RESPONSES OF ISOLATED WETLAND HERPETOFAUNA TO UPLAND FOREST MANAGEMENT

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Abstract: Because many amphibians and reptiles associated with wetlands also use adjacent terrestrial habitats to complete their life cycles, it has been suggested that undisturbed upland areas are required to maintain populations of these species. To date, however, measured responses of wetland herpetofauna to upland silviculture include only retrospective comparisons or anecdotes without true spatial and temporal references. We used an experimental approach to measure responses of herpetofauna at isolated wetlands in the Coastal Plain of South Carolina, USA, to disturbance of adjacent loblolly pine (*Pinus taeda*) forests. We used drift fences with pitfall traps to sample herpetofauna at 5 wetland sites for 1 year before (1997) and 2 years after (1998–1999) the following treatments were applied to the upland stands surrounding each site: (1) reference (unharvested), (2) clearcutting, and (3) clearcutting followed by mechanical site preparation. Although silvicultural treatments significantly altered overstory and ground-cover characteristics of upland stands, we did not observe any treatment-related changes in the overall richness, abundance, or community similarity of amphibian and reptile communities at the wetlands. Turtles and snakes were less abundant adjacent to clearcut and site-prepared stands 6 months after treatment but not after 1.5 years, possibly in response to physical disturbance of nest sites and changes in ground cover. Fifteen of the 17 species of herpetofauna with ≥30 individual captures showed no effects of treatments. Bronze frogs (*Rana clamitans*) entered the wetlands in proportionally higher numbers from clearcuts and site-prepared stands 1.5 years after treatment, possibly in relation to increased standing water in treated stands. In contrast, site preparation appeared to reduce the abundance of black racers (*Coluber constrictor*) 6 months after treatment. In the short term at least, many species of isolated wetland herpetofauna in the southeastern Coastal Plain may tolerate some disturbance in adjacent upland stands. Responses of isolated wetland herpetofauna to upland silviculture and the need for adjacent forested buffers likely depend on the specific landscape context (e.g., natural disturbance regimes) in which the wetlands occur and composition of the resident herpetofaunal community.

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Forest managers increasingly are challenged to balance production of forest products with maintenance of environmental quality, including function of wildlife habitats and conservation of biodiversity (Hunter 1990, Sharitz et al. 1992, Moore and Allen 1999). Concerns about even-aged management and specifically the practice of clearcutting have prompted considerable research on the effects of timber harvest on wildlife. However, most research has focused on mammals and birds, whereas other vertebrates such as amphibians and reptiles (herpetofauna) have received less attention (Harlow and Van Lear 1987, Gibbons 1988, deMaynadier and Hunter 1995, Moore and Allen 1999). Consequently, amphibians and reptiles often are not fully considered in forest management decisions (Bury 1988, Gibbons 1988, deMaynadier and Hunter 1995). This is despite recognition that herpetofauna are an important component of ecological communities and the most abundant vertebrates in many forests (Burton and Likens 1975, Congdon et al. 1986, Bury 1988).

Many species of amphibians and reptiles depend on isolated freshwater wetlands. Isolated wetlands are shallow basins that are not connected to streams or lakes, and the primary natural lentic habitats on the southeastern Coastal Plain of the United States (Sutter and Kral 1994, Sharitz and Gresham 1998, Kirkman et al. 1999). These wetlands support unique communities of plants and animals and are particularly important habitats for herpetofauna adapted to seasonal hydroperiods and the absence of predatory fish (Moler and Franz 1987, Dodd 1992, Semlitsch et al. 1996, Russell et al. 2002). Of the 29

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species of anurans (frogs and toads) native to the southeastern Coastal Plain, 10 breed primarily or exclusively in isolated wetlands and 10 others use these habitats opportunistically (Moler and Franz 1987). Many species of aquatic and semi-aquatic turtles and snakes use isolated wetlands for food and cover (Gibbons and Semlitsch 1991). The species richness and abundance of herpetofauna associated with even the smallest isolated wetlands indicate their contribution to regional biodiversity. In South Carolina, Pechmann et al. (1989) trapped 75,644 juveniles of 15 amphibian species from a 1.0-ha ephemeral wetland in 1 year, and Dodd (1992) captured 16,156 individuals of 16 amphibian and 26 reptile species over 5 years from a Florida temporary pond with an area of only 0.16 ha.

Many species of amphibians in the southeastern Coastal Plain exhibit biphasic life histories (Duellman and Trueb 1986). Adult salamanders and anurans migrate to isolated wetlands for mating and egg deposition but return to upland habitats for the remainder of the year (Duellman and Trueb 1986, Dodd 1996, Semlitsch et al. 1996, Semlitsch 1998). The eggs hatch as aquatic larvae that develop in the wetlands until metamorphosis. After metamorphosis, juveniles emigrate to adjacent terrestrial habitats where they develop to reproductive maturity. In contrast, many coastal plain turtles and snakes seek food and cover in isolated wetlands or their peripheries but migrate to adjacent uplands for egg laying and hibernation (Gibbons and Semlitsch 1991, Burke and Gibbons 1995, Russell and Hanlin 1999). Other species of southeastern turtles (e.g., yellowbelly sliders [*Trachemys scripta*]) migrate from isolated wetlands to nest in terrestrial habitats but overwinter in the wetlands (Gibbons and Semlitsch 1991).

Coastal plain managed forests are characterized by high densities of small isolated wetlands (Kirkman et al. 1999, Wigley 1999). Because most species of herpetofauna associated with isolated wetlands use adjacent uplands, several authors have suggested that large forested buffers (e.g., 275-m radius; Burke and Gibbons 1995) or complete exclusion of forest management surrounding coastal plain wetlands are necessary to protect herpetofaunal species and communities (Burke and Gibbons 1995; Dodd 1996; Dodd and Cade 1998; Semlitsch 1998, 2000; Kirkman et al. 1999). Isolated wetlands could be negatively impacted by indirect effects of upland timber harvest through altered water temperatures, evaporation rates, hydrology, and import of organic materials (deMaynadier and Hunter 1995, O'Neill 1995, Kirkman et al. 1999), although these impacts apparently are minor when compared to natural fluctuations (Sun et al. 2001). Clearcutting also may decrease suitability of adjacent terrestrial habitats for amphibians by increasing air and soil temperatures and decreasing soil moisture and ground cover (deMaynadier and Hunter 1995). Mechanical site preparation (e.g., disking, piling, bedding) following clearcutting may further reduce suitability of adjacent uplands for herpetofauna by removing coarse woody debris, leaf litter, understory shrubs, and other forest floor microhabitats (Enge and Marion 1986, deMaynadier and Hunter 1995). Mechanical site preparation also increases the magnitude of soil disturbance (Enge and Marion 1986), potentially destroying reptile burrows and nests (Diemer and Moler 1982, Burke and Gibbons 1995) and underground refugia used by amphibians (Dodd 1991, Semlitsch 1998). Clearcutting and site preparation also may isolate herpetofaunal populations and increase the risk of local extinction by leaving unsuitable habitats around wetlands that inhibit migration or dispersal (Gibbs 1993, Semlitsch 1998, Kirkman et al. 1999).

Although some data are available concerning effects of forest management on stream-associated amphibians, information about impacts of logging on herpetofauna associated with isolated wetlands and other aquatic systems is lacking (deMaynadier and Hunter 1995). Pechmann et al. (1991) speculated that the initial absence and then presence of marbled salamanders (*Ambystoma opacum*) at an isolated wetland in South Carolina resulted from regeneration of surrounding upland forests that previously were clearcut and burned. In Louisiana, Raymond and Hardy (1991) reported that a clearcut 156 m away from a breeding pond may have influenced the migratory movements and survivorship of a breeding population of mole salamanders (*A. talpoideum*). A study in Massachusetts found that the most important characteristic distinguishing isolated wetlands used by breeding amphibians was the percentage of forest within a 152-m radius of the wetlands (Stone 1992). However, we are aware of no studies that have directly (i.e., experimentally) demonstrated effects of upland forest management on isolated wetland herpetofauna or substantiated the efficacy of buffers.

