Responses of Arthropods to Large-Scale Manipulations of Dead Wood in Loblolly Pine Stands of the Southeastern United States

MICHAEL D. ULYSHEN[1] AND JAMES L. HANULA

USDA Forest Service, 320 Green St., Athens, GA 30602

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ABSTRACT Large-scale experimental manipulations of dead wood are needed to better understand its importance to animal communities in managed forests. In this experiment, we compared the abundance, species richness, diversity, and composition of arthropods in 9.3-ha plots in which either (1) all coarse woody debris was removed, (2) a large number of logs were added, (3) a large number of snags were added, or (4) no coarse woody debris was added or removed. The target taxa were ground-dwelling arthropods, sampled by pitfall traps, and saproxylic beetles (i.e., dependent on dead wood), sampled by flight intercept traps and emergence traps. There were no differences in total ground-dwelling arthropod abundance, richness, diversity, or composition among treatments. Only the results for ground beetles (Carabidae), which were more species rich and diverse in log input plots, supported our prediction that ground-dwelling arthropods would benefit from additions of dead wood. There were also no differences in saproxylic beetle abundance, richness, diversity, or composition among treatments. The findings from this study are encouraging in that arthropods seem less sensitive than expected to manipulations of dead wood in managed pine forests of the southeastern United States. Based on our results, we cannot recommend inputting large amounts of dead wood for conservation purposes, given the expense of such measures. However, the persistence of saproxylic beetles requires that an adequate amount of dead wood is available in the landscape, and we recommend that dead wood be retained whenever possible in managed pine forests.

KEY WORDS coarse woody debris, biodiversity, epigaeic, dispersal, colonization

Animal communities have been developing and diversifying in the presence of dead wood ever since the first forests appeared on earth >355 million years ago (Scheckler 2001). The extent to which species have come to rely, either directly or indirectly, on this important resource ranges from no association to complete dependence (i.e., saproxylic). Many species seem to fall somewhere between these two extremes, benefiting in some way from the presence of dead wood but not requiring it. Large-scale experiments are needed to determine how forest communities respond to changing amounts of dead wood in managed forests (Davies et al. 2008). Such information is critical if we hope to satisfy both timber demands and conservation goals in the long term. Here we present results from a study examining the responses of arthropods to large-scale manipulations of dead wood in loblolly pine (*Pinus taeda* L.) forests of the southeastern United States.

This research is part of a multidisciplinary effort to study the responses of animals to the addition and removal of coarse woody debris in loblolly pine forests on the Savannah River Site, SC. In this experiment, we compared the abundance, species richness, diversity, and composition of arthropods in plots in which either (1) all coarse woody debris were removed, (2) a large number of logs were added, (3) a large number of snags were added, or (4) no coarse woody debris was added or removed (i.e., for reference).

Two arthropod communities were targeted in this study, the first being ground-dwelling arthropods. Ground-dwelling arthropods have been shown to respond positively to dead wood at small-scales (Buddle 2001, Nittérus and Gunnarsson 2006, Varady-Szabo and Buddle 2006, Ulyshen and Hanula 2009a, and references therein), but the extent to which manipulations of dead wood over large areas affect them remains largely unknown. There have been too few large-scale experiments to adequately address this question, although several studies suggest that beetles (especially ground beetles) (Cárcamo and Parkinson 1999, Gunnarsson et al. 2004, Hanula et al. 2006, Latty et al. 2006) and spiders (Hanula et al. 2006) respond positively to dead wood at large scales. One of these studies took place in the reference and removal plots used in this project, soon after the plots were established in 1996. Hanula et al. (2006) sampled ground-dwelling arthropods in those plots for 5 yr (1997–2001) and found no differences in overall abundance or morphospecies richness. However, overall arthropod

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[1] Corresponding author, e-mail: mulyshen@hotmail.com.

diversity and evenness were significantly (α = 0.1) lower in removal plots than in reference plots, and several families differed in abundance between the two treatments. These differences were observed only in the first 2 full yr of sampling (i.e., 1998 and 1999), however. In this study, we sampled ground-dwelling arthropods using pitfall traps for a further 4 yr in the same reference and removal plots as well as the log input and snag input plots established in 2001. We predicted that arthropods overall and many individual orders and families would become more abundant, rich, and diverse in response to the addition of dead wood.

