THE ROLE OF DEAD WOOD IN MAINTAINING ARTHROPOD DIVERSITY ON THE FOREST FLOOR

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Abstract—Dead wood is a major component of forests and contributes to overall diversity, primarily by supporting insects that feed directly on or in it. Further, a variety of organisms benefit by feeding on those insects. What is not well known is how or whether dead wood influences the composition of the arthropod community that is not solely dependent on it as a food resource, or whether woody debris influences prey available to generalist predators. One group likely to be affected by dead wood is ground-dwelling arthropods. We studied the effect of adding large dead wood to unburned and frequently burned pine stands to determine if dead wood was used more when the litter and understory plant community are removed. We also studied the effect of annual removal of dead wood from large (10-ha) plots over a 5-year period on ground-dwelling arthropods. In related studies, we examined the relationships among an endangered woodpecker that forages for prey on live trees, its prey, and dead wood in the forest. The results of these and other studies show that dead wood can influence the abundance and diversity of the ground-dwelling arthropod community and of prey available to generalist predators not foraging directly on dead trees.

INTRODUCTION

Large dead wood or coarse woody debris (CWD) with a diameter >10 cm is an important resource for many arthropods and other animals that use it for food, oviposition sites, protection from environmental extremes, and foraging habitat (Elton 1966, Grove 2002b, Harmon and others 1986). Over 400 species of insects are known to use woody debris as a food resource in the Southeastern United States (Hanula 1996), and similar or greater numbers of arthropods have been reported to use it at other locations throughout the world (Grove 2002b). In addition to their direct contribution to forest diversity, these saproxylic arthropods are an important part of the forest food web (Harmon and others 1986). However, little work has been done on the role of terrestrial CWD in the forests of the Southeastern United States (McMinn and Crossley 1996).

Most of the research involving insects and CWD has focused on obligate saproxylic species (e.g., Grove 2002a, 2002b; Jonsell and others 1998; Sippola and others 2002; Speight 1989). Elton (1966) recognized that as wood decomposes it is increasingly colonized by generalists that do not require specific tree species or even depend on woody debris as their sole habitat. Relatively little is known about later successional communities in and around woody debris, and even less is known about the overall effect of woody debris on ground-dwelling arthropod communities. Recent work has begun to focus on these relationships, though (Evans and others 2003, Jabin and others 2004, Marra and Edmonds 1998).

During the past 8 years we have studied the role of CWD in relation to ground-dwelling arthropods in pine forests of the Southeastern United States. Our research examined results of trapping near CWD in unburned and frequently burned pine stands, and the effects of annual removal of dead wood from large plots over a 5-year period on ground-dwelling arthropods. In related studies we have examined interrelationships among the endangered red-cockaded woodpecker (RCW) (*Picoides borealis*), which forages for prey on live trees, its prey, and dead wood in the forest. The results of these and other studies are summarized here and show that dead wood influences the abundance and diversity of the ground-dwelling arthropod community, and may indirectly affect the prey available to at least some generalist predators.

USE OF CWD IN FREQUENTLY BURNED HABITATS BY GROUND-DWELLING ARTHROPODS

Longleaf pine (*Pinus palustris*) and its characteristic plant communities have experienced a long-term decline for a variety of reasons. Prescribed burning is considered one of the best options for restoring and maintaining this species and the characteristic plant communities associated with it, but little was known about the effects of fire on arthropods in these ecosystems. We conducted a 5-year study on long-term (40 years) research plots on the Osceola National Forest in northern Florida to examine the effects of frequent dormant-season burning on ground-dwelling arthropods (Hanula and Wade 2003). As part of that study we wanted to determine if CWD was an important arthropod habitat in areas receiving varying dormant-season burn frequencies. We hypothesized that the presence of woody debris would be important to ground-dwelling arthropods on annually burned plots where the understory vegetation and structure are more sparse compared to unburned plots (fig. 1). In addition, we measured the amount of CWD (diameter >10 cm) to determine if 40 years of frequent burning affected its abundance.

We hypothesized that logs could increase trap captures of arthropods in two ways: (1) they could be a preferred habitat resulting in concentrations of arthropods around them, or (2) they could act as drift fences concentrating and directing arthropods that normally wander across the forest floor into nearby traps. To determine which occurred, we placed 3-m lengths of longleaf pine logs (20 to 25 cm in diameter) in the center of each plot and installed pitfall traps along them (two

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Citation for proceedings: Grove, Simon J.; Hanula, James L., eds. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Gen. Tech. Rep. SRS-93. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 109 p.

Figure 1—Amount and height of vegetation on long-term burn plots on the Osceola National Forest near Olustee, FL, that received dormant season burns annually, biennially, quadrennially, or not at all over a 40-year period. The signs (arrows) in each photo are approximately the same height. Photos were taken at the end of each burn cycle so vegetation had the maximum amount of time to recover.

on each side within 0.5 m of each end) as close to the log as possible (fig. 2). A wedge-shaped piece of aluminum sheet metal was inserted in the space between the edge of each trap and the log to ground contact to prevent arthropods from bypassing the trap through the gap between the trap and the log. Four additional pitfall traps were installed along a 3-m long aluminum sheet metal drift fence located 10 m from and parallel to the center log (fig. 2). Traps were placed as the log pitfalls were except that the edge of each trap was in direct contact with the drift fence. Pitfall traps were opened for month-long periods six times per year and covered when not in use. Arthropods were identified to genus when possible.