We conducted a manipulative field experiment to test the effects of upland clearcut harvesting

and mechanical site preparation on isolated wetland amphibians and reptiles in the Coastal Plain of South Carolina. Our study objective was to provide a direct test of the hypothesis that disturbance in adjacent terrestrial forests negatively affects wetland-dwelling herpetofauna (Burke and Gibbons 1995, Dodd and Cade 1998, Semlitsch 1998).

STUDY AREA

We conducted our study at the Woodbury Tract, an 8,000-ha peninsula of managed 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 (Russell et al. 2002). The portion of the tract between the 2 river floodplains consists of sandhill ridges dominated by plantations of loblolly and longleaf (*Pinus palustris*) pine ranging from recent clearcuts to stands 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, respectively (National Oceanic and Atmospheric Administration 1992).

METHODS

We selected 5 small isolated wetlands—0.38 ha, 0.47 ha, 0.59 ha, 0.72 ha, and 1.06 ha in area—from within the upland sandhills as study sites. Sites were chosen to minimize differences in size, wetland and upland vegetation, and disturbance histories. We chose to focus our sampling at these sites rather than invest less effort at more wetlands because brief or infrequent surveys potentially underestimate both richness and abundance of ephemeral wetland herpetofauna (Dodd 1992). The wetlands were classified as coastal plain small depression ponds (Russell et al. 2002), with water inputs limited to precipitation, surface and subsurface flow, and water table fluctuations. Wetland vegetation was 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 supported no submerged, emergent, or floating vegetation but contained a thick layer of decomposing leaves. Wetland margins supported brushy plants, including blueberries (*Vaccinium* spp.), hollies (*Ilex* spp.), sweet bay (*Magnolia virginiana*), common wax myrtle (*Myrica cerifera*), greenbrier (*Smilax* spp.), and fetterbush (*Lyonia lucida*). Distances between the 5 wetlands ranged from 402 m to 1,509 m.

Surrounding uplands were dominated by 18- to 25-year-old stands of loblolly pine with turkey oak (*Quercus laevis*), southern red oak (*Q. falcata*), and post oak (*Q. stellata*) as major midstory components. Ground cover was dominated by conifer and deciduous litter. Pre-treatment monitoring revealed no significant differences among wetlands in precipitation or hydrology, but maximum air temperature, overstory structure, and microhabitat characteristics in the uplands varied among sites (Russell et al. 2002). Details of pre-treatment habitat conditions can be found in Russell et al. (2002).

Animal Sampling and Experimental Design

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 and silt fencing buried 10–15 cm in the ground (192-m, 226-m, 271-m, 302-m, and 366-m circumference, respectively). Paired pitfall traps (19-l plastic buckets) were buried on each side of the fence at 10-m intervals. Small holes were punched in the bottom of buckets to allow drainage and a moist sponge was placed in each bucket to prevent desiccation or drowning. We positioned drift fences just above the anticipated high water mark in the ecotone between the wetland depressions and upland stands. Thus, we were able to capture animals as they migrated to or from the wetlands, except for those species and age classes not effectively sampled with drift fences and pitfall traps (e.g., treefrogs, large adult snakes; Gibbons and Semlitsch 1981).

Prior to sampling, we divided the uplands surrounding each wetland into 3 stands of equal area (area varied among sites with wetland diameter but was ≥10 ha) and randomly assigned the 3 stands to 1 of the following silvicultural treatments: (1) reference, (2) clearcutting, or (3) clearcutting followed by mechanical site preparation. The reference stand at each wetland remained unharvested throughout the study. Treatments were applied in June 1998. On treated stands, all merchantable conifer and hardwood stems from the

high-water mark of each wetland to a ≥400-m radius were harvested using a feller-buncher and were tractor skidded to landings. Vegetation remained undisturbed in the wetlands. On clearcut-only stands, all residual slash was retained so that ground disturbance was limited to that caused by harvesting equipment. After harvest, stands assigned to site preparation treatments were disked and bedded. Site-prepared stands were then planted with 229 loblolly pine seedlings (6–9 mo old) per ha. Although selection of the 5 wetland sites was not random, our design included random order of treatments at each wetland, temporal (before and after) and spatial (reference vs. treatment) controls, and replication, as in an optimal impact study design (Green 1979).

We checked pitfall traps daily between 0700 and 1000 hr from June through December 1997 (pre-treatment), 1998 (6 mo post-treatment), and 1999 (1.5 yr post-treatment). We identified the species, sex (when possible), and age class (e.g., juvenile, adult) of each animal captured. Salamanders, anurans, and lizards were marked by toe-clipping (Ferner 1979) to indicate the wetland, year, and stand of capture. This marking scheme allowed us to assess the degree to which recaptured animals moved among the 3 stands surrounding a wetland before and after treatment. 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 ≥5 m from the point of capture and on the opposite side of drift fences to minimize the probability of immediate recapture.

Environmental and Vegetation Sampling

We recorded daily precipitation and air temperatures (maximum–minimum) 1.5 m above ground level using plastic rain gauges and Taylor maximum–minimum thermometers located at the periphery of each wetland. During April 1999, we characterized upland ground cover using 10 1-m^2 quadrats at 10-m intervals along a randomly located line transect (Mueller-Dombois and Ellenberg 1974) in each reference and treatment stand (10 plots/stand). For each plot, we made ocular estimates of percent cover woody debris, bare soil, conifer and deciduous litter, moss, herbaceous plants, and shrubs (≤1.5 m). We used a ruler to measure leaf litter depth at the center of each plot. Using a Kelway meter, we measured soil pH at the first, fifth, and tenth plots along each transect.

Analyses

Environmental and Vegetation Data.—Baseline characterization of the wetlands indicated that variation in abundance of herpetofauna was influenced by precipitation, air temperature, and upland vegetation (Russell et al. 2002). Therefore, we tested for differences in precipitation and temperature among years and differences in ground cover characteristics among treatments using 1-way analysis of variance (ANOVA). When an ANOVA yielded a significant F statistic, we used Tukey's honestly significant difference (HSD) to test significant differences among means. All variables were tested for normality (Shapiro-Wilk's W; SPSS 1999) and log or arcsine square root transformed when required (Sokal and Rohlf 1981). We also transformed percentages and converted pH values to hydrogen ion concentrations. Only nontransformed means and standard errors are reported.

Herpetofauna.—To examine effects of clearcutting and site preparation on herpetofauna, we compared richness, abundance, and community similarity of amphibians and reptiles among treatments and years. Presumably, effects of treatments on suitability of adjacent upland stands for herpetofauna should be reflected in numbers of animals migrating in or out of the wetlands (Raymond and Hardy 1991, Dodd and Cade 1998, Semlitsch 1998). We derived richness and abundance of immigrating, emigrating, and total herpetofauna in each stand for the pre-treatment (1997) and post-treatment (1998, 1999) sampling periods by separately pooling all pitfall trap captures from the outside and inside sections of drift fence. Because the number of pitfall traps per stand varied with wetland diameter, we weighted captures by trapping effort.

