3/0	5/1	3/0	2/0	13/1
Nerodia fasciata[b]	4/0	1/0	1/0	2/0	1/0	9/0
Nerodia taxispilota[b]	3/0	2/1	2/0	1/0	2/0	10/1
Opheodrys aestivus	2/0	2/1	0/0	2/0	0/0	6/1
Seminatrix pygaea[b,c]	0/0	1/0	0/0	0/0	0/0	1/0
Storeria dekayi	0/0	1/0	0/0	1/0	2/0	4/0
Storeria occipitomaculata[b]	7/0	4/0	5/0	3/0	10/0	29/0
Thamnophis sauritus	0/0	0/0	2/0	1/0	0/0	3/0
Thamnophis sirtalis[b]	0/0	3/0	2/0	2/0	3/0	10/0
Virginia valeriae	1/0	2/0	0/0	0/0	0/0	3/0
Total reptiles	219/23	203/7	144/5	223/18	209/23	998/76
Grand total	1435/170	2135/165	1963/234	883/110	2770/244	9186/923

[a] The first and second numbers represent unmarked individuals and recaptures, respectively.
[b] Reproduction documented by the presence of larvae, hatchlings, recent metamorphs, or juveniles.
[c] Species of Special Concern (South Carolina Department of Natural Resources, 1995).

Table 2
Number of species captured, evenness index (J'), and Shannon diversity index (H') for amphibian and reptile communities from five small isolated wetlands and adjacent upland stands, Woodbury Tract, South Carolina Coastal Plain[a]

Wetland (ha)	Community	Species captured	J'	H'
0.38	Amphibians	17	0.651	0.801 a
	Reptiles	21	0.686	0.907 I
0.47	Amphibians	19	0.398	0.509 b
	Reptiles	25	0.730	1.02 II
0.59	Amphibians	16	0.649	0.781 a
	Reptiles	24	0.884	1.22 IV
0.72	Amphibians	16	0.597	0.719 c
	Reptiles	27	0.755	1.08 II,III
1.06	Amphibians	17	0.523	0.644 d
	Reptiles	25	0.794	1.11 III

[a] Different letters, a–d (amphibians), or roman numbers, I–IV (reptiles), within columns denote significant differences in communities of same type among wetlands ($P \leq 0.05$).

individuals among species, was lowest at the 0.47 ha (second-smallest) wetland and highest at the 0.38 ha (smallest) wetland (Table 2). Likewise, amphibian diversity (H') was lowest at the 0.47 ha wetland and highest at the 0.38 ha wetland (Table 2). Differences in amphibian diversity (H') were significant for all wetland pairs ($3.3 \leq t \leq 17.8, P \leq 0.05$) except between the 0.38 and 0.59 ha wetlands (Table 2).

Reptile species richness ranged from a low of 21 at the smallest (0.38 ha) wetland to a high of 27 at the second-largest (0.72 ha) wetland (Table 2). Evenness (J') of reptiles ranged from 0.686 at the 0.38 ha wetland to a high of 0.884 at the 0.59 ha wetland (Table 2). Reptile diversity (H') was high for all five wetlands, ranging from 0.907 (0.38 ha wetland) to 1.22 (0.59 ha wetland). Diversity (H') of reptiles was significantly different among wetland pairs ($1.8 \leq t \leq 6.7, P \leq 0.05$) except that the 0.72 ha wetland was not statistically different from either the 0.47 or 1.06 ha wetlands (Table 2).

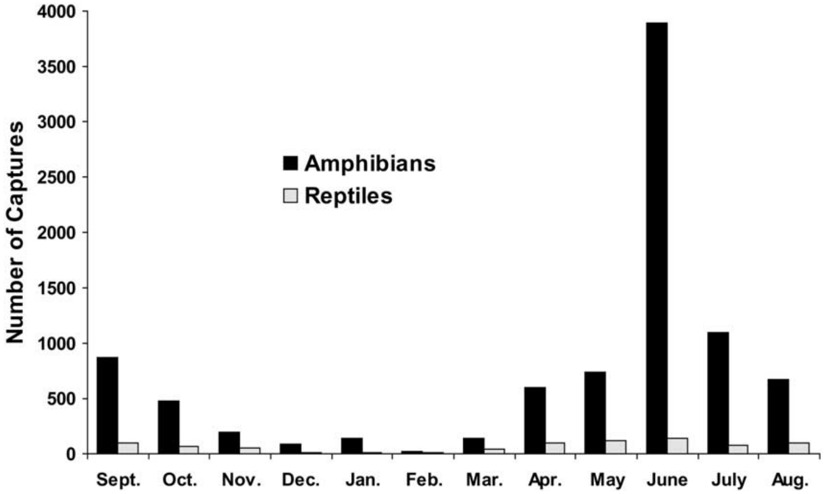

Fig. 2. Monthly captures of amphibians and reptiles from small isolated wetlands at the Woodbury Tract, South Carolina Coastal Plain, September 1996–August 1998.