Saproxylic beetles were the second arthropod community targeted in this study. Beetles are the most conspicuous and diverse arthropods in dead and dying wood. An estimated 20–25% of all beetle species are thought to be saproxylic (Elton 1966, Grove 2002), and many of those (e.g., ≈40% in Sweden) have become threatened in intensively managed landscapes (Jonsell et al. 2004, and references therein). Most evidence of imperilment comes from the boreal forests of Scandinavia, whereas the status of saproxylic beetles in other regions, including the southeastern United States, remains largely unknown. Saproxylic beetles were sampled in this study using flight intercept traps and emergence traps to determine how they differed in abundance, richness, diversity, and composition among treatments. We predicted that saproxylic beetles would become more abundant, rich, and diverse in response to the addition of dead wood.

Materials and Methods

Study Area. This research took place on the 80,267-ha Savannah River Site (SRS) located on the upper Coastal Plain Physiographic Province of South Carolina. The SRS, a facility owned and operated by the U.S. Department of Energy, was established in 1951, and was designated an Environmental Research Park in 1972 (Kilgo and Blake 2005). Innumerable studies have since been conducted to better understand the environmental impacts of human activities on forest ecosystems. Most of the land now owned by the Savannah River site was formerly used for agricultural purposes, and most forests currently standing, including those used in this study, were planted in the early 1950s (Kilgo and Blake 2005).

Stand Characteristics and Site Preparation. The loblolly pine (*Pinus taeda* L.) stands used in this study were planted between 1950 and 1953. Loblolly pine dominates much of the SRS and constitutes one of the most economically important forest types in the southeastern United States (Schultz 1997). Water oak (*Quercus nigra* L.), sweetgum (*Liquidambar styraciflua* L.), and several less common tree species were also present in low numbers. The stands were all thinned between 1991 and 1996 to achieve a standing basal area of 13.8–20.8 m^2/ha (McCay et al. 2002). The understory varied somewhat but was generally dominated by wax myrtle (*Myrica cerifera* L.), blackberry (*Rubus* spp.), kudzu [*Pueraria montana* (Lour.) Merr.], *Lespedeza bicolor* Turcz., and Japanese honeysuckle (*Lonicera japonica* Thunb.). To help control for differences in plant cover, all stands were treated with herbicide in 1996.

Fire history differed somewhat among the plots. Although most plots had been burned between 1990 and 1994, others had not been burned since 1983 or as early as 1972. To help control for differences in fire history, prescribed fires were administered in all plots between February 2000 and March 2001.

Experimental Design. In this randomized complete block design, four blocks were selected and divided into four square 9.3-ha plots (Fig. 1). Each plot consisted of a 6-ha core surrounded by a 3.3-ha buffer area (McCay et al. 2002). Each of the four plots within each stand was randomly assigned to one of the following treatments (Fig. 1), as outlined by Moseley et al. (2008).

1. Removal. Removal of all dead woody material, including snags, ≥10 cm in diameter and ≥60 cm in length. This began in 1996 and was repeated yearly for the duration of the study. All removed material was dumped in designated piles outside the plots.
2. Log input. Five-fold increase in log volume over average background levels. Logs were added in 2001 by felling trees within the plots.
3. Snag input. Twelve-fold increase in snag basal area over the average snag basal area on the plots before treatment. Snags were created by girdling and herbicide treatment in 2001.
4. Reference. Aside from being thinned between 1991 and 1996 (see above), the reference stands were not manipulated and were comparable to the forest matrix surrounding the plots.

Pitfall Trapping. Three rows of five pitfall traps were arranged in a grid-like pattern in the center (6-ha core area) of each plot for a total of 15 traps per plot. The traps were spaced 50 m apart and were therefore placed irrespective of dead wood and other features of the forest floor. Each trap consisted of a 480-ml plastic cup buried to ground level and was positioned at the intersection of four 0.5-m-long drift fences. A small funnel (8.4 cm diameter) inserted into the cup directed arthropods into a smaller 120-ml specimen cup below, which contained a 1% formaldehyde solution for specimen preservation. The traps ran for a week, and we sampled every other month for 4 yr beginning in March 2002 and ending in December 2005. Samples from the 15 traps in each plot were combined in the field and stored in 70% ethanol. Four laboratory technicians separated arthropods from the samples and sorted them by size and shape. Each technician was responsible for all samples within a given sampling period. Because samples from different sampling periods were processed by different people, we cannot meaningfully compare sampling periods and do not include time in our model (i.e., we combined all sampling periods before analysis). Samples were further sorted to morphospecies (MDU) using an established reference collection. Mites, Collembola, and other