Baseline data collected at the wetlands (Russell et al. 2002) revealed significant differences in abundance of herpetofauna among sites unrelated to wetland size. Preliminary analyses also indicated significant pre-treatment differences in captures of most species among the 3 stands (experimental units) surrounding each wetland. Thus, significant variation occurred in captures both among and within wetland sites that could mask treatment effects and was not controlled by standardizing trapping effort (Cole et al. 1997). We accounted for this variability by calculating the change (percent) in richness and abundance of herpetofauna in each stand for pre-treatment versus 6 months post-treatment and for pre-treatment versus 1.5 years post-treatment. We deter-

mined treatment effects by comparing the magnitude of change among treatments relative to pre-treatment conditions (Montgomery 1991). We calculated amphibian and reptile community similarity (percent similarity; Brower et al. 1998) for pre-treatment versus 6 months post-treatment and for pre-treatment versus 1.5 years post-treatment. We removed recaptures from the preceding data.

To assess whether amphibians used unharvested areas as refuges after cutting and site preparation of adjacent stands, we calculated the percentage of recaptured amphibians migrating into the wetlands from reference stands that originally were marked in clearcut and site preparation stands for 1997 (pre-treatment), 1998 (6 mo post-treatment), and 1999 (1.5 yr post-treatment) and compared the percentage of recaptured amphibians among years. Recaptures of reptiles were insufficient for analysis.

Capture data deviated from normal distributions and did not normalize following standard transformations. Significant pre-treatment variation in captures among the stands (experimental units) within each wetland block also violated assumptions of parametric tests (Montgomery 1991). Therefore, we used nonparametric Kruskal-Wallis rank sum tests to detect differences among treatment means for all herpetofaunal data. When Kruskal-Wallis tests yielded a significant H statistic, we used Wilcoxon rank sum tests to determine which treatments contributed to the overall differences (Saville 1990). We analyzed only species with ≥30 individual captures (Greenberg et al. 1994). Because captures of most reptile species were insufficient for individual analyses, we pooled captures of turtles, lizards, and snakes and analyzed these groups. Immigration accounted for ≥80% of individual turtles and snakes; captures of emigrating individuals were insufficient for analyses. Only analyses of total captures are reported for individual species if no significant differences were found for immigration or emigration.

All means are presented ± 1 standard error (SE), and the significance level for all statistical tests was $\alpha = 0.05$. We used SYSTAT 8.0 (SPSS 1999) for all statistical analyses.

RESULTS

Precipitation and Temperature

During the 1997, 1998, and 1999 sampling periods, precipitation totaled 86.5 cm, 44.5 cm, and 28.7 cm, respectively. As a result, mean weekly precipitation was significantly higher ($F = 7.16$; df = 2, 87; $P = 0.001$) in 1997 ($\bar{x} = 27.9 \pm 2.7$ mm) than in 1998 ($\bar{x} = 14.3 \pm 2.7$ mm) or 1999 ($\bar{x} = 9.9 \pm 2.6$ mm). Mean weekly maximum air temperatures were significantly higher ($F = 3.45$; df = 2, 87; $P = 0.036$) in 1998 ($\bar{x} = 32.7 \pm 0.8$ °C) than in 1997 ($\bar{x} = 29.1 \pm 1.2$ °C) or 1999 ($\bar{x} = 29.8 \pm 1.1$ °C), but we found no statistical differences in mean weekly minimum air temperatures among years ($F = 0.75$; df = 2, 87; $P = 0.477$).

Table 1. Ground cover characteristics of upland pine stands (unharvested reference stands, clearcuts, and clearcuts followed by mechanical site preparation) surrounding 5 isolated wetlands, Woodbury Tract, South Carolina Coastal Plain, Apr 1999.

	Reference		Clearcuts		Clearcuts with site preparation	
Habitat variable	Mean[a]	SE	Mean	SE	Mean	SE
Woody cover (%)	3.9A	0.7	39.6B	3.6	17.7C	1.9
Bare soil (%)	5.1A	1.9	17.9B	3.6	77.9C	2.3
Conifer litter (%)	44.0A	4.4	24.4B	2.4	1.2C	0.6
Deciduous litter (%)	34.7A	3.9	11.3B	2.3	0.3C	0.2
Moss (%)	5.8A	1.5	0.4B	0.2	0.0B	0.0
Herbaceous plants (%)	1.1A	0.4	3.7A	1.1	2.7A	0.9
Shrubs (≤1.5 m; %)	5.5A	1.8	2.8AB	1.0	0.2B	0.1
Litter depth (mm)	26.5A	1.7	15.7B	2.1	0.3C	0.2
Soil pH	6.6A	0.1	6.6A	0.1	6.9A	0.1

[a] Mean values followed by different letters across rows are significantly different using Tukey's HSD ($P \leq 0.05$).

Effects of Treatments on Ground Cover

Approximately 1 year following treatment, percent cover of woody debris was significantly different among treatments ($F = 56.58$; df = 2, 147; $P < 0.0001$), with clearcuts and unharvested reference stands containing the most and least woody debris, respectively (Table 1). Site-prepared clearcuts contained the greatest percentage of bare ground and unharvested reference stands contained the least bare ground ($F = 207.37$; df = 2, 147; $P < 0.0001$; Table 1). Percent cover of conifer ($F = 53.90$; df = 2, 147; $P < 0.0001$) and deciduous ($F = 63.76$; df = 2, 147; $P < 0.0001$) litter, and litter depth ($F = 71.56$; df = 2, 147; $P < 0.0001$) were highest in reference stands, intermediate in clearcuts, and lowest in site-prepared clearcuts (Table 1). Percent cover of moss was greater in unharvested reference stands than in clearcuts or site-prepared clearcuts ($F = 20.36$; df = 2, 147; $P < 0.0001$; Table 1). Unharvested reference stands contained a higher percentage of shrubs than site-prepared clearcuts ($F = 5.66$; df = 2, 147; $P = 0.004$; Table 1). Percent cover of herbaceous

plants (F= 1.38; df = 2, 147; P= 0.255) and soil pH (F = 3.10; df = 2, 147; P = 0.06) was not significantly different among treatments (Table 1).

Community Responses to Treatments

Between June 1997 and December 1999, we recorded 8,419 individuals and 769 recaptures of 19 amphibian species, and 683 individual captures and 61 recaptures of 37 reptile species (Appendix). Immigration accounted for 79.9% and 55.9% of individual amphibian and reptile captures, respectively. Southern leopard frogs (*Rana utricularia*), bronze frogs (*R. clamitans*), and southern toads (*Bufo terrestris*) were the most frequently captured amphibians, constituting 73% of all individuals (Appendix). Reptile captures were more evenly distributed among species, with the 3 most abundant reptiles (green anoles [*Anolis carolinensis*], worm snakes [*Carphophis amoenus*], and black racers [*Coluber constrictor*]) accounting for only 37% of individuals (Appendix). Canebrake rattlesnakes (*Crotalus horridus*), southern ringneck snakes (*Diadophis punctatus*), and rainbow snakes (*Farancia erytrogramma*) were captured only after implementation of silvicultural treatments (Appendix) and were represented by ≤6 individual captures.

Although species richness of both amphibians and reptiles declined at the wetlands between 1997 and 1999, these differences were independent of harvest treatments (Table 2). Similarly, we observed declines in the abundance of both immigrating and emigrating amphibians and reptiles, but these changes also were not significantly different among treatments for pre-treatment versus 6 months post-treatment or for pre-treatment versus 1.5 years post-treatment (Table 2). Proportionally fewer turtles immigrated to the wetlands from clearcuts when compared to reference (Wilcoxon Z = 3.12, P = 0.024) and site-prepared stands 6 months after treatment (Wilcoxon Z = 3.12, P = 0.014; Table 2). However, this difference was not significant after 1.5 years (Table 2). We also found proportionally fewer snakes immigrating to wetlands from clearcuts (Wilcoxon Z = 3.44, P = 0.047) and site-prepared stands (Wilcoxon Z = 2.63, P = 0.048) when compared with unharvested reference stands 6 months after treatment (Table 2). As with turtles, this effect was short-lived; the relative abundance of immigrating snakes did not differ among treatments after 1.5 years (Table 2).

