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# Rodent population and community responses to experimental, large scale, long-term coarse woody debris manipulations

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ABSTRACT

Coarse woody debris (CWD) is a structural feature in forests throughout the United States that provides unique cover, runways, and microclimate for various wildlife species. While use and selection of CWD for rodent foraging, travel, and nesting, which can impact an individual's fitness, has been demonstrated across numerous studies, the role of CWD presence and abundance in rodent population and community dynamics varies across studies. To better understand rodent and CWD relationships, we studied rodent populations across two periods of CWD manipulation in randomly assigned experimental treatments in South Carolina (Period I: March 1996–November 2000; removal of all snags and fallen logs, removal of fallen logs only, and Control, and Period II: January 2002–September 2006; downed woody debris addition, snag addition, and Control). Overall, we found minimal effects of experimental treatments on the rodent community composition and structure, and community level variation was mainly explained by cotton mouse (*Peromyscus gossypinus*) and southern flying squirrel (*Glaucomys volans*) captures. There were no experimental treatment effects on captures of cotton mice and southern flying squirrels, but we observed variation across seasons and years. Our study shows that over the long-term, rodent population and community dynamics are not affected by experimental manipulations of CWD in our study area.

## 1. Introduction

Coarse woody debris (CWD) is a structural feature in forests that provides unique cover, runways, and microclimates for various species, including fungi, amphibians, mammals, and birds (Fauteux et al., 2012; Naiman et al., 1999; Owens et al., 2008). However, managed forests, which are regularly harvested for timber, tend to have reduced CWD (Behjou et al., 2014; Debeljak, 2006; Gibb et al., 2005; McMinn and Hardt, 1996). As of 2010, 19% of southeastern United States forests are actively managed pine forests and that percentage is expected to increase as land use changes (Wear and Greis, 2012). Thus, managed forests in the southeastern United States may lack necessary structures for some wildlife species.

Rodents often use CWD as daytime refugia, protection from predators and extreme environmental conditions, and travel routes and feeding sites (Loeb 1996). However, results of studies of rodent use and selection of CWD, and the relationship between population dynamics and CWD, vary by species, region, and ecological scale (Fauteux et al., 2012). For example, studies conducted at the microhabitat scale often report strong positive relationships between rodent microhabitat use and selection and CWD presence and abundance (e.g., Greenberg, 2002; Hinkelman and Loeb, 2007; McCay, 2000). In contrast, studies conducted at the plot or stand scale often show weak relationships between rodent abundance or other demographic parameters and CWD abundance (Bowman et al., 2000; Craig et al., 2006; Jones and Lindquist, 2012) although Loeb (1999) found positive relationships between CWD abundance and cotton mouse (*Peromyscus gossypinus*) abundance, survival, and reproduction.

Research examining the relationship between rodents and CWD has taken a variety of approaches including natural additions of CWD due to large disturbance events (e.g., Craig et al., 2006; Greenberg, 2002; Loeb, 1999), comparisons among sites with natural variation in CWD (Jones and Lindquist, 2012), or removal of CWD, particularly for bioenergy (Boggs et al., 2020). Studies have also examined effects of downed woody debris (DWD) placed in piles and windrows (Sullivan et al., 2017). However, few studies have experimentally added CWD to explore its effects on rodents.

To better understand relationships between CWD and rodents, we

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investigated how rodent populations and communities were affected by experimentally manipulated levels of standing woody debris (SWD) or DWD over a multi-year period of CWD removal followed by a second multi-year period of CWD addition. The CWD addition period was designed to mimic a catastrophic event such as an ice or windstorm with the goal of increasing DWD levels to approximately six times background levels and SWD levels to 10 times background levels. To assess effects of treatment, season, and year, we measured: 1) rodent community structures (i.e., richness, diversity, and evenness), and 2) relative abundance or use of common species. Because of strong associations between rodents and CWD at the microhabitat scale, we predicted that rodent species richness, diversity, evenness and relative abundance or use would increase in plots with greater amounts of CWD. Specially, we predicted that southern flying squirrel use would be greater in plots with abundant snags (Taulman, 1999) and relative abundance of cotton mice would be greater in plots with greater amounts of DWD (Loeb, 1999).

## 2. Methods

### 2.1. Study area

Our study area was located at the US Department of Energy's Savannah River Site (SRS) in Aiken, Barnwell, and Allendale counties, South Carolina, USA. The SRS encompassed 80,267 ha of which approximately 68,800 ha were managed for natural resources. It was a National Environmental Research Park site located in the Southeastern Plains and Sandhills physiographic regions (Griffith et al. 2002). The natural resources of SRS were managed by the USDA Forest Service (Kilgo and Blake, 2005). The site was approximately 77% upland pine and hardwood forests with the remainder consisting of various bottomland and floodplain cover types (Imm and McLeod, 2005). Since the early 1950s, SRS has been actively managed for forest products, longleaf pine (*Pinus palustris*) and wetland restoration, conservation and recovery of the endangered red-cockaded woodpecker (*Dryobates* (=*Picoides*) *borealis*), and overall biodiversity. Study plots were situated in >45-yr old loblolly pine (*P. taeda*) stands with sandy and well-drained soils (Workman and McLeod, 1990). Additional species found in the overstory and midstory of plots were oaks (*Quercus* spp.), hickories (*Carya* spp.), sweetgum (*Liquidambar styraciflua*), and wax myrtle (*Morella cerifera*). Common understory species included poison oak (*Toxicodendron pubescens*), dog fennel (*Anthemis cotula*), and *Lespedeza* spp. All plots were thinned between 1991 and 1996 to achieve a standing basal area of 13.8–20.8 $m^2$/ha. Most of the plots were prescribed burned between 1990 and 1996 and were re-burned in 2000–2001 and 2004.

