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Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (*Pinus taeda*) forests

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ABSTRACT

Coarse woody debris (CWD) has been identified as a key microhabitat component for groups that are moisture and temperature sensitive such as amphibians and reptiles. However, few experimental manipulations have quantitatively assessed amphibian and reptile response to varying CWD volumes within forested environments. We assessed amphibian and reptile response to large-scale, CWD manipulation within managed loblolly pine stands in the southeastern Coastal Plain of the United States from 1998 to 2005. Our study consisted of two treatment phases: Phase I treatments included downed CWD removal (removal of all downed CWD), all CWD removal (removal of all downed and standing CWD), pre-treatment snag, and control; Phase II treatments included downed CWD addition (downed CWD volume increased 5-fold), snag addition (standing CWD volume increased 10-fold), all CWD removal (all CWD removed), and control. Amphibian and anuran capture rates were greater in control than all CWD removal plots during study Phase I. In Phase II, reptile diversity and richness were greater in downed CWD addition and all CWD removal than snag addition treatments. Capture rate of *Rana sphenocephala* was greater in all CWD removal treatment than downed CWD addition treatment. The dominant amphibian and snake species captured are adapted to burrowing in sandy soil or taking refuge under leaf litter. Amphibian and reptile species endemic to upland southeastern Coastal Plain pine forests may not have evolved to rely on CWD because the humid climate and short fire return interval have resulted in historically low volumes of CWD.

1. Introduction

Coarse woody debris (CWD), often defined as standing and downed dead trees, large boles, and downed branches greater than 10 cm in diameter and 60 cm in length (Harmon et al., 1986), has been identified as a key forest component that increases forest-floor structural diversity and serves as an important microhabitat for groups that are moisture and temperature sensitive such as reptiles and amphibians (deMaynadier and Hunter, 1995; Whiles and Grubaugh, 1996; Russell et al., 2004). Reduction of microhabitat features, such as CWD, is believed to be a major factor in suppressed amphibian and reptile populations therein (deMaynadier and Hunter, 1995; Russell et al., 2004). However, there have been no experimental studies examining effects of CWD removal and addition on herpetofaunal communities in managed forests of the southeastern Coastal Plain, or largely elsewhere.

Our study was a part of a long-term investigation on the role of CWD as an ecosystem component in upland loblolly pine forests of the southeastern Coastal Plain (McCay et al., 2002a). Our objective was to investigate effects of large-scale manipulation of CWD volume on amphibian and reptile communities using a randomized, replicated design. We hypothesized that captures of plethodontid salamander and reptile species would be greater in plots with CWD addition than in plots with CWD removed because of the dependence of these taxonomic groups on CWD for a variety of life history aspects (Petranka, 1998; Whiles and Grubaugh, 1996). Conversely, we hypothesized that captures of other

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amphibian species (excluding plethodontids) would not differ among CWD treatment types because in the Coastal Plain, most of these burrow into soil and leaf litter to avoid dry conditions (Clarke, 1974; Semlitsch, 1983).

2. Methods

2.1. Study area

Our study was conducted on the Savannah River Site (SRS; 33°0–25′N, 81°25–50′W), a 78,000-ha National Environmental Research Park administered by the U.S. Department of Energy, located in the Upper Coastal Plain and Sandhills physiographic region of South Carolina, USA. Upland forests in this region are characterized by a 3–7-year fire return interval, sandy soils, and gently sloping hills dominated by longleaf pine (*Pinus palustris*), loblolly pine (*P. taeda*) and slash pine (*P. elliottii*) interspersed with various oak (*Quercus* spp.) and hickory (*Carya* spp.) species in uplands and red maple (*Acer rubrum*) and sweetgum (*Liquidambar styraciflua*) in mesic bottomland sites. Climate is humid, warm-temperate to subtropical with a mean annual temperature of 18 °C and mean annual precipitation of 122.5 cm (Blake et al., 2005).

Our research plots were located in stands dominated by *P. taeda* planted between 1950 and 1953, though *P. elliottii* and *P. palustris* were also interspersed among the canopy. Understory vegetation was dominated by *Lespedeze* spp., broomsedge (*Andropogon virginicus*), poison oak (*Toxicodendron pubescens*), blackberry (*Rubus* spp.), black cherry (*Prunus serotina*), and sassafras (*Sassafras albidum*). As standard management, the USDA Forest Service conducted prescribed burns with low-intensity fires on plots every 3–4 years. Two of the three stands on which our plots (9 of 12 plots) were located were burned in February and March 2000. The remaining stand (and remaining 3 plots) was burned in March 2001. All study plots were burned again in May and June 2004.