Percentage similarity of herpetofaunal communities (relative to pre-treatment communities) declined at the wetlands 6 months and 1.5 years after treatment. Although the decline in amphibian community similarity was greater in clearcuts and site-prepared clearcuts than in reference stands, these differences were not significant for pre-treatment versus 6 months post-treatment (Kruskal-Wallis H = 0.87; df = 2, 12; P = 0.645) or for pre-treatment versus 1.5 years post-treatment (Kruskal-Wallis H = 1.26; df = 2, 12; P = 0.533). We also did not detect significant differences among treatments in reptile community similarity for pre-treatment versus 6 months post-treatment (Kruskal-Wallis H = 1.42; df = 2, 12; P = 0.522) or for pre-treatment versus 1.5 years post-treatment (Kruskal-Wallis H = 2.67; df = 2, 12; P = 0.263).

We found no evidence that amphibians dispersed into adjacent unharvested stands after application of harvest treatments. No significant differences occurred among pre-treatment (1997), 6 month post-treatment (1998), and 1.5 year post-treatment (1999) sampling periods in the percentage of amphibians recaptured in reference stands that originally were captured in clearcuts (Kruskal-Wallis H = 4.29; df = 2, 14; P = 0.118) or site-prepared stands (Kruskal-Wallis H = 3.87; df = 2, 14; P = 0.263; Fig. 1).

Species Responses to Treatments

We captured 10 species of amphibians, 6 species of reptiles, and 1 genus of lizards (*Eumeces* spp.) in sufficient numbers for individual analysis. Although the number of six-lined racerunners (*Cnemidophorus sexlineatus*) exceeded 30 individuals, insufficient captures occurred in 1998 or 1999 to allow us to test for treatment effects on this species. We detected treatment effects for 2 of the 17 species (Table 2).

Bronze frogs showed a delayed but positive response to treatment. Bronze frogs immigrated to the wetlands in proportionally higher numbers from clearcut (Wilcoxon Z = 2.02, P = 0.043) and site-prepared (Wilcoxon Z = 2.02, P = 0.043) stands 1.5 years after treatment (Table 2, Fig. 2A) when compared with unharvested reference stands. The proportion of juvenile bronze frogs immigrating to the wetlands was 66.7%, 80.8%, and 72.8% in 1997, 1998, and 1999, respectively. No treatment-related differences were found in the proportion of emigrating bronze frogs (Table 2).

Black racers immigrated to the wetlands in proportionally higher numbers from reference stands when compared with site-prepared stands 6 months after treatment (Wilcoxon Z = 3.37, P = 0.05; Table 2, Fig. 2B). However, we found no effects of treatments on abundance of racers after 1.5 years (Table 2, Fig. 2B). The proportion

Table 2. Mean change (percent) in richness and abundance of herpetofauna captured at the margins of 5 isolated wetlands surrounded by 3 upland pine stands (reference [RE], clearcut [CC], and clearcut with mechanical site preparation [SP]) for 1997 vs. 1998 (pre-treatment vs. 6 mo post-treatment) and 1997 vs. 1999 (pre-treatment vs. 1.5 yr post-treatment). Standard errors are in parentheses.

	1997 vs. 1998					1997 vs. 1999				
Variable	RE	CC	SP	*H*	*P*	RE	CC	SP	*H*	*P*
Amphibian richness	6.1A[a]	−0.9A	6.9A	1.44	0.486	−25.0A	−33.3A	−20.4A	3.18	0.204
	(6.5)	(6.5)				(2.8)	(11.4)	(6.9)		
Amphibian abundance										
Immigration	5.1A	109.9A	22.3A	0.86	0.651	−71.1A	−36.6A	−42.8A	3.44	0.179
	(32.4)	(83.2)	(35.9)			(6.2)	(12.2)	(21.3)		
Emigration	14.9A	−34.1A	−182.3A	1.86	0.395	−56.8A	−67.5A	−77.5A	0.42	0.811
	(23.7)	(14.1)	(165.1)			(20.4)	(13.1)			
Reptile richness	−27.5A	−45.2A	−26.5A	0.74	0.691	−71.9A	−66.4A	−58.7A	0.46	0.796
	(4.8)	(12.9)	(11.9)			(5.7)	(8.0)	(13.1)		
Reptile abundance										
Immigration	−55.1A	−53.6A	−42.6A	0.42	0.811	−77.1A	−79.1A	−69.7A	1.82	0.402
	(13.2)	(11.9)	(15.2)			(79.1)	(5.3)			
Emigration	−44.4A	−70.5A	−61.0A	3.62	0.164	−73.3A	−86.5A	−91.9A	0.764	0.683
	(11.1)	(6.8)	(9.8)			(12.8)	(7.1)			
Turtle abundance[b]	121.6A	−41.3B	183.2A	8.73	0.013	1.7A	10.6A	140.0A	0.29	0.863
	(48.4)	(19.4)	(107.7)			(52.5)	(59.2)	(112.3)		
Lizard abundance	−75.3A	−66.9A	−65.9A	0.38	0.827	−97.1A	−94.3A	−88.9A	2.28	0.320
	(6.5)	(9.7)	(14.1)			(2.9)	(3.6)			
Snake abundance[b]	−18.4A	−53.5B	−53.1B	6.30	0.043	−64.8A	−79.7A	−67.4A	0.06	0.970
	(14.8)	(5.4)	(12.5)			(19.1)	(4.4)	(21.6)		
Eastern newt	280.0A	240.0A	68.0A	1.69	0.430	−20.0A	60.0A	0.0A	0.24	0.887
Notophthalmus viridescens	(177.2)	(315.5)	(63.4)			(20.0)	(112.3)	(31.6)		
Mud salamander	44.2A	5.4A	−36.2A	0.339	0.844	34.2A	−62.7A	1.9A	0.65	0.723
Pseudotriton montanus	(65.1)	(51.1)	(19.8)			(92.9)	(18.5)	(54.9)		
Southern cricket frog	−96.3A	−97.6A	−93.6A	2.42	0.298	NA[c]	NA	NA	NA	NA
Acris gryllus	(2.5)	(1.4)	(2.2)							
Oak toad	−15.9A	−56.0A	131.1A	2.69	0.259	−5.0A	142.1A	64.5A	0.32	0.851
Bufo quercicus	(56.9)	(23.5)	(96.3)			(50.2)	(202.9)	(90.9)		
Southern toad	−29.2A	2.3A	−18.7A	0.96	0.619	−89.2A	−62.5A	−72.4A	0.42	0.811
Bufo terrestris	(52.7)	(76.3)	(55.9)			(5.2)	(29.2)	(18.5)		
Eastern narrowmouth toad	−24.1A	−14.5A	−19.9A	0.14	0.932	−78.4A	−73.9A	−75.5A	0.10	0.953
Gastrophryne carolinensis	(16.7)	(25.9)	(42.9)			(8.3)	(11.1)	(10.2)		
Bullfrog	108.8A	300.0A	248.0	0.63	0.729	−40.0A	−60.0A	−12.0A	1.34	0.511
Rana catesbeiana	(47.6)	(189.1)	(171.2)			(24.5)	(24.5)	(33.8)		
Bronze frog										
Rana clamitans										
Immigration	70.1A	146.6A	478.8A	1.46	0.482	29.6A	477.4B	494.1B	6.02	0.049
	(39.1)	(42.5)	(385.1)			(62.7)	(276.0)	(261.9)		
Emigration	70.3A	152.5A	50.0A	0.11	0.948	14.3A	26.3A	−38.8A	2.39	0.303
	(61.8)	(168.8)	(72.0)			(29.9)	(42.2)	(28.0)		
Southern leopard frog	321.9A	627.6A	1023.9A	1.50	0.472	70.1A	35.2A	109.9A	0.26	0.878
Rana utricularia	(109.8)	(206.9)	(600.3)			(85.2)	(44.6)	(77.5)		
Pickerel frog	372.8A	184.4A	240.3A	0.19	0.911	222.0A	334.3A	294.6A	1.46	0.481
Rana virgatipes	(264.2)	(66.7)	(182.7)			(245.2)	(159.6)	(269.4)		
Eastern mud turtle	−13.3A	20.0A	20.0A	0.12	0.944	−70.0A	80.0A	46.7A	3.25	0.197
Kinosternon subrubrum	(34.3)	(80.0)	(73.5)			(20.0)	(180.0)	(53.3)		
Green anole	81.7A	−36.0A	33.3A	3.58	0.167	−18.3A	−56.0A	−15.0A	0.04	0.981
Anolis carolinensis	(66.2)	(18.3)	(43.1)			(56.3)	(23.2)	(58.9)		
Skinks	−68.0A	−76.0A	−69.9A	0.03	0.957	−90.0A	−83.0A	−96.7A	0.922	0.631
Eumeces spp.	(19.3)	(11.2)	(15.5)			(10.0)	(12.9)	(3.3)		
Ground skink	−66.6A	−44.3A	−30.0A	2.04	0.361	NA	NA	NA	NA	NA
Scincella lateralis	(18.6)	(13.8)	(57.7)							
Worm snake	−86.0A	−93.5A	−78.0A	0.96	0.617	−100.0A	−100.0A	−84.2A	2.98	0.08
Carphophis amoenus	(9.8)	(4.4)	(10.2)			(0.0)	(0.0)	(20.5)		
Scarlet snake	−60.0A	−50.0A	14.1A	0.67	0.715	−60.0A	−36.7A	−55.0A	0.59	0.745
Cemophora coccinea	(24.5)	(22.4)	(73.3)			(24.5)	(18.6)	(22.9)		
Black racer[b]	110.0A	−3.3AB	−33.3B	4.63	0.058	60.0A	19.0A	−33.3A	0.10	0.951
Coluber constrictor	(60.0)	(18.6)	(27.9)			(81.2)	(72.2)	(21.1)		