### 2.2. Study design

Our study was a randomized complete block design with four treatments replicated across three blocks (Davis et al., 2010; McCay et al., 2002; Zarnoch et al. 2013). Each treatment plot was 9.3-ha and the central 4-ha of each plot was the core sampling area. Blocks were between 97.2 m and 1,008.9 m apart from one another (average 480.1 m) while our nearest core sampling plots within a block were between 93.2 m and 108.3 m apart (average 102.3 m). During Period I (March 1996–November 2000), randomly assigned experimental treatments were: 1) removal of all snags and fallen logs (All Removal), 2) removal of fallen logs only (Log Removal), and 3) Control. Initial removals of snags and logs were conducted July-August 1996 and then every January to March throughout Period I. For Period I, each block had two Control plots. During Period II (January 2002–September 2006) randomly assigned experimental treatments were 1) downed woody debris addition to the understory (DWD Addition), 2) snag addition (SWD Addition), and 3) Control. We used the same plots for both periods. One set of Control plots from Period I remained as Control plots for Period II. The Log Removal plots in Period I became the DWD Addition plots in Period II and the second set of Control plots in Period I became the SWD Addition plots in Period II. The DWD Addition plots were created by first removing all DWD from plots and then randomly selecting 12, 3.7 m wide strips that ran the length of the plot. Trees within these strips were cut and left as whole logs. The SWD Addition plots were implemented by girdling and later injecting herbicide into standing trees along 12 equally spaced strips that extended the length of each plot. Period II treatments were implemented during 2001. Control plots were thinned to a basal area of 13.8–20.8 $m^2$/ha in 2001 to maintain a similar canopy structure to the SWD and DWD Addition plots (see Davis et al., 2010; McCay et al., 2002; and below for details).

### 2.3. Trapping

We established trapping grids (8 × 8 array with 20 m spacing) in the center of each treatment plot. At each trap station, we placed one folding Sherman live trap (7.0 × 9.0 × 25.5 cm) on the ground and baited it with sunflower seeds. We placed traps at the grid point stake that marked that trap station and thus did not preferentially place traps near logs. However, if a log was at the trap station, the trap was placed near the log. We placed another trap approximately 1.5 m high on the nearest tree and baited it with peanut butter. We placed a Mosby-type wooden box trap (19 × 19 × 61 cm) at every other trap station. Additional details of the trapping procedure can be found in Loeb et al. (1999). We trapped small mammals bi-monthly from March 1997 through September 2006 for 7–9 nights around the new moon phase of the lunar cycle. The number of nights depended on weather or other logistical constraints that shortened the trapping period. All plots were trapped on the same nights to reduce risk of confounding trap night with treatment. Because southern flying squirrels suffer high mortality in aluminum traps in cold weather, we did not set tree traps when temperatures were predicted to drop below 1.7 °C. We checked traps each morning and recorded the following data for each captured small mammal: species, mass (g), sex, and age (adult or juvenile). More specifically, southern flying squirrel age classes were determined by mass: juveniles were ≤37 g, subadults 38–55 g, and adult >55 g (Linzey and Linzey, 1979; Riter and Vallowe, 1978; Sollberger, 1943). Cotton mouse age classes were based on pelage (i.e., whether they had completed their post-juvenile molt; Layne 1968) and cotton rats (*Sigmodon hispidus*) were considered adults if they weighed >80 g (Chipman 1965). We based age classes of other species on a combination of pelage and weight characteristics. We released striped skunks (*Mephitis mephitis*), Virginia opossums (*Didelphis virginiana*), and long-tailed weasels (*Mustela frenata*) without taking measurements. We tagged newly captured southern flying squirrels, cotton mice, cotton rats, golden mice (*Ochrotomys nutalli*), eastern cottontails (*Sylvilagus floridanus*), old field mice (*P. polionotus*), eastern harvest mice (*Reithrodontomys humulis*), and eastern woodrats (*Neotoma floridana*) with #1 Monel ear tags in each ear (National Band and Tag Co., Newport, KY). We either toe-clipped or PIT-tagged (Biomark, Inc., Boise, ID) newly captured gray squirrels (*Sciurus carolinensis*) and fox squirrels (*S. niger*). Upon recapture, we recorded tag or toe-clip number. Southern flying squirrels often lost one or both of their ear-tags. We therefore placed additional tags in their ears when possible. We also recorded whether a trap was not set or had been sprung or otherwise disturbed. We did not mark shrews. When a deceased shrew could be used as a specimen, it was collected and submitted to Clemson University's Department of Biological Sciences' Bob & Betsy Campbell Museum of Natural History. All handling procedures were within the guidelines approved by the American Society of Mammalogists (Sikes et al., 2016) and conducted under Clemson University Animal Use Protocols #99-056, #20006, and #50033.

### 2.4. Coarse woody debris and weather data

We conducted inventories of snags and logs on the plots within 16–50 m × 50 m subplots (four rows of four subplots each) in the central

4 ha of each plot, described as the core sampling area. We conducted inventories during January–February 1996 and during each summer (May-August) through 2000. In 2001, we conducted inventories during January–February just before application of the Period II treatments and in December to measure immediate effect of treatments. Additional Period II CWD measurements were made during winters (January–March) of 2003 through 2006 (Zarnoch et al., 2013). We measured length (m), diameter (cm), species group (pine or hardwood), and decomposition state of all logs ≥10 cm in diameter at the midpoint. We recorded species group, total height (m) or height (m) to 10 cm diameter at breast height (DBH), and DBH for all snags. We calculated total volume ($m^3$/ha) of SWD (snags) and DWD per plot per year. We calculated snag volume following Zarnoch et al. (2013). We used the volume equation of a cylinder to calculate volume of downed CWD. We then divided total CWD volume per plot by 4-ha (area of each sampling plot; Zarnoch et al., 2013) to obtain volume per hectare (Table 1). We did not distinguish between large and small snags.

We recorded hourly weather data on site with a weather station (Campbell Scientific, Inc., Logan, UT; Coleman et al., 2004). We calculated average temperature (°C), average minimum temperature (°C), average maximum temperature (°C), average rainfall (mm), and total rainfall (mm) per month for each year we had small mammal capture data (1997–2006).

We assigned months to season by averaging all temperatures by month across all years and finding distinct breaks in temperature. The assigned seasons, months, and corresponding temperature averages and ranges were Summer (June-August; 25.3 and 24.4–26.1 °C), Fall (September-November, 17.5 and 12.6–22.5 °C), Winter (December-February, 8.2 and 7.7–9.3 °C), and Spring (March-May, 16.9 and 13.1–21.4 °C).