In November 2003, we measured the volume of CWD on all plots. Down woody debris was sampled in five 10-m-wide transects equally spaced across each plot, and a 100 percent survey of standing dead wood was conducted at the same time. The midpoint diameter of standing dead trees was estimated using taper equations for Coastal Plain longleaf pine (Clark and others 1991), and CWD volume was estimated using Huber's equation (Avery 1975). Percent similarity (Southwood 1966) was used to compare arthropod communities captured in the two types of traps, and richness and the Shannon diversity index were used to measure arthropod community diversity. Calculations were based on the cumulative totals for the entire study period.

Analyses of variance were conducted to test for interactions between burn frequency and trap location, and trap location effects. Model effects were burn treatment, trap location, block, treatment x block interaction, and burn treatment x trap location interaction. We observed interactions between fire and arthropod use of logs in 30 taxa. In 11 taxa, more individuals were captured in traps near logs in some burn treatments than in other burn treatments. However, there was no consistent pattern; i.e., frequent burning was associated with greater

Figure 2—Pitfall traps were placed along 3-m long drift fences (top) and near 3-m sections of longleaf pine logs (bottom). Sheet metal squares were used to reduce trap flooding from rain.

numbers of some taxa near logs but infrequent or no burning was associated with greater numbers for other taxa. In only a few cases did frequent burning result in concentrations of arthropods near logs, although leaf litter, live herbaceous vegetation biomass, and structure were much lower on those plots than on unburned or quadrennially burned plots (Hanula and Wade 2003). Total volumes of CWD ranged from a mean of 8.0 m^3/ha (SE = 1.01) for unburned control plots to 9.1 m^3/ha (SE = 1.73) on annually burned plots. Volume of CWD was not significantly affected by burning, so differences in background levels of woody debris should not have affected the results.

Overall, we caught significantly more arthropods and a greater biomass of arthropods in pitfall traps near drift fences than in those near logs (fig. 3). The similarity of what was caught in the two types of traps ranged from 64.4 percent (SE = 3.6) in comparisons of annually burned plots to 69.2 percent (SE = 1.4 percent) in comparisons of similarity in the two trap locations on unburned controls. There were no significant differences in comparisons of similarity of arthropods captured in pitfall traps near logs to pitfalls near drift fences on the various burn treatments ($F_{5,3} = 1.06$, $P = 0.40$). Likewise, Shannon diversity, evenness, richness, and numbers of rare species were the same for traps near logs and drift fences regardless of burn frequency.

We captured over 932 genera in 5 years of trapping (Hanula and Wade 2003). Of those, 135 arthropod taxa were captured in higher numbers in one trap type or the other (table 1). When examining this many individual taxa one is very likely to encounter some apparently significant results simply by chance. However, the 135 taxa represent over 14 percent of the total number of arthropod taxa examined. At an alpha level of 0.05 one would only expect 5 percent to have been captured in statistically higher numbers by chance. Ninety-nine different arthropod taxa were captured in significantly ($P < 0.05$) higher numbers in pitfalls near drift fences while 36 arthropod taxa were captured in higher numbers near logs.

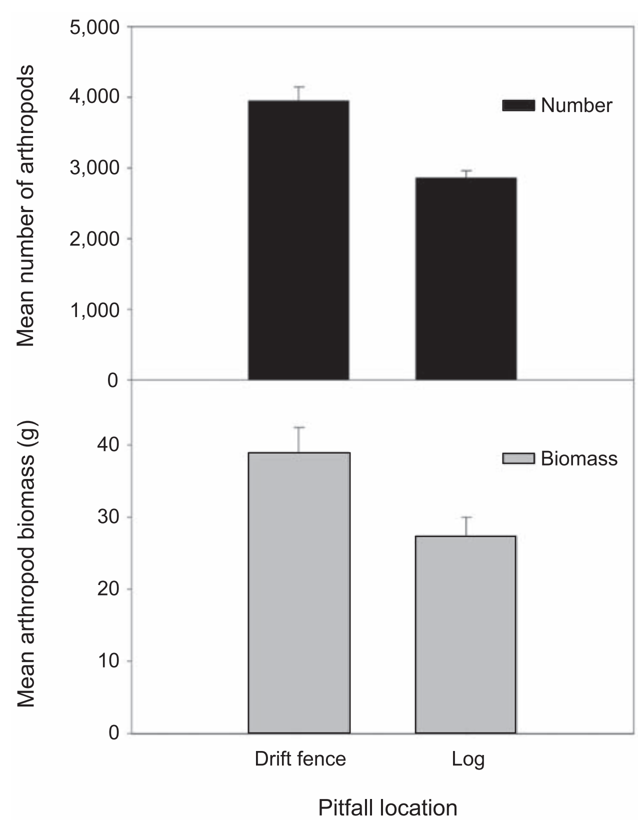

Figure 3—Pitfall traps near drift fences caught significantly higher numbers ($P < 0.0001$) and biomass ($P < 0.0001$) of arthropods than similar traps near logs.

