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Influence of coarse woody debris on herpetofaunal communities in upland pine stands of the southeastern Coastal Plain

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ABSTRACT

Coarse woody debris (CWD) is thought to benefit herpetofauna in a variety of ways including serving as feeding sites, providing a moist environment, and providing protection from temperature extremes. We investigated the importance of CWD to amphibian and reptile communities in managed upland pine stands in the southeastern United States Coastal Plain during years 6 and 7 of a long-term study. Using a randomized complete block design, 1 of the following treatments was assigned to 9.3-ha plots: removal ($n = 3$; all downed CWD $\geq$10 cm in diameter and $\geq$60 cm long removed), downed addition ($n = 3$; five-fold increase in volume of down CWD), snag ($n = 3$; 10-fold increase in volume of standing dead CWD), and control ($n = 3$; unmanipulated). Herpetofauna were captured seasonally using drift-fence pitfall trapping arrays within treatment plots. We compared abundance, diversity, and richness of anurans, salamanders, lizards, and snakes using analysis of covariance with topographic variables (slope, elevation, aspect, and distance to nearest stream) included as covariates. We captured 355 amphibians and 668 reptiles seasonally from January 2007 to August 2008. Abundance, species richness, and species diversity were similar among treatments for anurans, salamanders, and lizards. Snake abundance, species richness, and diversity were higher in removal than downed addition plots. Anuran abundance increased as distance to nearest stream decreased. The majority of species captured during this study are adept at burrowing into the sandy soils of the region. Lack of reliance on CWD may be the result of herpetofaunal adaptation to the longleaf pine (*Pinus palustris*) ecosystem that historically dominated the upland areas of the study area.

1. Introduction

The importance of coarse woody debris (CWD) as an ecosystem component is a topic of increasing concern. Most studies examining the value of CWD to herpetofauna in the United States were conducted in old-growth forests of the Pacific Northwest (Alkaslassy, 2005; Aubry et al., 1988; Bury et al., 1991; Butts and McComb, 2000; Dupuis et al., 1995; Welsh and Lind, 1991) or the Appalachian Mountains (Greenberg, 2001; Maidens et al., 1998), while relatively few studies have been conducted in the southeastern Coastal Plain (McCay et al., 2002; Whiles and Grubaugh, 1996). Average volumes of CWD in unmanaged forests in the Pacific Northwest approach 500 m^3/ha (Spies and Cline, 1988). Unmanaged forests in South Carolina average 17.5 m^3/ha while volumes in managed forests average 8.6 m^3/ha (McMinn and Hardt, 1996). Low CWD volume in southeastern forests, and particularly managed pine forests, is a product of common silvicultural practices, such as short rotation lengths and prescribed fire, in addition to high humidity which increases decay rate (McCay et al., 2002; Sharitz et al., 1992). Recent advances in wood utilization technology and an emerging biofuels market (i.e., wood chips, wood pellets, and cellulosic ethanol) have the potential to further decrease the amount of woody material left in forests following timber harvests (Bies, 2006; Hewett et al., 1981; Westbrook et al., 2007).

CWD within forested ecosystems provides multiple benefits to herpetofauna communities. CWD sustains stable temperature and moisture regimes, providing incubation sites and protection from desiccation (Boddy, 1983; Graham, 1925; Jaeger, 1980; Maser and Trappe, 1984; Maser et al., 1988; Whiles and Grubaugh, 1996). CWD provides an invertebrate prey base for many amphibian and reptile species by attracting larvae, termites, centipedes, earthworms, and other arthropods consumed by toads, frogs, lizards, salamanders, and small terrestrial snakes (Conant and Collins, 1998; Graham, 1925; Whiles and Grubaugh, 1996). Lizards and snakes may use downed logs and snags for courtship displays, egg

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deposition sites, and aestivation sites (Cooper and Vitt, 1994; Martof et al., 1980; Vitt and Cooper, 1986; Whiles and Grubaugh, 1996). CWD also provides habitat for small mammals including voles, shrews, and mice, providing prey for larger snake species such as rat snakes (*Elaphe* spp.), racers (*Coluber* spp.), coachwhips (*Masticophis* spp.), kingsnakes (*Lampropeltis* spp.), pine snakes (*Pituophis* spp.), and pit vipers (Viperidae; Gibbons and Dorcas, 2005; Martof et al., 1980; Loeb, 1999; Maser and Trappe, 1984; Tallmon and Mills, 1994).

Our study was a continuation of a 2-phase, long-term project investigating the importance of CWD as a habitat component in managed upland pine stands in the southeastern Coastal Plain. Phase I of the study was initiated in 1996 to determine if removing CWD had negative consequences on ecological processes. In Phase II, initiated in 2001, 2 additional treatments, a five-fold increase in downed CWD and a 10-fold increase in standing CWD (snags), were added to examine a broader range of processes and mechanisms by which CWD affects forest systems. Capture trends from previous years of the project indicate that amphibian and reptile communities in this study area do not rely strongly on the presence of CWD (Owens et al., 2008), although snake communities showed a positive response to removal treatments during years 2–4 of Phase II (2003–2005). Owens et al. (2008) suggested the lack of overall response was due to the burrowing capabilities of southeastern herpetofauna as an adaptation to low levels of CWD. While this may be true, the progression of decomposition results in CWD capable of holding more moisture and attracting a more diverse and abundant invertebrate community (Boddy, 1983; Graham, 1925; Maser and Trappe, 1984) potentially increasing herpetofauna use of treatment plots. Our primary objective was to assess the response of herpetofauna communities to the removal and addition of CWD (both downed and standing) as compared to control stands during years 6 and 7 of Phase II of the study. We also examined the relationship between rain events and amphibian and reptile captures among treatments under the premise that CWD retains moisture, allowing movement under dry conditions, whereas the absence of CWD restricts movement to precipitation events.

