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Ground-Dwelling Invertebrate Abundance Positively Related to Volume of Logging Residues in the Southern Appalachians, USA

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Abstract: Invertebrates, especially those dependent on woody debris for a portion of their life cycle, may be greatly impacted by the amount of downed wood retained following timber harvests. To document relationships between invertebrates and logging residues, we sampled invertebrates with pitfall traps placed near or far from woody debris in 10 recently (2013–2015) harvested sites in western North Carolina with varying levels of woody debris retention. We measured the groundcover and microclimate at each trap and estimated site-level woody debris volume. We modeled predictors (e.g., site-level woody debris volume, percent woody debris cover at the trap site, site type) of captures of spiders (Araneae), harvestmen (Opiliones), centipedes/millipedes (Chilopoda/Diplopoda), ground beetles (Carabidae), rove beetles (Staphylinidae), other beetles, ants (Formicidae), grasshoppers (Acrididae/Tetrigidae), crickets (Gryllidae), and cave crickets (Rhaphidophoridae). In addition, we modeled ant occurrence at a finer taxonomic resolution, including red imported fire ants (*Solenopsis invicta* Buren) and 13 other genera/species. Forest type, whether hardwood or white pine (*Pinus strobus* L.) overstory preharvest, was a predictor of invertebrate response for 21 of 24 taxonomic analyses. Invertebrate captures or the occurrence probability of ants increased with increasing site-level woody debris volume for 13 of the 24 taxa examined and increased with increasing coarse woody debris (CWD; diameter ≥ 10 cm) cover at the trap level for seven of 24 taxa examined. Our results indicate that woody debris in harvested sites is important for the conservation of a majority of the taxa we studied, which is likely because of the unique microclimate offered near/under woody debris. Stand-scale factors typically were more important predictors of invertebrate response than trap-level cover of woody debris. We recommend implementing sustainability strategies (e.g., Biomass Harvesting Guidelines) to retain woody debris scattered across harvested sites to aid in the conservation of invertebrates.

Keywords: ants; arachnids; bioenergy; downed wood; invertebrates; insects; logging residue; woody biomass

1. Introduction

Downed wood is a critical component of forest ecosystems and provides numerous ecological services, such as carbon sequestration [1,2], soil nutrient replenishment [1–3], and erosion control [1,4].

Downed wood can serve as "nurse logs" for tree seedlings, providing increased survival and/or decreased competition from other plants [5–8]. Downed wood provides cover that allows wildlife to avoid climate extremes, as temperature and moisture conditions in areas with downed wood present typically are cooler and wetter [4,9–12]. Downed wood also provides nesting and escape cover for a variety of wildlife, including small mammals, amphibians, and birds e.g., [13–16]. Numerous invertebrate taxa (e.g., species of wasps, bees, ants, and termites) nest in dead wood or associate with the nests of wood-nesting species [17]. Larger diameter downed wood (CWD) provides food for wildlife, either directly for saproxylic invertebrates (taxa directly or indirectly dependent on downed wood for some portion of their life cycle [18–20]) or indirectly by providing cover for invertebrates and small mammals that in turn serve as prey. CWD may provide a source of food for granivorous insects by trapping seeds, which is termed "seed-damming" [21–23]. Even invertebrates not directly dependent on CWD may use it as cover [23]. Furthermore, large pieces of wood provide refuge from hot, cold, or dry conditions [1,24]. Without dead and dying wood, populations of these valuable invertebrates would decline, along with the ecosystem services (e.g., decomposition) they provide [25,26].

Several studies show that saproxylic beetle species richness increases with increasing dead wood abundance, diversity [27,28], and decay level [29]. Other studies show that beetle, rove beetle, centipede, millipede, harvestman, and spider abundance are negatively associated with increasing distance from [30–35] or decreasing abundance [36] of woody debris. Both coarse and fine (FWD; diameter < 10 cm) woody debris may affect the abundance of some invertebrate taxa e.g., [37]. Populations of many invertebrate taxa would likely decrease with woody debris removal in forested ecosystems.

Reliance on downed wood by many invertebrate taxa suggests the importance of retaining downed wood, or logging residues, after timber harvest to provide the critical food, nest sites, cover, and microclimatic conditions they need. The abundance of ground beetles, crickets, cave crickets, millipedes, and native ants is positively affected by post-harvest retention of logging residue in the southeastern US Coastal Plain [23,38]; highly invasive red imported fire ant (*Solenopsis invicta* Buren) relative abundance increased in sites where woody debris was removed [38]. In Sweden, Carabid abundance decreased in sites when logging residue was removed [39]. Conversely, wild bee diversity may be enhanced by high levels of debris removal [40]. Logging residue could be especially critical in providing cover and suitable microclimatic conditions for ground-dwelling invertebrates because other forms of cover (i.e., leaf litter and vegetation) are temporarily reduced after timber harvests [41–43].

Expanding markets for low-value trees as a feedstock for bioenergy production could lead to reductions in logging residue and consequently downed wood following timber harvests, in turn affecting the availability of food and cover for invertebrates. As markets for wood pellets and other forms of bioenergy expand, low-value and small diameter trees, otherwise left as logging residue, may be removed from the harvest sites. Studies show that logging residue can decrease by more than 80% after removal for bioenergy markets in temperate and boreal forests [44,45]. As bioenergy harvests expand, such as in the southern Appalachians of the eastern USA, it is critical to document retention rates of downed wood with and without bioenergy harvests, as they may differ from other regions [44–47].