2.2. Study design

Our study was designed as a randomized complete block with four treatments (four 9.3 ha plots) randomly assigned within three blocks (three adjacent forest stands) (McCay et al., 2002a). Phase I treatments (1996–2001) included: downed CWD removal (removal of all downed CWD; $n = 3$), all CWD removal (removal of all downed and standing CWD; $n = 3$), pre-treatment snag ($n = 3$), and control ($n = 3$). Phase II treatments (2002–2005) included: downed CWD addition (downed CWD volume increased 5-fold; $n = 3$), snag addition (standing CWD volume increased 10-fold; $n = 3$), all CWD removal (removal of all downed and standing CWD; $n = 3$), and control ($n = 3$). We applied treatments to the entire 9.3 ha plot, but only sampled in the 6 ha core of each plot to avoid edge effects (McCay et al., 2002a). Annual removal of CWD ensured that downed CWD removal (Phase I) and all CWD removal (Phase I and Phase II) plots remained free of all limbs and downed trees ≥10 cm diameter and 60 cm length. For Phase II treatment implementation, we created snags in snag addition treatment plots by girdling and later injecting herbicide into trees in 20 12-ft strips resulting in a treated snag basal area of 15.9 m^2/ha during the summer of 2001. Similarly, we felled 20 12-ft strips of pines to increase CWD volume in each of the CWD Addition plots. To standardize remaining treatments, we thinned all treatment plots to 13.8–20.8 m^2/ha of live-tree basal area in September and October 2001. An ice storm in January 2004 created a pulse input of CWD that increased downed CWD volume on all plots; this input of downed CWD was removed from the all CWD removal treatment plots in February 2004.

2.3. Data collection

Although Phase I treatments were created in 1996, we started herpetofaunal sampling in 1998. We sampled amphibians and reptiles using drift-fence arrays installed on each plot (Gibbons and Bennett, 1974). Drift-fences consisted of aluminum flashing buried 15 cm below ground with 19 L plastic buckets buried flush to the ground. Each plot contained one cross-shaped drift fence array with four 30 m arms extending in each of the cardinal directions from the center of the plot, and four Y-shaped arrays with three 15 m arms located in each corner of the 6 ha core area. We maintained pitfall traps with a small amount of soil or water during sampling periods to prevent desiccation of captured animals. For each capture, we identified it to species, marked it with the removal of a single toe, and then released it on the other side of the fence from its capture. Although removal of multiple toes can decrease frog survival and recapture probability, removal of a single toe appears to have a negligible effect (McCarthy and Parris, 2004). Herpetofaunal capture and marking were approved by University of Georgia Institutional Animal Care and Use Committee (Permit number A2004-10204-m2). From summer 1998 to fall 2001 (Phase I), we conducted herpetofaunal sampling for 14 days during winter, summer, and fall and for 28 days during spring sampling periods. From summer 2002 to fall 2005 (Phase II), we conducted herpetofaunal sampling for 14 days during all seasons, except spring 2004, when we sampled for 28 days.

2.4. Statistical methods

We calculated the Shannon–Weiner species diversity index (H′; Pielou, 1977) and species richness/plot for amphibians and reptiles. To account for uneven trapping effort among years, we calculated captures rates for taxonomic groups by dividing plot captures by number of plot nights. Additionally, we calculated capture rates for individual species with ≥50 captures. We tested for normality using Shapiro–Wilks's test (Sokal and Rohlf, 1995). Variables not meeting assumptions of normality ($P < 0.05$) were rank transformed for analyses. We compared amphibian and reptile diversity, amphibian and reptile richness, and capture rates of amphibian, anuran, salamander, reptile, lizard, snake, and individual species among treatments in Phase I and Phase II using a one-way analysis of variance (ANOVA; Proc Mixed), with forest stand, year, and treatment × year treated as random effects. We used adjusted least square means pair-wise comparisons when ANOVA models indicated significant effects ($P < 0.05$). For Phase I, if no differences were detected among treatments, we used linear contrast statements to compare combined control and pre-treatment snag plots with all CWD removal treatments. We conducted all analyses using SAS statistical software (SAS Institute, 2005).

3. Results

3.1. Phase I

During Phase I, we captured 904 reptiles and 4348 amphibians over 266 sampling nights, representing 21 amphibian and 26 reptile species (see McCay et al., 2002b for species capture totals). Amphibian and reptile richness and diversity did not differ among treatments (Table 1). Total amphibian and anuran capture rates did not differ among treatments (Table 1); however, amphibian and anuran captures in combined control and pre-treatment snag plots were greater than in all CWD removal treatments ($F_{1,9} = 5.59$, $P = 0.042$; $F_{1,9} = 5.71$, $P = 0.041$ for amphibians and anurans, respectively).