### 2.5. Statistical analyses

For all Period I statistical analyses, we averaged data from the two Control plots within the same block. We calculated mean and standard error of the amount of SWD and DWD among each treatment during each year. Prior to analyses, we checked normality with Shapiro–Wilks' W test and equality of variances with Levene's test for all data to address assumptions of parametric statistical tests. If assumptions were not met for raw or log-transformed data, we rank transformed data. For analysis of variance (ANOVA) models with interactions and ranked data, we used aligned rank transformations (Beasley, 2002; Blair et al., 1987; Sawilowsky et al., 1989). For all analyses, we used an alpha of 0.05. Post hoc tests included Tukey HSD for main effect models and least-square mean contrasts for all interaction models. We used Program R for all analyses (R Core Team, 2019).

While we provide an overview of all small mammal captures, analyses are specific to rodents. To test our null hypothesis that rodent communities did not differ among treatments, years, nor an interaction of treatment and year (objective 1), we calculated relative population size of each rodent species using captures per 100 trap nights per treatment plot per month. We averaged captures across months to obtain a relative population size estimate for each plot per year. Assessing captures per 100 trap nights provided a balanced measure of the sampling effort across treatments, years, and months. We calculated corrected trap nights as 1 trap night subtracted from the total number of possible trap nights for each trap that was not set, and 0.5 trap night subtracted for each trap that was sprung (Nelson and Clark, 1973). We calculated Shannon-Weiner Diversity, Simpson's Diversity, Pielou's Index of Evenness (Pielou, 1966), and richness using relative population size of each species for each plot in program R (R Core Team, 2019), package Vegan (Oksanen et al., 2013). We tested the null hypothesis that diversity indices did not differ among treatments and years using repeated measures, randomized block design ANOVA models with treatment and year (repeated measure) as factors and a possible interaction. We also conducted a permutation multivariate analysis of variance (PerMANOVA) to assess any significant clustering by treatment, year, and an interaction between treatment and year. Lastly, we used a similarity of percentages (SIMPER) to assess which species contributed the most to treatment and year pairwise differences.

To test the null hypothesis that cotton mouse and southern flying squirrel captures per 100 trap nights did not differ among treatments, years, seasons or the interactions of treatments and years and treatments and seasons (objective 2), we used repeated measures, randomized block

**Table 1**
Summary of average (±SE) total standing woody debris (snag) volume ($m^3$/ha) and average (±SE) total down woody debris volume ($m^3$/ha) per treatment per year and separated by period. Coarse woody debris inventories were conducted annually at the US Department of Energy's Savannah River Site in Aiken, Barnwell, and Allendale counties, South Carolina, USA. Period I (1997–2000) treatments were: 1) removal of all snags and fallen logs (All Removal), 2) removal of fallen logs only (Log Removal), and 3) Control. All Removal plots were not sampled for snags. During Period II (2002–2006) treatments were 1) downed woody debris addition (DWD Addition), 2) snag addition (SWD Addition), and 3) Control.

| Treatments | | | | | |
|---|---|---|---|---|---|
| **AVERAGE SNAG VOLUME** | | | | | |
| ***Period I*** | | | | | |
| | *1997* | *1998* | *1999* | *2000* | |
| Control | 2.24 ± 0.32 | 2.07 ± 0.33 | 2.76 ± 0.83 | 2.84 ± 0.84 | |
| Log Removal | 2.21 ± 1.04 | 2.18 ± 0.94 | 3.31 ± 1.24 | 3.55 ± 1.23 | |
| ***Period II*** | | | | | |
| | *2002* | *2003* | *2004* | *2005* | *2006* |
| Control | 1.65 ± 0.82 | 1.91 ± 0.81 | 5.70 ± 0.72 | 6.30 ± 0.44 | 5.92 ± 0.85 |
| DWD Addition | 0.98 ± 0.36 | 0.66 ± 0.11 | 2.05 ± 0.44 | 1.81 ± 0.63 | 1.73 ± 0.62 |
| SWD Addition | 24.58 ± 2.34 | 23.25 ± 1.08 | 23.67 ± 0.83 | 20.72 ± 0.83 | 18.42 ± 2.08 |
| **AVERAGE DWD VOLUME** | | | | | |
| ***Period I*** | | | | | |
| | *1997* | *1998* | *1999* | *2000* | |
| Control | 7.36 ± 1.35 | 7.65 ± 1.06 | 8.33 ± 1.28 | 8.94 ± 1.25 | |
| All Removal | 0.96 ± 0.23 | 0.86 ± 0.16 | 0.51 ± 0.22 | 0.25 ± 0.20 | |
| Log Removal | 1.94 ± 0.36 | 1.85 ± 0.41 | 0.84 ± 0.12 | 0.67 ± 0.28 | |
| ***Period II*** | | | | | |
| | *2002* | *2003* | *2004* | *2005* | *2006* |
| Control | 9.28 ± 2.25 | 7.25 ± 2.52 | 10.89 ± 2.75 | 12.37 ± 2.97 | 13.37 ± 2.83 |
| DWD Addition | 22.21 ± 2.64 | 21.37 ± 2.59 | 21.82 ± 2.86 | 22.28 ± 2.82 | 22.36 ± 2.73 |
| SWD Addition | 3.72 ± 0.85 | 4.54 ± 1.28 | 7.27 ± 2.75 | 15.24 ± 7.32 | 14.37 ± 3.45 |

design ANOVA models. For southern flying squirrels, we used captures per 100 trap nights as an index of use, rather than relative abundance, because individuals moved among treatment plots (approximately 11% of known unique individuals) and individuals often lost their ear tags. Cotton mice rarely moved among treatment plots, so using captures per 100 trap nights is valid to compare relative abundances, but only when capture probabilities are homogenous among treatments (Skalski and Robson 1992). We did not have high enough cotton mouse recapture rates to effectively use mark-recapture population models to estimate capture probabilities, so we used capture histories to compare the number of individuals captured once to the number captured more than once among treatments with a Pearson's chi-square test of homogeneity for each Period. We found no statistical evidence for differences in capture probabilities among treatments (Period I: $x^2 = 0.97$, $p = 0.62$ and Period II: $x^2 = 0.04$, $p = 0.98$). Furthermore, to ensure we were not missing a potential treatment effect, we accounted for CWD and weather variables that could have either masked a treatment effect or aided in the explanation of any observed patterns. When we included SWD and DWD in our ANOVA models, we removed treatment because they were correlated. Similarly, when we included weather variables, we removed season from our models as weather variables were correlated with season. We did not find any significant effects of our continuous variables on abundances, nor did we find that the addition of our continuous variables altered our initial results. Thus, we do not present those results. However, to further explain year and season effects, we used Spearman's correlation to compare relationships of cotton mouse captures per 100 trap nights, southern flying squirrel captures per 100 trap nights, average temperature, and average precipitation.