2. Methods

2.1. Study area

The study plots were located on the Savannah River Site (SRS), a 78,000-ha National Environmental Research Park administered by the Department of Energy (DOE). The SRS is located in the Upper Coastal Plain and Sandhills physiographic region of South Carolina (White, 2005). This region is characterized by sandy soils and gently sloping hills dominated by pines with scattered hardwoods (Imm and McLeod, 2005). The climate of the SRS is humid subtropical with mean annual temperature and rainfall of 18 °C and 122.5 cm, respectively (Blake et al., 2005).

When the DOE acquired the SRS in 1951, old-field habitats dominated the site as a result of past land-use activities driven by crop and cotton production, as well as timber harvests (White, 2005). Today, the majority of the site has been reforested by the U. S. Forest Service (Imm and McLeod, 2005; White, 2005). Approximately 68% of the SRS is composed of upland pine stands, including loblolly (*Pinus taeda*), slash (*P. elliottii*), and longleaf (*P. palustris*) pines. While much of the land is managed for timber production, nearly two-thirds of the pine forests on SRS are 40–70 years old (Imm and McLeod, 2005).

Study plots were located in three loblolly pine stands planted between 1950 and 1953. Site index (base age 50) of the plots ranged from 80 to 100 (USDA Forest Service, unpublished data). Although the overstory in these stands was dominated by loblolly pine, slash and longleaf pine also were present. Understory vegetation was dominated by sassafrass (*Sassafrass albidum*), black cherry (*Prunus serotina*), lespedeza (*Lespedeza* spp.), blackberry (*Rubus* spp.), and poison oak (*Toxicodendron pubescens*).

2.2. Study design

Study design was a randomized complete block, with each of 4 treatments randomly assigned within each of the 3 forest stands (blocks). Blocks were chosen based on the following criteria: approximately 45-year-old loblolly pine plantations (at project initiation in 1996); ≥76 m from the nearest wetland, road, or power line; and large enough to accommodate four 9.3-ha square plots. Treatments were (1) control, where CWD was not manipulated; (2) snag, where standing CWD volume was increased 10-fold; (3) removal, where all downed CWD ≥10 cm in diameter and ≥60 cm in length was removed; and (4) downed, where volume of downed CWD was increased five-fold. Each treatment plot consisted of a 6-ha core trapping area, surrounded by a 3.3-ha buffer zone subject to the same treatment to minimize edge effect. Control and removal treatment plots were initiated in 1996 (Phase I), while downed and snag treatment plots were implemented in 2001 (Phase II). Downed treatments were created by removing existing downed CWD by hand and randomly felling trees within rows until a five-fold increase was obtained. Similarly, snag treatments were created by girdling and later injecting herbicide into trees within rows until a 10-fold increase was obtained. To standardize basal area, control and removal plots were thinned to a live pine basal area of between 13.8 and 20.8 m^2/ha in 2001. Annual removal of CWD ≥10 cm in diameter and ≥60 cm long was performed by hand in the removal treatment plots. All plots were prescribed burned in summer 2004.

2.3. Data collection

Downed woody debris measurements were taken from 2005 to 2008 to measure change in decay state during and 2 years prior to our study. Inventories were conducted in randomly selected subplots (50 m × 50 m) within the inner 4 ha of each treatment plot. Within each subplot, all logs with at least 50% of their measurable length within the subplot were measured, and logs ≥10 cm in diameter at the midpoint and ≥60 cm in length were included in the inventory. Logs were classified into 1 of 5 decay categories based on the Maser et al. (1979) decay scale, where stage 1 logs were sound, with intact bark; stage 2 logs had mostly sound wood with some bark starting to flake; stage 3 logs had broken branches and were missing bark; stage 4 logs were soft and blocky in texture; and stage 5 logs were powdery in texture and partly buried. Although log volumes were estimated assuming logs were cylindrical which may overestimate the true volume of downed wood, measurements were consistent among treatments and years.

Herpetofauna sampling was conducted using pitfall drift-fence arrays. Drift fences consisted of aluminum flashing buried approximately 15 cm below ground, with 19-l plastic buckets (pitfall traps) buried flush to the ground against each fence. Each plot contained one cross-shaped array with four 30-m arms extending out from the center of the plot in each of the cardinal directions, and four Y-shaped arrays with three 15-m arms located in each corner of the 6-ha core sampling area (Fig. 1). Pitfall traps were positioned on both sides drift fences to capture animals moving in either direction. Pitfall traps were maintained with 2.5–5 cm of soil in the bottom to provide captured animals cover from temperature extremes and desiccation during trapping periods. The bottoms of pitfall traps were perforated, allowing drainage of excess water after heavy rains.

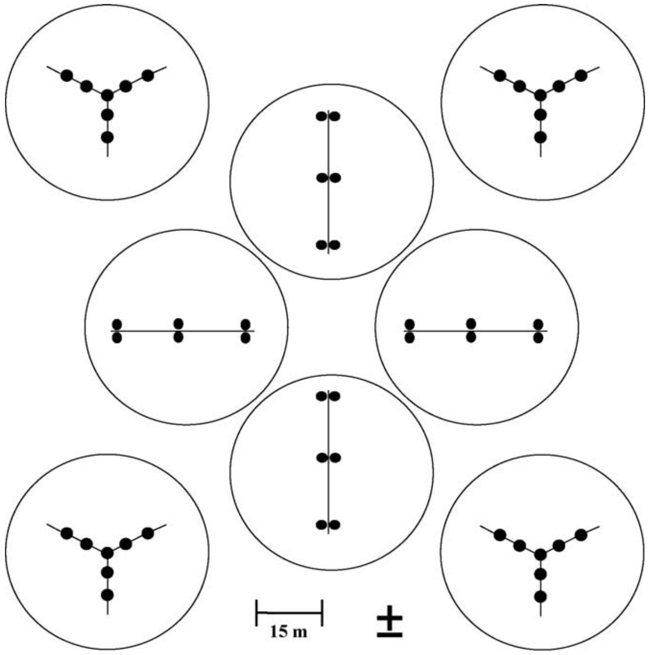

Fig. 1. Arrangement of drift-fence arrays and bucket traps used for sampling herpetofauna on 6-ha core area of a 9.3-ha treatment plot in an upland loblolly pine (*Pinus taeda*) stand at the Savannah River Site, Barnwell County, South Carolina. Also shown are buffers within which topographic variables were measured for covariate analyses.