Table 1
Phase I mean (±S.E.) amphibian and reptile diversity, richness, and capture rate (plot captures per plot night) in upland loblolly pine (*Pinus taeda*) stands subject to manipulations in coarse woody debris (CWD) volume in the upper Coastal Plain, South Carolina, 1998–2001

	Treatment				$F_{3,9}$	P
	Control	Pre-treatment snag addition	All CWD removal	Down CWD addition		
Amphibian diversity (H′)[a]	19.14 ± 3.02A	15.04 ± 2.09A	17.12 ± 2.69A	17.02 ± 2.63A	1.04	0.419
Amphibian richness	6.92 ± 0.57A	6.08 ± 0.45A	6.58 ± 0.60A	6.67 ± 0.61A	0.84	0.508
Reptile diversity (H′)	16.75 ± 1.30A	12.78 ± 1.62A	12.79 ± 1.60A	16.34 ± 2.60A	2.02	0.181
Reptile richness	7.33 ± 0.36A	6.17 ± 0.51A	6.00 ± 0.51A	7.08 ± 0.79A	1.86	0.206
Amphibian[a]	1.62 ± 0.56	1.66 ± 0.43	1.14 ± 0.26	0.99 ± 0.26	2.55	0.121
Anuran[a]	1.40 ± 0.52	1.32 ± 0.33	0.95 ± 0.22	0.86 ± 0.24	2.59	0.117
Salamander[a]	0.22 ± 0.07	0.34 ± 0.14	0.19 ± 0.05	0.13 ± 0.03	0.77	0.541
Reptile[a]	0.31 ± 0.04	0.21 ± 0.03	0.29 ± 0.03	0.31 ± 0.05	3.72	0.055
Snake[a]	0.11 ± 0.02	0.06 ± 0.01	0.07 ± 0.01	0.09 ± 0.02	3.34	0.070
Lizard[a]	0.20 ± 0.03	0.15 ± 0.02	0.22 ± 0.03	0.21 ± 0.04	2.81	0.100
Ambystoma talpoideum[a]	0.14 ± 0.06 (112)	0.29 ± 0.13 (234)	0.11 ± 0.05 (86)	0.06 ± 0.02 (47)	0.51	0.686
Bufo terrestris[a]	0.62 ± 0.19 (495)	0.45 ± 0.12 (366)	0.39 ± 0.10 (312)	0.40 ± 0.12 (322)	1.05	0.416
Gastrophryne carolinensis[a]	0.40 ± 0.29 (334)	0.43 ± 0.18 (360)	0.24 ± 0.11 (197)	0.22 ± 0.10 (181)	1.05	0.415
Plethodon chlorobryonis[a]	0.07 ± 0.02 (60)	0.05 ± 0.01 (41)	0.06 ± 0.03 (50)	0.06 ± 0.02 (53)	1.63	0.249
Pseudacris ornata[a]	0.11 ± 0.03 (88)	0.21 ± 0.09 (153)	0.07 ± 0.02 (54)	0.06 ± 0.02 (47)	4.04	0.045
Scaphiopus holbrookii[a]	0.24 ± 0.08 (180)	0.22 ± 0.07 (166)	0.25 ± 0.06 (191)	0.16 ± 0.06 (117)	2.70	0.109
Anolis carolinensis[a]	0.11 ± 0.02 (87)	0.05 ± 0.02 (44)	0.11 ± 0.03 (94)	0.08 ± 0.02 (62)	3.20	0.076
Scincella lateralis[a]	0.04 ± 0.01 (33)	0.03 ± 0.01 (22)	0.05 ± 0.01 (39)	0.07 ± 0.02 (60)	2.76	0.104
Sceloporus undulatus[a]	0.04 ± 0.01 (29)	0.05 ± 0.01 (38)	0.04 ± 0.01 (36)	0.06 ± 0.02 (43)	0.57	0.647
Tantilla coronata[a]	0.04 ± 0.01 (33)	0.02 ± 0.01 (17)	0.04 ± 0.01 (32)	0.02 ± 0.00 (19)	2.00	0.185

Phase I treatments included downed CWD removal ($n = 3$), all CWD removal ($n = 3$), pre-treatment snag ($n = 3$), and control ($n = 6$). For species, total captures are in parentheses following means. In rows, variable means not followed by the same letter were significantly different ($P < 0.05$) using least square means pairwise comparison.

[a] Analysis of variance performed on ranked data.