## 3. Results

### 3.1. Coarse woody debris data

During Period I, we only sampled snags in Control and Log Removal plots and total snag volume was similar between these two treatments (Table 1). In contrast, log volume was considerably higher in the Control sites than the All Removal and Log Removal plots during Period I (Table 1). During Period II, snag volume was over 10 times greater in the SWD Addition plots during 2002 and 2003, but this difference declined over time as snags began to fall in the SWD Addition plots and more snags were recruited in the Control sites (Table 1). Log volume in the DWD Addition plots during Period II was approximately 2–3 times the volume in Control plots and approximately 3–6 times greater than the volume in SWD Addition plots. However, the difference in log volume between DWD and SWD plots decreased in the latter two years of our study as snags fell and became logs (Table 1).

### 3.2. Objective 1: Rodent community

Across 9 years of trapping and 619,727 trap nights (adjusted for trap disturbance), southern flying squirrels and cotton mice were the most abundant species captured representing 44.9% and 42.6% of total captures and 46.8% and 37.7% of unique captures, respectively (Table 2). Golden mice, cotton rats, fox squirrels, and eastern cottontails were also commonly captured (Table 2).

There was no significant interaction between year and treatment for rodent assemblages in Period I (PerMANOVA: $F_{6,24} = 0.25$, $p = 0.99$). However, rodent assemblages significantly varied among treatments ($F_{2,24} = 2.85$, $p = 0.02$) and years ($F_{3,24} = 10.10$, $p < 0.01$) although year explained more of the variation than treatment (treatment $R^2 = 0.09$ and year $R^2 = 0.49$). Overall average dissimilarity between treatment pairs was similar (SIMPER, in descending order: Control and All Removal plots: 36.61; All Removal and Log Removal plots: 35.41; and Control and Log Removal plots: 35.39). There was more variation in the overall average dissimilarity between year pairs based on time gap length (in descending order: 1997 and 2000: 52.54; 1998 and 2000: 42.83; 1997 and 1999: 38.75; 1999 and 2000: 33.73; 1998 and 1999: 30.93; 1997 and 1998: 29.70). All pairwise comparisons were driven by differences in cotton mouse and southern flying squirrel captures per 100 trap nights, contributing cumulatively to at least 82% of each pairwise difference.

**Table 2**
All species captured throughout the study (1997–2006) across all treatments. Asterik (*) denotes species used in analyses. For species that we did not mark, we only included total captures as we could not differentiate recaptures ("na" for unique captures denotes those species we did not mark). We conducted small mammal trapping at the US Department of Energy's Savannah River Site in Aiken, Barnwell, and Allendale counties, South Carolina, USA.

| Species Code | Common Name | Scientific Name | Total Captures | Unique Captures |
|---|---|---|---|---|
| GLVO* | southern flying squirrels | *Glaucomys volans* | 4733 | 1820 |
| PGOS* | cotton mice | *Peromyscus gossypinus* | 4488 | 1466 |
| SIHI* | cotton rats | *Sigmodon hispidus* | 393 | 198 |
| SCNI* | fox squirrels | *Sciurus niger* | 276 | 126 |
| OCNU* | golden mice | *Ochrotomys nutalli* | 261 | 125 |
| SYFL | eastern cottontails | *Sylvilagus floridanus* | 170 | 77 |
| PPOL* | old field mice | *P. polionotus* | 41 | 20 |
| SCCA* | eastern gray squirrels | *Sciurus carolinensis* | 40 | 29 |
| BLCA | southern short-tailed shrew | *Blarina carolinensis* | 37 | na |
| DIVI | Virginia opossums | *Didelphis virginiana* | 29 | na |
| REHU* | eastern harvest mice | *Reithrodontomys humulis* | 23 | 19 |
| PRLO | common raccoon | *Procyon lotor* | 14 | na |
| MEME | striped skunks | *Mephitis mephitis* | 11 | na |
| NEFL* | eastern woodrats | *Neotoma floridana* | 11 | 6 |
| MUFR | long-tailed weasels | *Mustela frenata* | 3 | na |
| SOLO | southeastern shrews | *Sorex longirostris* | 3 | na |
| URCI | common gray foxes | *Urocyon cinereoargenteus* | 1 | na |

For Period II, neither the interaction between treatment and year nor the treatment main effect were significant for rodent assemblages ($F_{8,30} = 0.80$, $p = 0.75$ and $F_{2,30} = 1.63$, $p = 0.15$; respectively). However, rodent assemblages varied among years ($F_{4,30} = 5.86$, $p < 0.01$, $R^2 = 0.37$). Similar to Period I, the dissimilarity between years increased overall with increasing time gaps (in descending order: 2002 and 2006: 45.11; 2002 and 2005: 41.74; 2002 and 2004: 36.45; 2002 and 2003: 35.98; 2004 and 2006: 32.26; 2003 and 2006: 32.18; 2003 and 2004: 31.37; 2003 and 2005: 29.10; 2005 and 2006: 27.11; 2004 and 2005: 25.08). Similar to Period I, cotton mice and southern flying squirrels were the top two contributors to all but one (2004 and 2005) pairwise differences detected between years and contributed cumulatively to at least 63% of each pairwise difference.

In both Period I and Period II, community indices (Shannon diversity, Simpson's diversity, richness, and evenness) did not differ among treatments (all p-values $\geq 0.28$; Table 3). However, richness in Period I was significantly higher in 1997 than 2000 ($F_{3,18} = 4.31$, $p = 0.02$; Table 4).

