

## Short-term Response of Ground-dwelling Macroarthropods to Shelterwood Harvests in a Productive Southern Appalachian Upland Hardwood Forest

John Westby-Gibson, Jr., Cathryn H. Greenberg, Christopher E. Moorman, T.G. Forrest, Tara L. Keyser, Dean M. Simon, and Gordon S. Warburton



POREST SERVICE

Forest Service Southern Research Station e-Research Paper RP-SRS-59 December 2017

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#### **Cover Photo**

Abundance and dry biomass of Orthoptera (predominantly Rhaphidophoridae) were greater in forested controls than shelterwood plots. Pictured here is the camel cricket (*Ceuthophilus* sp.). (photo courtesy of Clemson University, USDA Cooperative Extension Slide Series, Bugwood.org)

#### ABSTRACT

Macroarthropods rarely are considered in forest management decisions, despite their ecological importance as decomposers, herbivores, pollinators, predators, and nutrient cyclers, and potential of some taxa as indicators of forest condition. We used a replicated design to experimentally determine if, and how, community composition, richness, and biomass of terrestrial macroarthropods differed between recent shelterwood harvests and unharvested controls in an intermediate quality upland hardwood forest. Richness of orders or families did not differ between treatments. Abundance and dry biomass of total macroarthropods and most orders or families were unaffected by shelterwood harvests despite substantial post-harvest reductions in tree density, canopy cover, and leaf litter cover and depth, at least in the short term. Among taxa, abundance and dry biomass of Opiliones (all Phalangiidae) and Lepidoptera (mostly larvae) were greater in shelterwoods than controls, whereas abundance and dry biomass of Orthoptera (predominantly Rhaphidophoridae) were greater in controls. Our results suggest that use of ground-dwelling macroarthropod taxa as indicators of forest disturbance be tempered with consideration of other site-related factors potentially affecting forest floor conditions and activity-abundance of macroarthropods, such as forest type, site quality, elevation, topographic position, and weather.

**Keywords:** Ground-dwelling macroarthropods; shelterwood harvest; southern Appalachians; upland hardwood forest.

#### ACKNOWLEDGMENTS

This is a contribution of the Regional Oak Study (ROS). This research was initiated by the U.S. Department of Agriculture, Forest Service, Southern Research Station, Upland Hardwood Ecology and Management Research Work Unit (RWU 4157) in partnership with the Forest Service Northern Research Station, the North Carolina Wildlife Resources Commission, the Stevenson Land Company, and the Mark Twain National Forest. We thank Kara Dziwulski, Austin Werner, Patrick Helm, and Ethan Green for making this study possible. We are grateful to Kenny Frick, Tracy Roof, Jacqui Adams, and many other Forest Service forestry technicians for assistance with logistics. We thank Mark Williams and many others from the North Carolina Wildlife Resources Commission and Haywood Community College who assisted with drift fence installation and in conducting prescribed burns. Three anonymous reviewers helped to improve an earlier version of this manuscript.

December 2017



Forest Service Research and Development Southern Research Station

e-Research Paper RP-SRS-59



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Focusing on key characteristics for identification, biological technician, John Westby-Gibson, Jr., examines arthropods under the microscope. (photo courtesy of John Westby-Gibson, Jr., University of North Carolina at Asheville)

## INTRODUCTION

Macroarthropods play ecologically important roles as decomposers, herbivores, pollinators, predators, and nutrient cyclers (Hanula and others 2016, Siira-Pietikainen and others 2003, Wilson 1987). They also are critical food resources for birds (Johnson and Sherry 2001) and salamanders (Hairston 1980). Many ground-dwelling species are sensitive to microclimatic features such as leaf litter depth, or moisture and light levels at the forest floor. Macroarthropod taxa are likely to vary in their response to forest disturbances that alter forest structure, flower and foliage production, and forest floor conditions (Niemela and others 1993). For example, richness and abundance of pollinators or foliage-eating taxa could increase in response to higher primary productivity following forest disturbance (Whitehead 2003, Wilson and others 2014), whereas ground-dwelling species associated with leaf litter may decrease in abundance (Duguay and others 2000, Greenberg and Forrest 2003, Haskell 2000, Whitehead 2003). Despite their ecological importance and the potential of some taxa as indicators of forest conditions (Pearce and Venier 2006), ground-dwelling macroarthropods in the upland hardwood forests of the Central Hardwood Region rarely are considered in forest management or restoration planning (Grodsky and others 2015).



Field technician, Meagan Bell, checks for captures in a pitfall trap. (photo by Cathryn H. Greenberg, U.S. Forest Service)

Restoration of structure and function of mixed-oak (Quercus spp.) forests is a focal issue of forest land managers in the Eastern United States. Widespread oak regeneration failure-the failure of oak seedlings or saplings to attain canopy status-is problematic, especially on intermediate and highly productive sites after canopy release because of competition from faster growing species such as yellowpoplar (Liriodendron tulipifera) (Aldrich and others 2005). Historically, mostly anthropogenic disturbances such as frequent burning, livestock grazing, loss of American chestnut (Castanea dentata), and widespread logging may have promoted understory light conditions conducive to oak development (Abrams 1992, McEwan and others 2011), but have been largely eliminated (Greenberg and others 2015). Silvicultural treatments to facilitate oak forest restoration involve altering forest structure to change light conditions and competition from other hardwood tree species to promote the growth of oak seedlings before canopy release, giving them a head start against faster growing competition. The resulting changes in forest structure alter microhabitat conditions such as leaf litter depth, moisture, and cover; ground-level temperature; and soil moisture (Moorman and others 2011) and could affect the abundance and community composition of ground-dwelling macroarthropods.

As part of the multi-disciplinary Regional Oak Study (Keyser and others 2008), we used a replicated design to experimentally assess how ground-dwelling macroinvertebrates responded to shelterwood harvests during the initial application of the shelterwood-burn treatment (Brose and others 1999) proposed to promote oak regeneration. Our objective was to compare community composition, richness, and biomass of terrestrial macroarthropods, focused at the family level, between recent shelterwood harvests and nearby unharvested mature forest controls.

## **METHODS**

#### **Study Area**

Our study was conducted in Haywood County, NC, on Cold Mountain Game Land (CMGL), which encompasses 1333 ha of second growth, upland mixed-oak forests with elevations ranging from 940 to 1280 m. CMGL is managed by the North Carolina Wildlife Resources Commission for diverse wildlife habitat and is located in the Blue Ridge physiographic province. Terrain is mountainous with gentle to steep slopes with predominant overstory trees of oak, hickory (*Carya* spp.), and yellow-poplar. Species composition in the midstory consisted primarily of shade-tolerant species, including sourwood (*Oxydendrum arboreum*), flowering dogwood (*Cornus florida*), silverbell (*Halesia tetraptera*), blackgum (*Nyssa sylvatica*), and red maple (*Acer rubrum*). The climate is characterized by warm summers and cool winters, and precipitation averages 1200 mm annually.