[a] Mean values followed by different letters across rows are significantly different ($P \leq 0.05$) using Kruskal-Wallis and Wilcoxon rank sum tests (*H*).

[b] Immigration only.

[c] NA indicates insufficient captures for analysis.

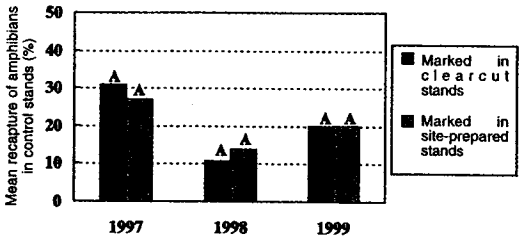

Fig. 1. Mean percentage of amphibians recaptured in reference stands that originally were marked in clearcut and site preparation stands for 1997 (pre-treatment), 1998 (6 mo post-treatment), and 1999 (1.5 yr post-treatment), Woodbury Tract, Marion County, South Carolina Coastal Plain. Within-treatment means with the same letter are not significantly different ($P \geq 0.05$) among years with Kruskal-Wallis and Wilcoxon rank sum tests.

of juvenile racers immigrating to the wetlands was 81.5%, 76.2%, and 75.0% in 1997, 1998, and 1999, respectively.

DISCUSSION

Treatment Effects on Ground Cover

Upland harvest treatments had predictable effects on ground-cover characteristics (White et al. 1975, Enge and Marion 1986, Hunter 1990). Leaf litter and understory shrubs were most abundant in reference stands, whereas bare soil dominated site-prepared clearcuts. Amounts of woody debris were highest in clearcuts without site preparation and lowest in reference stands. The paucity of woody debris in reference stands is a result of previous harvest and site preparation cycles, a history of agriculture prior to current forest management activities (Russell et al. 2002), low availability of source material (e.g., snags) in young pine stands, and rapid decomposition rates of woody material in southeastern forests (Olson 1963, Moorman et al. 1999).

Treatment Effects on Amphibians

Because most amphibian species we captured exhibit biphasic life histories (Duellman and Trueb 1986), the abundance, recruitment, and survival of these species at isolated wetlands presumably are influenced by characteristics of adjacent terrestrial habitats (Dodd and Cade 1998; Semlitsch 1998, 2000). Numerous retrospective studies have reported negative effects of clearcutting on amphibian richness and abundance (reviewed in deMaynadier and Hunter 1995). These declines typically are attributed to the loss of overstory shade and forest floor microhabitats (e.g., hardwood shrubs, leaf litter, woody debris) after harvest and site preparation (deMaynadier and Hunter 1995). Thus, to the extent these habitat components were reduced following treatments, we expected declines in the richness and abundance of amphibians at the wetlands.

Despite significant changes in upland habitats after clearcutting and mechanical site preparation, our manipulative study showed no treatment effects on amphibian richness or abundance, suggesting that, in the short term at least, isolated wetland amphibians in the southeastern Coastal Plain may tolerate some disturbance in adjacent upland stands. Palik et al. (2001) also found little compelling evidence that age of adjacent upland forests (0–100 years) in Minnesota influenced abiotic and biotic variables of ephemeral isolated wetlands, including hydroperiod, water depth, macroinvertebrate communities, or breeding activity and abundance of amphibians.

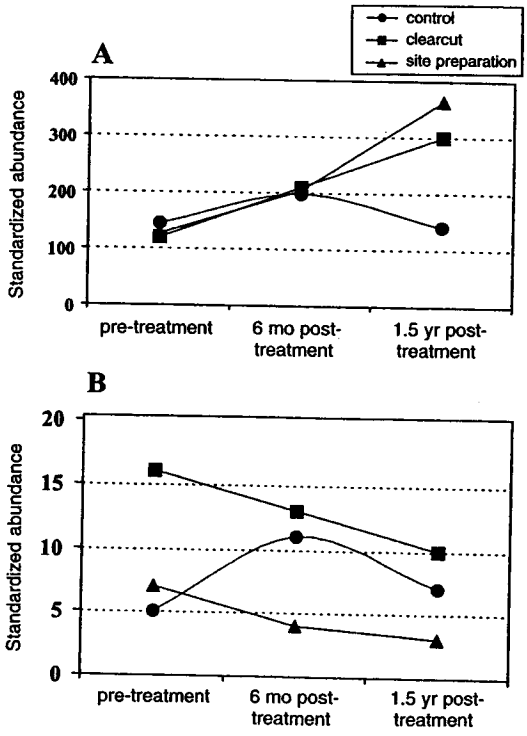

Fig. 2. Relative abundance (standardized by trapping effort, pooled across sites) of (A) bronze frogs, and (B) black racers captured from unharvested reference, clearcut, and clearcut with mechanical site preparation treatments adjacent to small isolated wetlands for pre-treatment (1997), 6 mo post-treatment (1998), and 1.5 yr post-treatment (1999). Data were collected from the Woodbury Tract, Marion County, South Carolina Coastal Plain.