Table 1—A list of arthropod taxonomic groups (order, family, or genus) captured in significantly (*P* < 0.05) higher numbers either in pitfall traps near drift fences or in pitfall traps near logs (within each row the lowest taxonomic level is significant)

Order	Family	Genus or subfamily
Scorpiones	Buthidae	*Centruroides*
Araneae	Ctenizidae	*Ummidia*
	Zoridae	*Zora*[a]
	Gnaphosidae	*Callilepis*
		Drassyllus
		Herpyllus[a,b]
		Sergiolus
	Theridiidae	*Dipoena*
	Linyphiidae	*Ceratinops*[a]
		Erigone[a]
		Meioneta
	Tetragnathidae	*Pachygnatha*[a]
	Thomisidae	*Ozyptila*[a]
	Corrinnidae	*Scotinella*[a]
	Agelenidae	*Cicurina*[a]
	Hahnidae	*Hahnia*
		Neoantistea[a]
	Lycosidae	*Allocosa*[a]
		Hogna
		Immatures[a]
		Pardosa
		Pirata[b]
		Schizocosa
		Sosippus
		Varacosa
	Salticidae	*Corythalia*[b]
		Habronattus
		Phlegra
		Sitticus[a]
Opiliones	Gagrellidae	*Leiobunum*
	Phalangidae[a]	
Isopoda[a]		
Spirobolida	Spirobolidae	*Narceus*
Lithobiomorpha	Lithobiidae	
Orthoptera	Tettigoniidae	*Atlanticus*
	Acrididae	Conocephalinae
	Gryllacrididae	*Ceuthophilus*
	Gryllidae	*Anaxipha*[a]
		Cycloptilum
		Gryllinae[a,b]
		Gryllus
		Miogryllus[a]
		Mogoplistinae[a,b]
		Orocharis
		Pictonemobius
Blattaria	Blattellidae	*Cariblatta*
Isoptera	Rhinotermitidae	*Reticulitermes*
Hemiptera	Reduviidae	*Repipta*[b]
		Stenopoda
Homoptera[b]	Cicadellidae	
	Delphacidae[a,b]	
	Cixiidae[b]	*Oliarus*[a,b]
	Achilidae[b]	*Catonia*[a,b]
	Aphididae	
Coleoptera	Carabidae	Larvae[a]
		Anisodactylus
Coleoptera (continued)		*Cyclotrachelus*
		Megacephala[a,b]
		Pasimachus
		Piemus[b]
		Pterostichini[b]
		Pterostichus
		Scaritini
	Dytiscidae	*Hydaticus*
	Scydmaenidae	
	Staphylinidae	Larvae[a]
		Aleochariinae[b]
		Osoriinae[b]
		Oxyteninae
		Steninae[b]
	Scarabaeidae	*Aphodius*[b]
		Bolbocerus
		Canthon
		Onthophagus
		Trox
	Elateridae	Larvae[b]
	Lycidae	*Plateros*[b]
	Cantharidae	*Larvae*[a]
	Endomychidae[b]	*Epipocus*[a,b]
	Melandryidae[b]	*Eustrophinus*[b]
	Tenebrionidae[b]	*Helops*
		Platydema[b]
	Cerambycidae[a,b]	*Prionus*[b]
	Chrysomelidae	*Metachroma*
		Myochrous
	Curculionidae	*Hylobius*
		Ips[b]
		Sphenophorus
Mecoptera	Panorpidae	*Panorpa*
Diptera	Tipulidae[b]	
	Mycetophilidae	Unidentified[a,b]
		Orfelia[a]
	Sciaridae	*Bradysia*[b]
		Corynoptera[a]
		Epidapus
		Pseudosciara[b]
		Sciara[a,b]
	Culicidae	*Culex*
	Chironomidae[b]	
	Empididae	*Drapetis*[b]
	Dolichopodidae[b]	*Medetera*[b]
	Phoridae	*Megaselia*
	Sphaeroceridae	*Leptocera*
Lepidoptera	Arctiidae	Larvae
	Noctuidae	Larvae
Hymenoptera	Diapriidae	
	Scelionidae	
	Mutillidae	*Dasymutilla*
		Timulla
	Pompilidae	*Priocnemella*
	Formicidae	*Formica*
		Leptothorax
		Monomorium
		Odontomachus
		Pheidole

[a] Denotes significant interaction between fire frequency and trap location.
[b] Groups that were captured in higher numbers near logs.