#### **Study Design**

We established ten 5-ha units (approximately 225 x 225 m) and randomly assigned treatments (shelterwood harvest or control), resulting in a completely randomized design with five replicate units per treatment (see Greenberg and others 2014 for map). All units were between 940–1240 m in elevation and separated by a >10-m buffer. Each contained mature (>70 years old), fully stocked, closed-canopy stands where oaks comprised at least 10 percent of the overstory tree basal area [ $\geq$ 25.0 cm diameter at breast height (dbh)]. We selected stands that contained abundant oak seedlings, few ericaceous shrubs, a well-developed midstory layer (stems 5.0–25.0 cm dbh), and no substantial disturbance within the last 15–20 years. All treatment units were intermediate- to high-quality sites, with site index ranging from 23.0 to 30.4 m (base age 50).

Treatments for the Regional Oak Study were designed to evaluate three oak regeneration practices on productive sites, but this study evaluated only one treatment, the establishment cut of a planned shelterwood-burn sequence (Brose and others 1999) (SW), and control (C). Trees were felled with standard chainsaws and grapple cutters, and dragged with rubber tire skidders to log landings where knuckle boom loaders filled forwarders and haul trucks; some units required



Abundance and dry biomass of Carabidae and Araneae, both indicators of environmental change, did not differ between shelterwood and control plots. Pictured here are the ground beetle (Carabidae) LEFT (photo by Joseph Berger, Bugwood.org) and wolf spider (Araneae) RIGHT. (photo by Karan A. Rawlins, University of Georgia, Bugwood.org)

skid trails due to steep slopes. Establishment cuts were implemented during winter 2009 through mid-summer 2010, with basal area retention of  $6.8-9.0 \text{ m}^2/\text{ha}$ .

#### **Macroarthropod Sampling**

We trapped macroarthropods during the first full growing season after the shelterwood harvests were completed (2011) using randomly oriented, 7.6-m-long aluminum drift fences spaced >10 m apart. Four drift fences were established at the lower one-third of each treatment unit and at the upper one-third of each unit for a total of eight fences per unit, except four in one C unit where steep, rocky terrain prevented establishment of the upper slope fences. Pitfall traps were 19-1 buckets buried flush with the ground at each end of the drift fences (two traps per fence). We placed a moist sponge in each bucket to provide moisture. Traps were designed to capture reptiles and amphibians (Greenberg and others 2016), but also captured abundant ground-dwelling macroarthropods.

Macroarthropods were collected (hand scooped) once weekly for 6 weeks (29 June 2011–3 August 2011) from all pitfall traps in all shelterwood and control units. Traps and sponges were cleared of macroarthropods and debris the day before collections so that each collection represented one day. Macroarthroods collected on a given sample date within a treatment unit (all pitfall traps) were combined and preserved in 70-percent ethyl alcohol and labeled by date, unit, and treatment. We later sorted, counted, and identified macroarthropods to the taxonomic order and family level, or lower if possible. Specimens were then air dried in a vacuum hood to a constant mass and weighed to obtain an estimate of average dry biomass. Because we did not use a killing agent, our trapping method likely under-sampled macroarthropods that could climb or fly from traps, and some macroarthropods were likely consumed by small mammals, herpetofauna, or other macroarthropods in the same traps. However, due to low capture rates of vertebrates in pitfall traps (Greenberg and others 2016), we assume that these potential biases were consistent between treatments and hence should not bias comparisons. Because differences in habitat structure and microclimate between SW and C could potentially affect both arthropod activity and abundance, our pitfall trapping method provided an 'activity-abundance' index (Perry and Herms 2016, Spence and Niemela 1994) as an indicator of treatment effects.

#### **Forest Structure Measurements**

We measured tree density and basal area of the overstory and midstory at plots and subplots, respectively, throughout the five SW and five C units in summer 2011. We established six 0.05-ha permanent circular plots at approximately 50 m, 112 m, and 175 m along each of two transects within each unit. Transects originated at a random distance from a corner of the downslope unit boundary line and ran parallel to and >30 m from side boundaries. Within each 0.05-ha circular plot, all live overstory trees  $\geq 25.0$  cm dbh were identified, measured for dbh, and tagged. Midstory trees  $\geq$ 5.0 cm and  $\leq$ 25.0 cm dbh were identified, measured for dbh, and tagged within a 0.01-ha subplot concentrically nested within the 0.05-ha plot. We combined midstory and overstory tree data (all trees >5.0 cm dbh) to estimate average density (stems/ha) and basal area (m<sup>2</sup>/ha) per treatment unit for data analyses (n=5 per treatment).

We measured percent ground cover [bare ground, coarse woody debris (CWD), and shrub cover] within 15 m of drift fence arrays in all five units per treatment; leaf litter and/or rocks occupied the ground surface unless bare ground was recorded. We measured ground cover along a 15-m, randomly oriented line transect at each of the drift fences (eight per unit, except four in one C unit), starting from the bucket furthest uphill. We recorded 'start' and 'stop' distance for each ground cover category along each transect and summed the total distance. Percent cover for each category was determined by dividing the sum of its cover by the transect length. Leaf litter depth (cm) was measured at the mid- and end-points of each line transect. Percent canopy cover was measured at each drift fence using a spherical densiometer held at breast height. For data analysis, we used means of each habitat variable across each of the five SW and five C units.

#### **Statistical Analyses**

We used t-tests (SAS 2012) to compare the relative abundance and dry biomass of each order and family and total macroarthropods, as well as richness of orders and families, between SW and C. We did not analyze taxa at the genus or species level because identifications at these taxonomic levels were inconsistent within and among families. All capture data were standardized for small differences in trapping efforts (fewer pitfall traps in one C unit) by using macroarthropod captures per 100 pitfall traps across the entire season [total captures per unit divided by 16 pitfall traps (or 8 for one C unit), multiplied by 100]. Larvae composed a small proportion of total captures and were included in statistical analyses with adults. We did not perform statistical analyses unless taxa (orders or families) included >30 specimens. We reported genus or species within families if identified, but did not perform statistical analyses because lower taxonomic levels were not identified consistently. We also used t-tests to compare habitat features between SW and C. Percentage data (bare ground,

CWD, shrub, and canopy cover) were arcsine-square-root transformed for analyses.