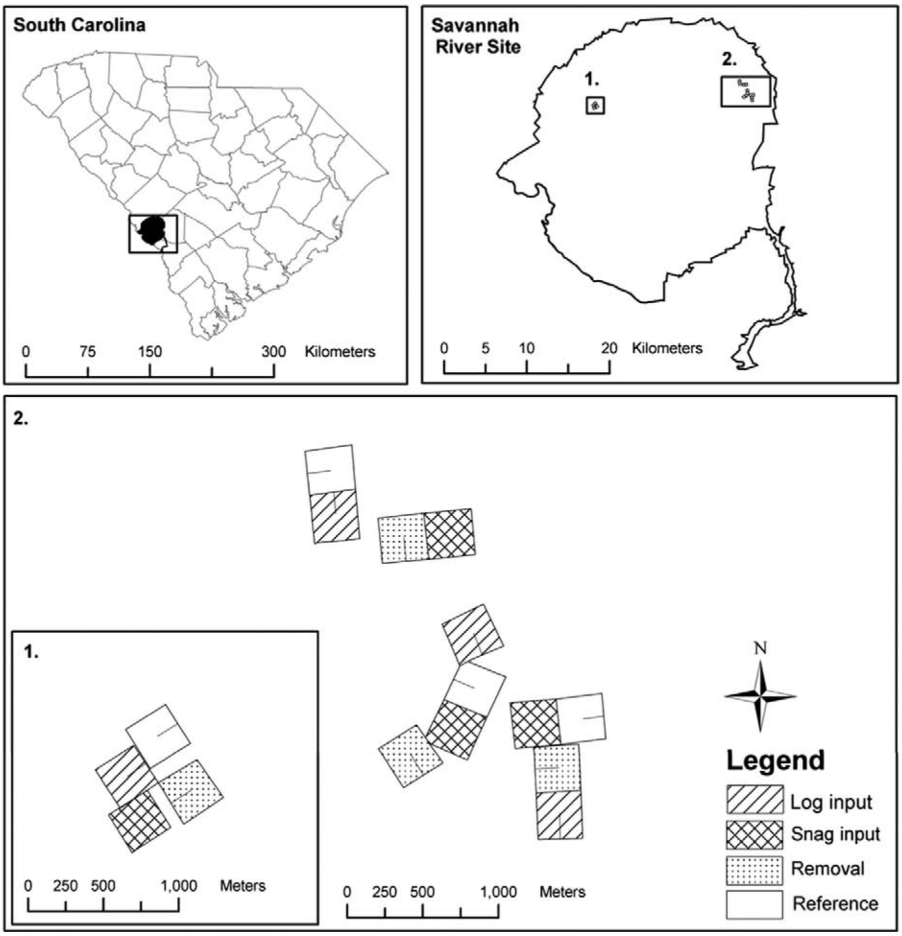

Fig. 1. Research plots (grouped by block) on the Savannah River Site, SC. Ground-dwelling arthropods were sampled in all plots using pitfall traps. To sample saproxylic beetles, groups of logs were placed on the edge, at the center, and halfway between the edge and center of each log input, log removal, and reference plot. Approximate placement is indicated by the lines half-bisecting each of those plots. Flight intercept traps were placed near the center of each log input, log removal, and reference plot.

micro-arthropod taxa were not counted, and holometabolous insect larvae were excluded from the dataset because of low taxonomic resolution. Analyses of variance were performed using SAS to determine whether there were any differences in abundance, species richness, or Shannon's diversity among treatments. Nonmetric multidimensional scaling (NMS) was performed on a dataset consisting of 654 morphospecies captured in at least three plots using PC-ORD (McCune and Mefford 2006). The same modified data set was used in PAST (Hammer et al. 2001) to perform ANOSIM with 10,000 permutations using a Bray-Curtis distance measure to quantitatively compare arthropod community similarity among treatments.

Flight Intercept Trapping. A pair of flight intercept traps (Ulyshen and Hanula 2007) were placed at the center of each reference, removal, and log input plot. The traps were placed 10 m apart and were suspended ≈0.5 m above the ground from metal poles. Propylene glycol was used as a preservative, and samples were collected every 2 wk. The traps ran continuously for 6 wk in 2007 (26 April–7 June). Specimens were sorted by species or morphospecies and those that are known to live in loblolly pine (i.e., based on emergence data collected in this and related studies) were categorized as "saproxylic." Data from the two traps in each plot and the different sampling periods were combined before analysis. Analyses of variance were performed using SAS to determine whether there were any differences in abundance, species richness, or Shannon's diversity among treatments. NMS was performed on a dataset consisting of 113 species captured in at least three plots using PC-ORD (McCune and Mefford 2006). The same modified data set was used in PAST (Hammer et al. 2001) to perform ANOSIM with 10,000 permutations using a Bray-Curtis distance measure to quantitatively compare beetle community similarity among treatments.