We quantified residual downed wood volumes and invertebrate communities in 10 recent timber harvest sites in the southern Appalachian region of western North Carolina, USA during 2016 and 2017 to determine the effects of residual downed wood volume and distribution on invertebrate populations. The 10 harvest sites included five that had white pine (*Pinus strobus* L.) overstory preharvest and five that had hardwood overstory preharvest, and they varied in the volume of debris retained. Using this mensurative experiment, our objectives were to (1) describe the relationships between downed wood (i.e., logging residue) volume and cover and invertebrate taxa at logged sites; and (2) evaluate the importance of downed wood as a predictor of invertebrate presence or abundance relative to other environmental factors (i.e., forest type and vegetation cover).

2. Materials and Methods

2.1. Study Area

We studied relationships between residual downed wood and invertebrates in 10 recent timber harvests, ranging in size from 3.2 to 16.6 ha, which were located on public land in western (Henderson and Transylvania County) North Carolina, USA (Figure 1). Six sites located in Pisgah National Forest (PNF) were harvested between 2013 and 2015 using a two-aged regeneration method with an average 4.98 m^2 of basal area retained per hectare (Figure 1). The remaining sites, three located in DuPont State Recreational Forest (DSRF) and one located in Holmes Educational State Forest (HESF), were harvested using a clearcut regeneration method between 2013 and 2015 (Figure 1). We assigned forest type (white pine or hardwood; $n = 5$ each) to each site based on overstory trees dominant before harvest based on conversations with U.S. Forest Service and North Carolina Forest Service staff and Google Earth imagery (Figure 1). Site preparation, which involved felling trees < 20 cm in diameter and treating the stumps of saplings of non-target species with herbicide, was conducted before sampling was initiated in 2016 at four sites in PNF and after sampling was completed in 2016 at two sites in PNF. All stands were allowed to regenerate naturally, with the exception of the hardwood site in DSRF, which was replanted with shortleaf pine (*Pinus echinata* Mill.). All harvests were conducted under the guidance of the U.S. Forest Service or North Carolina Forest Service and did not include a bioenergy harvest.

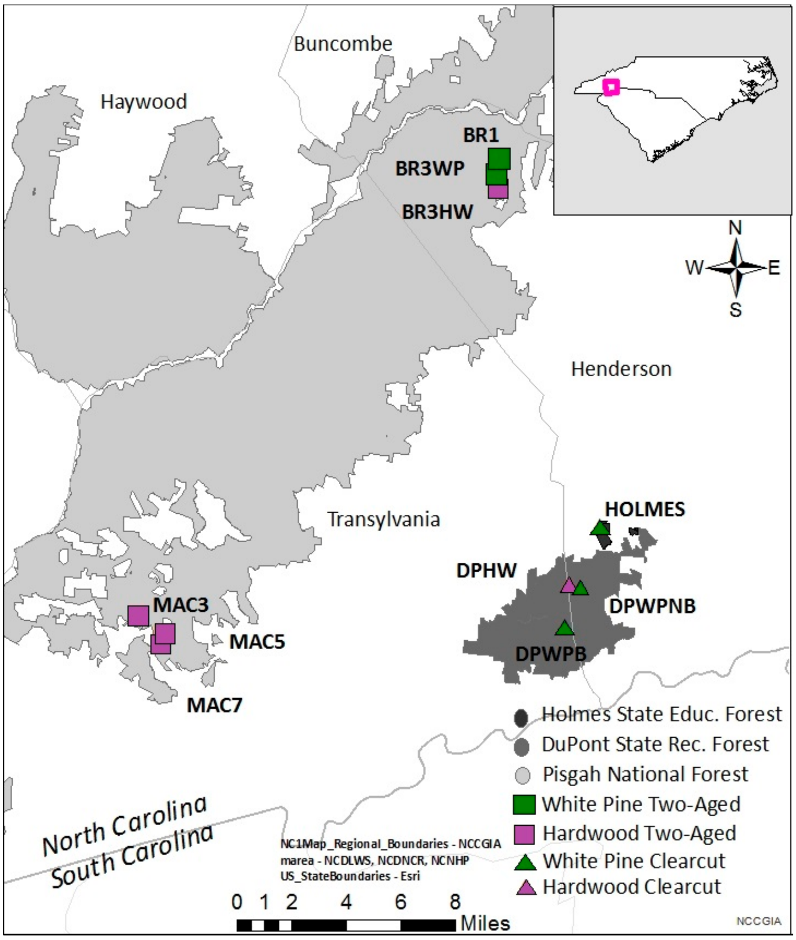

Figure 1. Map of sites in western North Carolina sampled using pitfall traps from July to August of 2016 and June to August of 2017. MAC3, MAC5, MAC7, BR3HW, BR3WP, and BR1 were located in Pisgah National Forest. DPWPNB, DPWPB, and DPHW were located in DuPont State Recreational Forest. HOLMES was located in Holmes Educational State Forest.

2.2. Invertebrate Sampling and Identification

We collected, stored, and identified ground-dwelling invertebrates from eight pairs of pitfall traps centered at piles of downed wood in each of the 10 harvested sites. Each pair of pitfall traps was centered at a pile of downed wood, with one pitfall trap located beside downed wood in the debris pile (near) and the other located 5 m away from the debris pile (far). A pile of downed wood consisted of many pieces of CWD and FWD tangled or stacked together. We chose piles of similar size when possible; however, the sizes of available piles varied widely within/across sites, necessitating accounting for the variation using the methods to quantify downed wood. We used 5 m as the separation distance, because we were unable to consistently locate distances further away from logging debris, indicating that the range of distances from debris was representative of what was available in harvest units. Pitfall traps consisted of a 0.47-L plastic cup buried with the top of the cup lower than or level with the ground [23,48–50]. Each pitfall trap contained a mixture of half propylene glycol and half water, with a drop of dish detergent added to reduce surface tension to ensure that insects could not walk on the surface of the solution [23]. The propylene glycol served as a temporary preservative until the invertebrate samples were strained and stored in 70% ethanol for later identification. We removed vegetation within 5 cm of pitfall traps [23,51]. We trapped insects between mid-July and mid-August of 2016 and between late June and early August of 2017. We opened each pitfall trap for a 2-day period in 2016 and 2017, for a total of 600 trap nights (300 trap nights for near traps and 300 trap nights for far traps; results from 10 pairs of pitfall traps were discarded due to trap failure from heavy rain or animal disturbance of traps). Traps were open for only two days per year per site due to high numbers of invertebrate captures and the difficulty associated with preserving and identifying large numbers of invertebrates. We identified invertebrates to order or family except for the classes Chilopoda (centipedes) and Diplopoda (millipedes), which we combined. We identified all ants to genus and/or species [52–54].