### RESULTS

Live tree density, basal area, and percent canopy cover were greater in C than SW (by 71, 58, and 50 percent, respectively; table 1). The percent cover and (marginally) depth of leaf litter also were greater in C than SW (by 65 and 12 percent, respectively). In contrast, the percent cover of CWD, shrubs, and (marginally) bare ground were greater in SW than C (by 48, 38, and 66 percent, respectively).

We captured 4,209 macroarthropods (462 g of dry biomass) within 17 orders and 55 families (table 2). Specimens identified to genus and species are presented in table 2 (footnotes). Dominant (>5 percent) orders based on abundance and/or dry biomass, respectively, were Coleoptera (46.2 percent and 36.4 percent), Orthoptera (18.3 and 13.6 percent), Polydesmida (14.0 and 20.1 percent), Spirobolida (1.9 and 22.3 percent), Opiliones (6.0 and 0.8 percent), and Araneae (5.1 and 0.8 percent).

The number and dry biomass of total macroarthropods did not differ between SW and C (table 2). Among the orders analyzed, relative abundance and dry biomass of Opiliones were greater in SW than C, and the relative abundance of Lepidoptera (primarily larvae) was also marginally (p=0.0676) higher in SW than C. In contrast, relative abundance and dry biomass of Orthoptera were higher in C than SW (table 2; fig. 1). Among families analyzed, the relative abundance and dry biomass of Phalangiidae (the only family captured within order Opiliones) were greater in SW than C. In contrast, relative abundance and dry biomass of Rhaphidophoridae (the predominant family within the order Orthoptera in our sites) were higher in C than SW. Richness of orders or families did not differ between C and SW (table 2).

Habitat feature	Control <sup>a</sup>	Shelterwood <sup>a</sup>	t <sub>d.f.=8</sub>	p-value	
Live tree density (ha)	666.0±60.4	192.6±38.4	6.61	0.0002	
Live tree basal area (m²/ha)	33.8±2.1	14.1±1.4	7.76	<0.0001	
Canopy cover (%)	83.6±1.6	41.6±7.1	5.27	0.0008	
Coarse woody debris (CWD) (%)	7.7±1.4	14.6±1.2	-3.78	0.0054	
Bare ground (%)	8.4±1.4	25.0±7.0	-2.03	0.0771	
Leaf litter (%)	73.2±5.8	25.8±9.3	3.79	0.0053	
Leaf litter depth (cm)	3.3±0.3	2.9±0.6	1.98	0.0831	
Shrub cover (%)	39.4±5.2	64.0±5.9	-3.24	0.0119	

# Table 1—Mean (+SE) habitat structural features and results of pooled t-tests comparing shelterwood harvests and controls

SE = standard error; d.f. = degrees of freedom

<sup>a</sup> Actual means are presented, but percentage values were arcsine-square-root transformed for t-tests.

# Table 2—Total and mean (±SE) number (first line) and dry biomass (g; second line) of terrestrial macroinvertebrate arthropod orders, families, and totals, per 100 pitfall traps in shelterwood harvests and controls