Herpetofauna were sampled in all plots for 14 days each season from January 2007 to August 2008, for a total of 7 sampling seasons. Traps were checked daily between 07:00 and 17:00. All captured individuals were identified to species, measured (snout-vent length; mm), and age (juvenile versus adult) was determined if possible. The array of capture and direction of movement (for cross-shaped arrays only) were noted for each animal captured (direction of movements for winter 2007 and the first 5 days of the spring 2007 sample seasons were not recorded). Rainfall data were collected from a weather station approximately 4 km from study plots.

Variations in slope, aspect, and relative elevation affect soil moisture (Famiglietti et al., 1998) which can influence herpetofauna distribution and abundance (Spight, 1968; Spotila and Berman, 1976). We therefore quantified topographic variables with the potential to influence herpetofauna abundance by affecting site moisture. Trap array locations were recorded using a Trimble GeoExplorer 3 handheld GPS unit and differentially corrected using data from a Continually Operating Reference Station (CORS) in Columbia County, Georgia (63 km from the study site). Array locations for Y-shaped arrays were taken at the middle bucket and array locations for each arm of the cross-shaped array were taken at the middle of each array arm. Y-shaped arrays and each arm of the cross-shaped array were considered separate arrays, yielding a total of 8 arrays with capture data per plot. We used a GIS to create a circular buffer with a radius of 15.5 m around array locations (Fig. 1). Buffer size was determined using home range estimates for Fowler's toad (*Bufo woodhousii fowleri*; Clarke, 1974) because no reliable home range estimates are available for the southern toad (*Bufo terrestris*), the most commonly captured anuran in our study. We assumed a home range size similar to Fowler's toads because of their similar habitat requirements and life histories (Buhlmann et al., 2005). The buffer size chosen encompasses home range size of most amphibians and reptiles captured in the study for which home range sizes are known. Mean elevation, degree of slope, and aspect were calculated for each buffered area using the Zonal Statistics tool in the Spatial Analyst extension of ArcGIS 9.2 (Environmental Systems Research Institute). All pixels (and their associated values) with $\geq$50% of their area within the buffer boundary were used for calculations. Distance to the nearest stream was calculated from the actual array location point (center point of the buffer). All stream orders were considered although intermittent streams may not have contained water during this study.

2.4. Statistical analysis

Amphibian and reptile abundance (captures), species diversity, and species richness were calculated for each Y-shaped array and each arm of cross-shaped arrays to allow inclusion of topographic variables as covariates in analyses. Species diversity was calculated using the Shannon–Weiner species diversity index (H'; Pielou, 1977). Values were standardized by dividing by length of fencing within each array. Treatment differences were examined using 2-way analysis of covariance (ANCOVA) with slope, elevation, aspect, and distance to nearest stream as covariates. All data were tested for normality using Shapiro–Wilks test. Non-normal data were ranked and ANCOVA was performed on ranks. Significant results were further analyzed using adjusted least square means pairwise comparisons. We used forest stand as the block for all ANCOVA analyses and SAS 9.1 (SAS Institute, 2008) to perform all statistical analyses.

Spearman correlation coefficient was used to examine the relationship between precipitation and amphibian and reptile captures within each treatment. Total number of each species captured per sample night was compared with the amount of precipitation 24- and 48-h prior to capture.

We examined directional data to determine if a significant portion of amphibians captured were migratory, as migration events might influence treatment responses. Because anurans made up 78% of all amphibian captures, movement was analyzed for this taxonomic group separately. Movement direction was inferred from the side of the drift fence on which individuals were captured. A chi-square test was used to test for equal captures among drift-fence sides. However, because small sample sizes yielded expected values <5 and chi-square tests underestimate P-values under these circumstances, Fisher's exact test was used to generate P-values for significance testing (Sokal and Rohlf, 1995; Zar, 1999). As migratory movements are generally seasonal, captures for both years were combined for each season. Total seasonal captures, as well as seasonal captures per site were analyzed, as the relative proximity of each site to potential breeding sites could influence animal movement.

3. Results

Mean volume ($\pm$SE) of downed CWD in 2007 was 59.4 m^3/ha ($\pm$7.9) in downed plots, 34.7 m^3/ha ($\pm$6.3) in snag plots, and 12.7 m^3/ha ($\pm$1.9) in control plots (Fig. 2). Downed CWD volume for removal plots was not measured in 2007, but was 0.29 m^3/ha ($\pm$0.14) and 0.24 m^3/ha ($\pm$0.15) in 2005 and 2006, respectively. Mean decay states of logs in downed, control, and snag plots in 2007 were 3.1, 3.3, and 3, respectively (Fig. 3).

Capture totals over 7 trapping seasons from January 2007 to August 2008 were 355 amphibians and 668 reptiles representing 11 and 25 species, respectively. Toads made up the majority (64.8%) of amphibian captures, whereas salamanders and frogs represented 22% and 13.2%, respectively (Table 1). Lizards made up the majority of reptile captures (77.2%) with snakes making up the remainder (22.8%) (Table 2).

Abundance, species richness, or species diversity did not differ among treatments for anurans, salamanders, and lizards ($P > 0.05$).