2.3. Microhabitat Characteristics

We quantified ground cover and temperature at each pitfall trap location and measured humidity at one randomly selected pair of pitfall traps in each site. We visually estimated groundcover percentages using a 1-m by 1-m Daubenmire frame centered on the pitfall trap [23,55]. We recorded groundcover as CWD (>10 cm diameter), FWD (<10 cm diameter), bare ground, leaf litter, or vegetation. We measured humidity and temperature each trapping season with Hygrochron^{TM} iButtons® (Maxim Integrated, San Jose, CA, USA) placed at a randomly selected pair of traps at each site. Additionally, we placed Thermochron® iButtons® (Maxim Integrated, San Jose, CA, USA) measuring temperature only at all remaining pitfall traps. At the "near" traps, we placed sensors directly under a piece of downed wood close to the pitfall trap. At the "far" traps, we placed sensors within 15 cm of the pitfall trap. Since we had fewer iButtons than sampling locations, we placed sensors at trapping locations for a 2-day period up to six weeks after trapping occurred.

2.4. Downed Wood Volumes

We estimated downed wood volumes once in each site during the winter months in late 2016 and early 2017. We measured "scattered" and "piled" downed wood volumes using the prism sweep sampling method [56,57] at 15 systematically spaced plots across each of the 10 sites and summed both estimates to calculate site-level woody debris volume. We used a wedge prism to determine if scattered pieces of CWD and FWD were "in" each plot before measuring the length of pieces of FWD and CWD within the plots to estimate the volume of downed wood [56,57]. For piles of woody debris, we estimated the volume of woody debris located within 7.32 m of the center of the plot [57]. If the midpoint of a pile was within 7.32 m of the plot center, we estimated the proportion of the pile located within 7.32 m of the plot center and estimated how much of the pile consisted of debris (versus air) [57]. We determined the shape of each pile and took height, width, and/or length measurements based on the associated shape code [57]. We used volume equations associated with each shape code to calculate volume estimates for each pile and used the volumes for each pile to calculate the volume of debris per hectare [57].

2.5. Statistical Analysis

We did not include temperature and humidity metrics in the analysis of invertebrate detections but rather investigated these factors only relative to the proximity to downed wood. We used PROC ANOVA in SAS® Enterprise Guide (version 7.15 HF3) [58] to determine if there was a significant difference in minimum temperature, maximum temperature, minimum humidity, maximum humidity, and the range of humidity measured over the course of two days between "near" and "far" pitfall traps. We determined the minimum and maximum values of temperature and humidity and the range of humidity across the two-day period for each sensor, and we used these values to run an analysis of variance (ANOVA) with proximity to debris (near or far) as the dependent variable for each category (minimum temperature, maximum temperature, minimum humidity, maximum humidity, and range of humidity).

We analyzed invertebrate captures by fitting Poisson generalized linear models in the glmulti package in R [59] with the number of captures for each invertebrate taxa as the dependent variable and environmental and temporal covariates, including proximity (near or far), forest type, site-level debris volume, bare ground cover, CWD cover, FWD cover, vegetation cover, and year as the independent variables. All analyses were conducted with the trap site as the experimental unit. We used the vif function in the car package [60] in R (version 3.4.3) [61] to test for multicollinearity. The variance inflation factors for the covariates indicated a problem with multicollinearity; after removing leaf litter percent cover, the variance inflation factors for the remaining covariates were less than 8, so we retained all remaining covariates (see above) in models. We chose to remove leaf litter percent cover as a covariate because we determined it was not as essential as the other covariates, and it was correlated with multiple covariates, which were determined using PROC CORR in SAS® Enterprise Guide (version 7.15 HF3) [58]. We standardized all continuous response variables by subtracting the mean and dividing by the standard deviation [62]. We analyzed only invertebrate taxa with greater than 90 individuals captured, because this was a natural break in capture numbers and was deemed an appropriate threshold for a minimum number of captures for analysis. We conducted automated model selection using an exhaustive screening of all possible models containing no interactions with glmulti in R, and we selected the best model based on the lowest Akaike information criterion corrected for small sample size (AICc) value [63].

For ants, we used the presence or absence of ant genera/species as a binomial response and analyzed the data using logistic regression. We used logistic regression because we captured many ant genera/species in high numbers at relatively few traps. Independent covariates were proximity (near or far), year, forest type (white pine or hardwood), percent CWD cover, percent FWD cover, percent vegetation cover, percent bare ground, and site-level debris volume. We conducted automated model selection using an exhaustive screening of all possible model combinations without interactions with glmulti in R and selected the most competitive model based on AICc score.

3. Results

3.1. Microhabitat Characteristics

In total, we obtained 636 sensor days of temperature measurements (318 days of measurements for far sensors and 318 days of measurements for near sensors) and 80 sensor days of humidity measurements (40 days of measurements for far sensors and 40 days of measurements for near sensors). Minimum humidity and minimum temperature across the 2-day periods were greater near piles of woody debris, whereas the maximum temperature and range of humidity were greater far from piles of woody debris (Table 1).