Individual species with ≥50 captures included *Bufo terrestris* (southern toad, $n = 1495$), *Ambystoma talpoideum* (mole salamander, $n = 479$), *Gastrophryne carolinensis* (eastern narrowmouth toad, $n = 1072$), *Plethodon chlorobryonis* (slimy salamander, $n = 204$), *Pseudacris ornata* (ornate chorus frog $n = 342$), *Scaphiopus holbrookii* (eastern spadefoot , $n = 654$), *Anolis carolinensis* (green anole, $n = 287$), *Scincella lateralis* (ground skink, $n = 154$), *Sceloporus undulatus* (eastern fence lizard, $n = 146$), and *Tantilla coronata* (southeastern crowned snake, $n = 101$). For individual amphibian species analyzed, *A. talpoideum*, *B. terrestris*, *G. carolinensis*, *P. chlorobyonis*, *S. holbrookii* capture rate did not differ among treatments (Table 1). Using linear contrasts, *P. ornata* capture rate was greater in pre-treatment snag than in downed CWD removal ($F_{1,9} = 11.07$, $P = 0.009$). For individual reptile species, *S. lateralis*, *S. undulatus* and *T. coronata* did not differ among treatments (Table 1).

Table 2
Phase II mean ± S.E. amphibian and reptile diversity, richness, and capture rates (plot captures per plot night) in upland loblolly pine (*Pinus taeda*) stands subject to manipulations in coarse woody debris (CWD) volume in the upper Coastal Plain, SC, 2003–2005

	Treatment				$F_{3,9}$	P
	Control	Downed CWD Addition	CWD removal	Snag addition		
Amphibian diversity (H′)	18.65 ± 2.16	17.27 ± 1.39	18.17 ± 1.45	16.75 ± 1.73	0.32	0.810
Amphibian richness[a]	6.83 ± 0.47	6.42 ± 0.42	7.00 ± 0.37	6.50 ± 0.50	0.71	0.570
Reptile diversity (H′)	13.40 ± 0.88AB	16.69 ± 1.68AB	17.39 ± 1.56A	10.42 ± 1.81B	5.01	0.026
Reptile richness[a]	6.50 ± 0.29AB	7.17 ± 0.47A	7.42 ± 0.45A	5.33 ± 0.54B	5.70	0.018
Amphibian	1.78 ± 0.29	1.91 ± 0.31	1.79 ± 0.26	1.34 ± 0.15	1.34	0.321
Anuran	1.60 ± 0.27	1.77 ± 0.30	1.65 ± 0.27	1.11 ± 0.15	1.93	0.196
Salamander	0.18 ± 0.05	0.15 ± 0.03	0.14 ± 0.03	0.23 ± 0.09	0.79	0.528
Reptile	0.37 ± 0.07AB	0.45 ± 0.07AB	0.50 ± 0.08A	0.27 ± 0.05B	4.55	0.033
Snake	0.14 ± 0.03AB	0.15 ± 0.02AB	0.19 ± 0.04A	0.09 ± 0.03B	4.44	0.036
Lizard	0.22 ± 0.05	0.28 ± 0.06	0.27 ± 0.05	0.18 ± 0.03	1.91	0.198
Ambystoma talpoideum[a]	0.12 ± 0.05 (70)	0.08 ± 0.03 (51)	0.09 ± 0.03 (63)	0.19 ± 0.09 (134)	0.14	0.933
Bufo terrestris	0.67 ± 0.19 (345)	0.88 ± 0.28 (486)	0.80 ± 0.25 (406)	0.52 ± 0.13 (288)	0.8	0.525
Gastrophryne carolinensis	0.62 ± 0.16 (398)	0.67 ± 0.21 (396)	0.47 ± 0.10 (259)	0.34 ± 0.06 (203)	1.29	0.337
Plethodon chlorobryonis[a]	0.05 ± 0.02 (25)	0.06 ± 0.02 (27)	0.04 ± 0.02 (19)	0.02 ± 0.02 (11)	3.19	0.077
Pseudacris ornata	0.02 ± 0.01 (18)	0.02 ± 0.01 (18)	0.04 ± 0.01 (29)	0.04 ± 0.01 (24)	1.66	0.244
Rana sphenocephala[a]	0.04 ± 0.02AB (30)	0.02 ± 0.01A (16)	0.11 ± 0.04B (78)	0.03 ± 0.01AB (23)	4.39	0.037
Scaphiopus holbrookii	0.22 ± 0.08 (160)	0.15 ± 0.05 (110)	0.19 ± 0.03 (133)	0.17 ± 0.05 (122)	0.56	0.656
Anolis carolinensis[a]	0.07 ± 0.02 (39)	0.06 ± 0.02 (30)	0.10 ± 0.03 (57)	0.06 ± 0.02 (37)	1.16	0.377
Scincella lateralis[a]	0.02 ± 0.01 (10)	0.02 ± 0.01 (10)	0.04 ± 0.01 (20)	0.02 ± 0.01 (11)	0.51	0.683
Sceloporus undulatus	0.10 ± 0.02 (49)	0.18 ± 0.05 (95)	0.12 ± 0.03 (56)	0.08 ± 0.02 (44)	3.27	0.073
Tantilla coronata	0.09 ± 0.02 (47)	0.09 ± 0.02 (49)	0.13 ± 0.03 (70)	0.06 ± 0.02 (31)	3.46	0.065