3.2. Community composition

A total of 8188 individual amphibians was captured 9035 times (Table 1). Amphibians entered and exited the wetlands throughout the year, but almost 90% of captures occurred between April and September (Fig. 2). Although amphibian abundance was highest at the largest wetland (Table 1), the overall distribution of captures was disproportionate to wetland size. Total captures of amphibians were significantly different among the five wetlands ($\chi^2 = 899.7, P < 0.001$), with more amphibians captured at the three smallest wetlands (0.38, 0.47, and 0.59 ha) than expected ($P < 0.05$) and fewer amphibians captured at the second-largest (0.72 ha) wetland than expected ($P < 0.05$). Anurans were the dominant amphibians at all five wetlands (Table 1). *Rana utricularia* was captured most often and composed 37% of all amphibian captures, followed by *Bufo terrestris* (27%), *Acris gryllus* (15%), *Rana clamitans* (8%), *Gastrophryne carolinensis* (4%), and *Rana virgatipes* (4%). The numerical dominance of *R. utricularia* at the 0.47 and 1.06 ha wetlands (Table 1) largely contributed to the lower values of evenness and diversity for these sites (Table 2). Of the five species of salamanders captured, only *Pseudotriton montanus* was relatively common (2% of captures; Table 1).

A total of 998 individual reptiles was captured 1074 times (Table 1). Reptiles were captured in relatively low numbers throughout the year but rarely were encountered between December and February (Fig. 2). Total captures of reptiles were significantly different among wetlands ($\chi^2 = 21.9, P < 0.001$), with more reptiles captured from the 0.38 ha wetland than expected ($P < 0.05$). Lizards were the most abundant reptiles at all sites, except at the 0.59 ha wetland, where snakes dominated reptile captures (Table 1). *Scincella lateralis* was most abundant and composed 24% of all reptile captures, followed by *Carphophis amoenus* (13%), *Anolis carolinensis* (11%), *Eumeces inexpectatus* (7%), *Eumeces laticeps* (6%), and *Coluber constrictor* (4%). Captures of turtles typically were characterized by a relatively small number of individuals recaptured multiple times. Most (75%) species of snakes were represented by $\leq$10 individual captures.

Sorenson Coefficients of Similarity indicated a high degree of herpetofaunal species overlap among all five wetlands (Table 3). The two largest wetlands (0.72 and 1.06 ha) exhibited the highest degree of community similarity and the 0.47 and 0.59 ha wetlands exhibited the lowest degree of similarity (Table 3).

3.3. Environmental and habitat attributes

Daily maximum air temperatures were significantly higher ($F = 3.6, P = 0.007$, 4 d.f.) at the 0.72 ha wetland than at the other four sites, but there were no

Table 3
Sorenson coefficient of community similarity (C_{C_S}) for herpetofaunal communities from five small isolated wetlands and adjacent upland stands, Woodbury Tract, South Carolina Coastal Plain[a]

	Wetland (ha)			
	0.38	0.47	0.59	0.72
0.47	0.805			
0.59	0.795	0.786		
0.72	0.790	0.828	0.795	
1.06	0.825	0.837	0.878	0.871

[a] Values closer to 1.0 indicate greater community similarity between wetlands.

significant differences among wetlands in daily minimum air temperature, precipitation, or water depth (Table 4). All five wetlands were acidic, and pH was significantly lower at the 0.47 ha wetland than at the other four sites ($F = 5.2, P = 0.008$, 4 d.f.; Table 4). Canopy closure was extensive (96–99%) within all five wetlands (Table 4).