### 3.3. Objective 2: Common species captures per 100 trap nights

In Period I, neither treatment ($F_{2,6} = 0.22$, $p = 0.80$, Fig. 1A) nor the interaction between treatment and year ($F_{6,18} = 0.42$, $p = 0.86$) had a significant effect on cotton mouse captures per 100 trap nights. When averaged across years, cotton mouse captures per 100 trap nights differed among seasons ($F_{3,18} = 22.47$, $p < 0.01$) with the highest captures in spring followed by summer and the lowest average captures in fall and winter (Fig. 1B). Cotton mouse captures per 100 trap nights also

**Table 3**
Mean diversity indices (±SE) averaged across blocks and years per period. Trapping data were collected at the US Department of Energy's Savannah River Site, in Aiken, Barnwell, and Allendale counties, South Carolina, USA. Period I (1997–2000) treatments were: 1) removal of all snags and fallen logs (All Removal), 2) removal of fallen logs only (Log Removal), and 3) Control. During Period II (2002–2006) treatments were 1) downed woody debris addition (DWD Addition), 2) snag addition (SWD Addition), and 3) Control. Shannon and Simpson's indices of diversity, richness, and evenness indices were calculated using captures per 100 trap nights and did not significantly differ among treatments ($\alpha = 0.05$).

| Treatment | N | Shannon | Simpson | Richness | Evenness |
|---|---|---|---|---|---|
| ***Period I*** | | | | | |
| **Control** | 12 | 0.94 ± 0.05 | 0.54 ± 0.02 | 4.91 ± 0.38 | 0.62 ± 0.04 |
| **All Removal** | 12 | 0.79 ± 0.04 | 0.48 ± 0.02 | 3.67 ± 0.22 | 0.62 ± 0.03 |
| **Log Removal** | 12 | 0.84 ± 0.05 | 0.51 ± 0.03 | 3.83 ± 0.30 | 0.65 ± 0.03 |
| | | $F_{2,4} = 0.70$, $p = 0.55$ | $F_{2,4} = 0.65$, $p = 0.57$ | $F_{2,4} = 1.75$, $p = 0.28$ | $F_{2,4} = 0.68$, $p = 0.56$ |
| ***Period II*** | | | | | |
| **Control** | 15 | 1.02 ± 0.05 | 0.57 ± 0.03 | 4.47 ± 0.22 | 0.69 ± 0.03 |
| **DWD Addition** | 15 | 1.03 ± 0.04 | 0.57 ± 0.02 | 4.73 ± 0.30 | 0.68 ± 0.02 |
| **SWD Addition** | 15 | 1.05 ± 0.05 | 0.58 ± 0.02 | 4.60 ± 0.21 | 0.70 ± 0.02 |
| | | $F_{2,4} = 0.03$, $p = 0.98$ | $F_{2,4} = 0.05$, $p = 0.96$ | $F_{2,4} = 0.03$, $p = 0.97$ | $F_{2,4} = 0.16$, $p = 0.86$ |

**Table 4**
Mean diversity indices (±SE) averaged across blocks and treatments per period. Trapping data were collected at the US Department of Energy's Savannah River Site, in Aiken, Barnwell, and Allendale counties, South Carolina, USA. Diversity indices were calculated using captures per 100 trap nights. In Period I (1997–2000) richness was higher in 1997 than 2000 (different letters indicate significant differences among treatments; $\alpha = 0.05$). In Period II (2002–2006), diversity indices were not different among years.

| Year | N | Shannon | Simpson | Richness | Evenness |
|---|---|---|---|---|---|
| ***Period I*** | | | | | |
| **1997** | 9 | 0.89 ± 0.05 | 0.51 ± 0.02 | 4.89 ± 0.54 **a** | 0.60 ± 0.04 |
| **1998** | 9 | 0.84 ± 0.04 | 0.52 ± 0.02 | 4.22 ± 0.36 **ab** | 0.61 ± 0.02 |
| **1999** | 9 | 0.86 ± 0.06 | 0.52 ± 0.02 | 3.89 ± 0.20 **ab** | 0.64 ± 0.02 |
| **2000** | 9 | 0.84 ± 0.07 | 0.48 ± 0.04 | 3.56 ± 0.29**b** | 0.68 ± 0.05 |
| | | $F_{3,18} = 0.24$, $p = 0.87$ | $F_{3,18} = 0.02$, $p = 0.99$ | $F_{3,18} = 4.31$, **$p = 0.02$** | $F_{3,18} = 1.00$, $p = 0.41$ |
| ***Period II*** | | | | | |
| **2002** | 9 | 1.01 ± 0.07 | 0.54 ± 0.04 | 4.56 ± 0.29 | 0.67 ± 0.03 |
| **2003** | 9 | 0.93 ± 0.04 | 0.53 ± 0.02 | 4.44 ± 0.34 | 0.64 ± 0.03 |
| **2004** | 9 | 1.06 ± 0.04 | 0.59 ± 0.02 | 4.67 ± 0.24 | 0.70 ± 0.02 |
| **2005** | 9 | 1.07 ± 0.06 | 0.60 ± 0.02 | 4.44 ± 0.34 | 0.73 ± 0.03 |
| **2006** | 9 | 1.10 ± 0.08 | 0.60 ± 0.03 | 4.89 ± 0.39 | 0.71 ± 0.03 |
| | | $F_{4,24} = 1.87$, $p = 0.15$ | $F_{4,24} = 2.21$, $p = 0.10$ | $F_{4,24} = 0.53$, $p = 0.72$ | $F_{4,24} = 1.31$, $p = 0.29$ |

differed among years ($F_{3,18} = 18.05$, $p < 0.01$) with highest captures in 1997, intermediate in 1998 and 1999, and lowest in 2000 (Fig. 1C). Temperature and rainfall fluctuated on a yearly basis (Supplementary Fig. 1) and cotton mouse captures per 100 trap nights were positively correlated with average temperature and average rainfall in Period I ($r = 0.82$, $p < 0.001$; $r = 0.61$, $p < 0.001$, respectively; Supplementary Fig. 2).

In Period II, neither the treatment by year interaction ($F_{8,24} = 1.07$, $p = 0.42$) nor treatment ($F_{2,6} = 1.18$, $p = 0.37$; Fig. 1D) had a significant effect on cotton mouse captures per 100 trap nights. Cotton mouse captures were affected by season in Period II and were higher in both spring and winter compared to summer and fall ($F_{3,18} = 17.75$, $p < 0.01$; Fig. 1E). Cotton mouse captures were also affected by year and lower in 2002 compared to all other years ($F_{4,24} = 7.78$, $p < 0.01$; Fig. 1F). Cotton mouse captures per 100 trap nights were not correlated with average temperature nor average rainfall in Period II ($r = -0.14$, $p > 0.05$; $r = 0.04$, $p > 0.05$, respectively; Supplementary Fig. 3).