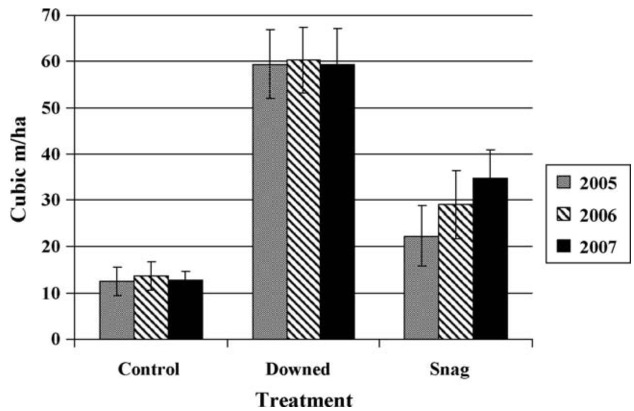

Fig. 2. Mean volume of down woody debris accumulations over 3 years in control ($n = 3$; CWD was not manipulated), downed ($n = 3$; volume of downed CWD was increased five-fold), removal ($n = 3$; all downed CWD ≥10 cm in diameter and ≥60 cm in length was removed), and snag ($n = 3$; standing CWD volume was increased 10-fold) treatment plots in loblolly pine (*Pinus taeda*) stands on the Savannah River Site, Barnwell County, South Carolina.

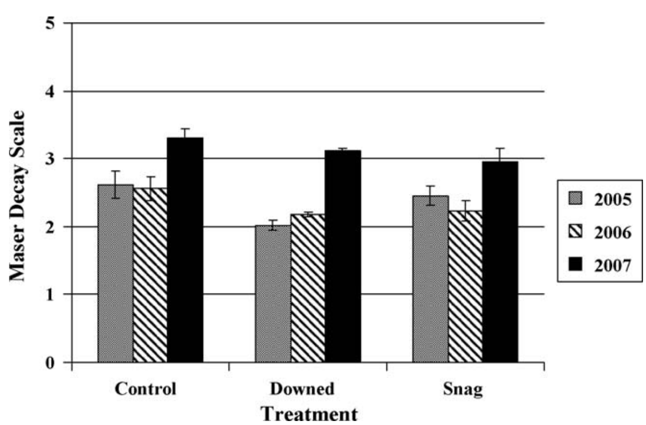

Fig. 3. Mean decay stage of downed wood, based on Maser et al. (1979), over 3 years in control ($n = 3$), downed addition ($n = 3$), and snag ($n = 3$) treatment plots in loblolly pine (*Pinus taeda*) stands on the Savannah River Site, Barnwell County, South Carolina.

Snake abundance ($F_{3,86} = 3.07$, $P = 0.0321$), species richness ($F_{3,86} = 2.91$, $P = 0.0392$), and species diversity ($F_{3,86} = 3.39$, $P = 0.0216$) were higher in removal than downed addition plots (Table 3). Anuran abundance was influenced by block ($F_{2,86} = 3.62$, $P = 0.031$) and distance to nearest stream ($F_{1,86} = 6.71$, $P = 0.0112$).

Daily captures for anurans and salamanders were positively correlated with rainfall 24 h prior to capture in all treatment plots with strongest correlations occurring in removal plots (Table 4). Daily captures for anurans and salamanders also were positively correlated with rainfall 48 h prior to capture in control and downed addition plots, respectively ($r = 0.2143$, $P = 0.0341$; $r = 0.2443$, $P = 0.0154$; Table 4). Lizard captures were negatively correlated with rainfall 48 h prior to capture in control and snag plots ($r = -0.2587$, $P = 0.0101$; $r = -0.3916$, $P < 0.0001$). All amphibian and anuran movement direction did not differ ($P > 0.05$) for total seasonal captures or seasonal captures per site, suggesting that treatment responses were not influenced by seasonal migratory movements.

4. Discussion

The lack of a treatment response by amphibians in our study was consistent with trends from the previous 10 years (encompassing both Phases I and II) of the long-term project (McCay et al., 2002; Owens et al., 2008). Ornate chorus frogs (*Pseudacris ornata*), eastern spadefoot toads (*Scaphiopus holbrookii*), *A. talpoideum*, and *B. terrestris* together comprised 71% of amphibian captures. These species are fossorial and prefer sandy soils to accommodate burrowing activities (Brown and Means, 1984; Carr, 1940; Martof et al., 1980; Semlitsch, 1983). While it has been shown that invertebrate abundance can be positively influenced by the presence of CWD (Jabin et al., 2004), sampling within study plots 5 years following initiation of removal treatments showed no significant effect of CWD removal on average arthropod abundance (Hanula et al., 2006). Further, invertebrate communities in southeastern pine stands can be highly abundant on the forest floor (Hanula and Wade, 2003). Most previous studies that have demonstrated positive relationships between CWD and amphibian communities were conducted in regions of the U.S. characterized by high CWD volumes (Spies and Cline, 1988) compared to the Southeast (McMinn and Hardt, 1996). Amphibians in the Southeast may have adapted to avoid desiccation and predation by burrowing rather than relying solely on CWD for cover and invertebrate production.

Snakes were the only group of herpetofauna for which we demonstrated a treatment response. Snake abundance was higher in removal than in downed addition plots, consistent with results from years 2 to 4 (2003–2005) of Phase II (Owens et al., 2008). We also found higher snake diversity and richness in removal compared to downed addition plots. In contrast, Owens et al. (2008) who reported no difference in diversity among treatments and lower species richness in snag plots. Small, litter-dwelling

Table 1
Total number of amphibians captured using drift-fence pitfall arrays in control ($n = 3$; CWD was not manipulated), downed ($n = 3$; volume of downed CWD was increased five-fold), removal ($n = 3$; all downed CWD ≥10 cm in diameter and ≥60 cm in length was removed), and snag ($n = 3$; standing CWD volume was increased 10-fold) treatment plots in upland loblolly pine (*Pinus taeda*) stands in Barnwell County, South Carolina, 2007–2008.