Emergence Trapping. On 4–5 May 2006, we cut 180 0.5-m sections (mean diameter, 29.8 ± 0.3 cm; range,

Fig. 2. Circular arrangement of logs used to sample saproxylic beetles at three locations in each log input, log removal, and reference plot. Saproxylic beetles were reared from logs removed randomly from each location after 2, 6, 10, and 22 mo. (Online figure in color.)

23.6–37.3 cm) of loblolly pine from nine freshly felled trees. The lower 2 m were discarded to minimize differences in bark thickness. Five logs were placed in a circular arrangement (Fig. 2) at the edge, center, and half-way between the edge and the center of log removal, log input, and reference plots (Fig. 1). Care was taken to ensure logs placed on the edges of plots were not adjacent to other treatments (Fig. 1). The five logs in each group were randomly assigned a number (1–5). Two months after cutting (5 July), we returned to collect log 1 from each location. Logs 2, 3, and 4 were collected after ≈6 (12 November), 10 (17 March), and 22 mo (7 March), respectively (note: the fifth log was not collected). Logs were loaded onto trucks and transported to an emergence facility in Athens, GA. Although the logs were handled as carefully as possible, some bark loss or loosening occurred. Loose bark was reaffixed to logs with string or wire, when possible. Beetles emerging from each set of logs were collected for 6 mo using rearing bags (Ulyshen and Hanula 2009b) and later identified by MDU. Sampling followed a split-split plot design consisting of three treatments (i.e., whole factor: log removal, log input, and reference), three locations (i.e., split factor: edge, center, and half-way between edge and center), and four dates (i.e., split-split factor: 2, 6, 10, and 22 mo). Analyses of variance were performed using SAS with species richness as the response variable. The same analysis was performed on abundance data for the 25 most numerous (i.e., >100 individuals) taxa. NMS was performed on a dataset consisting of 91 species captured in at least three plots using PC-ORD (McCune and Mefford 2006). The same modified dataset was used in PAST (Hammer et al. 2001) to perform ANOSIM with 10,000 permutations using a Bray-Curtis distance measure to quantitatively compare beetle community similarity among treatments.

Results

Pitfall Trapping. Pitfall traps captured 210,656 specimens representing 1,206 morphospecies. There were no significant differences in abundance, species richness, or Shannon's diversity among treatments for arthropods overall, and only five significant differences for the individual taxa examined (Table 1). The beetle family Carabidae was significantly more species rich and diverse in log input plots than in the other treatments (Table 1). Distinct treatment groupings were not apparent on NMS ordination (data not shown),

Table 1. Mean ± SE ($n = 4$) abundance, richness, and Shannon's diversity of arthropods captured in South Carolina