Without species-level identifications and studies it is difficult to know if these organisms are dependent on CWD or occasional users that can survive in its absence. However, the results of this study show that a variety of arthropods were captured in higher numbers near CWD. Some of these were clearly saproxylic and fed on dead wood, e.g., some Curculionidae, while others such as spiders and planthoppers were not. The fact that traps along drift fences were more efficient in capturing arthropods, as demonstrated by the much higher numbers of arthropods captured in those traps, suggests that the taxa that were caught in greater abundance in pitfalls near logs spent more time in that habitat and that logs were not just acting as drift fences for these organisms. Clearly, logs provide a resource that benefits these arthropods, but more detailed studies are needed to determine what role logs play in their biology and population dynamics.

DOES ANNUAL REMOVAL OF CWD AFFECT FOREST FLOOR ARTHROPODS?

This question is being addressed as part of a larger interdisciplinary effort to investigate how CWD affects the diversity and abundance of animal populations in mature, managed loblolly pine (*P. taeda*) forests (McCay and others 2002). The evidence is clear that CWD is important to animals in upland forests and that many organisms would disappear without it. A number of arthropod species that are not dependent on woody debris use it as a resource, but their association with it is not clear. However, few studies have been conducted under conditions that remove confounding factors to insure that CWD is the likely reason for observed differences in species abundance (Harmon and others 1986, McCay and others 2002). Loblolly pine was chosen for this study because it is the most common and commercially important species of tree in the Southern United States, where it makes up over one-half of the standing pine volume and occupies about 11.7 million ha (Baker and Langdon 1990). Loblolly pine management is often more intensive than management of other species in this region or similar species in other regions of North America. The large area covered by loblolly pine forests makes them important to regional biodiversity, and intensive management has the potential to reduce CWD in these forests. If CWD is important not only to species that depend on it for food but also to other species, then this impact will be even greater. Thus, the question addressed in this study was whether maintaining low levels of CWD by regularly removing it would affect the diversity and abundance of the general forest floor arthropod community.

The study was initiated in the summer of 1996 at the Savannah River Site, an 80 270-ha U.S. Department of Energy nuclear production facility and a National Environmental Research Park located in the upper Atlantic Coastal Plain Physiographic Province near Aiken, SC. Both longleaf and loblolly pine forests are prevalent on the site, covering approximately 14 924 ha and 25 677 ha, respectively (Knox and Sharitz 1990). Historically, longleaf pine dominated the dry, sandhill habitats, while loblolly pine was found mostly in riparian areas. The site now contains artificially regenerated, even-aged stands of loblolly, longleaf, and slash pines (*P. elliottii*).

The study was a randomized complete block design consisting of four blocks of four treatments. Blocks consisted of even-aged stands of 45-year-old loblolly pine large enough to accommodate four treatment plots. The stands selected for the study had received periodic thinning and prescribed burns. Treatment plots were 9.3-ha squares. Each plot consisted of a 6-ha core area and a 3.3-ha buffer zone to reduce edge effects. The entire 9.3-ha plot was treated, but CWD measurements and arthropod sampling were conducted only in the central 6-ha area. Treatments included a control in which all woody debris was left in place and woody debris removal in which both standing (snags) and fallen (logs) CWD was removed annually.

CWD was removed from the plots during January to February 1997, February to March 1998, March 1999, January 2000, and April to May 2001. At each annual removal all CWD was removed. Wood was removed by crews who used chainsaws to fell standing dead trees and to cut logs into sections that could be lifted by hand onto a trailer pulled by a small tractor or all-terrain vehicle. The initial removal treatment was more invasive than later ones, but removal of CWD caused little noticeable damage to the understory plants, litter, or soil.

All dead wood >10cm in diameter was measured annually in a 4-ha area in the center of each treatment plot. Volumes for logs and portions of standing dead trees < 2 m long were estimated using Huber's formula (Avery 1975), and regional volume equations (Clark and others 1991) were used to calculate volumes of larger snags.

Arthropods were sampled in each plot with 15 pitfall traps identical to those used in a previous study (Hanula and others 2002). Pitfalls were evenly spaced in three lines of five traps with approximately 50 m between traps within lines and 80 m between lines. Traps were opened for 1 week every 2 months and covered when not in use. Arthropod sampling began in November 1997 so only one sample was collected that year. Four were collected in 1998, six in 1999, five in 2000, and two in 2001. Macroarthropods from the 15 traps per plot were pooled into a single sample, preserved in 70 percent alcohol, sorted to morphologically similar groups, and identified to morphospecies by trained entomologists using a reference collection. If possible, following identification, 30 or more specimens were oven-dried at 40 °C for 48 hours and weighed to estimate biomass. In many cases biomass estimates were available from previous studies conducted in similar habitats (e.g., Hanula and Franzreb 1998), so those estimates were used to calculate biomass for this study. All immature insects and spiders were ovendried and weighed because of variation in their sizes.

Arthropod community characteristics were compared using Shannon's diversity index, evenness, morphospecies richness, and Horn's (1966) simplification of Morista's index (1959) for measuring community overlap. Differences in biomass and abundance were compared using a two-way analysis of variance (SAS 1982). Data were transformed using a $\log_{10}(x+1)$ or $\sqrt{x + 0.5}$ transformation to stabilize the variance.