Species	Treatment				Total
	Control	Downed	Removal	Snag	
Ambystoma tigrinum (Tiger salamander)	0	0	1	0	1
Ambystoma talpoideum (Mole salamander)	15	14	14	26	69
Bufo terrestris (Southern toad)	10	22	30	20	82
Gastrophryne carolinensis (Eastern narrowmouth toad)	28	18	18	24	88
Hyla gratiosa (Barking tree frog)	0	0	1	0	1
Hyla sp. (unidentifiable hylid species)	1	0	2	0	3
Plethodon chlorobryonis (Atlantic coast slimy salamander)	3	0	2	1	6
Pseudacris ornata (Ornate chorus frog)	3	4	13	22	42
Pseudotriton ruber (Southern red salamander)	0	0	2	0	2
Rana sp. (unidentifiable ranid species)	1	0	0	0	1
Schaphiopus holbrookii (Eastern spadefoot toad)	16	14	10	20	60
Total	77	72	93	113	355

Table 2
Total number of reptiles captured using drift-fence pitfall arrays in control (n = 3; CWD was not manipulated), downed (n = 3; volume of downed CWD was increased five-fold), removal (n = 3; all downed CWD ≥10 cm in diameter and ≥60 cm in length was removed), and snag (n = 3; standing CWD volume was increased 10-fold) treatment plots in upland loblolly pine (*Pinus taeda*) stands in Barnwell County, South Carolina, 2007–2008.

Species	Treatment				Total
	Control	Downed	Removal	Snag	
Agkistrodon contortrix (Copperhead)	0	1	0	0	1
Anolis carolinensis (Green anole)	21	30	28	10	89
Cemophora coccinea (Scarlet snake)	1	3	7	2	13
Cnemidophorus sexlineatus (Six-lined racerunner)	12	3	16	13	44
Coluber constrictor (Black racer)	2	0	3	0	5
Diadophis punctatus (Southern ringneck snake)	1	0	0	0	1
Elaphe guttata (Corn snake)	1	1	0	1	3
Elaphe obsoleta (Gray rat snake)	1	0	2	0	3
Eumeces fasciatus (Five-lined skink)	13	15	4	30	62
Eumeces inexpectatus (Southeastern five-lined skink)	4	10	3	3	20
Eumeces laticeps (Broadhead skink)	10	17	5	21	53
Eumeces sp. (unidentifiable skink species)	2	1	1	2	6
Heterodon platyrhinos (Eastern hognose snake)	1	0	0	0	1
Heterodon simus (Southern hognose snake)	2	1	2	1	6
Lampropeltis triangulum (Scarlet kingsnake)	0	0	1	0	1
Nerodia fasciata (Banded water snake)	0	0	2	2	4
Nerodia floridana (Florida green water snake)	0	0	1	0	1
Scincella lateralis (Ground skink)	11	5	11	6	33
Sceloporus undulatus (Eastern fence lizard)	30	59	67	53	209
Sistrurus miliarius (Pygmy rattlesnake)	1	0	0	0	1
Storeria dekayi (Brown snake)	1	0	0	0	1
Storeria occipitomaculata (Red-bellied snake)	3	1	1	4	9
Tantilla coronata (Southeastern crowned snake)	21	9	32	13	75
Thamnophis sauritus (Eastern ribbon snake)	1	0	0	0	1
Thamnophis sirtalis (Common garter snake)	0	0	1	1	2
Virginia valeriae (Smooth earth snake)	5	9	8	2	24
Total	144	165	195	164	668

terrestrial snakes, including the smooth earth snake (*Virginia valeriae*), southern ringneck snake (*Diadophis punctatus*), scarlet kingsnake (*Lampropeltis triangulum*), brown snake (*Storeria dekayi*), red-bellied snake (*S. occipitomaculata*), scarlet snake (*Cemophora coccinea*), and southeastern crowned snake (*Tantilla coronata*) constituted almost 82% of all snakes captured during our study. These species commonly forage for soft-bodied arthropods, earthworms, slugs, and spiders under leaf and pine litter, but also can be found in decaying logs and stumps and under rocks (Gibbons and Dorcas, 2005; Martof et al., 1980). Todd and Andrews

Table 3
Mean (SE) number of captures, species richness, and species diversity per m of drift fence for all herpetofauna and taxonomic groups captured in control (n = 3; CWD was not manipulated), downed (n = 3; volume of downed CWD was increased five-fold), removal (n = 3; all downed CWD ≥10 cm in diameter and ≥60 cm in length was removed), and snag (n = 3; standing CWD volume was increased 10-fold) treatment plots from January 2007 to August 2008 in upland loblolly pine (*Pinus taeda*) stands in Barnwell County, South Carolina. Different letters indicate significant differences among treatments.

	Treatment			
	Control	Downed	Removal	Snag
Abundance	(n = 24)	(n = 24)	(n = 24)	(n =24)
Herpetofauna	0.23(0.03)	0.27(0.03)	0.33(0.03)	0.31(0.03)
Amphibians	0.07(0.02)	0.09(0.02)	0.11(0.01)	0.13(0.02)
Anurans	0.06(0.01)	0.07(0.01)	0.09(0.01)	0.09(0.01)
Salamanders	0.02(0.01)	0.02(0.01)	0.02(0.01)	0.03(0.01)
Reptiles	0.15(0.02)	0.18(0.02)	0.22(0.02)	0.18(0.02)
Lizards	0.01(0.12)	0.15(0.02)	0.15(0.02)	0.15(0.02)
Snakes	0.04(0.01)ab	0.03(0.01)b	0.07(0.01)a	0.03(0.01)ab
Richness				
Herpetofauna	0.16(0.02)	0.15(0.01)	0.19(0.01)	0.18(0.02)
Amphibians	0.05(0.01)	0.05(0.01)	0.08(0.01)	0.07(0.01)
Anurans	0.04(0.01)	0.04(0.01)	0.06(0.01)	0.06(0.01)
Salamanders	0.01(0.003)	0.01(0.003)	0.01(0.003)	0.01(0.003)
Reptiles	0.11(0.01)	0.09(0.01)	0.12(0.01)	0.10(0.01)
Lizards	0.07(0.01)	0.07(0.01)	0.07(0.01)	0.08(0.01)
Snakes	0.04(0.01)ab	0.02(0.01)b	0.04(0.01)a	0.02(0.01)ab
Diversity				
Herpetofauna	0.04(0.003)	0.04(0.003)	0.05(0.003)	0.05(0.003)
Amphibians	0.01(0.003)	0.02(0.003)	0.02(0.003	0.02(0.003)
Anurans	0.01(0.003)	0.01(0.003)	0.02(0.003)	0.02(0.003)
Salamanders	0.001(0.001)	−0.0002(0.001)	0.001(0.001)	0.001(0.001)
Reptiles	0.03(0.004)	0.03(0.003)	0.03(0.003)	0.03(0.003)
Lizards	0.02(0.003)	0.02(0.003)	0.02(0.003)	0.02(0.003)
Snakes	0.01(0.002)ab	0.003(0.002)b	0.01(0.002)a	0.004(0.002)ab