For species, total captures are given in parentheses following means. In rows, variable means not followed by the same letter were significantly different ($P < 0.05$) using least square means pairwise comparisons. Phase II treatments included downed CWD addition ($n = 3$), all CWD removal ($n = 3$), snag addition ($n = 3$), and control ($n = 3$). Phase II treatments included downed CWD addition ($n = 3$), all CWD removal ($n = 3$), snag addition ($n = 3$), and control ($n = 3$). For species, total captures are given in parentheses following means. In rows, variable means not followed by the same letter were significantly different ($P < 0.05$) using least square means pairwise comparisons.

[a] Analysis of variance performed on ranked data.

3.2. Phase II

During Phase 2, we captured 879 reptiles and 4040 amphibians over 210 sampling nights, representing 14 amphibian and 24 reptile species (see Moseley, 2004 and Owens, 2006 for complete list of species captured). Amphibian diversity and richness did not differ among treatments (Table 2). Reptile diversity was greater in all CWD removal than snag addition treatments, and reptile richness was greater in downed CWD addition and all CWD removal treatments than snag addition treatments (Table 2). Total amphibian, anuran, and salamander capture rates did not differ among treatments (Table 2). Reptile and snake capture rates were greater in removal than snag treatments and (Table 2). Lizard capture rates did not differ among treatments (Table 2).

Individual species with $\geq$50 captures included *B. terrestris* (*n* = 1525), *A. talpoideum* (*n* = 318), *G. carolinensis* (*n* = 1256), *P. chlorobryonis* (*n* = 82), *P. ornata* (*n* = 89), *S. holbrookii* (*n* = 525), *Rana sphenocephala* (southern leopard frog) (*n* = 147), *A. carolinensis* (*n* = 163), *S. lateralis* (*n* = 51), *S. undulatus* (*n* = 244), and *T. coronata* (*n* = 197). For individual amphibian species analyzed, *A. talpoideum*, *B. terrestris*, *G. carolinensis*, *P. chlorobryonis*, *P. ornata*, and *S. holbrookii* capture rates did not differ among treatments (Table 2). *Rana sphenocephala* capture rate was greater in all CWD removal than downed CWD addition treatments (Table 2). For individual reptile species examined, *A. carolinensis*, *S. lateralis*, *S. undulatus*, and *T. coronata* capture rates did not differ among treatments (Table 2).

4. Discussion

4.1. Amphibian response

Although CWD has been identified as an important structural component maintaining amphibian diversity in forested environments (deMaynadier and Hunter, 1995), overall we found few differences in amphibian parameters measured among our CWD treatments. Amphibian captures were dominated by *B. terrestris*, *G. carolinensis*, and *S. holbrookii*, which together accounted for 74 and 82 % of amphibian captures in Phases I and II, respectively. Combined capture rates of the three dominant species was over 1.4 times greater in control than all CWD removal plots during Phase I. However, overall amphibian and anuran capture rates did not differ among treatments in Phase II of our study. Terrestrial anurans often rely on burrowing under leaf litter or soil to escape adverse climatic conditions (Greenberg and Tanner, 2005; Baughman and Todd, 2007). Similarly, ambystomatid salamanders use subterranean burrows created by small mammals such as moles (Talpidae) and rodents, as well as pre-existing cracks and crevices in the soil, during unsuitable surface conditions (Semlitsch, 1983). Dependence on CWD by many of these species probably is negligible, especially where sufficient litter cover is available. However, dependence on CWD may increase following reductions in litter depth and cover (Chazal and Niewiarowski, 1998; Moseley et al., 2004; Rothermel and Luhring, 2005).