Attributes of the upland stands surrounding each wetland varied considerably (Table 4). Structure of the upland stands adjacent to the 0.72 ha wetland were markedly different from that of the other sites, including fewer trees per hectare ($F = 16.4, P = 0.0002$, 4 d.f.), lower basal area of conifers ($F = 9.6$, $P = 0.002$, 4 d.f.), and less conifer litter ($F = 9.2$,

Table 4
Environmental and habitat attributes of small isolated wetlands and adjacent upland stands, Woodbury Tract, South Carolina Coastal Plain[a]

	Wetland (ha)				
	0.38	0.47	0.59	0.72	1.06
Maximum air temperature (°C)	27.6 ± 0.5 a (8.0–42.0)	27.6 ± 0.5 a (9.0–45.0)	27.5 ± 0.5 a (9.0–40.0)	29.6 ± 0.5 b (9.0–42.0)	27.5 ± 0.5 a (10.0–40.0)
Minimum air temperature (°C)	14.4 ± 0.5 a (−5.0–25.0)	14.5 ± 0.5 a (−5.0–28.0)	14.8 ± 0.5 a (−5.0–26.0)	13.3 ± 0.5 a (−6.0–25.0)	14.7 ± 0.5 a (−5.0–26.0)
Rainfall (mm)	7.3 ± 1.2 a (0.0–116.0)	8.6 ± 1.3 a (0.0–130.0)	8.6 ± 1.4 a (0.0–148.0)	8.6 ± 1.4 a (0.0–132.0)	8.1 ± 1.3 a (0.0–142.0)
Maximum water depth (cm)	13.7 ± 0.8 a (0.0–35.8)	15.6 ± 0.9 a (0.0–39.5)	12.8 ± 0.9 a (0.0–47.0)	14.9 ± 1.0 a (0.0–51.0)	14.6 ± 1.1 a (0.0–64.0)
Wetland pH	4.3 ± 0.1 a (4.2–4.3)	4.0 ± 0.1 b (3.9–4.1)	4.3 ± 0.03 a (4.2–4.3)	4.2 ± 0.1 ab (4.2–4.3)	4.3 ± 0.1 a (4.1–4.4)
Wetland canopy closure (%)	98.9 ± 1.1 a (94.5–100)	96.6 ± 2.5 a (87.6–100)	99.5 ± 0.5 a (97.6–100)	96.0 ± 2.9 a (84.9–100)	97.9 ± 1.3 a (94.0–100)
Distance to nearest wetland (m)	60.4	160.9	80.5	80.5	120.7
Tree diameter (dbh; cm)					
Conifer	21.8 ± 0.9 a (12.7–36.1)	18.9 ± 1.0 a (12.7–33.8)	22.4 ± 1.0 a (12.7–32.5)	21.6 ± 1.0 a (12.7–32.5)	21.1 ± 0.6 a (12.7–33.3)
Deciduous	17.4 ± 1.0 a (12.7–24.5)	13.6 ± 7.3 a (12.7–35.6)	17.3 ± 1.1 a (12.7–25.9)	19.6 ± 1.9 a (12.7–32.0)	9.9 ± 5.0 a (13.2–19.8)
Trees per hectare	448.1±31.4 ab (148.3–790.7)	556.8±45.8 a (148.3–889.6)	342.6±34.9 bc (148.3–543.6)	214.2±21.6 c (49.4–543.6)	504.1±30.2 a (197.7–840.1)
Hardwood component (%)	19.6 ± 4.8 ab (15.6–27.5)	8.8 ± 4.4 a (0.0–14.0)	22.3 ± 8.6 ab (10.0–38.9)	47.4 ± 16.6 b (30.0–80.7)	3.5 ± 2.6 a (0.0–8.5)
Basal area (m^2/ha)					
Conifer	13.5 ± 1.0 a (3.9–27.9)	14.3 ± 1.7 a (1.1–31.9)	10.6 ± 2.0 ab (1.0–21.0)	3.7 ± 0.9 b (0.0–13.6)	17.0 ± 2.2 a (4.0–44.6)
Hardwood	2.0 ± 0.1 ab (0.0–5.9)	1.8 ± 1.1 ab (0.0–9.3)	1.6 ± 0.5 ab (0.0–6.9)	3.1 ± 1.2 a (0.0–13.2)	0.3 ± 0.2 b (0.0–2.2)

Table 4 (*Continued*)