Table 4
Correlation coefficients (*r*) and *P*-values from Spearman correlation tests between the amount of precipitation 24- and 48-h prior to capture in control (*n* = 3; CWD was not manipulated), downed (*n* = 3; volume of downed CWD was increased five-fold), removal (*n* = 3; all downed CWD ≥10 cm in diameter and ≥60 cm in length was removed), and snag (*n* = 3; standing CWD volume was increased 10-fold) treatment plots for daily captures of all herpetofauana, amphibians, anurans, salamanders, reptiles, lizards, and snakes. Herpetofauna were captured using drift fences pitfall traps from January 2007 to August 2008 in upland loblolly pine stands at the Savannah River Site in Barnwell County, South Carolina.

	Control		Downed		Removal		Snag	
	r	*P*-value	*r*	*P*-value	*r*	*P*-value	*r*	*P*-value
24-h prior to capture								
Herpetofauna	0.037	0.719	0.084	0.409	0.147	0.150	0.207	0.040[a]
Amphibians	0.370	<0.0001[a]	0.388	<0.0001[a]	0.452	<0.0001[a]	0.433	<0.0001[a]
Anurans	0.309	0.002[a]	0.331	<0.0001[a]	0.518	<0.0001[a]	0.453	<0.0001[a]
Salamanders	0.267	0.008[a]	0.213	0.035[a]	0.366	0.0002[a]	0.281	0.005[a]
Reptiles	−0.199	0.049[a]	−0.106	0.297	−0.160	0.116	−0.105	0.305
Lizards	−0.175	0.085	−0.070	0.491	−0.120	0.240	−0.087	0.395
Snakes	−0.119	0.242	−0.147	0.149	−0.090	0.380	0.020	0.845
48-h prior to capture								
Herpetofauna	−0.171	0.093	−0.120	0.240	−0.314	0.002[a]	−0.128	0.208
Amphibians	0.188	0.064	0.180	0.076	0.015	0.884	0.142	0.163
Anurans	0.214	0.034[a]	0.049	0.630	−0.017	0.866	−0.073	0.478
Salamanders	−0.027	0.789	0.244	0.015[a]	−0.047	0.642	0.137	0.178
Reptiles	−0.256	0.011[a]	−0.228	0.024[a]	−0.391	<0.0001[a]	−0.198	0.051
Lizards	−0.259	0.010[a]	−0.184	0.070	−0.392	<0.0001[a]	−0.174	0.086
Snakes	−0.112	0.273	−0.174	0.087	−0.137	0.179	−0.169	0.097

[a] Indicates a significant correlation at $\alpha = 0.05$.

(2008) suggested that small terrestrial snakes may use CWD for daytime refugia, foraging, or nesting. Snakes in removal plots may range farther in search of invertebrate prey and adequate nesting sites while snakes in downed addition plots centralize their movements around downed CWD for foraging and nesting activities. Increases in movement rate and distance in removal plots would increase the possibility of capture, thus explaining higher abundance and diversity levels seen in those plots compared to downed addition plots. Additionally, the inadequacy of pitfall traps in capturing all snake species present within plots may have influenced snake capture results. For example, while 19-l buckets are capable of capturing the young-of-year (YOY) for some large-bodied snake species (e.g. racers, rat snakes, kingsnakes, coachwhips, and pitvipers), adults easily escape (Todd et al., 2007). Todd et al. (2007) determined that drift fences using a combination of funnel traps and 19-l plastic buckets yielded the greatest number of individual captures. Therefore, snake species richness, diversity, and abundance estimates based solely on pitfall trap captures may underestimate true values.

We found that reptile captures were negatively correlated with rainfall. The evolution of scales in the epidermis of reptiles reduces water loss (Zug et al., 2001), and likely explains their independence from moisture-regulating habitat variables and weather conditions. Conversely, the positive correlation we observed between amphibian captures and precipitation is a well-documented phenomenon driven by physiological requirements (Carr, 1940; Semlitsch, 1981; Spight, 1968; Spotila and Berman, 1976). Further, correlation coefficient (*r*) values suggest that amphibian movement is more strongly dictated by rain events in removal plots, possibly due to the lack of moisture-holding CWD on the forest floor.

5. Conclusion

Our results suggest that amphibians and reptiles in the southeastern Coastal Plain do not rely heavily on CWD as a habitat component. Lack of response may be a result of adaptation to the longleaf pine ecosystem that historically dominated the uplands on our study area (White, 2005). The frequent fires that maintain longleaf pine forests, coupled with increased decomposition rates due to high humidity, yield ecosystems low in aboveground structural diversity (McCay et al., 2002; Sharitz et al., 1992). However, the sandy soils of the region provided herpetofauna an avenue for adapting to the paucity of forest floor structure. The majority of species captured during this study are adept at burrowing into the sandy forest floor below the litter layer (Carr, 1940; Pearson, 1955; Pearson, 1957; Semlitsch, 1981; Semlitsch, 1983). A thick layer of pine and leaf litter provides invertebrate prey, protection from predators, and a buffer from temperature and moisture extremes (Geiger et al., 1995; Hanula and Wade, 2003). Utilizing a combination of existing burrows, ground litter, decomposing root systems, CWD, and stumps, amphibian and reptile communities in the Southeast appear able to thermoregulate and mitigate moisture loss, as well as survive periodic ground fires, without relying completely on CWD (Gibbons and Dorcas, 2005; Martof et al., 1980).