The interaction between treatment and year had no significant effect on southern flying squirrel captures per 100 trap nights in Period I ($F_{6,18} = 1.15$, $p = 0.38$). However, there was a significant treatment effect ($F_{2,6} = 5.45$, $p = 0.04$). Southern flying squirrel captures were higher in All Removal plots than Log Removal plots, with Control plots having intermediate levels (Fig. 2A). When averaged across years, southern flying squirrel captures per 100 trap nights in Period I differed among seasons ($F_{3,18} = 176.67$, $p < 0.01$), with the highest captures in summer, then spring, fall, and winter (Fig. 2B). Southern flying squirrel captures were higher in 1998 than in 1999 and 2000, with 1997 being intermediate and only significantly higher than 2000 ($F_{3,18} = 17.40$, $p < 0.01$; Fig. 2C). Southern flying squirrel captures per 100 trap nights were positively correlated with average temperature and average rainfall in Period I ($r = 0.57$, $p < 0.001$; $r = 0.50$, $p < 0.01$, respectively; Supplementary Fig. 2).

In Period II, southern flying squirrel captures did not differ among treatments ($F_{2,6} = 1.30$, $p = 0.34$; Fig. 2D). Southern flying squirrel captures were higher in summer and spring when compared to fall, and were lowest in winter ($F_{3,18} = 70.97$, $p < 0.01$; Fig. 2E). Southern flying squirrel captures per 100 trap nights were higher in 2003 than in any other year in Period II ($F_{4,24} = 12.91$, $p < 0.01$; Fig. 2F). There was a marginal interaction between treatment and season on southern flying squirrel captures per 100 trap nights in Period II with higher captures in Control plots during the summer and SWD Addition plots in winter ($F_{6,18} = 2.50$, $p = 0.06$; Fig. 3). Southern flying squirrel captures per 100 trap nights were negatively correlated with average temperature and positively correlated with average rainfall in Period II ($r = -0.43$, $p < 0.01$; $r = 0.35$, $p < 0.05$, respectively; Supplementary Fig. 3).

## 4. Discussion

In a unique experimental study that examined the effects of CWD on rodents over almost a decade, we found surprisingly few effects of CWD on rodents. Although rodents are often associated with CWD at the microsite scale in some cover types (e.g., Greenberg, 2002; Hinkelman and Loeb, 2007; McCay, 2000; McMillan and Kaufman, 1995) we did not find strong population or community responses to SWD or DWD. Our results are similar to other studies that did not find strong responses of rodents to CWD (e.g., Bowman et al., 2000; Craig et al., 2006; Jones and Lindquist, 2012) and also similar to those of Moseley et al. (2008) who did not find any treatment response for shrews in the same plots as our study.

Stand age, elevation, and CWD decay stage likely affect the relationship between rodents and CWD. For example, coarse woody debris stays on the landscape for different lengths of time across regions. Our study was conducted in thinned loblolly pine stands with trees >45-years old in a relatively low elevation area. Most studies that have found inconsistent or no association between rodent population size and CWD were conducted in young, regenerating stands (Fritts et al., 2017; Homyack et al., 2014; Marshall et al., 2012). At lower elevations in the southeastern U.S., high humidity and temperatures lead to faster CWD decomposition than in cooler, less humid regions such as the Pacific Northwest US and mountainous areas (Woodall, 2007). Therefore, rodent response to CWD is more likely in the Pacific Northwest US (e.g., Butts and McComb, 2000; Carey and Johnson, 1995) than in eastern