Not only did we fail to observe declines in amphibian populations associated with clearcutting (deMaynadier and Hunter 1995), we found that bronze frogs immigrated into the wetlands in higher numbers from treated stands when compared with unharvested areas after 1.5 years. The similar proportion of juveniles in 1997 and 1999 and lack of treatment effects on emigrating frogs suggest that these increases were not an artifact of increased reproduction (i.e., increased emigration of juveniles masking declining immigration of adult frogs).

We believe that regional and taxonomic influences largely explain the divergence between our results and many previous studies. Most reports of amphibian declines after clearcutting have focused on terrestrial salamanders in the Pacific Northwest or Appalachians (deMaynadier and Hunter 1995, Petranka 1998). In contrast, several studies from the southeastern United States have reported increased numbers of amphibians, including bronze frogs, in clearcut stands when compared to unharvested reference sites (Pais et al. 1988, O'Neill 1995, Clawson et al. 1997, Perison et al. 1997). Wigley (1999) recently reported that of 40 amphibian species and 37 reptile species sampled from 444 temporary isolated wetlands across the southeastern Coastal Plain, retention of an adjacent forested buffer was correlated with the presence of only 1 species, the pine woods treefrog (*Hyla femoralis*). In Texas, Anderson et al. (1999) also found no correlation between the richness of anurans at isolated playa wetlands and the type or intensity of adjacent land use.

Compared with salamanders, anurans have relatively high operating and tolerance temperatures and the ability to store and reabsorb large quantities of water in the bladder (e.g., 20–30% of body mass; Duellman and Trueb 1986), which may explain their tolerance to warmer conditions found in harvested stands (deMaynadier and Hunter 1995). Also, in the flat and humid Coastal Plain, elevated water tables, increased soil saturation, and ruts created by tree removal, skidding, and bedding often increase amounts of standing water in clearcuts (Shepard 1994, O'Neill 1995, Perison et al. 1997). We often observed standing water in treated stands, particularly after heavy rains, and these fish-free pools may attract increased numbers of anurans to clearcuts when compared with unharvested stands (O'Neill 1995, Clawson et al. 1997, Perison et al. 1997, Cromer 1999).

Alternatively, increased immigration of bronze frogs into the wetlands from treated stands may reflect the unsuitability of upland habitats after clearcutting and site preparation, rather than an increase in abundance. Often, only part of an amphibian population migrates to breeding sites in a given year; the rest remain nonreproductive in upland habitats (Alford and Richards 1999). After we implemented treatments, an increasing proportion of the bronze frog population at each site may have moved to the cool, moist wetlands to escape harsh conditions in clearcut and site-prepared stands. If this were the case, we also would expect frogs to seek refuge in adjacent unharvested stands during the nonbreeding season and subsequently enter the wetlands from those stands. However, neither numbers of immigrating bronze frogs nor the percentage of previously marked amphibians were proportionally more abundant in unharvested stands after implementation of treatments.

Mud salamanders (*Pseudotriton montanus*) were the only abundant salamander species at the wetlands, and they did not appear to be affected by harvest treatments. Although mud salamanders occasionally disperse into upland stands, typically they are confined to the muddy margins (e.g., ≤1 m) of wetland and stream habitats (Petranka 1998), which may buffer them from the effects of upland timber harvest. In a manipulative experiment, Chazal and Niewiarowski (1998) found no significant differences in the number of captures, body mass and length, and clutch size of pond-breeding mole salamanders after 6 months exposure to a 4-month-old clearcut and a 40-year-old pine stand (animals were captured from an isolated wetland breeding site and placed in 100-m^2 pens installed post-harvest). Ambystomatid salamanders were largely absent from our study area (Russell et al. 2002), and additional research is needed to evaluate effects of upland forest management on these species (Semlitsch 2000).

In 1 of the only other studies to examine effects of mechanical site preparation on amphibians, Enge and Marion (1986) compared populations of 15 species from 3 pine flatwoods stands in Florida: a 40-year-old pine stand and 2 clearcuts receiving minimum (roller-drum chop, bed, plant) and maximum (stump removal, burn, windrow, harrow, bed, plant) site-preparation treatments. They found no significant differences in amphibian species richness among the 3 stands, but they reported lower abundance of amphibians in both site-preparation treatments when compared with the reference stand. However, the study lacked treatment replication, and

variation in captures among stands might have reflected the proximity and quality of adjacent aquatic habitats, rather than a treatment effect (Alford and Richards 1999).

Declining richness and abundance of amphibians between 1997 and 1999, independent of treatment, corresponded with marked decreases in precipitation during the same period. Annual population sizes of amphibians at isolated wetlands often fluctuate dramatically with environmental conditions (Pechmann et al. 1991, Semlitsch et al. 1996). Also, the low number of recaptures indicates that substantial turnover of amphibian populations may have occurred at the wetlands (Alford and Richards 1999). Natural variability and even occasional extinctions of amphibian populations at small isolated wetlands, independent of habitat modification, may be common and increase the difficulty of separating natural fluctuations from human-caused declines (Pechmann et al. 1991).

Treatment Effects on Reptiles

Clearcutting and mechanical site preparation adjacent to isolated wetlands appeared to have short-term negative effects on black racers and other snakes. For black racers, the similar proportion of juveniles and adults between 1997 and 1999 suggests impacts on both age classes. Most snake captures were juveniles that presumably hatched from upland nests adjacent to the wetlands and were trapped in pitfalls as they dispersed (Dodd 1992, Russell et al. 2002). Many of the snake species we captured nest during late spring and early summer (Ernst and Barbour 1989), which corresponded with the timing of our harvest treatments. The physical disturbance to soil and ground cover from clearcutting and site preparation probably destroyed many nests and temporarily reduced suitability of adjacent uplands for snakes.

Enge and Marion (1986) attributed the lower abundance of snakes and other reptiles in a maximum-site-prepared clearcut to elimination of woody debris and other cover objects that serve as refugia and nesting sites. For example, black racers use vegetation, downed wood, and other surface cover in open habitats to forage, avoid predators, and thermoregulate (Ernst and Barbour 1989). Racers also lay eggs in and under cover objects such as logs. Because treatments consisted of a single application, however, nest destruction did not occur in subsequent years.

Potential effects of treatments on snakes were short-lived. Accelerated shrub development in site-prepared stands (White et al. 1975) and lack of repeated applications may have provided sufficient cover and protection of nest sites for racers and other snakes by 1.5 years after treatment. In contrast, Enge and Marion (1986) observed negative effects of site preparation on reptiles 3–4 years after treatment. Although exact methods of site preparation may not be comparable among studies (e.g., we did not employ chopping), the intensity of our treatments was most similar to the minimum-intensity treatment of Enge and Marion (1986). With high-intensity site preparation, we may have observed the more substantial effects on snake populations reported by Enge and Marion (1986).

We were surprised that numbers of immigrating turtles declined in the first 6 months after clearcutting when compared with both reference and site-preparation treatments. Because the turtles we captured nest in the sandy uplands adjacent to wetlands (Burke and Gibbons 1995), we expected soil disturbance associated with site preparation treatments to have the greatest impact (Diemer and Moler 1982). Although the negative response of turtles to clearcutting but not site preparation may be a sampling artifact, this trend was evident at all 5 wetlands. The large amounts of slash and other debris left from logging may have limited use of landmarks by turtles to navigate or otherwise orient themselves toward wetlands (Woodbury and Hardy 1948, Gourley 1974), or provided insufficient solar exposure for nesting (Janzen 1994, Kolbe and Janzen 2002).