Order and family		Reference[a]	Log input	Removal	Snag input
Araneae	Abundance[b]	2,553.0 ± 164.2	2,028.3 ± 215.5	2,156.5 ± 353.7	2,015.3 ± 172.0
	Richness[c]	86.3 ± 2.7	82.3 ± 3.3	83.0 ± 4.1	86.0 ± 4.1
	Diversity[c]	3.1 ± 0.1	3.1 ± 0.1	3.2 ± 0.1	3.1 ± 0.0
Agelenidae	Abundance	161.0 ± 23.5	123.8 ± 19.4	120.3 ± 18.9	122.0 ± 43.1
Anyphaenidae	Abundance	2.0 ± 1.0	4.0 ± 2.5	76.8 ± 72.5	3.0 ± 1.2
Araneidae	Abundance	12.8 ± 2.0	5.3 ± 1.8	7.5 ± 1.0	4.5 ± 1.7
Clubionidae	Abundance	10.3 ± 3.0	15.0 ± 5.5	14.3 ± 3.4	12.0 ± 2.2
Corinnidae	Abundance	62.5 ± 8.7	40.8 ± 9.5	60.0 ± 10.1	53.0 ± 10.7
Ctenizidae	Abundance	7.8 ± 2.5	9.5 ± 2.0	10.5 ± 3.1	7.8 ± 1.7
Dictynidae	Abundance	11.5 ± 4.8	8.5 ± 1.0	12.0 ± 2.2	20.5 ± 3.9
Gnaphosidae	Abundance	403.5 ± 53.5	398.3 ± 76.4	417.8 ± 98.0	351.0 ± 37.7
Hahniidae	Abundance	324.5 ± 101.0	160.8 ± 93.4	154.8 ± 57.0	160.8 ± 89.0
Linyphiidae	Abundance	396.8 ± 61.0	311.5 ± 89.8	350.3 ± 37.4	316.8 ± 61.0
	Richness	16.5 ± 1.0	17.5 ± 1.7	16.8 ± 0.9	17.3 ± 1.3
	Diversity	2.0 ± 0.1	1.9 ± 0.2	1.9 ± 0.1	1.9 ± 0.1
Lycosidae	Abundance	972.0 ± 119.8	827.5 ± 113.2	816.0 ± 125.1	834.5 ± 59.8
Pisauridae	Abundance	9.0 ± 1.8	8.3 ± 1.7	9.0 ± 2.9	9.3 ± 0.8
Salticidae	Abundance	116.8 ± 46.5	65.5 ± 10.2	54.3 ± 2.9	63.3 ± 19.0
Theridiidae	Abundance	14.0 ± 1.5	8.5 ± 4.3	9.5 ± 2.1	15.5 ± 2.0
Thomisidae	Abundance	30.0 ± 11.8	28.0 ± 12.3	24.5 ± 7.5	29.0 ± 7.9
Blattaria	Abundance	188.5 ± 20.1	175.3 ± 28.8	181.0 ± 59.1	191.8 ± 33.0
Chordeumida	Abundance	32.0 ± 8.6	41.0 ± 8.9	36.5 ± 20.3	30.0 ± 9.7
Coleoptera	Abundance	1,654.8 ± 144.9	1,385.3 ± 186.9	1,488.0 ± 146.6	1,479.3 ± 170.3
	Richness	138.0 ± 7.6	141.0 ± 6.1	136.0 ± 3.4	131.3 ± 3.1
	Diversity	3.6 ± 0.1	3.8 ± 0.1	3.6 ± 0.1	3.6 ± 0.1
Carabidae	Abundance	324.0 ± 62.1	286.5 ± 53.1	291.0 ± 46.3	303.3 ± 44.6
	Richness[d,e,f]	22.3 ± 1.4	26.8 ± 1.3	22.0 ± 1.4	22.3 ± 0.3
	Diversity[f]	1.7 ± 0.1b	2.3 ± 0.1a	1.7 ± 0.1b	1.8 ± 0.1ab
Chrysomelidae	Abundance	19.8 ± 5.4	16.5 ± 2.8	10.0 ± 2.4	14.8 ± 6.6
Ciidae	Abundance	9.8 ± 2.3	11.0 ± 3.1	5.3 ± 2.3	10.0 ± 3.3
Cryptophagidae	Abundance	44.8 ± 16.6	18.8 ± 4.1	33.5 ± 2.9	31.0 ± 1.8
Curculionidae	Abundance	182.5 ± 18.6	184.5 ± 13.6	168.3 ± 38.4	188.3 ± 9.7
	Richness	14.5 ± 1.3	14.8 ± 1.1	13.5 ± 1.7	13.0 ± 1.9
	Diversity	1.7 ± 0.1	1.6 ± 0.1	1.7 ± 0.2	1.5 ± 0.1
Elateridae	Abundance	13.3 ± 1.8	10.8 ± 2.9	19.3 ± 2.7	15.8 ± 3.1