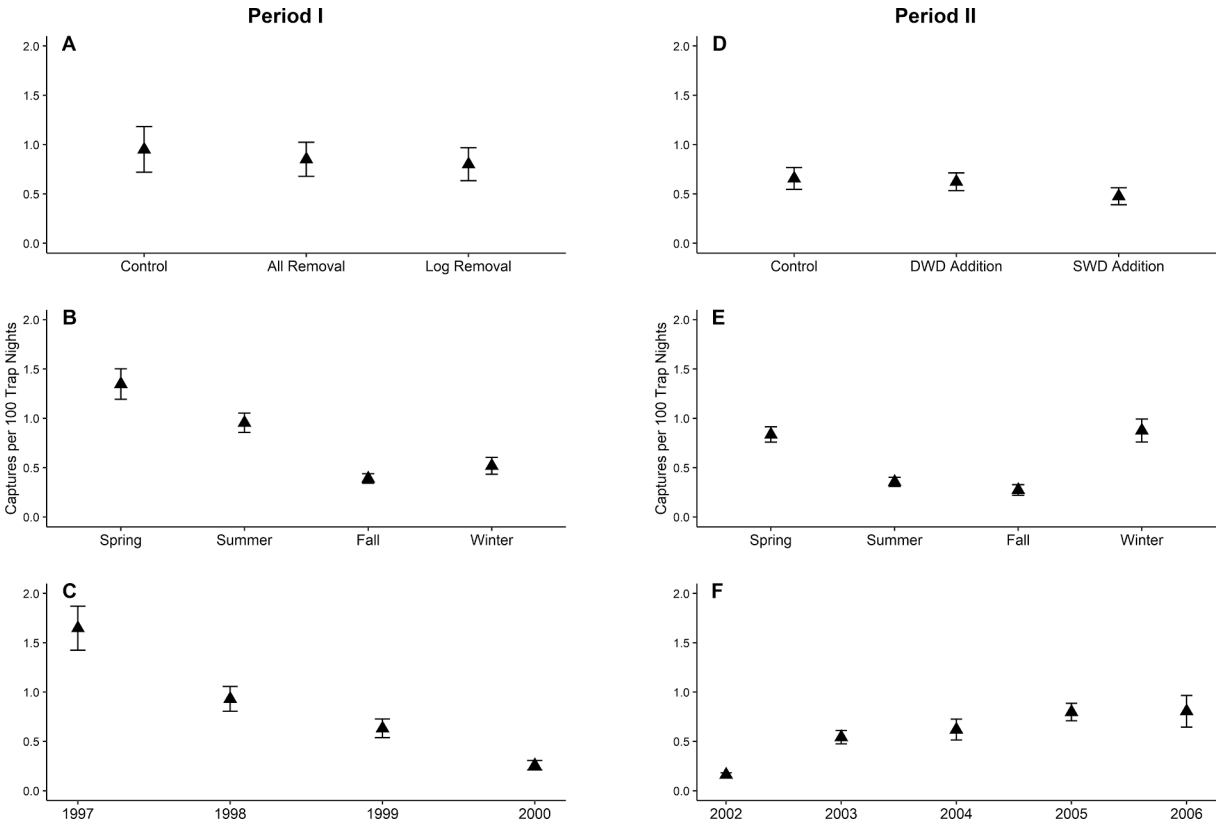


**Fig. 1.** Cotton mouse (*Peromyscus gossypinus*) mean (±SE) captures per 100 trap nights by A) treatment, B) season, and C) year in Period I (1997–2000) and D) treatment, E) season, and F) year in Period II (2002–2006). Trapping data were collected at the US Department of Energy's Savannah River Site, in Aiken, Barnwell, and Allendale counties, South Carolina, USA. In Period I, treatments were: 1) removal of all snags and fallen logs (All Removal), 2) removal of fallen logs only (Log Removal), and 3) Control and in Period II, treatments were: 1) downed woody debris addition (DWD Addition), 2) snag addition (SWD Addition), and 3) Control.

North America (e.g., Bowman et al., 2000; Osbourne and Anderson, 2002). However, in low elevation sites in British Columbia, deer mouse population size is associated with lower volume of CWD, but not in high elevation areas (Craig et al., 2006). Boggs et al. (2020) found white-footed mouse population size increased with increasing CWD in North Carolina, but these sites were relatively high elevation within the southern Appalachians, where it is likely CWD would persist longer than in the warmer piedmont or coastal regions of the eastern U.S.

Characteristics of CWD may also be important in explaining rodent population responses. In a metanalysis, Riffell et al. (2011) found that small mammals do not respond strongly to CWD in experimental studies (incorporating Loeb, 1999; Moseley et al., 2008; Osbourne and Anderson, 2002) but the amount of advanced decayed CWD has more of an effect on rodent population size than overall amount of CWD in correlative studies. Boggs et al. (2020) suggested that regional differences that affect downed wood volumes, management histories, stand ages, and rodent communities may be relevant factors in explaining variation in rodent responses to CWD across studies. We recommend future studies focus on sampling across regions, and across various elevations within a region while including potential factors such as masting and seasonal nesting selection to better understand the relationship between rodents and CWD.

Our study showed that over the long-term, rodents in our study area did not respond strongly to the addition of CWD. While rodents may respond to oak masting (Ostfeld and Keesing, 2000) or periodical cicadas (*Magicicada* spp.; Marcello et al., 2008) via higher reproductive rates and greater population sizes (Clotfelter et al., 2007; Ostfeld et al., 1996), responses to the addition of CWD may be more subtle (e.g., changes in nesting behavior). Thus, even though CWD is important in refuge selection by individual cotton mice in our study area (Hinkelman and Loeb 2007, McCay 2000), other resources such as food availability may have had a greater effect on populations and communities.

Although we did not find anticipated effects of treatment on community structure, we found year effects and where we found differences in community structure, cotton mice and southern flying squirrels were the main drivers. Rodent population sizes are known to fluctuate (Kelt et al., 2019; Oli, 2019, for reviews), and this includes evidence from SRS (Smith et al., 1974). In Period I, community assemblages differed slightly by treatment, and in Period II there was not a treatment effect, but in both Periods, variation was explained by year. As trees on the plots aged, with concomitant understory changes, there was also a loss of some early successional associated species. For example, old field mice were only captured in 1997 and 1998, and eastern harvest mice were only captured in 1997–1999, and a few individuals were captured in 2005. Golden mouse population size was high in 1997 but was relatively low throughout the following years. Fox squirrel population size remained relatively low throughout Period I but was high at the beginning of Period II and then gradually decreased. Eastern woodrats were only captured in 2002, 2005, and 2006. Overall, the species-specific responses over time are similar to Fauteux et al. (2012). Rodent population size is known to fluctuate by year (Ivey, 1949; Jones and Lindquist, 2012; McCarley, 1954; Smith et al., 1974) and season, and our study detected these patterns independent of treatment.

Rodent population size often responds to precipitation. This is true in arid environments where water is limiting (Thibault et al., 2010) but also in forested habitats at SRS where cotton mice, short-tailed shrews, golden mice, and southeastern shrews positively respond to precipitation (Smith et al. 1974). Smith et al. (1974) speculated that soil moisture during summer would have a large influence on the food supply of both insectivorous and omnivorous species. Although we saw a positive relationship between cotton mouse and southern flying squirrel captures and temperature and rainfall during Period I, in Period II we saw no