Although we found few treatment-related differences in the richness or abundance of reptiles, the infrequent capture of many species (and thus low power of subsequent analyses) may have prevented detection of significant effects. Also, several reptiles we captured are strictly upland species (e.g., green anoles, skinks [*Scincella lateralis, Eumeces* spp.], six-lined racerunners) that have no association with isolated wetlands and whose home ranges only incidentally contacted our drift fences (Dodd 1992, Russell et al. 2002). Because our study was not designed to sample upland herpetofauna away from breeding sites and the sampling biases of drift fences, our pitfall captures probably underestimate the abundance of these species in adjacent stands. Although the physical disturbance of treatments may have caused short-term declines in abundance of some populations, the array of early-successional habitats created by clearcutting and site preparation likely benefited many upland reptile species (Campbell and Christman 1982, Enge and Marion 1986, Greenberg et al. 1994).

Reasons for declining reptile populations independent of treatment are unclear but may be linked to decreased precipitation in 1998 and 1999. Many snake and turtle species are common at isolated wetlands when prey (amphibians, invertebrates) are abundant, but probably disperse to more permanent wetland habitats as prey and water levels decline with decreasing precipitation (Dodd 1992). Abundance of upland reptile species also may be impacted by decreases in prey (e.g., forest floor invertebrates) that are sensitive to changes in soil moisture (Rollo 1982, McCay 1996). Moisture-sensitive species such as worm snakes were common at the wetlands in 1997 but virtually absent by 1999. This species is associated with the damp peripheries of isolated wetlands in the study area (Russell and Hanlin 1999) and probably dispersed to more moist areas to avoid desiccation.

MANAGEMENT IMPLICATIONS

Our study examined stand-level effects of upland forest management on isolated wetland herpetofauna and did not address landscape-level effects of upland silviculture on wetland connectivity (Kirkman et al. 1999). We also addressed short-term effects of clearcutting and mechanical site preparation. It is possible that populations of herpetofauna at our wetland sites will change in response to treatment over the next several years. However, because we implemented treatments in the early summer, when peak movement of herpetofauna from adjacent uplands into the wetlands occurs (Russell et al. 2002), we expected the physical disturbances of clearcutting and site preparation to have a strong immediate effect.

Applying forested buffers around coastal plain isolated wetlands is a widely suggested (Burke and Gibbons 1995; Dodd and Cade 1998; Semlitsch 1998, 2000; Kirkman et al. 1999) but untested management strategy for protecting herpetofaunal communities in the southeastern Coastal Plain. Discussions have focused on buffer widths and structures (Burke and Gibbons 1995, Dodd and Cade 1998, Semlitsch 1998, Kirkman et al. 1999) without addressing the fundamental question of necessity. The limited geographical and temporal scope of our study requires that our results be interpreted cautiously. Our data suggest, however, that many species of wetland-associated amphibians and reptiles in the southeastern Coastal Plain may tolerate some disturbance in adjacent upland stands. Our results also indicate the importance of separating timber-removal and site-preparation impacts. Even if forest buffers are not retained, excluding mechanical site preparation from the immediate margins of isolated wetlands may protect the nesting, cover, and foraging habitats of several reptile species. We caution it is premature to suggest that upland forested buffers surrounding isolated wetlands are unnecessary, but clearly, previous assumptions about effects of forest management on isolated wetland herpetofauna must be reassessed with additional experimental studies.

The proper historical context often has been missing when considering effects of forest management on isolated wetland herpetofauna. The upland harvest treatments in our study were only the latest in a 300-year continuum of forest clearing, intensive agriculture, forest regrowth, and short-rotation (e.g., 25-yr intervals) timber harvest on the study area (and across the southeastern Coastal Plain; Sharitz et al. 1992). Prior to human influence, frequent and intense natural disturbances (e.g., fire, windthrow) played a dominant role in shaping coastal plain forests (Sharitz et al. 1992, Myers and Van Lear 1998). Thus, many vertebrates in the region, including herpetofauna, have tolerated and adapted to stand-replacing events throughout much of their evolutionary histories (Campbell and Christman 1982, Greenberg et al. 1994, McCoy and Mushinsky 1999, Russell et al. 1999). In fact, periodic disturbance may be a critical factor in maintaining biota of fire-dependent ecosystems of the southeastern Coastal Plain and elsewhere (Campbell and Christman 1982, Enge and Marion 1986, Greenberg et al. 1994), and the lack of dramatic treatment effects in our study may not be surprising.

Ironically, a little-considered but important management issue for isolated wetland herpetofauna may be the continuing increase in forest cover and succession across much of the eastern United States (Skelly et al. 1999, Werner and Glennemeier 1999). Skelly et al. (1999) reported that succession to closed-canopy conditions over a 30-year period appeared to be a major factor contributing to local extirpations of amphibian assemblages in Michigan ponds. Closed-canopy conditions may decrease survivorship and productivity of amphibians via changes in pond hydroperiod, dissolved oxygen concentrations, and invertebrate prey communities (Werner and Glennemeier 1999), or decrease suitability of upland nest sites for reptiles (Kolbe and Janzen 2002). Management strategies for isolated wetlands must consider not only the resident her-

petofaunal community but also the landscape ecology of surrounding forests, including the scales and intensities of disturbance to which species and communities are adapted.

Our study represents an initial test of the hypothesis that disturbance in adjacent terrestrial forests negatively affects wetland-associated herpetofauna. Additional research is required to evaluate and improve management of isolated wetland herpetofauna in conjunction with timber harvest in adjacent upland stands. Although short-term measures of richness and abundance of most wetland herpetofauna were not impacted by upland forest management, these metrics may not be good predictors of habitat quality (Van Horne 1983), and changes in upland habitats could have longer-term consequences for reproductive success, survival, and dispersal of amphibians and reptiles. Of particular need are manipulative experiments that evaluate (1) longer-term (e.g., over a rotation age) and demographic consequences to wetland herpetofauna of timber harvest in adjacent uplands, (2) effects of upland forest management on isolated wetland herpetofauna in regions with natural disturbance regimes that occur at smaller scales and intensities than in the southeastern Coastal Plain, and (3) different approaches to forest management to provide resource managers with realistic options for protecting isolated wetland herpetofauna.

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Appendix. Total numbers of amphibian and reptile species captured (and recaptured) at the margin of 5 small isolated wetlands surrounded by 3 upland pine stands (unharvested reference, clearcut, and clearcut with mechanical site preparation) during Jun–Dec 1997 (pre-treatment), 1998 (6 mo post-treatment), and 1999 (1.5 yr post-treatment), Woodbury Tract, South Carolina Coastal Plain. Data are pooled across the 5 sites.

	1997 (pre-treatment)			1998 (6 mo post-treatment)			1999 (1.5 yr post-treatment)			
Species	Ref.	Clearcut	Site prep.	Ref.	Clearcut	Site prep.	Ref.	Clearcut	Site prep.	Total
Salamanders										
Ambystoma mabeei	1 (0)	1 (0)	2 (0)	0 (0)	1 (0)	1 (0)	0 (0)	2 (0)	0 (0)	8 (0)
Ambystoma opacum	0 (0)	1 (0)	0 (0)	0 (0)	3 (1)	0 (0)	0 (0)	0 (0)	0 (0)	4 (1)
Notophthalmus viridescens	1 (0)	3 (0)	4 (0)	7 (0)	6 (1)	4 (0)	0 (0)	3 (0)	2 (0)	30 (1)
Pseudotriton montanus	16 (0)	42 (3)	35 (1)	11 (0)	29 (0)	15 (0)	7 (0)	18 (0)	22 (0)	195 (4)
Anurans										
Acris gryllus	229 (0)	305 (0)	400 (0)	12 (0)	5 (34)	29 (4)	0 (0)	0 (0)	0 (0)	980 (38)
Bufo quercicus	23 (1)	28 (6)	21 (6)	3 (0)	2 (3)	7 (1)	6 (0)	11 (1)	15 (0)	116 (18)

Appendix. continued.