Rana sphenocephala was the only amphibian to respond positively to CWD removal treatments. During Phase II, capture rates were 3.3 and 4.8 times greater in all CWD removal than snag addition and downed CWD addition plots, respectively. Insufficient sample size precluded analyses of *R. sphenocephala* capture rates for Phase I, thus we are unable to determine if treatment effects were consistent between phases. However, some ranid species, including *R. sphenocephala*, have been found to prefer open forested habitats that facilitate rapid, unimpeded movement (Birchfield and Deters, 2005; Graeter et al., 2008; Mazerolle and Desrochers, 2005). The large amount of CWD in our downed CWD addition treatments may have hindered *R. sphenocephala* migration across plots. Several of our plots were located near an ephemeral wetland; therefore, our amphibian captures may have been more influenced by the proximity of our treatment plots to a breeding site than by CWD manipulations.

Contrary to our initial hypothesis, plethodontid salamanders did not exhibit a response to our CWD treatments. Unlike ambystomatid salamanders, members of the family Plethodontidae rely entirely upon dermal respiration, requiring moist skin to facilitate efficient oxygen exchange (Stebbins and Cohen, 1997). Plethodontid salamander abundance has been positively correlated with CWD volume in various hardwood forest types in the Appalachians (Maidens et al., 1998; Moore et al., 2001) and coniferous forests of the Pacific Northwest and Canada (Dupuis et al., 1995; Butts and McComb, 2000). Coarse woody debris in advanced decay stages has greater water holding ability (Jaeger, 1980) and therefore should serve as better cover for plethodontids in xeric upland pine stands. *Plethodon chlorobryonis* densities may increase as CWD reaches more advanced decay stages in our treatments.

4.2. Reptile response

Phase I differences in reptile capture rates between pretreatment snag and control plots make interpretation of snag-treatment effects difficult. However, our results suggest Snag plots supported lower reptile richness and diversity than downed CWD addition and all CWD removal plots, particularly for snakes. Of the 15 snake species captured in Phase II, only 6 occurred in snag addition plots. There is little available research on the impacts of habitat alteration on snake communities. Snake occurrence and abundance are influenced by a variety of factors including prey abundance, habitat structure, and predation (Vitt, 1987). Although snag presence can influence invertebrate prey abundance (Hanula et al., 2006), forest floor invertebrate abundance did not differ among our CWD treatments (Moseley et al., 2006; Hanula et al., 2006). Therefore, prey availability influence on snake occurrence probably was negligible. Avian predators can be particularly abundant in pine forests with high snag densities (Land et al., 1989; Lohr et al., 2002), and in the snag addition treatments surface dwelling snake species occurrence or abundance may have been reduced because of increased predation. However, because our sampling method was biased towards smaller snakes (Enge, 2001), we do not know what the impact was for larger snakes.

Despite evidence suggesting most terrestrial snake species captured rely to some extent on CWD as a source of refugia and insect prey substrate (Brode and Allison, 1958; Semlitsch, 1981), we found no differences in snake captures among downed CWD addition treatment and controls. Conversely, increased abundance of *Diadophus punctatus* (southern ringneck snake), *Lampropeltis triangulum* (scarlet kingsnake), and *Virginia striatula* (rough earth snake) in central Florida flatwoods stands subject to clearcut harvesting and minimum site preparation was presumably a result of greater CWD abundance (Greenberg et al., 1994). Semlitsch (1981) found that xeric microhabitat with sufficient logs and rotting stumps were more important for *T. coronata* than vegetation type or macrohabitat. Sufficient leaf litter cover and uncompacted soils may be sufficient for supporting these species. Furthermore, small, cryptozoic snakes may become more abundant as CWD reaches advanced stages of decay.

5. Conclusion

Overall, our study suggests that herpetofauna of the southeastern Coastal Plain do not respond strongly to CWD manipulations; however, our ability to detect treatment effects may have been reduced by low replication, a common drawback to large-scale experimental studies. Nonetheless, our study represents one of only several large-scale, experimental studies investigating the role of CWD manipulations on amphibian and reptile communities. Historically, upland areas of our study region were characterized by the longleaf pine-wiregrass (*Aristida stricta*) community (Landers et al., 1995; Van Lear and Harlow, 2002). The frequent, low intensity ground fires that maintained this community combined with high decomposition rates contributed historically to low level of CWD (Van Lear and Waldrop, 1994; Van Lear, 1996). Additionally, CWD in advanced stages of decay probably did not persist for long periods (Moorman et al., 1999). Mature southeastern pine stands contain lower CWD volumes than do mature hardwood forests in the region (McMinn and Hardt, 1996; Moorman et al., 1999). Pine litter contains abundant invertebrate prey (Hanula and Wade, 2003) and buffers soil burrows from extreme temperature and moisture fluctuations (Geiger et al., 1995). A number of forest floor microhabitat features including litter, CWD, and underground burrows probably act synergistically to sustain amphibian and reptile abundance and diversity within upland pine stands of the southeastern Coastal Plain.