Order, Family*     Total*     Order     Family     Control     Shelterwood     t <sub>uns</sub> *     p-value*       Araneidae     214     5.1     115.02±14.87     161.26±22.57     -1.71     0.1255       Araneidae     143     66.8     81.28±0.27     102.24±28.04     -0.76     0.4932       Lycosidae     71     63.2     33.78±7.02     56.78±0.74     -1.28     0.2432       Lycosidae     28     0.7     1126±5.73     26.28±0.66	% of Total								
Arane     214     5.1     115.02±14.67     161.26±2.25.7     1.71     0.1255       Araneidae     143     66.8     81.28±10.27     102.54±26.04     -0.76     0.4952       Lycosidae     7.1     33.2     33.78±7.02     58.78±17.08     -0.82     0.4952       Bittodea     2.85     3.5.8     0.64±0.19     1.04±0.24     -1.28     0.2254       Bittodea     2.86     0.7     11.26±5.73     2.8.28±0.60        Cyptocercidae*     2.6     7.1     2.80±2.50     0.00±0.00        Cyptocercidae*     2.631     9.96     6.76±0.81     2.8.23±0.60     -0.52     0.52±1.40       Coleoptera*     1.945(22.1)     4.62     1.166.28±2.46.16     133.50±1.47.07     -0.59     0.5724       Brentidae*     1.61.22.2     0.01.0.0.02.29.40.20     0.00±0.00	Order, Family <sup>b</sup>	Total <sup>a</sup>	Order	Family	Control	Shelterwood	t <sub>d.f.=8</sub> c	p-value <sup>d</sup>	
Araneidae     3.785     0.8     2.209.045     2.68±0.38     -0.82     0.482       Lycosidae     71     3.32     3.78±7.02     5.8±0.47     1.05.42.64.04     -0.76     0.4893       Bittodea     1.355     3.58     0.64.019     1.04±0.24     -1.28     0.2128       Ectobildae*     2.8     0.7     1.12.65.7     22.62.84.66	Araneae	214	5.1		115.02±14.87	161.26±22.57	-1.71	0.1255	
Araneidae     143     66.8     91.28±10.27     102.54±28.04     -0.76     0.4693       Lycosidae     71     33.2     33.78±7.02     58.78±17.08     -1.35     0.2128       Blattodea     28     0.7     11.28±5.73     26.28±0.06		3.785	0.8		2.20±0.45	2.68±0.38	-0.82	0.4352	
243     64.2     1.52+0.27     1.60+0.44     -0.16     0.8804       Lycosidae     1.355     35.8     0.64+0.19     1.04+0.24     -1.28     0.2254       Bittodea     28     0.7     11.265.73     26.284.06	Araneidae	143		66.8	81.28±10.27	102.54±26.04	-0.76	0.4693	
Lycosidae     71     33.2     33.782.702     58.782.1708     -1.35     0.2128       Blattodea     2.8     0.7     11.2825.73     26.284.606		2.43		64.2	1.52±0.27	1.60±0.44	-0.16	0.8804	
1385     35.8     0.64+019     10.40.24     -1.28     0.2354       Blattodea     28     0.7     11265.73     26.286.06	Lycosidae	71		33.2	33 78+7 02	58 78+17 08	-1.35	0.2128	
Blattodea     28     0.7     11.24±5.73     28.24±0.6	Lybboldub	1.355		35.8	0.64+0.19	1 04+0 24	-1.28	0.2354	
Ectobilidae <sup>b</sup> 5.455     1.2     2.00±1.28     5.52±1.96	Blattodea	28	0.7		11 26+5 73	26 28+6 06		0.2001	
Ectobilidae <sup>b</sup> 2     1     2     2     1     2     2     0	Diattodea	5.455	1.2		2 00+1 28	5 52+1 06			
	Ectobiidae	2.400	1.2	71	2.00±1.20	0.00±0.00			
Cryptocercidae <sup>b</sup> D.02     D.42     D.44     D.044,04     D.044,02     D.046,04     D.046,02     D.066,06     D.024,07     D.046,02     D.066,06     D.024,07     D.024,07 <thd.024,07< th="">     D.024,07     <th< td=""><td>LCIODIIdae</td><td><u> </u></td><td></td><td>7.1</td><td>2.30±2.30</td><td>0.00±0.00</td><td></td><td></td></th<></thd.024,07<>	LCIODIIdae	<u> </u>		7.1	2.30±2.30	0.00±0.00			
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	Om mate a smallele sh	0.024		0.4	0.04±0.04	0.00±0.00			
5.443     99.6     1.961/28     5.524196	Cryptocercidae	26		92.9	8.76±4.68	26.28±6.06			
Coleoptera*     1,945(22L)     46.2     1166.262246.16     1335.02247.07     -0.59     0.5724       Agyrtidae <sup>b</sup> 3     0.2     2.52±1.54     11.98±22.15     -0.25     0.8068       Brentidae <sup>b</sup> 1     0.1     1.26±1.26     0.064.0.00        Carabidae <sup>b, b</sup> 1,751(7L)     90.0     1010.02±39.07     1235.02±153.64     -0.79     0.4514       149.037     88.6     88.6 2±25.16     101.22±20.22     -0.39     0.7064       Carabidae <sup>b, b</sup> 1.717(7L)     90.0     1010.02±239.07     1235.02±153.64     -0.79     0.4514       149.037     88.6     88.62±25.16     101.2±20.22     -0.39     0.7064       Carabidae <sup>b</sup> 1     0.1     0.00±0.00     128±1.26        Curculionidae <sup>b</sup> 1     0.1     0.00±0.00     128±1.26        Curculionidae <sup>b</sup> 1     0.1     1.26±1.26     0.00±0.00        Curculionidae <sup>b</sup> 0.31     0.2     0.02±0.02     0.02±0.02        Dy		5.431		99.6	1.96±1.28	5.52±1.96			
Agyrtidae <sup>b</sup> 168.196 $36.4$ 103.20.26.76     111.98.22.15     -0.25     0.806       Brentidae <sup>b</sup> 0.068     <0.11	Coleoptera <sup>a</sup>	1,945(22L)	46.2		1166.26±246.16	1335.02±147.07	-0.59	0.5724	
Agyridae <sup>b</sup> 3     0.2     2.52±1.54     1.26±1.26		168.196	36.4		103.20±26.76	111.98±22.15	-0.25	0.8068	
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Agyrtidae <sup>b</sup>	3		0.2	2.52±1.54	1.26±1.26			
Brentidae <sup>b</sup> 1     0.1     1.26±1.26     0.000		0.068		<0.1	0.04±0.02	0.06±0.06			
	Brentidae <sup>b</sup>	1		0.1	1.26±1.26	0.00±0.00			
		0.022		<0.1	0.02±0.02	0.00±0.00			