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References

Alkaslassy, E., 2005. Abundance of plethodontid salamanders in relation to coarse woody debris in a low elevation mixed forest of the western cascades. Northwest Sci. 79, 156–163.
Aubry, K.B., Jones, L.L.C., Hall, P.A., 1988. Terrestrial amphibian communities in southern Washington Cascade Range. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Management of Amphibians, Reptiles, and Small Mammals in North America. USDA For. Serv. Gen. Tech. Rep. RM-166, pp. 327–338.
Bies, L., 2006. The biofuels explosion: is green energy good for wildlife? Wildl. Soc. Bull. 34, 1203–1205.
Blake, J.I., Hunter Jr., C.H., Bayle, B.A., 2005. Climate and air quality. In: Kilgo, J.C., Blake, J.I. (Eds.), Ecology and Management of a Forested Landscape: Fifty Years of Natural Resource Stewardship on the Savannah River Site. Island Press, Washington, D.C., pp. 16–23.

Boddy, L., 1983. Microclimate and moisture dynamics of woody decomposing in terrestrial ecosystems. Soil Biol. Biochem. 15, 149–157.
Brown, L.E., Means, D.B., 1984. Fossorial behavior and ecology of the chorus frog *Pseudacris ornata*. Amphibia-Reptilia 5, 261–273.
Buhlmann, K.A., Tuberville, T.D., Leiden, Y., Ryan, T.J., Poppy, S., Winne, C.T., Greene, J.L., Mills, T.E., Scott, D.E., Gibbons, J.W., 2005. Biotic communities: amphibians and reptiles. In: Kilgo, J.C., Blake, J.I. (Eds.), Ecology and Management of a Forested Landscape: Fifty Years of Natural Resource Stewardship on the Savannah River Site. Island Press, Washington, D.C., pp. 203–223.
Bury, R.B., Corn, P.S., Aubry, K.B., 1991. Regional Patterns of Terrestrial Amphibian Communities in Oregon and Washington. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA For. Serv. Gen. Tech. Rep. PNW-GNR-285, pp. 340–350.
Butts, S.R., McComb, W.C., 2000. Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. J. Wildl. Manag. 64, 95–104.
Carr Jr., A.F., 1940. Dates of frog choruses in Florida. Copeia 1940, 50.
Clarke, R.D., 1974. Activity and movement patterns in a population of Fowler's Toad, *Bufo woodhousei fowleri*. Am. Midl. Nat. 92, 257–274.
Conant, R., Collins, J.T., 1998. A Field Guide to Reptiles and Amphibians of Eastern/Central North America, 3rd edition. Houghton Mifflin Co., Boston, MA.
Cooper Jr., W.E., Vitt, L.J., 1994. Tree and substrate selection in the semi-arboreal scincid lizard *Eumeces laticeps*. Herpetol. J. 4, 20–23.
Dupuis, L.A., Smith, J.N.M., Bunnell, F., 1995. Relation of terrestrial-breeding amphibian abundance to tree-stand age. Conserv. Biol. 9, 645–653.
Famiglietti, J.S., Rudnicki, J.W., Rodell, M., 1998. Variability in surface moisture content along a hillslope transect: Rattlesnake Hill, Texas. J. Hydrol. 210, 259–281.
Geiger, R., Aron, R.H., Todhunter, P., 1995. The Climate Near the Ground. Harvard University Press, Cambridge.
Gibbons, W., Dorcas, M., 2005. Snakes of the Southeast. University of Georgia Press, Athens, Georgia.
Graham, S.A., 1925. The felled tree trunk as an ecological unit. Ecology 6, 397–411.
Greenberg, C.H., 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. For. Ecol. Manag. 148, 135–144.
Hanula, J.L., Wade, D.D., 2003. Influence of long-term dormant-season burning and fire exclusion on ground-dwelling arthropod populations in longleaf pine flatwoods ecosystems. For. Ecol. Manag. 175, 163–184.
Hanula, J.L., Horn, S., Wade, D.D., 2006. The role of dead wood in maintaining arthropod diversity on the forest floor. Insect biodiversity and dead wood. In: Grove, S.J., Hanula, J.L. (Eds.), Proceedings of the Symposium for the 22nd International Congress of Entomology. USDA For. Serv. Gen. Tech. Rep. SRS-93, pp. 57–66.
Hewett, C.E., High, C.J., Marshall, N., Wildermuth, R., 1981. Wood energy in the United States. Ann. Rev. Energy 6, 139–170.
Imm, D.W., McLeod, K.W., 2005. Plant Communities. In: Kilgo, J.C., Blake, J.I. (Eds.), Ecology and Management of a Forested Landscape: Fifty Years of Natural Resource Stewardship on the Savannah River Site. Island Press, Washington, D.C., pp. 106–160.
Jabin, M., Mohr, D., Kappes, H., Topp, W., 2004. Influence of deadwood on density of soil macro-arthropods in a managed oak-beech forest. For. Ecol. Manag. 256, 61–69.
Jaeger, R.G., 1980. Microhabitats of a terrestrial forest salamander. Copeia 1980, 265–268.
Loeb, S.C., 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. J. Mammal. 80, 460–471.
Maidens, D.A., Menzel, M.A., Laerm, J., 1998. Notes on the effect of size and level of decay of course woody debris on relative abundance of shrews and salamanders in the southern Appalachian Mountains. Georgia J. Sci. 56, 226–233.
Martof, B.S., Palmer, W.M., Bailey, J.R., Harrison III, J.R., 1980. Amphibians and Reptiles of the Carolinas and Virginia. The University of North Carolina Press, Chapel Hill, North Carolina.