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References

Baughman, B., Todd, B.D., 2007. Role of substrate cues in habitat selection by recently metamorphosed *Bufo terrestris* and *Scaphiopus holbrooki*. J. Herpetol. 41, 154–157.

Birchfield, G.L., Deters, J.E., 2005. Movement paths of displaced northern green frogs (*Rana clamitans melanota*). Southeast. Nat. 4, 63–76.

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, DC, pp. 16–23.

Brode, W.E., Allison, P., 1958. Burrowing snakes of the panhandle counties of Mississippi. Herpetologica 14, 37–40.

Butts, S.R., McComb, W.C., 2000. Associations of forest-floor vertebrates with coarse woody debris in managed forests of western Oregon. J. Wildlife Manage. 64, 95–104.

Chazal, A.C., Niewiarowski, P.H., 1998. Responses of mole salamanders to clearcutting: using field experiments in forest management. Ecol. Appl. 8, 1133–1143.

Clarke, R.D., 1974. Activity and movement patterns in a population of Fowler's toad, *Bufo woodhousei fowleri*. Am. Midl. Nat. 92, 257–274.

deMaynadier, P.G., Hunter, M.L., 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environ. Rev. 3, 230–261.

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.

Enge, K.M., 2001. The pitfalls of pitfall traps. J. Herpetol. 35, 467–478.

Geiger, R., Aron, R.H., Todhunter, P., 1995. The Climate Near the Ground. Harvard University Press, Cambridge.

Gibbons, J.W., Bennett, D.H., 1974. Determination of anuran terrestrial activity patterns by a drift fence method. Copeia 1974, 236–243.

Graeter, G.J., Rothermel, B.B., Gibbons, J.W., 2008. Habitat selection and movement of pond-breeding amphibians in experimentally fragmented pine forests. J. Wildl. Manage. 72, 473–482.

Greenberg, C.H., Neary, D.G., Harris, L.D., 1994. Effects of high-intensity wildfire and silvicultural treatments on reptile communities in sand-pine scrub. Conserv. Biol. 8, 1047–1057.

Greenberg, C.H., Tanner, G.W., 2005. Spatial and temporal ecology and eastern spadefoot toads on a Florida landscape. Herpetologica 61, 20–28.

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. Manage. 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 Fors. Serv. Gen. Tech. Rep. SRS-93. pp. 57–66.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.

Jaeger, R.G., 1980. Microhabitats of a terrestrial forest salamander. Copeia 1980, 265–268.

Land, D., Marion, W.R., O'Meara, T.E., 1989. Snag availability and cavity-nesting birds in slash pine plantations. J. Wildl. Manage. 53, 1165–1171.

Landers, J.L., Van Lear, D.H., Boyer, W.D., 1995. The longleaf pine forests of the Southeast: requiem or renaissance. J. For. 93, 39–44.

Lohr, S.M., Gauthreaux, S.A., Kilgo, J.C., 2002. Importance of coarse woody debris to avian communities in loblolly pine forests. Conserv. Biol. 16, 767–777.

Maidens, D.A., Menzel, M.A., Laerm, J., 1998. Notes on the effect of size and level of decay of coarse woody debris on relative abundance of shrews and salamanders in the southern Appalachian mountains. GA J. Sci. 56, 226–233.

Mazerolle, M.J., Desrochers, A., 2005. Landscape resistance to frog movements. Can. J. Zool. 83, 455–464.

McCarthy, M.A., Parris, K.M., 2004. Clarifying the effect of toe clipping on frogs using Bayesian statistics. J. Appl. Ecol. 41, 780–786.

McCay, T.S., Hanula, J.L., Loeb, S.C., Lohr, S.M., McMinn, J.W., Wright-Miley, B.D., 2002a. The role of coarse woody debris in southeastern pine forests: preliminary results from a large-scale experiment. In: Proceedings of the USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181, Southern Research Station, New Ellenton, SC, pp. 135–144.

McCay, T.S., Forschler, B.T., Komoroski, M.J., Ford, W.M., 2002b. Responses of mammalian insectivores, amphibians and reptiles to broad-scale manipulations of coarse woody debris. In: Proceedings of the USDA For. Serv. Fin. Proj. Rep. SRS 00-CA-11330138-197, Southern Research Station, New Ellenton, SC, pp. 1–54.

McMinn, J.W., Hardt, R.A., 1996. Accumulations of coarse woody debris in southern forests. Biodiversity and coarse woody debris in southern forests. In: McMinn, J.W., Crossley, Jr., D.A. (Eds.), Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Fors. Serv. Gen. Tech. Rep. SE-94, Southern Research Station, Asheville, NC, pp. 1–9.