$\begin{array}{c} 149.03^7 & 88.6 & 88.62.825.16 & 101.222.20.22 & -0.39 & 0.7064 \\ \hline 12 & 0.6 & 7.50\pm3.06 & 8.76\pm2.50 & & \\ 10.199 & 6.1 & 6.10\pm3.08 & 7.44\pm4.52 & \\ \hline 10.199 & 6.1 & 6.10\pm3.08 & 7.44\pm4.52 & \\ \hline 0.009 & -0.1 & 0.00\pm0.00 & 1.26\pm1.26 & & \\ \hline 0.009 & -0.1 & 0.00\pm0.00 & 0.02\pm0.00 & \\ \hline 0.001 & -0.1 & 0.00\pm0.00 & 0.02\pm0.00 & \\ \hline 0.011 & -0.1 & 0.00\pm0.00 & 0.02\pm1.26 & \\ \hline 0.011 & -0.1 & 0.00\pm0.00 & 0.02\pm1.26 & \\ \hline 0.031 & 0.01\pm0.26 & 0.00\pm0.00 & 0.02\pm0.02 & \\ \hline 0.031 & 0.1 & 1.26\pm1.26 & 0.00\pm0.00 & 0.00\pm0.00 & \\ \hline 0.011 & -0.1 & 1.26\pm1.26 & 0.00\pm0.00 & 0.00\pm0.00 & \\ \hline 0.011 & -0.1 & 1.26\pm1.26 & 0.00\pm0.00 & 0.00\pm0.00 & \\ \hline 0.011 & -0.1 & 1.26\pm1.26 & 0.00\pm0.00 & 0.00\pm0.00 & \\ \hline 0.011 & -0.1 & 0.00\pm0.00 & 0.00\pm0.00 & \\ \hline 0.011 & -0.1 & 0.00\pm0.00 & 0.00\pm0.00 & \\ \hline 0.011 & -0.1 & 0.00\pm0.00 & 0.00\pm0.00 & \\ \hline 0.0463 & 0.3 & 0.30\pm0.30 & 0.28\pm0.28 & \\ \hline 0.044 & -0.2 & 3.76\pm2.50 & 1.26\pm1.26 &$	Carabidae <sup>a, b</sup>	1.751(7L)		90.0	1010.02±239.07	1235.02±153.64	-0.79	0.4514	
$\begin{array}{c cccc} Cerambycidae^b & 12 & 0.6 & 7.50\pm 3.06 & 8.76\pm 2.50 & \cdots & \cdots & 10.199 & 6.1 & 6.10\pm 3.08 & 7.64\pm 5.50 & \cdots & \cdots & 10.199 & 6.1 & 6.10\pm 3.08 & 7.64\pm 5.50 & \cdots & \cdots & 0.009 & 0.01 & 0.00\pm 0.00 & 1.26\pm 1.26 & \cdots & \cdots & 0.009 & 0.01 & 0.00\pm 0.00 & 1.26\pm 1.26 & \cdots & \cdots & 0.011 & 0.1 & 0.00\pm 0.00 & 0.02\pm 0.02 & \cdots & \cdots & 0.011 & 0.1 & 0.00\pm 0.00 & 0.02\pm 0.02 & \cdots & \cdots & 0.011 & 0.1 & 0.00\pm 0.00 & 0.02\pm 0.02 & \cdots & \cdots & 0.011 & 0.1 & 0.00\pm 0.00 & 0.02\pm 0.02 & \cdots & \cdots & 0.011 & 0.1 & 1.26\pm 1.26 & \cdots & \cdots & \cdots & 0.011 & 0.01 & 1.26\pm 1.26 & 0.00\pm 0.00 & \cdots & \cdots & \cdots & 0.011 & 0.01 & 1.26\pm 1.26 & 0.00\pm 0.00 & \cdots & \cdots & \cdots & 0.011 & 0.01 & 1.26\pm 1.26 & 0.00\pm 0.00 & \cdots & \cdots & \cdots & 0.011 & 0.01 & 1.26\pm 1.26 & 0.00\pm 0.00 & \cdots & \cdots & \cdots & 0.011 & 0.01 & 1.26\pm 1.26 & 0.00\pm 0.00 & \cdots & \cdots & \cdots & 0.011 & 0.04 & 0.00 & 0.00\pm 0.00 & \cdots & \cdots & \cdots & 0.0711 & 0.4 & 0.40\pm 0.09 & 0.56\pm 0.27 & \cdots & \cdots & 0.0711 & 0.4 & 0.40\pm 0.09 & 0.56\pm 0.27 & \cdots & \cdots & 0.0711 & 0.4 & 0.40\pm 0.09 & 0.56\pm 0.27 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & \cdots & \cdots & 0.001 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.0072 & 0.01 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.0072 & 0.01 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.0072 & 0.01 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.0072 & 0.01 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.0072 & 0.01 & 0.00\pm 0.00 & \cdots & \cdots & 0.0072 & 0.01 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.0072 & 0.01 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & \cdots & 0.0072 & 0.01 & 0.00\pm 0.00 & 0.00\pm 0.00 & \cdots & $		149 037		88.6	88 62+25 16	101 22+20 22	-0.39	0 7064	
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Cerambycidae	12		0.6	750+3.06	8 76+2 50	0.00	0.7004	
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Ocrambyeldae	10 100		6.1	6 10+2 08	744+4.50			
$\begin{array}{c} {\rm Cleft(labe^{o})} & 1 & 0.1 & 0.000.00 & -0.000.00 & -0.000.00 \\ \hline 0.000 & -0.000.00 & -0.000.00 & -0.000.00 \\ \hline 0.011 & -0.1 & 0.000.00 & 0.024.00 & -0.000.00 \\ \hline 0.011 & -0.1 & 0.000.00 & 0.024.00 & -0.0000 \\ \hline 0.011 & -0.1 & 0.0000 & 0.024.00 & -0.0000 \\ \hline 0.031 & 0.2 & 0.180.18 & 0.244.01 & \\ \hline 0.031 & 0.2 & 0.180.18 & 0.244.01 & \\ \hline 0.001 & -0.1 & 1.261.26 & 0.0000 & \\ \hline 0.001 & -0.1 & 1.261.26 & 0.0000 & \\ \hline 0.001 & -0.1 & 1.261.26 & 0.0000 & \\ \hline 0.001 & -0.1 & 0.0000 & 0.0000 & 0.0000 &$	Claridaah	10.199		0.1	0.10±0.00	1.06.1.06			
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Ciendae	1		0.1	0.00±0.00	1.20±1.20			
$\begin{array}{c} \mbox{Cocclean} \label{eq:Cocclean} \la$		0.009		<0.1	0.00 0.00	<0.00±0.00			
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Coccinellidae <sup>b</sup>	1		0.1	0.00±0.00	1.26±1.26			
		0.011		<0.1	0.00±0.00	0.02±0.02			
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	Curculionidae <sup>b</sup>	<u>11</u>		0.6	7.50±5.00	7.54±1.24			
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		0.331		0.2	0.18±0.18	0.24±0.10			
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Dytiscidae	1		0.1	1.26±1.26	0.00±0.00			
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		0.004		<0.1	<0.00±0.00	0.00±0.00			
$ \begin{array}{ c c c c c c c c c c c c c c c c c c c$	Elateridae <sup>a, b</sup>	26(1L)		1.3	13.78±2.34	20.02±7.75			
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		0.741		0.4	0.40±0.09	0.56±0.27			
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	Endomychidae	1		0.1	0 00+0 00	1 26+1 26			
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		0.001		<01	0.00+0.00	0.00+0.00			
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Frotylidae	2		0.1	1 26+1 26	1 26+1 26			