Table 1. Mean (±SE) temperature and humidity collected by sensors placed near and far from piles of woody debris over a 2-day period in 10 harvested sites in western North Carolina during summer 2016 and 2017. The *p*-value given is from an analysis of variance with proximity as the dependent variable. Means are presented by year and proximity to show that relationships were consistent across the two years.

Values Compared	Mean (±SE)				*p*-Value
	2016		2017		
	Near	Far	Near	Far	
Minimum Temperature (°C)	19.76 (1.83)	18.50 (1.49)	18.07 (1.46)	16.29 (1.78)	<0.0001
Maximum Temperature (°C)	28.78 (4.34)	48.77 (11.90)	26.10 (3.90)	44.29 (12.24)	<0.0001
Minimum Humidity (%)	85.91 (16.91)	50.82 (25.47)	93.62 (7.81)	45.02 (26.31)	<0.0001
Maximum Humidity (%)	103.39 (1.70)	102.85 (3.45)	103.29 (1.20)	102.40 (3.25)	0.3888
Range of Humidity (%)	17.47 (16.08)	52.03 (23.82)	9.67 (8.03)	57.38 (27.01)	<0.0001

3.2. *Site-Level Woody Debris Volumes*

Estimates of debris volume per site ranged from 56.05 to 376.61 m^3 ha^{-1}, with a mean of 176.66 m^3 ha^{-1} and a standard error of 28.71 m^3 ha^{-1} (Table 2).

Table 2. Scattered, piled, and site-level woody debris volumes at each of 10 harvest sites in western North Carolina based on measurements taken winter 2016–2017. We classified each site as white pine or hardwood based on the overstory trees present before harvest.

Site	Forest Type	Scattered Woody Debris Volume (m^3 ha^{-1})	Piled Woody Debris Volume (m^3 ha^{-1})	Site-Level Woody Debris Volume (m^3 ha^{-1})
BR1	White Pine	81.06	72.76	153.82
BR3WP	White Pine	60.92	32.13	93.05
DPWPB	White Pine	76.11	70.55	146.66
DPWPNB	White Pine	52.57	3.48	56.05
HOLMES	White Pine	145.28	75.86	221.14
BR3HW	Hardwood	71.29	32.47	103.76
DPHW	Hardwood	40.39	133.65	174.05
MAC3	Hardwood	102.32	112.51	214.83
MAC5	Hardwood	93.10	133.49	226.59
MAC7	Hardwood	83.34	293.26	376.61
White Pine	Mean	83.19	50.96	134.14
	Standard Error	16.35	14.30	28.20
Hardwood	Mean	78.09	141.08	219.17
	Standard Error	10.74	42.36	44.84
Overall	Mean	80.64	96.02	176.66
	Standard Error	9.26	25.88	28.71

3.3. *Capture Summary*

We identified 11,293 individual invertebrates captured from mid-July to mid-August 2016 and late June to early August 2017 (Table 3). Invertebrates that were captured infrequently (e.g., katydids (Tettigoniidae)) or that are not typically ground-dwelling (e.g., flies (Diptera) and butterflies/moths (Lepidoptera)) were not identified, tallied, or included in the statistical analysis. Captured invertebrates included spiders (Araneae), harvestmen (Opiliones), pseudoscorpions (Pseudoscorpiones), centipedes/millipedes (Chilopoda/Diplopoda), ground beetles (Carabidae), rove beetles (Staphylinidae), ants (Formicidae), grasshoppers (Acrididae/Tetrigidae), crickets (Gryllidae), and cave crickets (Rhaphidophoridae) (Table 3). Ants comprised 55% of captures and were identified to the species level when possible (Table 3). Collembolans were typically small and present in high numbers within samples, making accurately collecting and tallying all individuals impractical and necessitating omitting them from analyses. Red imported fire ants and minute (tiny) species within the genus *Solenopsis* comprised 51% of ant captures (Table 3).

Table 3. Total captures of each invertebrate taxon in 10 harvested sites in western North Carolina, USA (2016–2017).

Class	Order	Family	Subfamily	Species	Number of Captures
Arachnida					
	Araneae				1313
	Opiliones				400
	Pseudoscorpiones				78
Chilopoda/Diplopoda					265
Insecta					
	Coleoptera				
		Carabidae			613
		Staphylinidae			811
		Other			553
		Larvae			314
	Hymenoptera				
		Formicidae			6244
			Amblyoponinae	*Stigmatomma palipes* Haldeman	1
			Formicinae	*Brachymyrmex depilis* Emery	45
				Camponotus spp.	160
				Formica spp.	306
				Lasius spp.	172
				Nylanderia spp.	122
			Dolichoderinae	*Forelius* spp.	32
				Tapinoma sessile Say	96
			Myrmicinae	*Aphaenogaster* spp	969
				Crematogaster spp.	91
				Monomorium spp.	16
				Myrmecina spp.	128
				Myrmica spp.	122
				Pheidole spp.	402
				Solenopsis spp. (minute)	1831
				Solenopsis invicta Buren	1325
				Stenamma spp.	27
				Strumigenys spp.	55
				Temnothorax spp.	8
				Tetramorium spp.	148
			Ponerinae	*Brachyponera chinensis* Emery	11
				Hypoponera spp.	50
				Ponera spp.	92
			Proceratiinae	*Proceratium croceum* Roger	1
	Orthoptera				
		Acrididae/Tetrigidae			95
		Gryllidae			467
		Rhaphidophoridae			140
TOTAL					11293

3.4. Invertebrate Responses

Relationships between invertebrate captures and covariates varied among invertebrate taxa (Table 4). Within the class Arachnida, we analyzed the orders Araneae (spiders) and Opiliones (harvestmen). We captured fewer spiders at traps near than far from piles of woody debris, and captures decreased with increasing bare ground, CWD, and FWD cover (Figure 2, Table 4). Spider captures were greater at white pine than hardwood sites, and they increased with increases in vegetation cover and site-level woody debris volume (Figure 3, Table 4). Harvestmen captures were lower at white pine sites than at hardwood sites, and they were lower in 2017 than in 2016 (Figure 3, Table 4). Harvestmen captures decreased with increasing bare ground cover and decreasing CWD cover (Table 4).