Maser, C.R., Anderson, R.G., Cromack Jr., K., Williams, J.T., Martin, R.E., 1979. Dead and downed woody material. In: Thomas, J. (Ed.), Wildlife habitats in Managed Forests, the Blue Mountains of Oregon and Washington. USDA For. Serv. Agr. Hdbk., pp. 78–95.
Maser, C., Trappe, J.M., 1984. The seen and unseen world of the fallen tree. USDA For. Serv. Gen. Tech. Rep. PNW-164.
Maser, C., Tarrant, R.F., Trappe, J.M., Franklin, J.F., 1988. From the forest to the sea: a story of fallen trees. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-229.
McCay, T.S., Forschler, B.T., Komoroski, M.J., Ford, W.M., 2002. Responses of mammalian insectivores, amphibians, and reptiles to broad-scale manipulation of coarse woody debris. In: Proceedings of the USDA For. Serv. Fin. Proj. Rep. SRS 00-CA-11330138-197, pp. 1–54.
McMinn, J.W., Hardt, R.A., 1996. Accumulation of coarse woody debris in southern forests. In: McMinn, J.W., Crossley, Jr., D.A. (Eds.), Biodiversity of Coarse Woody Debris in Southern Forests. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA For. Serv. Gen. Tech. Rep. SE-94, pp. 1–9.
Owens, A.K., Moseley, K.R., McCay, T.S., Castleberry, S.B., Kilgo, J.C., Ford, W.M., 2008. Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (*Pinus taeda*) forests. For. Ecol. Manag. 256, 2078–2083.
Pearson, P.G., 1955. Population ecology of the spadefoot toad, *Scaphiopus h. holbrooki* (Harlan). Ecol. Monogr. 25, 233–267.
Pearson, P.G., 1957. Further notes on the population ecology of the spadefoot toad. Ecology 38, 580–586.
Pielou, E.C., 1977. Mathematical Ecology. Wiley and Sons, New York, New York.
SAA Institute, 2008. SAS/STAT Software, Version 9. 1. 3. SAS Institute, Inc., Cary, NC.
Semlitsch, R.D., 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Can. J. Zool. 59, 315–322.
Semlitsch, R.D., 1983. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. Can. J. Zool. 61, 616–620.
Sharitz, R.R., Boring, L.R., Van Lear, D.H., Pinder III, J.E., 1992. Integrating ecological concepts with natural resource management of southern forests. Ecol. Appl. 2, 226–237.
Sokal, R.R., Rohlf, F.J., 1995. Biometry: The Principles and Practice of Statistics in Biological Research, 3rd edition. W.H. Freeman, New York, New York.
Spies, T.A., Cline, S.P., 1988. Coarse woody debris in forests and plantations of coastal Oregon. In: Maser, C., Cline, S.P., Cromack, Jr., K., Trappe, J.M., Hansen, E. (Eds.), From the Forest to the Sea: A Story of Fallen Trees. USDA For. Serv. Gen. Tech. Rep. PNW-229, pp. 5–24.
Spight, T.M., 1968. The water economy of salamanders: evaporative water loss. Physiol. Zool. 41, 195–203.
Spotila, J.R., Berman, E.N., 1976. Determination of skin resistance and the role of the skin in controlling water loss in amphibians and reptiles. Comp. Biochem. Physiol. 55A, 407–411.
Tallmon, D., Mills, L.S., 1994. Use of logs within home ranges of California red-backed voles on a remnant forest. J. Mammal. 75, 97–101.
Todd, B.D., Andrews, K.M., 2008. Response of a reptile guild to forest harvesting. Conserv. Biol. 22, 753–761.
Todd, B.D., Winne, C.T., Willson, J.D., Gibbons, J.W., 2007. Getting the drift: examining the effects of timing, trap type and taxon on herpetofaunal drift fence surveys. Am. Midl. Nat. 158, 292–305.
Vitt, L.J., Cooper Jr., W.E., 1986. Foraging and diet of a diurnal predator (*Eumeces laticeps*) feeding on hidden prey. J. Herpetol. 20, 408–415.
Welsh, H.H., Jr., Lind, A.J., 1991. The structure of the herpetofaunal assemblage in the Douglas-fir hardwood forests of northern California and southwestern Oregon. In: Ruggiero, L.F., Aubry, K.B., Carey, A.B., Huff, M.H. (Eds.), Wildlife and Vegetation of Unmanaged Douglas-fir Forests. USDA For. Serv. Gen. Tech. Rep. PNW-GNR-285, pp. 395–414.
Westbrook Jr., M.D., Greene, W.D., Izlar, R.L., 2007. Utilizing forest biomass by adding a small chipper to a tree-length southern pine harvesting operation. South. J. Appl. For. 31, 165–169.
Whiles, M.R., Grubaugh, J.W., 1996. Importance of coarse woody debris to southern forest herpetofauna. In: McMinn, J.W., Crossley, Jr., D.A. (Eds.), Biodiversity and Coarse Woody Debris in Southern Forests. Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA For. Serv. Gen. Tech. Rep. SE-94, pp. 94–100.
White, D.L., 2005. Land-use history. In: Kilgo, J.C., Blake, J.I. (Eds.), Ecology and Management of a Forested Landscape: Fifty Years of Natural Resource Stewardship on the Savannah River Site. Island Press, Washington, D.C., pp. 2–12.
Zar, J.H., 1999. Biostatistical Analysis, 4th edition. Prentice Hall, Upper Saddle River, New Jersey.
Zug, G.R., Vitt, L.J., Caldwell, J.P., 2001. Herpetoglogy: An Introductory Biology of Amphibians and Reptiles, 2nd edition. Academic Press, San Diego, CA.