In the year 2000, the volume of CWD averaged 0.5 m^3/ha (SE = 0.20) on removal plots and 10.8 m^3/ha (SE = 2.4) on control plots. About 40 percent of the dead wood on the plots was in the form of standing dead trees, and CWD volume was relatively consistent throughout the treatment blocks.

An average of 8,581 arthropods (SE = 1,013.5) were captured in pitfall traps per control stand, and an average of 9,981 (SE = 598.9) were captured per CWD removal stand. CWD removal had no significant effect on the average number of arthropods caught per plot or the average biomass ($\bar{x}$ = 108.9 g per control plot, SE = 6.51; $\bar{x}$ = 148.5 g per removal plot, SE = 28.1).

Although removal of CWD did not result in a reduction in total number of forest floor arthropods, it did result in a significant overall reduction in morphospecies diversity ($P < 0.06$; H′ = 4.27 on control plots, SE = 0.16; H′ = 3.61 on CWD removal plots, SE = 0.18) and evenness ($P < 0.07$; J = 0.70 on control plots, SE = 0.03; J = 0.59 on CWD removal plots, SE = 0.03) for the 5 years combined. When morphospecies diversity in each year of the study is examined (table 2) it is found that CWD removal resulted in significant reductions in diversity and evenness in 1998 and 1999 but that both diversity and evenness were similar for the two treatments by 2000 and into 2001. Although overall diversity of ground-dwelling arthropods was reduced by CWD removal, morphospecies richness (control = 444.3 ± 5.6 species; removal = 434.3 ± 6.2 species) and the numbers of rare (< 5 captured) morphospecies (control = 304.8 ± 11.1 species; removal = 305.3 ± 13.3 species) were unaffected.

Community similarity was 58.5 percent (SE = 4.60) for comparison of control stands to stands with CWD removed. To provide a standard, we compared faunal similarity in half of the control stands with faunal similarity in the other half. Faunal similarity among similar untreated stands was 72.8 percent, considerably higher than in the comparison of control to treated stands.

Thirteen families of arthropods were significantly affected by removal of CWD (table 3). Of those, 3 families benefited from removal and the remaining 10 were reduced. The latter included three families of spiders, three families of beetles including the Carabidae, two families of Hemiptera, one family of Diptera, and Xystodesmidae millipedes.

These data show that 5 years of removal of CWD lowered overall diversity and community similarity of arthropods in mature loblolly pine stands. Total number and biomass of ground-dwelling arthropods captured in pitfalls were unaffected by annual removal of dead wood, although the removal clearly affected many organisms that lived in the logs but were not sampled using pitfall traps. Likewise, organisms that stay close to logs and do not move readily would not be sampled adequately. However, removal of wood had an impact on a number of groups whose association with woody debris is not clearly understood, and it is important to understand how these organisms interact with dead wood. Five years is not a long time in the life of a forest, so it is difficult to know if the trends we observed will continue. However, our results show that the relatively low levels of CWD found in our study areas play a role in the biology of a diverse array of arthropods.

INTERRELATIONSHIP OF AN ENDANGERED WOODPECKER, ITS PREY, AND CWD

The RCW constructs nest cavities in live pine trees and spends approximately 95 percent of its time foraging on the boles and branches of mature live pines. For this reason its relationship to CWD, unlike many other woodpeckers, is not readily apparent.

As a high-profile endangered species, RCW has received a lot of attention and research. Much of that effort has focused on its foraging behavior and territories, but prior to 1990 only two studies examined the diet of RCW and neither of these studies was definitive (Beal 1911, Harlow and Lennartz 1977). In 1985 the RCW recovery plan (U.S. Fish and Wildlife Service 1985) focused attention on foraging habitat and the lack of understanding about the arthropod prey in it, and how forest management affects prey abundance and availability. Therefore, we studied the diet of RCW and how those arthropods are associated with live and dead trees.

One of the first goals was to develop a detailed understanding of the diet. To do this we monitored 31 groups of RCW over 5 years at 4 sites in the Southeastern United States using automatic cameras to record nest visits with prey (Hanula and Engstrom 2000, Hanula and Franzreb 1995, Hanula and others 2000). Collectively, RCW used 41 different arthropods to feed nestlings, but 9 of these arthropods made up over 90 percent of the diet. Wood cockroaches (*Parcoblatta* spp.) (Blattaria: Blattellidae), were recorded in over 6,500 nest visits and represented 54.7 percent of the diet of all 31 RCW groups combined. RCW consistently used the same types of

Table 2—Shannon diversity (H′), evenness (J), and morphospecies richness for arthropods captured in pitfall traps in 9.3-ha plots receiving annual removal of all coarse woody debris ≥ 10 cm in diameter from 1996 to 2001 at the Savannah River Site, Barnwell County, SC

	H′ (mean ± SE)		J (mean ± SE)		Richness (mean ± SE)	
Year	Control	Removal	Control	Removal	Control	Removal
1997	2.7 ± 0.26	1.8 ± 0.42	0.6 ± 0.06	0.4 ± 0.08	101 ± 6.9	75 ± 14.3
1998	4.1 ± 0.09[a]	3.4 ± 0.21	0.8 ± 0.02[a]	0.6 ± 0.04	207 ± 7.6	197 ± 8.2
1999	4.1 ± 0.08[a]	3.6 ± 0.11	0.8 ± 0.01[a]	0.7 ± 0.01	216 ± 4.0	222 ± 13.1
2000	3.4 ± 0.32	3.1 ± 0.21	0.7 ± 0.06	0.6 ± 0.04	155 ± 2.3	158 ± 4.1
2001	2.8 ± 0.30	2.7 ± 0.19	0.6 ± 0.06	0.6 ± 0.03	98 ± 8.4	92 ± 8.0

SE = standard error.
[a] Controls were significantly different (P < 0.05) from removals within a given year.