	Wetland (ha)				
	0.38	0.47	0.59	0.72	1.06
Upland canopy closure (%)	97.9 ± 0.9 a (88.8–100.0)	91.3 ± 4.9 ab (25.1–100.0)	84.7 ± 5.1 b (36.8–100.0)	85.6 ± 3.1 b (63.3–98.9)	90.3 ± 2.6 ab (70.6–99.7)
Woody cover (%)	4.9 ± 0.7 a (0.0–15.0)	2.2 ± 0.6 b (0.0–10.0)	4.2 ± 0.9 abc (0.0–25.0)	2.0 ± 0.4 bc (0.0–5.0)	5.7 ± 1.1 a c (0.0–25.0)
Bare soil (%)	0.3 ± 0.2 a (0.0–5.0)	6.1 ± 1.6 bd (0.0–30.0)	5.4 ± 2.5 abcd (0.0–60.0)	11.2 ± 3.8d (0.0–70.0)	0.8 ± 0.4 ab (0.0–10.0)
Conifer litter (%)	66.0 ± 4.0 a (2.5–95.0)	38.4 ± 5.5 bc (0.0–97.5)	44.2 ± 5.0 b (0.0–100.0)	25.8 ± 4.4 c (0.0–80.0)	45.1 ± 5.0 b (0.0–95.0)
Deciduous litter (%)	17.2 ± 3.3 a (0.0–70.0)	25.4 ± 4.8 a c (0.0–90.0)	37.7 ± 4.0 bc (0.0–100.0)	51.2 ± 4.7 b (0.0–97.5)	34.4 ± 5.0 bc (0.0–100.0)
Moss (%)	2.5 ± 1.1 ab (0.0–25.0)	0.8 ± 0.5 a (0.0–10.0)	4.8 ± 2.2 ab (0.0–50.0)	6.3 ± 1.7 b (0.0–30.0)	6.2 ± 2.2 ab (0.0–30.0)
Herbaceous plants (%)	0.4 ± 0.2 a (0.0–5.0)	7.6 ± 1.9 b (0.0–25.0)	1.3 ± 0.5 a (0.0–10.0)	0.8 ± 0.1 a (0.0–25)	1.2 ± 0.4 a (0.0–5.0)
Shrubs (<1.5 m; %)	8.7 ± 2.8 a (0.0–60.0)	19.5 ± 4.5 b (0.0–80.0)	2.4 ± 1.2 a (0.0–25.0)	3.5 ± 1.3 a (0.0–27.5)	6.8 ± 2.8 a (0.0–50.0)
Litter depth (mm)	29.7 ± 1.5 a c (15.0–40.0)	21.3 ± 2.0 b (10.0–50.0)	27.2 ± 2.0 abc (0.0–45.0)	21.2 ± 2.3 b (2.5–40.0)	32.5 ± 2.2 c (10.0–60.0)
Soil pH	6.3 ± 0.1 a (5.6–6.6)	6.6 ± 0.1 ab (6.2–6.8)	6.8 ± 0.1 b (6.6–7.0)	6.5 ± 0.2 ab (5.8–7.0)	6.8 ± 0.1 b (6.6–7.0)

[a] Mean values (±S.E.) followed by the same letter (a, b, c, d) are not significantly different across rows by Tukey's HSD ($P \geq 0.05$). Ranges are in parentheses.

$P < 0.0001$, 4 d.f.), but higher percent hardwoods ($F = 4.6, P = 0.02$, 4 d.f.), higher basal area of hardwoods ($F = 2.9, P = 0.05$, 4 d.f.), higher percent cover of deciduous litter ($F = 8.6, P < 0.0001$, 4 d.f.), and higher percentage of bare soil ($F = 4.7$, $P = 0.001$, 4 d.f.; Table 4). The uplands adjacent to the 0.38 ha wetland had higher canopy closure ($F = 3.2, P = 0.02$, 4 d.f.), higher percent cover of conifer litter ($F = 9.2, P \leq 0.0001$, 4 d.f.), and lower soil pH ($F = 4.6, P = 0.004$, 4 d.f.) than the other four sites (Table 4). The uplands surrounding the 0.47 ha wetland had lower percent cover of moss ($F = 2.5, P = 0.05$, 4 d.f.) but more trees per hectare ($F = 16.4, P = 0.0002$, 4 d.f.), higher percent cover of herbaceous plants ($F = 12.0, P < 0.0001$, 4 d.f.), and higher percent cover of shrubs ($F = 6.9$, $P < 0.0001$, 4 d.f.) than the other four sites (Table 4), the latter resulting from a dense ring of *Lyonia lucida* in the wetland-upland ecotone. Upland litter depth was highest at the 0.38 and 1.06 ha wetlands and lowest at the 0.47 and 0.59 ha wetlands ($F = 6.2, P < 0.0001$, 4 d.f.; Table 4).