Endomychidae	Abundance	8.5 ± 1.9	9.8 ± 2.0	6.0 ± 1.9	3.5 ± 1.0
Erotylidae	Abundance	46.5 ± 20.6	26.3 ± 8.1	95.3 ± 54.7	68.5 ± 32.5
Histeridae	Abundance	7.0 ± 3.2	5.0 ± 1.1	10.3 ± 4.6	7.0 ± 2.5
Leiodidae	Abundance	40.8 ± 9.6	28.0 ± 2.7	33.3 ± 8.5	26.5 ± 1.4
Melyridae	Abundance	10.3 ± 9.3	5.5 ± 3.1	8.8 ± 5.7	1.8 ± 1.8
Nitidulidae	Abundance	40.0 ± 13.3	34.0 ± 12.3	26.8 ± 6.4	18.0 ± 5.1
Scarabaeidae	Abundance	93.3 ± 15.5	97.8 ± 12.0	105.3 ± 16.8	119.5 ± 40.7
	Richness	18.0 ± 1.1	18.3 ± 1.3	17.5 ± 0.6	18.3 ± 2.2
	Diversity	2.3 ± 0.2	2.4 ± 0.1	2.3 ± 0.1	2.1 ± 0.2
Scydmaenidae	Abundance[f]	116.0 ± 8.4a	63.3 ± 16.8ab	66.8 ± 18.8ab	53.0 ± 13.7b
Staphylinidae	Abundance	595.5 ± 129.1	486.5 ± 130.7	518.5 ± 162.5	511.0 ± 114.0
	Richness	22.8 ± 1.2	19.5 ± 2.7	19.8 ± 1.0	20.5 ± 1.3
	Diversity	1.8 ± 0.1	1.9 ± 0.0	2.0 ± 0.1	1.9 ± 0.1
Tenebrionidae	Abundance	60.0 ± 11.7	56.8 ± 5.7	49.5 ± 3.8	73.8 ± 33.1
Diptera	Abundance	1,297.3 ± 235.0	1,297.3 ± 296.5	966.5 ± 143.1	1,205.0 ± 228.8
	Richness	53.0 ± 1.6	51.3 ± 1.4	49.0 ± 2.7	47.8 ± 1.9
	Diversity	2.4 ± 0.1	2.3 ± 0.1	2.4 ± 0.1	2.2 ± 0.1
Geophilomorpha	Abundance	16.8 ± 2.0	12.3 ± 0.5	22.3 ± 2.2	16.0 ± 4.1
Hemiptera	Abundance	188.8 ± 25.6	242.0 ± 64.4	131.3 ± 24.7	193.3 ± 24.9
	Richness	33.8 ± 1.8	35.8 ± 4.3	32.0 ± 4.3	32.5 ± 0.6
	Diversity	2.7 ± 0.1	2.5 ± 0.1	2.7 ± 0.1	2.4 ± 0.1
Hymenoptera	Abundance	5,422.5 ± 174.4	5,006.0 ± 997.8	7,004.8 ± 912.3	6,687.0 ± 1485.3
	Richness	88.0 ± 2.5	79.8 ± 4.8	80.3 ± 3.1	82.8 ± 1.7
	Diversity	2.5 ± 0.0	2.2 ± 0.2	2.2 ± 0.1	2.1 ± 0.2
Julida	Abundance	1,055.8 ± 282.3	744.8 ± 180.0	1,162.3 ± 299.5	631.3 ± 123.0
Lepidoptera	Abundance	5.8 ± 1.5	6.5 ± 2.9	5.5 ± 1.2	7.5 ± 1.5
Microcoryphia	Abundance	48.5 ± 29.4	69.8 ± 40.4	48.8 ± 32.1	19.5 ± 16.0
Opiliones	Abundance	110.5 ± 25.5	105.8 ± 33.5	120.3 ± 14.8	39.0 ± 6.0
Orthoptera	Abundance[f]	666.5 ± 55.3a	663.3 ± 83.7a	598.0 ± 127.7ab	408.5 ± 64.2b
	Richness	18.8 ± 1.4	19.0 ± 1.1	20.0 ± 0.4	16.8 ± 0.9
	Diversity	1.7 ± 0.0	1.8 ± 0.1	1.9 ± 0.1	1.9 ± 0.1
Polydesmida	Abundance[f]	44.0 ± 24.1ab	96.5 ± 58.2a	86.0 ± 65.4ab	52.0 ± 43.4b
Pseudoscorpiones	Abundance	10.5 ± 4.6	13.8 ± 2.0	12.5 ± 3.7	18.0 ± 6.2
Psocoptera	Abundance	13.3 ± 4.4	9.5 ± 4.1	8.5 ± 0.9	18.8 ± 10.0
Scolopendromorpha	Abundance	42.0 ± 5.3	49.5 ± 10.0	60.0 ± 19.0	46.0 ± 8.6
Thysanura	Abundance	4.8 ± 1.8	11.3 ± 4.5	9.8 ± 6.5	6.3 ± 2.1