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Elotylidae	0.463		0.1	0.20±0.20	0.28+0.28			
Geourupidae <sup>b</sup> 2   0.1   1.20±1.20   1.20±1.20   1.20±1.20   1.20±1.20     Histeridae <sup>b</sup> 4   0.2   3.76±2.50   1.26±1.26       Lampyridae <sup>a</sup> 0.044   <0.1	Contrupidooh	0.403		0.3	1.06+1.06	1.20±0.20			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Geotiupidaes	<u> </u>		0.1	0.10.0.10	1.20±1.20			
Histeridaeb4 $0.2$ $3.76\pm2.50$ $1.26\pm1.26$ $$ $$ Lampyridaea $0.044$ $<0.1$ $0.02\pm0.02$ $0.04\pm0.040$ $$ $$ Lucanidaeb $0.72$ $<0.1$ $0.02\pm0.02$ $0.06\pm0.06$ $$ $$ Lucanidaeb $2$ $0.1$ $0.02\pm0.02$ $0.06\pm0.06$ $$ $$ Meloidaeb $8$ $0.4$ $8.76\pm4.68$ $3.73\pm1.54$ $$ $$ Nitidulidae $2$ $0.1$ $0.20\pm0.10$ $0.02\pm0.02$ $0.00\pm0.00$ $$ Nitidulidae $2$ $0.1$ $2.50\pm2.50$ $0.00\pm0.00$ $$ $$ Nitidulidae $2$ $0.1$ $2.50\pm2.50$ $0.00\pm0.00$ $$	l liste viele s b	0.200		0.1	0.10±0.10	0.00±0.00			
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Histeridae	4		0.2	3.76±2.50	1.26±1.26			
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		0.044		<0.1	0.02±0.02	0.04±0.040			
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	Lampyridae <sup>a</sup>	14(14L)		0.7	2.50±2.50	15.02±13.50			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		0.072		<0.1	0.02±0.02	0.06±0.06			
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Lucanidae <sup>b</sup>	2		0.1	0.00±0.00	2.52±1.54			
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		0.214		0.1	0.00±0.00	0.28±0.21			
Nitidulidae $0.155$ $0.1$ $0.20\pm0.10$ $0.06\pm0.04$ $\cdots$ $\cdots$ $\cdots$ $2$ $0.1$ $2.50\pm2.50$ $0.00\pm0.00$ $\cdots$ $\cdots$ $\cdots$ $\cdots$ $\cdots$ $0.004$ $<0.1$ $0.00\pm0.00$ $0.00\pm0.00$ $\cdots$ $\cdots$ $\cdots$ $\cdots$ Pyrochroidae <sup>b</sup> 1 $0.1$ $1.26\pm1.26$ $0.00\pm0.00$ $\cdots$ $\cdots$ $\cdots$ $0.027$ $<0.1$ $0.04\pm0.04$ $0.00\pm0.00$ $\cdots$ $\cdots$ $\cdots$ Scarabaeidae <sup>b</sup> 19 $1.0$ $11.26\pm4.14$ $15.02\pm1.54$ $\cdots$ $\cdots$ $1.302$ $0.8$ $1.02\pm0.48$ $0.88\pm0.36$ $\cdots$ $\cdots$ $21$ $1.1$ $26.28\pm10.71$ $3.76\pm2.50$ $\cdots$ $\cdots$ $2.080$ $1.2$ $2.34\pm1.24$ $0.46\pm0.29$ $\cdots$ $\cdots$ $2.080$ $1.2$ $2.34\pm1.24$ $0.46\pm0.29$ $\cdots$ $\cdots$ $0.146$ $0.1$ $0.12\pm0.07$ $0.06\pm0.06$ $\cdots$ $\cdots$ Tenebrionidae <sup>b</sup> 51 $2.6$ $52.54\pm28.21$ $12.52\pm3.43$ $1.41$ $0.1966$ $2.615$ $1.6$ $3.10\pm1.67$ $0.22\pm0.13$ $1.72$ $0.1244$ Tetratomidae <sup>b</sup> 5 $0.3$ $5.00\pm3.06$ $1.26\pm1.26$ $\cdots$ $\cdots$ $20$ pheridae <sup>b</sup> 1 $0.1$ $1.26\pm1.26$ $0.00\pm0.00$ $\cdots$ $\cdots$ $2.0113$ $0.72$ $0.40\pm0.25$ $0.06\pm0.06$ $\cdots$ $\cdots$ $\cdots$ $0.369$ $0.2$ $0.40\pm0.25$ $0.06\pm0.00$ $\cdots$ $\cdots$ $\cdots$ $0.076$ $<0.1$ <td>Meloidae<sup>b</sup></td> <td>8</td> <td></td> <td>0.4</td> <td>8.76±4.68</td> <td>3.78±1.54</td> <td></td> <td></td>	Meloidae <sup>b</sup>	8		0.4	8.76±4.68	3.78±1.54			
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		0.155		0.1	0.20±0.10	0.06±0.04			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Nitidulidae	2		0.1	2.50±2.50	0.00±0.00			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		0.004		<0.1	$0.00 \pm 0.00$	0.00±0.00			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Pyrochroidae <sup>b</sup>	1		0.1	1 26+1 26	0.00+0.00			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	i yrooniolado	0.027		<01	0.04+0.04	0.00+0.00			
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Scarabaeidae	10		1.0	11 26+4 14	15 02+1 5/			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Scarabaeidae	1 200		1.0	1 02 0 49	0.00,0.26			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Oile hide a h	1.302		0.0	1.02±0.40	0.00±0.00			
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	Silphidae	21		1.1	20.20±10.71	3.70±2.50			
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Staphylinidae <sup>b</sup>	2.080		1.2	2.34±1.24	0.46±0.29			
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		5		0.3	5.02±2.34	1.26±1.26			
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		0.146		0.1	0.12±0.07	0.06±0.06			
$2.615$ $1.6$ $3.10\pm1.67$ $0.22\pm0.13$ $1.72$ $0.1244$ Tetratomidae <sup>b</sup> $5$ $0.3$ $5.00\pm3.06$ $1.26\pm1.26$ $$ $$ $0.369$ $0.2$ $0.40\pm0.25$ $0.06\pm0.06$ $$ $$ $1$ $0.1$ $1.26\pm1.26$ $0.00\pm0.00$ $$ $0.076$ $<0.1$ $0.10\pm0.10$ $0.00\pm0.00$ $$	Tenebrionidae <sup>b</sup>	51		2.6	52.54±28.21	12.52±3.43	1.41	0.1966	
Tetratomidae <sup>b</sup> 5     0.3     5.00±3.06     1.26±1.26         0.369     0.2     0.40±0.25     0.06±0.06         Zopheridae <sup>b</sup> 1     0.1     1.26±1.26     0.00±0.00        0.076     <0.1		2.615		1.6	3.10±1.67	0.22±0.13	1.72	0.1244	
Zopheridae <sup>b</sup> $0.369$ $0.2$ $0.40\pm0.25$ $0.06\pm0.06$ $$ $$ 10.1 $1.26\pm1.26$ $0.00\pm0.00$ $$ $$ 0.076<0.1	Tetratomidae <sup>b</sup>	5		0.3	5.00±3.06	1.26±1.26			
Zopheridae <sup>b</sup> 1     0.1     1.26±1.26     0.00±0.00        0.076     <0.1		0.369		0.2	0.40±0.25	0.06±0.06			
0.076 <0.1 0.10±0.10 0.00±0.00	Zopheridae <sup>b</sup>	1		0.1	1.26±1.26	0.00±0.00			
		0.076		<0.1	0.10±0.10	0.00±0.00			