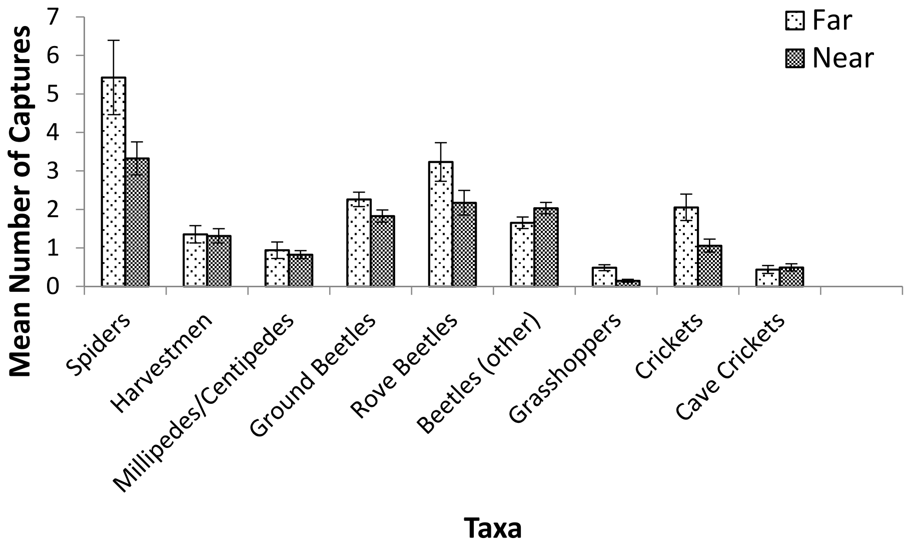

Figure 2. Mean (+SE) number of invertebrate captures near and far from piled woody debris in 10 harvested sites in western North Carolina (2016–2017).

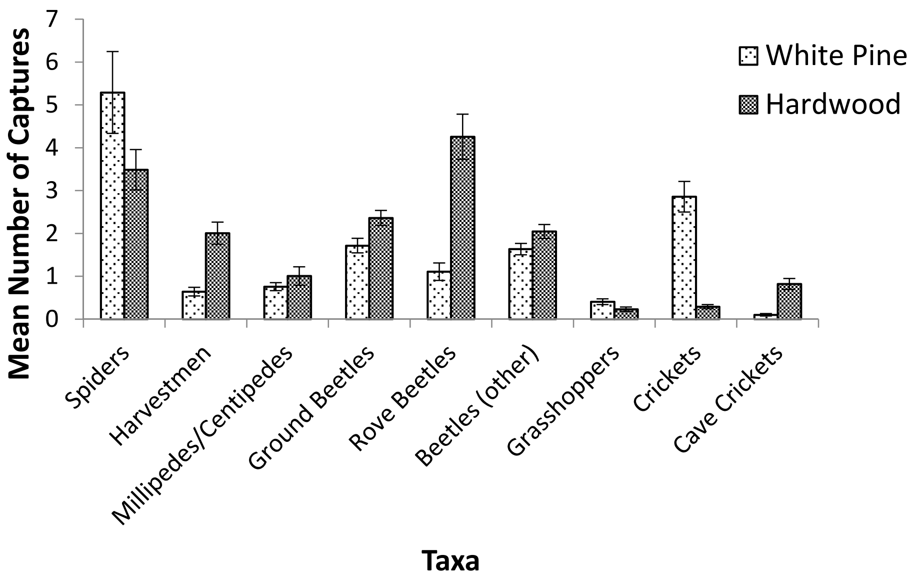

Figure 3. Mean (+SE) number of invertebrate captures by forest type in 10 harvested sites in western North Carolina (2016–2017).

We combined classes Chilopoda (centipedes) and Diplopoda (millipedes) for analyses because of the relatively few captures of each group, although we recognize that these are ecologically distinct taxa. We captured 265 millipedes and centipedes during 2016 and 2017 (Table 3). Captures were lower at white pine than hardwood sites, and they decreased with increasing bare ground cover and CWD cover (Figure 3, Table 4).

Coleoptera (class Insecta) were grouped into the families Carabidae (ground beetles) and Staphylinidae (rove beetles); all remaining beetles were grouped as "other beetles". We included only captures of adult beetles in analyses. Ground beetle captures were lower at white pine than hardwood sites, lower in 2017 than in 2016, and declined with increasing CWD cover (Figure 3, Table 4). Rove beetle captures were lower in white pine than hardwood sites and lower near rather than far from piles of woody debris (Figure 2, Table 4). Rove beetle captures increased with increasing CWD, FWD, vegetation cover, and site-level woody debris volume (Table 4). Other beetle captures were lower at white pine than hardwood sites, and captures declined with increasing bare ground and vegetation cover (Figure 3, Table 4).

Ants (order Hymenoptera and family Formicidae) comprised 55% of the invertebrates we identified (Table 3). Overall, ant captures were lower at white pine than hardwood sites (Table 4). Ant captures were greater near compared with far from woody debris piles and increased with increasing bare ground and CWD cover (Table 4).