Table 3—Mean (SE) number of arthropods captured in pitfall traps in 9.3-ha plots receiving annual removal of all coarse woody debris with diameters ≥ 10 cm from 1996 to 2001 at the Savannah River Site, Barnwell County, SC

Family	Control	CWD removal	P > F
Araneae			
Clubionidae	20.8 (2.14)	12.8 (2.95)	0.007
Hahniidae	384.3 (131.2)	173.5 (80.3)	0.05
Lycosidae	370.3 (41.6)	291.5 (34.9)	0.01
Coleoptera			
Carabidae	330.0 (45.8)	258.8 (34.2)	0.04
Meloidae	1.25 (0.63)	0.25 (0.25)	0.06
Diptera			
Phoridae	259.8 (58.3)	115.5 (27.6)	0.04
Homoptera			
Cicadellidae[a]	1 (0.4)	4.5 (0.96)	0.02
Hemiptera			
Largidae	15.0 (6.26)	3.75 (1.75)	0.06
Lygaeidae	10.5 (1.66)	5.5 (1.32)	0.03
Reduviidae[a]	4.5 (0.96)	7.3 (1.49)	0.01
Hymenoptera			
Mutillidae[a]	22.3 (4.15)	35.0 (8.12)	0.04
Polydesmida			
Xystodesmidae	80.3 (37.3)	42.3 (27.3)	0.03

SE = standard error; CWD = coarse woody debris.
[a] Denotes more captured in CWD removal plots. The remaining families were captured in significantly higher numbers in control plots.

prey despite differences in location, forest type, physiography, or year of observation (table 4) (Hanula and Horn 2004). In every case wood cockroaches were the most frequently used prey making up about half of the diet at three of the four sample locations and about a quarter of it at the fourth.

Most arthropods found on tree boles do not live there exclusively (Hanula and Franzreb 1998) so we were interested in finding other habitats that might be important to them. We found that prey of RCW were primarily detritivores and predators based on published records of their behavior and feeding habits (table 4). In addition to prey able to move freely between

Table 4—Proportions of the most common prey groups fed to red-cockaded woodpecker nestlings at four locations in the Southeastern United States sampled during 1993 to 1997 (from Hanula and Horn 2004)

	Nest visits (percent)			
Prey item	Upper Atlantic Coastal Plain[a b c]	Lower Atlantic Coastal Plain[b]	Piedmont[b]	Gulf Coastal Plain[c]
Wood cockroach	59.6	26.0	49.9	46.8
Woodborer larva	7.3	1.2	0.5	2.9
Caterpillar	7.7	9.1	9.3	8.9
Spider	6.4	7.2	5.2	8.3
Ants	2.5	7.2	0	1.1
Centipede	5.6	4.9	3.2	6.7
Insect larva	2.4	1.3	4.1	7.4
Insect larvae	1.9	6.0	1.0	2.5
Year studied	1993–1997	1994	1995	1995–1997

[a] Data from Hanula and Franzreb 1998.
[b] Data from Hanula and others 2000.
[c] Data from Hanula and Engstrom 2000.

habitats, the RCW also fed on woodborer larvae taken from dead pine trees or dead limbs in live trees. Therefore, only a small proportion of the diet is composed of herbivores dependent on live vegetation and, in most cases, those prey feed on pine cones (Hanula and Horn 2004).

Dead Wood as Prey Habitat

Since the RCW feed primarily on detritivores and predators, what habitats are important to these arthropods? We believe that detritus, particularly standing and fallen dead trees, provides important habitat for arthropods that spend time on tree boles where they are preyed upon by RCW and other bark-foraging birds.

Support for this comes from a number of studies. First, diet studies show that RCW feed on wood cockroaches, centipedes, spiders, and ants (Beal 1911, Hanula and Engstrom 2000, Hanula and Franzreb 1995, Hanula and others 2000, Hess and James 1998); i.e., detritivores, predators, and omnivores. All of these major prey items are commonly found in or on dead wood. Second, dead branches of live trees contain as much or more arthropod biomass as any other part of the tree (Hanula and Franzreb 1998, Hooper 1996). Hooper (1996) found more arthropod biomass in dead branches than in bark at other positions on the tree bole. Likewise, Hanula and Franzreb (1998) found dead branches contained as much arthropod biomass as bark at the base of the tree, and both of these locations contained more biomass than any other position on tree boles. Third, wood cockroaches are abundant in standing dead trees (snags) and downed dead wood (logs). Snags contained almost three times as many as logs on the ground (fig. 4), but snags and logs on the ground contained approximately equal numbers of wood cockroaches because log volumes were nearly three times as great as volumes of standing dead trees (Horn and Hanula 2002a).