Moore, A.L., Williams, C.E., Martin, T.H., Moriarity, W.J., 2001. Influence of season, geomorphic surface and cover item on capture, size and weight of *Desmognathus ochrophaeus* and *Plethodon cinereus* in Allegheny Plateau riparian forest. Am. Midl. Nat. 145, 39–45.

Moorman, C.E., Russell, K.R., Sabin, G.R., Guynn Jr., D.C., 1999. Snag dynamics and cavity occurrence in the South Carolina Piedmont. For. Ecol. Manage. 118, 37–48.

Moseley, K.R., 2004. Response of herpetofauna and soricids to coarse woody debris manipulations in upland loblolly pine stands. M.S. Thesis, University of Georgia, Athens.

Moseley, K.R., Castleberry, S.B., Ford, W.M., 2004. Coarse woody debris and pine litter manipulation effects on movement and microhabitat use of *Ambystoma talpoideum* in a *Pinus taeda* stand. For. Ecol. Manage. 191, 387–396.

Moseley, K.R., Castleberry, S.B., Hanula, J.L., Ford, W.M., 2006. Diet of southern toads (*Bufo terrestris*) in loblolly pine (*Pinus taeda*) stands subject to coarse woody debris manipulations. Am. Midl. Nat. 153, 327–337.

Owens, A.K. 2006. Coarse woody debris manipulations and the response of soricid and herpetofaunal communities in mature loblolly pine (*Pinus taeda*) stands. M.S. Thesis, University of Georgia, Athens.

Petranka, J.W., 1998. Salamanders of the United States and Canada. Smithsonian Institute Press, Washington, DC.

Pielou, E.C., 1977. Mathematical Ecology. Wiley and Sons, New York.

Rothermel, B.B., Luhring, T.M., 2005. Burrow availability and desiccation risk of mole salamanders (*Ambystoma talpoideum*) in harvested versus unharvested forest stands. J. Herpetol. 39, 619–626.

Russell, K.R., Wigley, T.B., Baughman, W.M., Hanlin, H.G., Ford, W.M., 2004. Responses of southeastern amphibians and reptile to forest management: a review. In: Rauscher, H.M. (Ed.), Proceedings of the Gen. Tech. Rep. SRS-75, Southern Research Station, Asheville, NC, pp. 319–334.

SAS Institute, 2005. SAS/STAT Software, Version 9.1. 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., 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Herpetologica 37, 40–46.

Semlitsch, R.D., 1983. Burrowing ability and behavior of salamanders of the genus Ambystoma. Can. J. Zool. 61, 616–620.

Sokal, R.R., Rohlf, F.J., 1995. Biometry: The Principles and Practice of Statistics in Biological Research, 3rd ed. Freeman, New York.

Stebbins, R.C., Cohen, N.W., 1997. A Natural History of Amphibians. Princeton University Press, New Jersey.

Van Lear, D.H., Waldrop, T.A., 1994. Coarse woody debris considerations in southern silviculture. In: Edwards, M.B. (Ed.), Proceedings of the Eighth Biennial S. Silvicul. Res. Conf. US For. Serv., Gen. Tech. Rep. SRS-1. pp. 281–288.

Van Lear, D.H., 1996. Dynamics of coarse woody debris in southern forest ecosystems, biodiversity of coarse woody debris in southern forests. In: McMinn, J.W., Crossley, Jr., D.A. (Eds.), Proceedings of the Work. Coarse Woody Debris in S. For.: Effects on Biodiversity. US For. Serv., Gen. Tech. Rep. SE-94. pp. 10–17.

Van Lear, D.H., Harlow, R.F., 2002. Fire in the eastern United States: influence on wildlife habitat, the role of fire in nongame wildlife management and communitiy restoration. In: Ford, W.M., Russell, K.R., Moorman, C.E. (Eds.), Proceedings of the Traditional Uses and new directions proc. Special workshop. US For. Serv., Gen. Tech. Rep. NE-288. pp. 2–10.

Vitt, L.J., 1987. Communities. In: Seigel, R.A., Collins, J.T., Novak, S.S. (Eds.), Snakes: Ecology and Evolutionary Biology. MacMillan Publishing Co., New York, pp. 335–365.

Whiles, M.R., Grubaugh, J.W., 1996. Importance of coarse woody debris to southern forest herpetofaunal, biodiversity and coarse woody debris in southern forests. In: McMinn, J.W., Crossley, Jr., D.A. (Eds.), Proceedings of the Workshop on Coarse Woody Debris in Southern Forests: Effects on Biodiversity. USDA Fors. Serv. Gen. Tech. Rep. SE-94, Southern Research Station, Asheville, NC, pp. 94–100.