(continued)

# Table 2–(*Continued*) Total and mean ( $\pm$ SE) number (first line) and dry biomass (g; second line) of terrestial macroinvertebrate arthropod orders, families, and totals, per 100 pitfall traps in shelterwood harvests and controls

% of Total							
Order, Family <sup>b</sup>	Total <sup>a</sup>	Order	Family	Control	Shelterwood	t <sub>d.f.=8</sub> c	p-value <sup>d</sup>
Diptera <sup>a</sup>	3(1L)	0.1		2.50±2.50	1.26±1.26		
	0.193	<0.1		0.06±0.06	0.18±0.18		
Asilidae	1		33.3	1.26±1.26	0.00±0.00		
	0.045		23.3	0.06±0.06	0.00±0.00		
Tipulidae	1		33.3	1.26±1.26	0.00±0.00		
	0.009		4.7	0.02±0.02	0.00±0.00		
Gordioidea	9	0.2		10.00±6.23	3.76±2.50		
	0.388	0.1		0.40±0.35	0.10±0.06		
Hemiptera	37	0.9		12.50±6.85	33.78±15.14	-1.28	0.2362
	1.741	0.4		1.08±0.57	0.18±0.36	-0.00	1.0000
Coreidae	1		2.7	0.00±0.00	1.26±1.26		
	0.011		0.6	0.00±0.00	0.02±0.02		
Pentatomidae <sup>b</sup>	7		18.9	1.26±1.26	7.52±3.65		
	0.367		21.1	0.16±0.16	0.32±0.18		
Reduviidae <sup>b</sup>	27		73.0	11.26±5.74	22.52±10.93		
	1.352		77.7	0.92±0.50	0.76±0.31		
Thyreocoridae	2		5.4	0.00±0.00	2.50±2.50		
There are a state of	0.011		0.6	0.00±0.00	0.02±0.00		
Hymenoptera	12	1./		56.28±16.66	37.54±12.80	0.89	0.3983
A second second	0.625	0.1	1.0	0.05±0.21	0.28±0.07	0.97	0.3603
Apidae	3		4.2	1.26±1.26	2.52±1.54		
	0.124		19.8	0.06±0.06	0.10±0.06		
Formicidae	0.470		91.7	<u>53.76±15.50</u>	32.54±12.25	1.07	0.3143
le bre e um e mide e b	0.473		/5./	0.42±0.21	0.18±0.09	1.04	0.3268
Ichneumonidae	2		2.8	1.20±1.20	1.20±1.20		
Pompilidaa	1		2.0	0.020±0.020	0.00±0.00		
Pompilidae	0.010		1.4	0.00±0.00	1.20±1.20		
leepeda	15	0.4	1.9	0.00±0.00	0.02±0.02		
Isopoda	0.063	0.4		$10.70\pm4.42$	-0.00+0.00		
Oniscidae	10	<0.1	66.7	11 26±5 00	1 26+1 26		
Oniscidae	0.051		81.0	0.06+0.04	1.20±1.20		
Porcellionidae <sup>b</sup>	2		13.3	2 50+2 50	0.00±0.00		
1 oroemonidae	0.002		3.2	0.00+0.00	0.00±0.00		
Trachelinodidae	1		6.7	2 50+2 50	0.00±0.00		
Indenenpedidae	0.002		3.2	<0.00+0.00	0.00±0.00		
Julida	100	24	0.2	75 02+22 63	52 50+15 00	0.83	0 4309
	10 293	22		8 82+2 24	4 50+1 50	1 60	0 1479
Julidae <sup>b</sup>	10.200			75 02+22 63	52 50+15 00	0.83	0 4309
cunado				8 82+2 24	4.50+1.50	1.60	0.1479
Lepidoptera <sup>a</sup>	38(29L)	0.9		13.76±5.00	35.04±8.75	-2.11	0.0676
	7.127	1.5		3.26±1.75	5.94±2.29	-0.93	0.3799
Arctiidae (Erebidae) <sup>a</sup>	9(9L)		23.7	8.76±3.76	3.78±1.54		
· · · · · · · · · · · · · · · · · · ·	0.925		13.0	0.88±0.52	$0.56 \pm 0.33$		
Lvmantriidae (Erebidae) <sup>a</sup>	1(1L)		2.6	1.26±1.26	0.00±0.00		
<b>,</b> ,	0.532		7.5	0.66±0.66	0.00±0.00		
Papilionidae <sup>a, b</sup>	28(20L)	73.7		3.78±1.54	31.28±8.62		
	5.670	79.6		1.72±1.07	5.38±2.17		
Lithobiomorpha	30	0.7		22.52±10.20	15.02±7.56	0.59	0.5709
	1.672	0.4		1.38±0.81	0.70±0.39	0.76	0.4704
Lithobiidae				22.52±10.20	15.02±7.56	0.59	0.5709
				1.38±0.81	0.70±0.39	0.76	0.4704
Mecoptera <sup>a</sup>	2(1L)	<0.1		5.00±5.00	0.00±0.00		
Panorpidae <sup>a</sup>	0.007	<0.1		0.02±0.02	0.00±0.00		
	2(1L)		100.0	5.00±5.00	0.00±0.00		
	0.007		100.0	0.02±0.02	0.00±0.00		
Microcoryphia	24	0.6		15.00±10.00	15.04±5.46		
	0.089	<0.1		0.04±0.02	0.06±0.02		
Machilidae	24		100.0	15.00±10.00	15.05±5.46		
	0.089		100.0	0.04±0.02	0.06±0.02		
Opiliones	253	6.0		57.52±12.09	260.02±53.64	-3.68	0.0062
	3.646	0.8		0.84±0.19	3.72±0.79	-3.53	0.0078

(continued)

#### Table 2-(Continued) Total and mean (±SE) number (first line) and dry biomass (g; second line) of terrestial macroinvertebrate arthropod orders, families, and totals, per 100 pitfall traps in shelterwood harvests and controls

% of Total							
Order, Family <sup>b</sup>	Total <sup>a</sup>	Order	Family	Control	Shelterwood	$t_{d.f.=8}^{c}$	p-value <sup>d</sup>
Phalangiidae	253		100.0	57.52±12.09	260.02±53.64	-3.68	0.0062
-	3.646		100.0	0.84±0.19	3.72±0.79	-3.53	0.0078
Orthoptera	772	18.3		725.04±137.70	282.52±51.45	3.01	0.0168
	62.703	13.6		62.24±12.31	19.32±5.06	3.22	0.0122
Acrididae	11		1.4	10.02±4.25	5.02±3.66		
	0.526		0.8	0.50±0.21	0.22±0.14		
Gryllidae	4		0.5	1.26±1.26	3.76±2.50		
	0.094		0.1	0.02±0.02	0.10±0.06		
Rhaphidophoridae <sup>b</sup>	752		97.4	713.78±139.41	267.52±55.40	2.97	0.0177
	62.036		98.9	61.70±12.40	18.92±5.18	3.18	0.0129
Tetrigidae	5		0.6	0.00±0.00	6.26±2.80		
	0.047		0.1	0.00±0.00	0.06±0.06		
Polydesmida	589	14.0		328.76±79.05	448.78±98.69	-0.95	0.3703
	92.964	20.1		73.56±18.48	53.66±10.83	0.93	0.3800
Xystodesmidae <sup>b</sup>				328.76±79.05	448.78±98.69	-0.95	0.3703
				73.56±18.48	53.66±10.83	0.93	0.3800
Spirobolida	78	1.9		41.26±17.64	56.26±21.10	-0.55	0.6004
	103.041	22.3		47.84±22.15	80.96±27.85	-0.93	0.3791
Spirobolidae	78		100.0	41.26±17.64	56.26±21.10	-0.55	0.6005
	103.041		100.0	47.84±22.15	80.96±27.85	-0.93	0.3791
TOTAL	4,209			2676.28±431.28	2765.02±225.02	-0.18	0.8598
	461.988			307.50±39.08	290.68±55.27	-0.25	0.8100
RICHNESS (Orders)				12.6±0.6	13.2±0.6	-0.60	0.5651
RICHNESS (Families)				24.4±3.3	25.4±2.0	-0.26	0.8023

SE = standard error; d.f. = degrees of freedom

<sup>a</sup> Totals include both adults and larvae; larvae also denoted separately in parentheses.