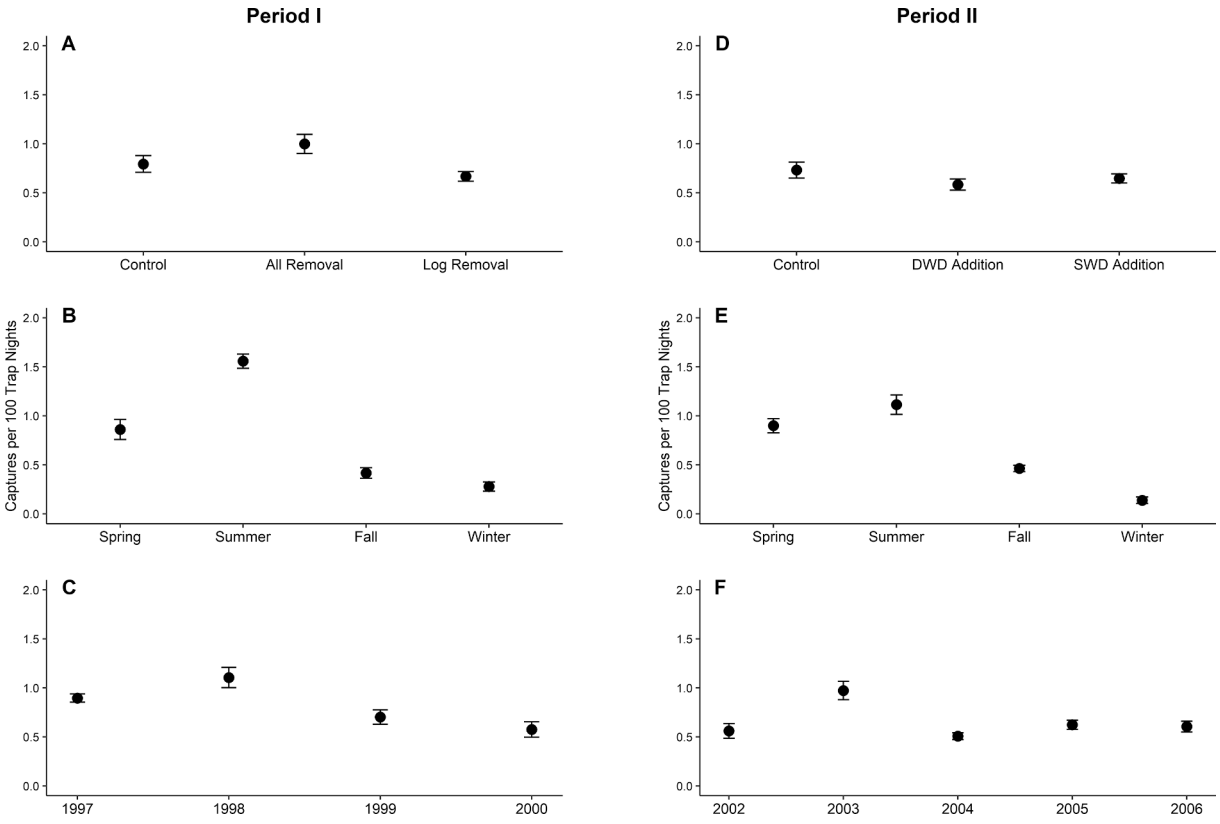


**Fig. 2.** Southern flying squirrel (*Glaucomys volans*) mean (±SE) captures per 100 trap nights by A) treatment, B) season, and C) year in Period I (1997–2000) and D) treatment, E) season, and F) year in Period II (2002–2006). Trapping data were collected at the US Department of Energy's Savannah River Site, in Aiken, Barnwell, and Allendale counties, South Carolina, USA. In Period I, treatments were: 1) removal of all snags and fallen logs (All Removal), 2) removal of fallen logs only (Log Removal), and 3) Control and in Period II, treatments were: 1) downed woody debris addition (DWD Addition), 2) snag addition (SWD Addition), and 3) Control.

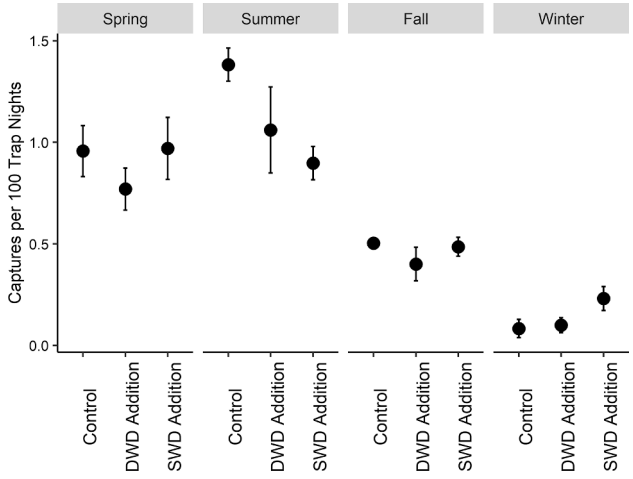


**Fig. 3.** Southern flying squirrel (*Glaucomys volans*) mean (±SE) captures per 100 trap nights by treatment and season in Period II (2002–2006). Trapping data were collected at the US Department of Energy's Savannah River Site, in Aiken, Barnwell, and Allendale counties, South Carolina, USA. Treatments were 1) downed woody debris addition (DWD Addition), 2) snag addition (SWD Addition), and 3) Control.

relationship between cotton mouse captures and weather variables, and the relationship between southern flying squirrel captures and average temperatures was negative. Weather (including temperature and precipitation) also affects masting, although there are other factors that influence masting (Pearse et al., 2016). Variation in responses to temperature and rainfall between periods emphasizes the need for long-term data to understand how rodent population dynamics respond to weather.

Variation in cotton mouse and southern flying squirrel captures was seasonal. Cotton mouse captures were highest in spring during Period I and winter and spring during Period II. Cotton mouse reproduction occurs mainly in fall, winter, and spring (Bigler and Jenkins, 1975; McCarley, 1954; Wolfe and Linzey, 1977) and peak cotton mouse population size tends to occur in winter (McCarley, 1954). Southern flying squirrel offspring are born in fall and late winter (Goertz et al., 1975; Raymond and Layne, 1988; Sollberger, 1943), which results in increased numbers of individuals in the summer. During summer, southern flying squirrel captures were higher in Control plots than in SWD Addition plots whereas in winter they were more abundant in SWD Addition plots and this change in relative use of treatments may have been due to changes in nesting behavior. Southern flying squirrels often use outside nests (drays) particularly in pine stands (Taulman, 1999) and outside nest use may be higher in summer than in winter due to temperatures (Goertz et al., 1975). Further, the use of live trees instead of snags by southern flying squirrels is more likely in the summer in Virginia (Bendel and Gates, 1987). We would expect similar nesting behavior in South Carolina, which may explain seasonal differences among treatments in southern flying squirrel captures in our study.

### 4.1. Conclusions

Although CWD is a resource that is often used by small mammals for nesting, foraging, traveling, and refuge, we found that it was not a significant driver of rodent populations and communities in our study area. The key finding from our study is that there was a minimal relationship between rodents and CWD at this study site, even when considered over the long-term with various addition and removal treatments. However,

CWD is important for other taxa in this system including bark dwelling arthropods (Horn and Hanula, 2008) and several bird species (Kilgo and Vukovich, 2014; Lohr et al., 2002), and these taxa should also be considered in future research and management.

## CRediT authorship contribution statement

**Angela L. Larsen-Gray:** Conceptualization, Formal analysis, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Susan C. Loeb:** Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing, Visualization, Supervision, Project administration, Funding acquisition. **Matina C. Kalcounis-Rueppell:** Resources, Writing - review & editing, Visualization, Project administration.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119427.

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