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Table 1. Continued

Order and family		Reference[a]	Log input	Removal	Snag input
Total	Abundance	13405.0 ± 637.3	12006.8 ± 1384.0	14143.0 ± 1537.8	13109.3 ± 1481.2
	Richness	440.5 ± 11.2	434.3 ± 16.5	425.8 ± 7.8	421.5 ± 6.6
	Diversity	4.2 ± 0.0	4.1 ± 0.1	3.9 ± 0.1	3.8 ± 0.2

[a] Arthropods were collected with pitfall traps placed in plots with different amounts of coarse woody debris (reference: no manipulation of dead wood; log input: 5-fold increase in log volume; removal: removal of all dead woody material, including snags, ≥10 cm in diam and ≥60 cm in length; snag input: 12-fold increase in snag basal area).

[b] Abundance data are presented for orders (and families of Araneae and Coleoptera) represented by ≥100 specimens.

[c] Richness and diversity data are presented for those taxa represented by ≥25 species.

[d] For each taxon, means followed by different letters are statistically different (α-0.05) based on Tukey's studentized range test. Log(x + 1)-transformed abundance data were used for this test, but untransformed data are presented here.

[e] Carabidae richness varied significantly among treatments based on ANOVA but there were no differences among means based on Tukey's studentized range test.

[f] Significant differences ($P < 0.05$).

and there were no significant differences in arthropod community similarity among treatments (ANOSIM: $R = 0.05$, $P = 0.29$).

Flight Intercept Trapping. The flight intercept traps captured 11,600 beetle specimens representing ≥240 species overall. Of these, 1,769 (15%) specimens and 60 (25%) species are known to be saproxylic on loblolly pine (Ulyshen 2009). There were no differences in species richness or diversity among treatments for beetles overall or for saproxylic species alone (Table 2). Distinct treatment groupings were not apparent on NMS ordination (data not shown), and there were no significant differences in beetle community similarity among treatments (ANOSIM: $R = -0.06$, $P = 0.65$).

Emergence Trapping. A total of 16,347 beetle specimens representing ≥155 species emerged from the 144 logs sampled in this study. Species richness did not differ among treatments or among locations, and there were no significant interactions (Table 3). However, species richness did differ significantly among sampling dates (Table 3). Similarly, none of the most common taxa differed in abundance among treatments or locations but most differed in abundance among sampling dates. There were significant interaction terms for some species but no more than expected by chance (data not shown). Distinct treatment groupings were not apparent on NMS ordination (data not shown), and there were no significant differences in beetle community similarity among treatments (ANOSIM: $R = -0.09$, $P = 0.71$).

Table 2. Mean ± SE ($n = 4$) richness and diversity of Coleoptera collected in flight intercept traps placed in plots with different amounts of coarse woody debris (there were no significant differences among treatments)

		Reference[a]	Log input	Removal
All species	Richness	76.3 ± 3.5	76.5 ± 3.1	80.3 ± 2.7
	Diversity	3.0 ± 0.2	2.9 ± 0.2	2.8 ± 0.2
Saproxylic species only	Richness	23.5 ± 1.2	26.0 ± 3.1	22.0 ± 1.6
	Diversity	2.2 ± 0.1	2.4 ± 0.1	2.2 ± 0.2

[a] Reference: no manipulation of dead wood; log input: 5-fold increase in log vol; removal: removal of all dead woody material, including snags, ≥10 cm in diam and ≥60 cm in length.

Discussion

Ground-Dwelling Arthropods. There were no differences in total arthropod abundance, richness, diversity, or composition among treatments. For the 73 comparisons made on individual taxa, only five showed significant differences, about the number expected by chance at the $\alpha = 0.05$ level of significance. Only the results for ground beetles (Carabidae), which were more species rich and diverse in log input plots, support our prediction that arthropods would become more abundant, species rich, or diverse in response to additions of dead wood. These results are consistent with previous studies that have shown positive associations between ground beetles and coarse woody debris (Cárcamo and Parkinson 1999, Pearce et

Table 3. ANOVA table for a split-split plot design with saproxylic beetle species richness as the response variable

Source	df	MS	F
Whole factor[a]			
Treatment	2	25.76	$F_{2,6} = 0.63$
Block	3	10.04	$F_{3,6} = 0.24$
Treatment × block	6	40.99	—
Split factor[b]			
Location	2	12.72	$F_{2,18} = 0.30$
Treatment × location	4	19.69	$F_{4,18} = 0.47$
Block × location	6	73.36	—
Block × treatment × location	12	25.91	—
Error (location)	(18)	41.73	—
Split-split factor[c]			
Date	3	330.71	$F_{3,81} = 16.51$[d]
Treatment × date	6	5.02	$F_{6,81} = 0.25$
Location × date	6	17.03	$F_{6,81} = 0.85$
Treatment × location × date	12	28.61	$F_{12,81} = 1.43$
Block × date	9	19.90	—
Block × treatment × date	18	21.64	—
Block × location × date	18	22.18	—
Block × treatment × location × date	36	18.18	—
Error (date)	(81)	20.03	—
Total	143		

[a] This randomized complete block design consisted of three treatments (i.e., log removal, log input, and reference).