Horn and Hanula (2002b) estimated that in their study area a hectare of mature loblolly pine forest contained approximately 725 wood cockroaches in logs and snags. However, an average of 10.8 wood cockroaches per live tree were collected when entire tree boles were sprayed with insecticide (Horn and Hanula 2002a). The study area contained an average of 156 trees per ha, so if each tree contained ca. 11 cockroaches, there were approximately 1,716 wood cockroaches per ha on live trees—more than twice as many as found in logs and snags (fig. 5). However, the stands contained an average volume of 8.6 m^3/ha of dead wood over 10 cm in diameter compared to 188 m^3/ha of live trees. Therefore, dead trees contained almost 10 times more wood cockroaches per unit volume than live trees (fig. 5). The fact that wood cockroaches are more concentrated in dead wood suggests that it is important to their biology.

Larvae of wood-boring beetles (Coleoptera: Cerambycidae or Buprestidae), which are found in dead trees or dead branches of live trees, are also common and important prey of RCW. Likewise, the two common ant prey, carpenter ants (*Camponotus* spp.) and *Crematogaster* spp. ants, are found nesting in dead branches of live trees (Hanula and Franzreb 1998) and in dead trees. In fact, carpenter ants were six times more abundant in dead branches than at any other sample position on live trees. *Crematogaster* spp. ants were equally abundant in dead branches and in the bark 1.5 m above the ground.

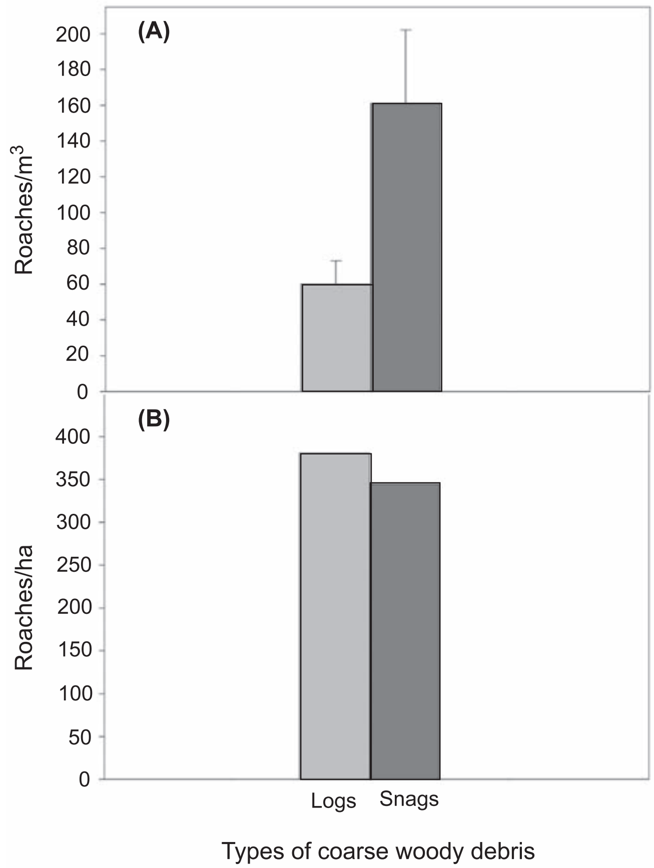

Figure 4—Densities (A) of wood cockroaches were significantly higher ($P = 0.0003$) in standing dead trees (snags) than in logs in loblolly pine stands on the Savannah River Site, SC. Estimated numbers (B) of wood cockroaches per hectare at the same location (from Horn and Hanula 2002b).

Both sample positions contained five times the numbers of ants found at the midbole or crown sample locations.

If logs and snags are important habitat for arthropods that serve as prey for RCW, what happens when they are removed from the system? We are currently investigating that question on the large-scale, long-term research plots on the Savannah River Site mentioned above. In addition to installing pitfall traps, we attached crawl traps (Hanula and New 1996) to 15 trees widely distributed throughout the plots and monitored them monthly from October 1997 to September 1999. Burlap bands also were placed on 30 trees per plot and monitored monthly from July 1998 to September 1999 (Horn 2000).