The number of amphibian captures increased significantly with precipitation and temperature (maximum and minimum), whereas reptile captures were positively correlated only with maximum air temperature (Table 5). Reptile captures also decreased significantly with increasing wetland depth (Table 5).

Differences among wetlands in herpetofaunal abundance and diversity were related to variation in habitat attributes. Amphibian abundance was positively correlated with basal area of conifers but negatively correlated with diameter, basal area, and percentage of hardwoods (Table 5). Diversity (H') of amphibians was positively correlated with conifer diameter but negatively correlated with increasing distance to nearest wetland (Table 6). Abundance of reptiles was not significantly correlated with any

Table 5
Relationships between environmental and habitat attributes and captures of amphibians and reptiles from small isolated wetlands at the Woodbury Tract, South Carolina Coastal Plain, 1996–1998[a]

Variable	Amphibians		Reptiles	
	r_s	P	r_s	P
Maximum air temperature	0.349	0.007	0.297	0.024
Minimum air temperature	0.342	0.009	0.213	0.108
Rainfall	0.325	0.002	−0.132	0.325
Water depth	−0.184	0.167	−0.384	0.003
Wetland pH	0.112	0.858	0.671	0.215
Wetland canopy closure	0.200	0.747	0.300	0.624
Conifer dbh	−0.500	0.391	0.300	0.624
Deciduous dbh	−1.00	0.000	−0.300	0.624
Trees per hectare	0.800	0.104	−0.300	0.624
Hardwood (%)	−0.900	0.037	−0.100	0.873
Basal area (conifer)	0.900	0.037	0.100	0.873
Basal area (hardwood)	−0.900	0.037	−0.600	0.285
Upland canopy closure	0.100	0.873	−0.600	0.285
Woody cover	0.600	0.285	0.500	0.391
Bare soil	−0.300	0.624	−0.200	0.747
Conifer litter	0.300	0.624	0.200	0.747
Deciduous litter	−0.300	0.624	0.500	0.391
Moss	−0.300	0.624	0.700	0.188
Herbaceous plants	0.600	0.285	−0.100	0.873
Shrubs	0.300	0.624	−0.700	0.188
Litter depth	0.600	0.285	0.500	0.391
Soil pH	0.718	0.172	0.667	0.219
Distance to nearest wetland	0.718	0.172	−0.051	0.935

[a] Values are based on Spearman rank correlations (r_s).

habitat attribute, but reptile diversity (H') was positively correlated with soil pH and negatively correlated with upland canopy closure (Table 6).

4. Discussion

Species inventories provide the essential foundation for conserving biological diversity (Dodd, 1992; Oliver and Beattie, 1993) and even acquiring data on species perceived to be common is an important aspect of conservation efforts (Dodd and Franz, 1993; Gibbons et al., 1997). The Woodbury Tract supports the highest known richness of herpetofauna in South Carolina with the exception of the US Department of Energy's Savannah River Site, a much larger tract where ecological research has been conducted since the 1950s (Gibbons et al., 1997; Leiden et al., 1999). The 56 species documented from our five wetland sites represent 74% (20/27) and 80% (36/45) of the amphibians and reptiles, respectively, known to occur within the study area (Leiden et al., 1999). In comparison, simultaneous surveys for herpetofauna in neighboring upland stands with similar age and structure characteristics but lacking small isolated wetlands revealed the presence of only eight amphibian and 17 reptile species (Y.A. Leiden, personal communication).

Because captures of amphibians and reptiles fluctuate with temporal variations in environmental conditions, long-term sampling (i.e. years or decades) may be necessary to fully characterize patterns and variability of herpetofaunal richness, abundance, and diversity at isolated wetlands (Pechmann et al., 1991; Semlitsch et al., 1996; Gibbons et al., 1997). Thus, we offer our data as representing a "snapshot" of small wetland herpetofaunal communities within a managed forest landscape. However, other short- and long-term surveys of coastal plain small wetlands (0.1–2.5 ha) have yielded comparable numbers of amphibian

Table 6
Relationships between environmental and habitat attributes and diversity (H') of amphibians and reptiles from small isolated wetlands at the Woodbury Tract, South Carolina Coastal Plain, 1996–1998[a]