Within the order Orthoptera, we analyzed grasshoppers (families Acrididae and Tetrigidae), crickets (family Gryllidae), and cave crickets (family Rhaphidophoridae). We captured fewer crickets near rather than far from piled woody debris (Figure 2, Table 4). Cricket captures declined with increasing FWD cover and increased with increasing bare ground, increasing CWD cover, and greater site-level woody debris volume; cricket captures were greater at white pine than hardwood sites and were greater in 2017 than in 2016 (Figure 3, Table 4). Grasshopper captures were lower near rather than far from woody debris piles (Figure 2, Table 4). Grasshopper captures were greater at white pine than hardwood sites, and they increased with increasing FWD, vegetation cover, and site-level woody debris volume (Figure 3, Table 4). Grasshopper captures were greater in 2017 than in 2016 (Table 4). More cave crickets were captured at hardwood than white pines sites, and captures were greater in 2016 than in 2017; captures increased with increasing site-level woody debris volume and decreasing bare ground cover (Figure 3, Table 4).

3.5. Ant Responses

We captured and identified 6244 ant individuals representing six subfamilies, 23 genera, and six species (Table 3). We conducted logistic regressions for the 14 taxa that had at least 90 captures. Multiple ant taxa were captured fewer than 20 times, including the invasive Asian needle ant (*Brachyponera chinensis* Emery) (Table 3). The ant subfamilies Amblyoponinae and Proceratiinae were represented by only one individual and therefore were not included in the analysis (Table 3).

Within the ant subfamily Formicinae, we captured individuals representing *Brachymyrmex depilis* Emery, carpenter ants (*Camponotus*), field ants (*Formica*), *Lasius*, and *Nylanderia*. We did not encounter *Brachymyrmex depilis* frequently enough for analysis. The capture probability of *Camponotus* increased as the site-level woody debris volume increased and as trap-level bare ground cover decreased; capture probability was greater at white pine sites than at hardwood sites (Table 5). *Formica* capture probability increased with increasing site-level woody debris volume but declined with increasing FWD cover; capture probability was lower in white pine sites than at hardwood sites (Table 5). *Lasius* capture probability was lower at white pine sites than hardwood sites and increased as CWD cover and vegetation cover increased (Table 5).

Table 4. Coefficients for the relationship between number of captures of each invertebrate taxa and the habitat covariates (bare ground, coarse woody debris (CWD), fine woody debris (FWD), vegetation, and woody debris volume) included in the most competitive linear regression model based on captures at 10 harvested locations in western North Carolina USA (2016–2017). Standard errors are noted in parentheses. A "−" means that the specific variable was not included in the top model for the taxa. * Indicates *p*-value < 0.05.

Taxa (Order or Family)	Proximity (Near)	Type (White Pine)	Year (2017)	Bare Ground (% cover)	CWD (% cover)	FWD (% cover)	Vegetation (% cover)	Site-Level Woody Debris Volume (m^3 ha^{-1})
Acrididae/Tetrigidae	−1.05 (0.29) *	0.84 (0.27) *	−0.88 (0.23) *	-	-	0.34 (0.13) *	0.42 (0.14) *	0.28 (0.13) *
Araneae	−0.44 (0.10) *	0.54 (0.07) *	-	−0.07 (0.03) *	−0.12 (0.05) *	−0.22 (0.04) *	0.29 (0.04) *	0.08 (0.03) *
Beetles (other)	-	−0.24 (0.08) *	-	−0.15 (0.05) *	-	-	−0.10 (0.04)*	-
Carabidae	-	−0.31 (0.08) *	−0.27 (0.08) *	-	−0.14 (0.04) *	-	-	-
Chilopoda/Diplopoda	-	−0.30 (0.12) *	-	−0.34 (0.10) *	−0.20 (0.07) *	-	-	-
Formicidae	0.23 (0.05) *	−0.47 (0.03) *	0.54 (0.03) *	0.06 (0.01) *	0.09 (0.02) *	-	0.31 (0.02)*	-
Gryllidae	−0.71 (0.18) *	3.07 (0.19) *	0.20 (0.09) *	0.21 (0.03) *	0.16 (0.08) *	−0.17 (0.07) *	-	0.56 (0.07) *
Opiliones	-	−1.120 (0.13) *	−1.22 (0.12) *	−0.41 (0.09) *	0.10 (0.05)	-	-	-
Rhaphidophoridae	-	−1.82 (0.29) *	−0.48 (0.17) *	−0.35 (0.14) *	-	-	-	0.26 (0.08) *
Staphylinidae	−0.86 (0.15) *	−0.99 (0.10) *	-	-	0.29 (0.07)*	0.32 (0.05) *	0.30 (0.05) *	0.35 (0.04) *

Table 5. Coefficients for the relationship between probability of capture of each ant genus/species and the habitat covariates included in the most competitive logistic regression model based on captures at 10 harvested locations in western North Carolina USA (2016–2017). Standard errors are noted in parentheses. BG stands for Bare Ground and VEG stands for Vegetation. A "−" means that the specific variable was not included in the top model for the taxa. * Indicates *p*-value < 0.05.

Taxa	Prox. (Near)	Type (White Pine)	Year (2017)	BG (% Cover)	CWD (% Cover)	FWD (% Cover)	VEG (% cover)	Site-Level Woody Debris Vol.
Aphaenogaster	-	−1.46 (0.36) *	−0.60 (0.30) *	−0.88 (0.20) *	0.47 (0.16) *	−0.25 (0.16)	-	0.42 (0.21) *
Camponotus	-	0.52 (0.36)	-	−0.34 (0.20)	-	-	-	0.51 (0.17) *
Crematogaster	-	-	1.03 (0.50) *	−0.80 (0.49)	-	-	0.54 (0.23) *	−1.37 (0.39) *
Formica	-	−0.78 (0.30) *	-	-	-	−0.39 (0.15) *	-	0.60 (0.16) *
Lasius	-	−1.13 (0.47) *	-	-	0.62 (0.30) *	-	1.02 (0.31) *	-
Myrmecina	-	-	0.42 (0.28)	−0.39 (0.19) *	-	-	-	0.50 (0.14) *
Myrmica	-	−0.89 (0.41) *	-	-	-	-	-	0.48 (0.17) *
Nylanderia	-	3.92 (0.83) *	0.75 (0.41)	-	-	-	-	2.33 (0.36) *
Pheidole	-	1.19 (0.51) *	1.25 (0.42) *	0.29 (0.16)	−0.61 (0.26) *	−0.54 (0.27) *	-	0.75 (0.24) *
Ponera	-	−0.56 (0.31)	-	−0.43 (0.26)	0.31 (0.15) *			
Solenopsis (minute)	-	-	-	-	-	-	0.39 (0.27) *	-
Solenopsis invicta	-	1.79 (0.36) *	1.05 (0.28) *	0.33 (0.15) *	−0.29 (0.14) *	0.27 (0.15)	-	0.45 (0.17) *
Tapinoma sessile	0.91 (0.41) *	−0.68 (0.41)	0.90 (0.40) *	-	-	−1.11 (0.45) *	0.66 (0.25) *	-
Tetramorium	-	1.76 (0.47) *	0.89 (0.42) *	-	-	−1.03 (0.35) *	−0.46 (0.23) *	-