Arthropod abundance on tree boles as measured under the burlap bands was significantly ($P < 0.04$) reduced by removal of CWD but arthropod abundance in crawl traps was not (Horn 2000). No one group, e.g., ants or wood cockroaches, was significantly affected by the removal, but all groups in general were reduced slightly, resulting in the overall significant reduction in arthropod abundance beneath burlap bands. Although interesting, these preliminary results are not clear evidence of an essential role of CWD in the food web supporting RCW. Burlap bands are an efficient, nonlethal sampling method for assessing arthropods available for foraging by

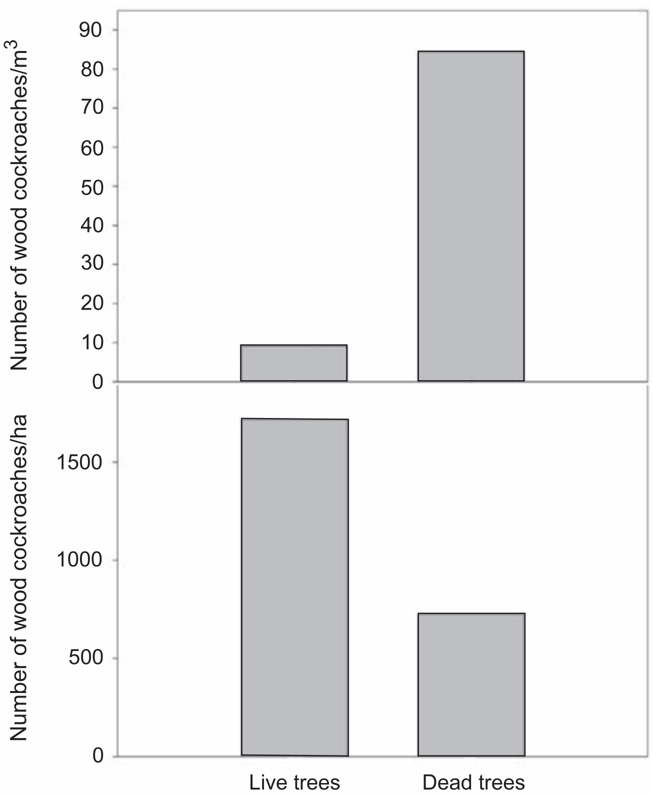

Figure 5—The number of Parcoblatta spp. wood cockroaches per unit volume (top) found in live and dead pine trees, and estimated number per unit area (bottom) in the same habitats. Wood cockroaches are concentrated in dead trees but the volume of live trees is much greater so approximately equal numbers occur in both habitats on a given hectare of pine forest (from Hanula and Horn 2004).

woodpeckers and they sample them in proportions similar to the proportions the woodpeckers actually use (Hanula and Horn 2004). They were particularly effective in sampling wood cockroaches, but abundance of these insects beneath burlap bands and in crawl traps were not affected by removal of woody debris. Thus, one of the main prey of RCW, wood cockroaches, were not reduced by the removals even though so many can be found in dead trees. The results show that the initial 2 to 3 years of CWD removal had some effect. Whether long-term absence of woody debris will affect the community of arthropods that RCW depend on is unclear, but it is a question that we are currently investigating. Likewise, it is not known whether absence of dead wood in a forest would affect population viability of RCW. Few studies have looked at such linkages. However, MacNally and others (2002) demonstrated that the brown treecreeper (*Climacteris picumnus*) in an Australian floodplain forest responded rapidly to the addition of woody debris, and Lohr and others (2002) found that removing dead wood from an upland pine forest in South Carolina reduced overall breeding bird abundance and richness as well as the abundance of several species. These studies from very different habitats are indicative of the importance of dead wood in forests and the subtle relationships between woody debris and other organisms. Clearly, more work is needed on how CWD is affecting these species.

SUMMARY

The role of CWD in the ecology of forest floor arthropods in the Southeastern United States is not clear. Logs did not increase the total abundance or biomass of arthropods captured near them and annual removal of woody debris did not result in a general decrease in arthropod abundance. However, a number of arthropods from a wide variety of taxonomic groups were captured in higher numbers near logs, and removal of CWD resulted in lower overall diversity and evenness of ground-dwelling arthropods on large scale plots. In addition, CWD removal negatively affected the abundance of a number of arthropod families. What is not clear is whether these groups were affected by the physical removal, i.e., they were removed with the wood, or whether the removal affects their ability to maintain populations within a forest. Studies are underway to determine if removal over extended periods results in further declines in their populations, and if addition of large amounts of standing or down woody debris results in population increases. Other studies are underway on the biology of specific groups, particularly wood cockroaches because of their importance as prey for the RCW, to determine their specific habitat needs and relationship to woody debris. Clearly, wood cockroaches were abundant in dead wood and are important as prey of the RCW, but whether a certain level of dead wood input is necessary to sustain populations of either the wood cockroaches or the woodpeckers is not yet clear. Dead wood in forests does influence populations of a variety of generalist, ground-dwelling arthropods, but determining to what degree and how critical it is to sustaining their populations will require further study.

ACKNOWLEDGMENTS

Funding for this work was provided in part by the U.S. Department of Energy, Savannah River Operations Office through the U.S. Department of Agriculture Forest Service, Savannah River, under Interagency Agreement DE–AI09–00SR22188 and by The Nature Conservancy's A.W. Mellon Foundation Ecosystem Research Program. We also thank the numerous colleagues, cooperators, graduate students, and technicians who worked with us on these projects. Finally, we thank Simon Grove and Staffan Lindgren for helpful comments on earlier drafts of this paper.

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