Variable	Amphibians		Reptiles	
	r_s	P	r_s	P
Maximum air temperature	0.000	1.000	−0.633	0.252
Minimum air temperature	−0.100	0.873	0.700	0.188
Rainfall	−0.472	0.450	0.447	0.450
Water depth	−0.800	0.104	−0.400	0.505
Wetland pH	0.671	0.215	0.335	0.581
Wetland canopy closure	0.600	0.285	0.300	0.624
Conifer dbh	0.900	0.037	0.300	0.624
Deciduous dbh	0.600	0.285	−0.300	0.624
Trees per hectare	−0.600	0.285	−0.300	0.624
Hardwood (%)	0.500	0.391	0.100	0.873
Basal area (conifer)	−0.500	0.391	−0.100	0.873
Basal area (hardwood)	0.300	0.624	−0.600	0.285
Upland canopy closure	0.000	1.000	−0.900	0.037
Woody cover	0.200	0.747	0.100	0.873
Bare soil	−0.500	0.391	0.200	0.747
Conifer litter	0.500	0.391	−0.200	0.747
Deciduous litter	0.100	0.873	0.700	0.188
Moss	0.100	0.873	0.500	0.391
Herbaceous plants	−0.700	0.188	0.400	0.501
Shrubs	−0.400	0.505	−0.800	0.104
Litter depth	0.200	0.747	0.100	0.873
Soil pH	−0.410	0.493	0.872	0.054
Distance to nearest wetland	−0.975	0.005	0.205	0.741

[a] Values are based on Spearman Rank correlations (r_s).

(16–27) and reptile (22–26) species (Dodd, 1992; Cash, 1994; O'Neill, 1995; citations in Semlitsch and Bodie, 1998), indicating that our data are representative of the region. Clearly, small isolated wetlands on the Woodbury Tract, and those within other intensively managed forests (O'Neill, 1995; T.B. Wigley, unpublished data) of the southeastern Coastal Plain make a contribution to herpetofaunal diversity that is disproportionate to either their size or ephemeral hydrology. The capture of several South Carolina Species of Special Concern underscores the importance of these habitats for conserving regional biodiversity.

Values of species richness and diversity are useful measures of community composition and structure but their limitations must be recognized (Magurran, 1988; Noss, 1990; Dodd, 1992). Also, constraints on sample size limit the scope of our data. Nevertheless, this study represents one of the few efforts to compare herpetofaunal abundance and diversity among coastal plain small wetlands with intensive, sustained sampling. Although species richness and composition were similar at the five sites, we found significant differences among wetlands in the abundance and diversity of herpetofauna. These differences did not vary with wetland size, but were related to variation in upland habitat attributes. Because large isolated wetlands (e.g. >4.0 ha; Semlitsch and Bodie, 1998) tend to be more permanent and support a greater variety of fish and invertebrate predators, they may support less diverse or abundant amphibian assemblages than small wetlands (Moler and Franz, 1987; Semlitsch et al., 1996). However, our results suggest that among small wetlands, variations in size may be unimportant when compared to the influence of wetland or upland habitat conditions. Amphibian diversity increased among wetlands with increasing conifer diameter. Amphibian abundance also varied positively among wetlands with the diameter of conifers in the surrounding upland stands but was negatively correlated with the presence, diameter, and basal area of hardwoods. The latter trend was most evident at the 0.72 ha wetland, which exhibited amphibian species richness comparable with the other four sites but yielded only 54% of the captures from the smallest wetland. When compared to the other sites, the 0.72 ha wetland also had significantly fewer trees per hectare and lower basal area of conifers but a conspicuously higher hardwood component in its surrounding upland stands.

The negative relationship between amphibian abundance and upland hardwood composition in our study conflicts with previous reports (Bennett et al., 1980; deMaynadier and Hunter, 1995; Hanlin et al., 2000), but we believe this finding largely reflects a historical artifact of stand management unique to the 0.72 ha wetland. The uplands surrounding this wetland were not replanted after the previous harvest but allowed to regenerate naturally (A.W. Smith, personal communication), resulting in a stand dominated by scrub oaks with only scattered residual pines. In contrast, the other four wetlands, surrounded by densely stocked pine plantations, yielded 46–75% more individual amphibians. The sparse pine overstory adjacent to the 0.72 ha wetland resulted in significantly higher maximum air temperatures and reduced ground cover, factors that may limit the suitability of surrounding uplands for amphibians during the non-breeding season (deMaynadier and Hunter, 1995; Semlitsch, 1998). However, as conifers eventually reestablish themselves in the uplands surrounding the 0.72 ha wetland, a process accelerated at the other four sites by replanting, we suspect concomitant increases in amphibian abundance will occur.