Within the ant subfamily Dolichoderinae, we captured *Forelius* and the odorous house ant (*Tapinoma sessile* Say); *Forelius* had too few encounters for analysis. *T. sessile* capture probability was lower in white pine than hardwood sites (Table 5) and increased with decreasing FWD cover, proximity to piled woody debris, and as vegetation cover increased (Table 5).

The subfamily Myrmicinae comprised 82% of the ants captured (Table 3). Genera/species within Myrmicinae included *Aphaenogaster*, acrobat ants (*Crematogaster*), *Monomorium*, *Myrmecina*, *Myrmica*, *Pheidole*, minute *Solenopsis*, red imported fire ants (*Solenopsis invicta*), *Stenamma*, *Strumigenys*, *Temnothorax*, and *Tetramorium*. We did not analyze *Monomorium*, *Stenamma*, *Strumigenys*, and *Temnothorax* due to a low number of captures. The most competitive logistic regression model for *Aphaenogaster* indicated that capture probability was lower at white pine than hardwood sites and was lower in 2017 than in 2016; capture probability increased with decreasing bare ground cover, decreasing FWD cover, increasing CWD cover, and increasing site-level woody debris volume (Table 5). *Crematogaster* capture probability decreased as site-level woody debris volumes increased, bare ground cover increased, and vegetation cover decreased (Table 5). *Myrmecina* capture probability increased as trap-level bare ground cover decreased and as site-level woody debris volume increased (Table 5). *Myrmica* capture probability was lower at white pine than hardwood sites and increased with increasing woody debris volume (Table 5). *Pheidole* capture probability was greater at white pine than hardwood sites and greater in 2017 than in 2016; capture probability increased as FWD cover, site-level woody debris volume, and bare ground cover increased, and as CWD cover decreased (Table 5). Capture probability of the most abundant ant taxon encountered, minute *Solenopsis*, only showed a positive relationship with vegetation cover (Table 5). Capture probability for red imported fire ants was greater at white pine than hardwood sites and greater in 2017 than 2016; capture probability increased as site-level woody debris volume, FWD cover, and bare ground cover increased, and as CWD cover decreased (Table 5). *Tetramorium*, similar to many other ant taxa, was negatively associated with FWD cover and positively associated with white pine (Table 5). *Tetramorium* capture probability declined as vegetation cover increased (Table 5).

Within the ant subfamily Ponerinae, we captured individuals representing Asian needle ants (*Brachyponera chinensis*), *Hypoponera*, and *Ponera*. Only *Ponera* had sufficient captures for analysis. *Ponera* capture probability was lower at white pine than hardwood sites and declined as bare ground cover increased and CWD cover decreased (Table 5).

4. Discussion

The consistent positive correlations between woody debris and invertebrate detections indicated that downed wood attracted several invertebrate taxa at both the trap and site level. At the trap level, captures of rove beetles (Staphylinidae), crickets (Gryllidae), ants (at the family level), and multiple genera of ants increased as CWD cover increased. Similarly, captures of red imported fire ants (*Solenopsis invicta*), grasshoppers (Acrididae/Tetrigidae), and rove beetles increased with increasing amounts of FWD cover. Relationships with site-level woody debris volume were overwhelmingly positive; capture numbers or capture probabilities for 54% of analyzed taxa increased with increasing woody debris volumes and decreased with increasing woody debris volumes only for *Crematogaster* ants. Such positive relationships with woody debris may be due to the greater availability of food, cover, and nesting sites, or the lower maximum temperatures and greater humidity under coarse woody debris.

The lack of a consistently positive relationship between proximity to piles of downed wood and captures of most invertebrate taxa, combined with frequent positive relationships between captures and CWD cover or site-level woody debris volume, indicates that most were able to use the scattered woody debris resources and may not require piles of woody debris. The models for only six of the invertebrate taxa (grasshoppers, rove beetles, crickets, spiders, ants at the family level, and odorous house ants) indicated either a negative or a positive relationship with near proximity to piled woody debris. Moreover, grasshoppers, rove beetles, crickets, and spiders each declined near piled downed wood. Only ant captures at the family level, and at the species level for odorous house ants, were greater near piled downed wood. Downed wood was widely dispersed across most of the 10 study sites, potentially reducing the biological relevance of distance from piled downed wood for most invertebrate taxa. A greater connectivity of downed wood across an area is associated with greater species richness of saproxylic flies (Diptera) and beetles (Coleoptera) [64], which is a relationship that may hold for other taxa. Some saproxylic beetle species are characteristic of areas with high connectivity, indicating that the connectivity of downed wood should be sustained when possible [65]. Site preparation, such as windrowing or shearing after a timber harvest, can greatly reduce the connectivity of downed wood and potentially restrict invertebrates to windrows or piles of downed wood [23].