Species	1997 (pre-treatment)			1998 (6 mo post-treatment)			1999 (1.5 yr post-treatment)			
	Ref.	Clearcut	Site prep.	Ref.	Clearcut	Site prep.	Ref.	Clearcut	Site prep.	Total
Bufo terrestris	314 (83)	277 (122)	367 (114)	126 (27)	121 (12)	157 (25)	20 (1)	43 (1)	60 (3)	1485 (388)
Gastrophryne carolinensis	69 (2)	45 (9)	96 (5)	45 (2)	36 (3)	36 (6)	11 (0)	9 (0)	18 (1)	365 (28)
Hyla chrysoscelis	0 (0)	1 (0)	0 (0)	0 (0)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (0)
Hyla cinerea	1 (0)	2 (0)	1 (0)	0 (0)	2 (0)	0 (0)	0 (0)	1 (0)	1 (0)	8 (0)
Hyla femoralis	1 (0)	3 (0)	4 (0)	2 (0)	1 (0)	2 (0)	1 (0)	0 (0)	0 (0)	14 (0)
Hyla squirella	0 (0)	1 (0)	0 (0)	0 (0)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (0)
Pseudacris crucifer	0 (0)	0 (0)	4 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	4 (0)
Rana catesbeiana	5 (1)	7 (4)	5 (1)	8 (0)	12 (1)	10 (0)	0 (0)	2 (0)	1 (0)	50 (7)
Rana clamitans	94 (23)	72 (12)	92 (13)	113 (8)	119 (3)	138 (1)	88 (9)	170 (1)	286 (6)	1172 (76)
Rana palustris	11 (2)	8 (6)	3 (6)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	23 (14)
Rana utricularia	157 (21)	152 (13)	195 (19)	534 (29)	1054 (3)	857 (36)	104 (3)	133 (3)	263 (2)	3449 (129)
Rana virgatipes	26 (11)	29 (5)	28 (13)	67 (18)	64 (2)	101 (3)	22 (1)	75 (3)	78 (8)	490 (64)
Scaphiopus holbrookii	0 (0)	0 (0)	0 (0)	3 (0)	0 (1)	3 (0)	5 (0)	4 (0)	5 (0)	20 (1)
Total amphibians	948 (144)	977 (180)	1257 (178)	931 (84)	1459 (64)	1361 (76)	264 (14)	471 (9)	751 (20)	8419 (769)
Turtles										
Chelydra serpentina	1 (2)	1 (1)	0 (0)	3 (0)	0 (0)	1 (0)	1 (1)	0 (0)	0 (0)	7 (4)
Clemmys guttata	2 (4)	1 (2)	0 (0)	4 (4)	0 (1)	3 (0)	3 (2)	1 (0)	1 (0)	15 (14)
Kinosternon baurii	1 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)
Kinosternon subrubrum	7 (1)	3 (3)	2 (1)	4 (0)	5 (0)	4 (1)	2 (1)	3 (0)	3 (1)	33 (8)
Sternotherus odoratus	1 (1)	4 (0)	0 (0)	6 (2)	1 (0)	3 (0)	1 (0)	0 (0)	0 (0)	16 (3)
Terrapene carolina	1 (0)	2 (0)	2 (0)	3 (0)	0 (2)	2 (1)	0 (0)	2 (2)	0 (0)	12 (5)
Trachemys scripta	0 (0)	0 (0)	0 (0)	2 (5)	1 (2)	10 (3)	1 (0)	5 (0)	2 (2)	21 (12)
Lizards										
Anolis carolinensis	22 (0)	18 (0)	16 (1)	10 (0)	10 (0)	10 (0)	1 (0)	2 (0)	4 (0)	93 (1)
Cnemidophorus sexlineatus	8 (0)	13 (0)	8 (1)	0 (0)	1 (0)	1 (0)	1 (0)	0 (0)	1 (0)	33 (0)
Eumeces fasciatus	0 (0)	3 (0)	0 (0)	0 (0)	2 (0)	1 (0)	1 (0)	1 (0)	1 (0)	9 (0)
Eumeces inexpectatus	8 (1)	8 (0)	4 (0)	2 (0)	1 (0)	1 (0)	0 (0)	0 (0)	0 (0)	24 (1)
Eumeces laticeps	11 (1)	10 (1)	18 (1)	0 (0)	1 (0)	5 (0)	0 (0)	1 (0)	0 (0)	46 (3)
Ophisaurus attenuatus	0 (0)	1 (0)	2 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (0)
Ophisaurus ventralis	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)
Scincella lateralis	31 (0)	19 (0)	21 (0)	6 (0)	7 (0)	8 (0)	1 (0)	0 (0)	4 (0)	97 (0)
Snakes										
Agkistrodon contortrix	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)
Carphophis amoenus	18 (0)	23 (0)	30 (0)	3 (0)	3 (0)	4 (0)	2 (0)	0 (0)	2 (0)	85 (0)
Cemophora coccinea	6 (2)	5 (1)	10 (1)	1 (0)	1 (0)	4 (0)	1 (0)	2 (0)	1 (0)	31 (4)
Coluber constrictor	4 (0)	10 (1)	5 (0)	6 (0)	10 (0)	4 (0)	3 (0)	6 (0)	4 (0)	52 (1)
Crotalus horridus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)
Diadophis punctatus	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	1 (0)
Elaphe obsoleta	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)
Farancia abacura	2 (0)	1 (0)	1 (1)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	1 (0)	6 (1)
Farancia erytrogramma	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	1 (0)
Heterodon platyrhinos	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)	1 (0)	1 (0)	0 (0)	1 (1)	5 (1)
Lampropeltis getulus	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	1 (0)	1 (0)	4 (0)
Lampropeltis triangulum	2 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (0)
Masticophis flagellum	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)
Nerodia erythrogaster	2 (1)	1 (0)	2 (0)	0 (0)	3 (0)	2 (0)	1 (0)	1 (0)	0 (0)	12 (1)
Nerodia fasciata	2 (0)	2 (0)	0 (0)	3 (0)	2 (0)	2 (0)	2 (0)	0 (0)	1 (0)	14 (0)
Nerodia taxispilota	0 (0)	2 (0)	2 (0)	1 (0)	1 (0)	1 (0)	0 (0)	0 (0)	0 (0)	7 (0)
Seminatrix pygaea	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)
Storeria dekayi	2 (0)	0 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	3 (0)
Storeria occipitomaculata	3 (0)	7 (0)	7 (0)	2 (0)	4 (0)	2 (0)	0 (0)	0 (0)	0 (0)	25 (0)
Thamnophis sauritus	0 (0)	1 (0)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (0)
Thamnophis sirtalis	2 (0)	2 (0)	3 (0)	1 (0)	0 (0)	0 (0)	0 (0)	1 (0)	0 (0)	9 (0)
Virginia valeriae	0 (0)	0 (0)	1 (0)	0 (0)	3 (0)	1 (0)	0 (0)	1 (0)	0 (0)	6 (0)
Total reptiles	140 (14)	138 (9)	137 (6)	59 (12)	58 (5)	72 (5)	22 (4)	29 (2)	28 (4)	683 (61)
Total species	1088 (158)	1115 (189)	1394 (184)	990 (96)	1517 (69)	1433 (81)	286 (18)	500 (11)	779 (24)	9102 (830)