The abundance and diversity of reptiles also were unrelated to wetland size. The disproportionately large number of reptiles at the smallest wetland is largely explained by captures of *Scincella lateralis* in the surrounding uplands. Unlike many species of coastal plain lizards, *S. lateralis* is most abundant in wooded habitats with a thick layer of ground litter (Gibbons and Semlitsch, 1991), and its abundance at the 0.38 ha wetland may reflect the significantly greater upland canopy closure and conifer litter at this site. In general, however, the negative correlation of reptile species diversity with increasing canopy closure probably reflects the association of many coastal plain reptiles (e.g. *Eumeces inexpectatus*, *Cnemidophorus sexlineatus*) with more open or disturbed habitats (Gibbons and Semlitsch, 1991; Greenberg et al., 1994; Russell et al., 1999).

The high diversity but generally low abundance of reptiles at the five wetlands, and snakes in particular, can in part be attributed to sampling biases of pitfall traps (Gibbons and Semlitsch, 1981; Greenberg et al., 1996), but also reflects differences in wetland use by reptiles when compared to amphibians (Dodd, 1992). Although most amphibian species at our sites are facultative or obligate users of isolated wetlands for breeding and larval development, reptiles captured along the wetland peripheries include (1) purely terrestrial species whose home range incidentally contacts the drift fences (e.g. *Anolis carolinensis*, *Cnemidophorus sexlineatus*, *Eumeces* spp.); (2) wide ranging terrestrial and semi-aquatic species that actively forage at the wetlands (e.g. *Nerodia* spp., *Coluber constrictor*; Plummer and Congdon, 1994); and (3) species that nest in the adjacent uplands but inhabit the wetlands for much of the year (e.g. turtles; *Farancia abacura*). The abundance of *Carphophis amoenus*, a terrestrial snake typically associated with cool deciduous microclimates and considered uncommon across much of the pine-dominated Coastal Plain, was notable and may reflect a preference by this species for the moist but unsaturated conditions of wetland peripheries (Russell and Hanlin, 1999).

The numerical dominance of anurans (e.g. *Rana utricularia*) at our sites and the paucity of amphibian captures between October and March (Fig. 2) resulted from the almost complete absence of fall and winter breeding amphibians (*Ambystoma* spp., *Pseudacris* spp.). Because these species often are abundant at coastal plain isolated wetlands (Gibbons and Semlitsch, 1991; Semlitsch et al., 1996), their absence from our sites is problematic. Many amphibians in the region, including *Ambystoma* spp., use isolated wetlands for reproduction but spend the remainder of the year in surrounding upland forests (Dodd, 1996; Semlitsch et al., 1996; Semlitsch, 1998). Although studies that explicitly (i.e. experimentally) demonstrate the need for terrestrial buffers surrounding isolated wetlands currently are lacking, several researchers have suggested that intact terrestrial habitats are necessary to maintain the integrity of wetland herpetofaunal communities (Burke and

Gibbons, 1995; Dodd and Cade, 1998; Semlitsch, 1998). Thus, it is possible that previous forest management in the uplands surrounding our wetland sites reduced or eliminated populations of *Ambystoma* spp. or *Pseudacris* spp. Although our sample size is small, the positive correlations of amphibian abundance and diversity with increased basal area and diameter of conifers indicate the condition of adjacent upland stands may influence composition of small wetland herpetofauna.

However, previous studies have demonstrated that wetland-associated amphibians, including *Ambystoma* spp. and *Pseudacris* spp., often are abundant in intensively managed forests (Bennett et al., 1980; Grant et al., 1994; Baughman, 2000; Hanlin et al., 2000). Opportunistic surveys across the Woodbury Tract also indicate that at least one species, *A. mabeei*, is more common than indicated by sampling at our five sites. We also note that current harvest regimes are only the latest in a long history ($\geq$150 years) of forest management and prior to that, farming, on the Woodbury Tract (A.W. Smith, International Paper, personal communication). Thus, the generally high richness, abundance, and diversity of herpetofauna at small isolated wetlands surrounded by young growth forests indicate that overall these communities may be resilient to disturbance, a finding that corresponds with historical disturbance regimes in the southeastern Coastal Plain (Sharitz et al., 1992; Russell et al., 1999). Although perhaps counterintuitive, we speculate that the absence of some amphibian species may in part be related to the lack of disturbance. Historically, wildfires entered coastal plain isolated wetlands from the surrounding fire-adapted uplands during periods of drought. These periodic upland fires (1–5 year intervals; Russell et al., 1999) maintained open palustrine wetlands with abundant herbaceous vegetation (Sharitz and Gresham, 1998) favored by many species of amphibians, including the threatened flatwoods salamander (*Ambystoma cingulatum*; Palis, 1997). In the absence of fire, accumulation of organic matter creates substrate conditions that allow succession of small isolated wetlands to closed-canopy hardwood stands and eventual permanent drying of ponds (Means and Moler, 1979; Russell et al., 1999).