[b] Sampling took place at three locations (i.e., edge, center, and half-way between edge and center) within each plot.

[c] Sampling took place at four different times (i.e., 2, 6, 10, and 22 mo) at each location.

[d] Significant difference ($P < 0.05$).

al. 2003, Hanula et al. 2006, Latty et al. 2006, Nittérus and Gunnarsson 2006). Although previous studies have also shown positive associations between spiders (Araneae) and dead wood (Buddle 2001, Hanula et al. 2006, Varady-Szabo and Buddle 2006), there were no differences in spider abundance, richness, or diversity among treatments in this study.

We recently sampled litter-dwelling arthropods near and away from logs in the same forests used in this study (Ulyshen and Hanula 2009a). Arthropod abundance was significantly higher near logs than away from them as has been shown in the broad-leaved forests of Europe (Jabin et al. 2004; Topp et al. 2006a, b; Kappes 2006, Kappes et al. 2006, Jabin et al. 2007). These results are seemingly incongruous with those of this study. However, it is possible that dead wood affects the distribution of arthropods without affecting their abundance. The pitfall traps used in this study were independently placed with respect to dead wood, and the samples were combined from each plot. Any differences in abundance, richness, and diversity caused by dead wood proximity were likely canceled out.

It is interesting to note that predators seem to benefit the most from dead wood compared with other ground-dwelling arthropod taxa. In this study, only ground beetles showed a positive response to the addition of dead wood. Similarly, of the 10 arthropod families collected more commonly in reference plots than removal plots by Hanula et al. (2006), 4 were entirely predatory (Carabidae, Clubionidae, Hahniidae, and Lycosidae). Predators may benefit from dead wood if it affects the distribution of their prey, even if it has no effect on prey abundance. It may be easier to locate prey in forests with dead wood given that the abundance of many ground-dwelling arthropod taxa increases with increasing proximity to dead wood (Ulyshen and Hanula 2009a, and references therein).

Saproxylic Beetles. There were no differences in total saproxylic beetle abundance, richness, diversity, or composition among treatments based on flight intercept trapping or emergence trapping. Furthermore, there were no differences in abundance among treatments for any individual species examined in this study. These results suggest that saproxylic beetles in loblolly pine forests of the southeastern United States have strong dispersal abilities and are little affected by changing amounts of dead wood at the scale of the 9.3-ha plots used in this study. It is important to keep in mind, however, that the plots were embedded in a hospitable forest matrix. Our results may have been quite different had the plots been isolated fragments of forests or surrounded by forests from which all woody material had been removed. It is also important to consider the history of the Savannah River Site because site history is known to strongly influence saproxylic beetle communities. For example, Goßner et al. (2008) found that saproxylic beetles, especially those associated with old wood, were less species rich in forests established on former agricultural land than in forests reestablished on ancient woodland sites. Because the forests used in this study were recently established on former farmland, it is possible that the species most sensitive to manipulations of dead wood were already absent from the forests before the study began. Comparisons between old-growth and second-growth forests are needed to determine whether there are species restricted to old-growth patches in the region before we can fully understand the implications of this research.

Management Implications. The results from this study are encouraging in that arthropods seem less sensitive than expected to manipulations of dead wood in managed pine forests of the southeastern United States. Because log input plots and removal plots supported equally diverse communities of arthropods, we cannot recommend inputting large amounts of dead wood for conservation purposes, given the expense of such measures. This conclusion is supported by data on shrews, reptiles, and amphibians collected by other researchers involved in this study (Moseley et al. 2008, Owens et al. 2008). However, the persistence of saproxylic beetles and other organisms requires that an adequate amount of dead wood is available, and we strongly recommend that dead wood be protected whenever possible in managed pine forests. A long history of intensive management in the boreal forests of Finland has resulted in a 90–98% reduction in dead wood at the landscape scale, perhaps threatening more than one half of all saproxylic species with regional extinction (Siitonen 2001). If we wish to avoid a similar fate in the southeastern United States, efforts must be made to accommodate dead wood in managed forests. Saproxylic beetles and other arthropods sampled in this study likely owe their apparent resiliency to the quality of the surrounding forest matrix. We support Seymour and Hunter (1999) in their assertion that the best way to both satisfy timber demands and meet conservation goals is to practice balanced forestry, which they define as "a triad of production forestry and ecological reserves embedded in a matrix of ecological forestry." This compromise allows for the creation of essential reserves (Niemelä 1997) without decreasing productivity. It also recognizes the importance of the matrix in maintaining diversity at the landscape scale.

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