Forest type was the most consistent predictor of invertebrate captures. Of the 21 taxa displaying a response to forest type, 13 were less likely to be detected at white pine than hardwood sites, while the remaining eight were more likely to be detected at white pine than hardwood sites. The consistent influence of forest type on captures may be because of differences in vegetation composition and structure, associated harvest methods (clearcut or two-aged), elevation, topography, or downed wood characteristics (e.g., species and diameter) [23,66–69]. Taxa also may have a greater association with specific forest types [70–74], and mixed forest types may contribute more to biodiversity conservation than monotypic types, as in the white pine stands we studied [75]. However, it is difficult to determine whether differences in invertebrate abundance or species richness among forest types are due to forest structure or composition, especially where plant cover and diversity is low due to age or management history [76].

Site-level woody debris and trap-level CWD cover were consistent positive predictors of invertebrate captures. Captures or capture probability increased with increasing site-level woody debris volume for 13 taxa of invertebrates/genera of ants, suggesting that site-level woody debris volume is an important factor for many invertebrate taxa within harvested sites in the southern Appalachians. Additionally, captures or capture probability increased with increasing trap-level CWD cover for seven taxa of invertebrates/genera of ants, indicating that both volume and characteristics (e.g., cover, size) of downed wood are influential for a variety of invertebrates. Grodsky et al. [23,38] also reported a positive relationship with post-harvest site-level debris volume and CWD cover for crickets, cave crickets, and various genera/species of ants in the southeastern Coastal Plain.

Our research supports the previously documented importance of logging debris for a variety of saproxylic and non-saproxylic invertebrate taxa, but it differs from prior research for ground beetles (Carabidae) and red imported fire ants. We documented a negative relationship between ground beetles and CWD cover and no relationship between ground beetles and site-level woody debris volume, which contrasts with results of other studies [23,39,77]. Such a discrepancy may be due to the high amount of scattered downed wood in multiple sites in our study, allowing ground beetles to move freely due to increased connectivity of cover. Although prior studies showed that downed wood retention either negatively or neutrally impacts red imported fire ants, we showed that red imported fire ants were negatively correlated with downed wood (CWD percent cover) at the trap level and positively correlated with woody debris volume at the site level [38,78]. However, Grodsky et al. [38] did note a negative response to windrows in Georgia during the first year of their study, which is in agreement with our findings and indicates that the response of red imported fire ants to CWD may be scale-specific. Differing results for Carabids and fire ants between our study and others e.g., [38,78] may be due to differences in the degree of landscape disturbance, geographic area, trapping methods, or the adaptability of red imported fire ants.

There was little consistency in relationships between invertebrate taxa and covariates measured at the trap level, but most taxa had a positive relationship with vegetation cover or a negative relationship with bare ground cover, indicating that some form of cover is important for invertebrates in harvested sites. Other studies similarly have documented positive relationships between invertebrate presence and vegetation cover [23,38,79]. A positive relationship with vegetation cover is expected for most invertebrates, as vegetation provides food, escape cover, and potential anchor points for spider webs.

However, some taxa, such as tiger beetles (Carabidae family, Cicindelinae subfamily), use bare ground, especially as larvae [80].

Our results indicated that site-level characteristics such as forest type and woody debris volume may be more important than local microsite characteristics for many invertebrates. Forest type and site-level woody debris volumes were the two most consistent predictors of invertebrate captures. However, trap level covariates were predictors of captures for many taxa, especially the availability of some form of ground cover, indicating that it is important to consider both site and local factors when integrating conservation measures in managed forest systems.

Invertebrates had variable relationships with local microhabitat characteristics, but overall, they had consistent, positive relationships with site-level woody debris volumes. Due to the positive response of multiple invertebrate taxa to downed wood at the trap level and site level, sufficient down downed wood should be retained as a resource for invertebrate taxa in an operational context where debris is to be removed. We recommend leaving as much downed wood as economically feasible in sites after timber harvests, especially those including an operational removal of downed wood. Since our study is correlative in nature and we did not experimentally test invertebrate response to specific levels of woody debris volume, we are unable to recommend an optimal woody debris retention level. However, considering the positive response of many invertebrate taxa to increasing woody debris volume and/or cover, retaining more debris rather than less is better for invertebrates. In the Coastal Plain, Grodsky et al. [23] recommended the retention of at least 15% of the merchantable woody biomass in areas where debris is to be removed, which is similar to some Biomass Harvesting Guidelines [44]. The average volume of downed wood in our sites (176.66 m^3 ha^{-1}) was greater than the average volume in the Coastal Plain sites (108.20 m^3 ha^{-1}) sampled by Grodsky et al. [81] and Fritts et al. [44], suggesting that 15% retention in the southern Appalachians (26.50 m^3 ha^{-1}) will be greater than 15% retention in the Coastal Plain sites (16.23 m^3 ha^{-1}). We encourage forest managers to consider retaining as much debris as economically feasible and including a variety of downed wood types, such as large and small stems, tops, and branches. Post-harvest downed wood retention in the form of logging residue aids in maintaining various ecosystem services, including decomposition and the prey-base provided by invertebrates [75]. Future research should focus on manipulating downed wood levels after timber harvests to mimic operational woody biomass harvests and to determine the optimum level of residue retention for assorted invertebrate taxa.

5. Conclusions

With the potential of biomass markets expanding into new regions of the eastern U.S., it is essential to determine the impacts of downed wood removal on invertebrates. Our research indicates that downed wood, at both the site and trap level, positively influences various invertebrate taxa. As such, we recommend leaving as much downed wood as economically feasible as a resource for invertebrates and other wildlife following all timber harvests. Additionally, managers may consider establishing and following voluntary Biomass Harvesting Guidelines, which emphasize the conservation of biodiversity, water quality, and soil productivity on sites with wood bioenergy harvests [44,82].

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