We suggest that extensive closed canopies at the five wetlands and consequent absence of herbaceous vegetation, rather than upland forest management, may explain the absence of selected amphibian species. In a recent survey of coastal plain ponds, the presence of a dense leaf pack in wetland basins associated with closed canopies was negatively correlated with amphibian species richness (T.B. Wigley, unpublished data). Skelly et al. (1999) reported that over a 30-year period, ponds undergoing succession to closed canopy conditions in Michigan exhibited the greatest number of amphibian species extinctions. Closed-canopy ponds may limit the presence of some amphibian species because of lower dissolved oxygen concentrations, elimination of herbaceous vegetation, and changes in food resources (Werner and Glennemeier, 1999). Our point is not to discount potential impacts of surrounding forest management on wetland communities but to suggest that the effect of hardwood succession on the herpetofaunal composition of coastal plain small wetlands is a conservation issue warranting equal attention (Means and Moler, 1979; Russell et al., 1999; S.H. Bennett, personal communication).

5. Conclusion

Our study demonstrates that small wetlands are important for maintaining diversity of herpetofauna in commercially managed forests. The biological significance of small wetlands may extend far beyond their edges, however. Amphibians may constitute the greatest biomass among vertebrates in some forest ecosystems (Burton and Likens, 1975), and the biphasic life cycle of salamanders and anurans constitutes one of the few biotic mechanisms for transporting nutrients from eutrophic water bodies into terrestrial ecosystems (Wasserug, 1975). Because small isolated wetlands tend to be scattered over landscapes (Gibbs, 1993; Semlitsch and Bodie, 1998), they are an important source of prey for wide-ranging terrestrial vertebrates. For example, Moler and Franz (1987) suggested that toads from an inconspicuous 1 ha isolated wetland conceivably could support a population of hognosed snakes occupying over 1000 ha of upland habitat. The diverse and abundant herpetofaunal communities of small isolated wetlands undoubtedly play an important role in food web dynamics of the southeastern Coastal Plain. The loss of small wetlands also could impede source–sink processes and increase the probability of population extinctions at remaining wetlands (Gibbs, 1993; Semlitsch and Bodie, 1998). Our finding that amphibian diversity decreased with increasing distance to nearest wetland is suggestive, but requires validation with increased sampling effort.

Clearly, size alone is not an adequate index of wetland values and functions (Gibbs, 1993; Semlitsch and Bodie, 1998). Small isolated wetlands, while superficially similar with respect to dominant species, support variable levels of herpetofaunal diversity and abundance which can only be conserved by protecting a range of sites. However, in order to determine which sites to protect, more knowledge is needed on the variability of these unique communities (Dodd, 1992). We strongly urge additional characterization of small isolated wetland herpetofaunal communities in managed forests and the determinants of among-wetland variability. Particularly valuable would be studies that explicitly test influences of upland disturbance on wetland herpetofauna and the need for adjacent terrestrial buffers (Semlitsch and Bodie, 1998). The data collected in this study will provide the baseline from which to experimentally evaluate impacts of upland forest management practices on wetland herpetofauna.

The increasing trend towards intensively site prepared, high density, short-rotation pine plantations in the southeastern United States has important implications for biodiversity within the region (Moore and Allen, 1999). An important question for the forest products industry is how this approach to management influences the diversity and abundance of herpetofauna (deMaynadier and Hunter, 1995). Our results indicate that small isolated wetlands are focal points of herpetofaunal richness and abundance in young growth forests of the southeastern Coastal Plain. Land managers can significantly enhance the contribution of our extensive commercial forests to regional biodiversity by incorporating ecological values, including those of isolated wetland herpetofauna, into their forest planning objectives.

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