<sup>b</sup> Taxa within families, if identified to genus or species, are as follows:

Agyrtidae includes Necrophilus spp.;

Brentidae includes Arrhenodes minutus;

Carabidae includes Agonum spp., Amara spp., Calosoma externum, other Calosoma spp., Chlaenius tricolor, Galerita spp., Harpalus spp., Pterostichus spp. (at least four morphospecies), Scaphinotus spp., Sphaeroderus spp., Stenolophus spp.;

Cerambycidae includes Anelaphus spp., Clytus spp., Knulliana spp., Monochamus spp., Prionus laticollis, other Prionus spp.;

Cleridae includes Chariessa spp.;

Coccinellidae includes Coccinella septempunctata;

Cryptoceridae includes Cryptocercus punctulatus;

Curculionidae includes Myosides spp., Otiorhynchus sulcatus;

Ectobiidae includes Parcoblatta spp.;

Elateridae includes Limonius spp., Melanotus spp;

Erotylidae includes Megalodacne heros;

Formicidae includes Camponotus spp.;

Geotrupidae includes Geotrupes spp.;

Histeridae includes Hister spp., Hololepta fossularis;

Ichneumonidae includes Pimpla spp.;

Julidae includes Julida (two morphospecies);

Lucanidae includes Dorcus parallelipipedus, Sinodendron rugosum;

Meloidae includes Meloe impressus, other Meloe spp.;

Papilionidae includes Battus philenor, other Battus spp.;

Pentatomidae includes Acrosternum spp., Menecles insertus, Mormidea spp., Perillus spp.;

Porcellionidae includes Porcellio spp.;

Pyrochroidae includes Neopyrochroa flabellata;

Reduviidae includes Apiomerus spp., Empicoris spp., Rhiginia cruciata, Stenopoda spinulosa;

Rhaphidophoridae includes Ceuthophilus spp.;

Scarabaeidae includes Aphodius spp., Melolonthinae spp., Onthophagus orpheus;

Silphidae includes Oiceoptoma noveboracense; Nicrophorus spp., N. marginatus, N. orbicollis;

Staphylinidae includes *Platydracus* spp.;

Tenebrionidae includes Alobates spp., Meracantha contracta; Arthromacra spp.;

Tetratomidae includes Penthe obliguata;

Xystodesmidae includes *Polydesmida* (three morphospecies); Zopheridae includes Phellopsis obcordata.

<sup>c</sup>T-tests were conducted only if n>30 specimens.

<sup>d</sup>Lines bolded if p<0.10.



Figure 1—Mean (+standard error) number of individuals (A), and dry biomass (g) (B) of terrestrial macroarthropods within taxonomic orders, captured per 100 pitfall traps in recent shelterwood harvests and controls, Cold Mountain Game Land, Haywood County, NC, 2011.

### DISCUSSION

Our results indicate that community composition and richness of orders or families did not differ between recent shelterwood harvests and mature forest. Similarly, the relative abundance and dry biomass of total macroarthropods and most orders and families were unaffected by shelterwood harvests in the short term, despite substantial post-harvest reductions in tree density, canopy cover, and leaf litter cover and depth. The direction of responses varied among the few taxa responding to harvests.

Effects of harvesting may be more pronounced at the genus or species levels, and thus our analyses at the family level may have missed some responses (Siira-Pietikainen and others 2003). However, family-level data are more likely to be used in management decisions (Bennett and Gratton 2013), and species-level patterns are often strongly correlated with higher levels of taxonomic resolution (Timms and others 2013).



More Lepidopteran larvae were captured in the shelterwood plots than the controls, likely due to more open conditions, a flush of young foliage, and flowers that attracted butterflies for egg laying. Pictured here is the pipevine swallowtail (*Battus philenor*). (photo by Ansel Oommen, Bugwood.org.)

Ground-dwelling macroarthropod response to canopy reduction is known to vary among taxa, favoring some and negatively impacting others. Further, taxa-specific responses are not always predictable. We found fewer Phalangiidae but a greater abundance of Rhaphidophoridae in C than SW, and no difference in abundance of Carabidae, Araneae, Julidae, or Spirobolidae. In contrast, several studies indicate that some ground-dwelling macroarthropod taxa, including Araneae, Carabidae, Julidae, Opiliones, Scolopendromorpha, Spirobolidae, and Rhaphidophoridae, are more abundant in closed-canopy forest than canopy gaps, harvested areas, or other forest openings, suggesting an association with greater litter depth and moisture (Brown and others 2011, Duguay and others 2000, Greenberg and Forrest 2003, Harper and others 2001, Haskell 2000, Perry and Herms 2016, Schowalter and others 1981, Shure and Phillips 1991, Whitehead 2003). Healy (1985) reported increasing macroinvertebrate abundance across a gradient of herbaceous ground cover

for some, but not all taxa. Yet other studies report few differences in abundance of these taxa among disturbance treatments in hardwood forests (Greenberg and others 2010, McCord and others 2014). Our finding of no response by Carabidae or Araneae was especially surprising, given that they are considered indicators of environmental change (Pearce and Venier 2006).

Although our study was not designed to sample flying and foliar insects, we captured more Lepidopteran larvae in SW than C. This was likely due to the more open conditions; a flush of young foliage by shrubs, seedlings, and stump sprouts; and possibly flowering by some herbaceous plants and shrubs that attracted butterflies for egg laying (Hanula and others 2016). Other studies indicated greater abundance and family richness (Wilson and others 2014) of flying/foliar insects and pollinators in open- than closed-canopy forest and a positive association with herbaceous vegetation cover (Campbell and others 2007, Hanula and others 2016, Healy 1985, Hollifield and Dimmick 1995, Whitehead 2003).

Inconsistent results among studies of macroarthropod response to heavy disturbances could be at least partly attributed to different sampling methods. For example, colored pan traps attract flying/foliar pollinators (Campbell and others 2007, Wilson and others 2014), and sweep-nets collect flying arthropods and from shrub- or ground-level vegetation (Harper and others 2001). In contrast, pitfall traps are a metric of activity-abundance by primarily groundand litter-dwelling taxa. Other factors that may influence study results and confound interpretation and potential generalizations regarding macroarthropod response to disturbances include differences in the seasonal timing of sampling (Greenberg and Forrest 2003, Greenberg and others 2010, Johnston and Holberton 2009, Whitehead 2003); post-disturbance forest floor and microclimatic conditions; taxonomic levels (e.g., order, family, species) reported; and the geographic locations and ecosystems where studies are conducted (Pearce and Venier 2006). Time since disturbance could also affect results of studies addressing macroinvertebrate response (Pearce and Venier 2006, Perry and Herms 2016). For example, decreased abundance of salamanders in our study sites was not apparent until 2 to 3 years post-harvest, despite rapid recovery of leaf litter and

shrub cover during that period (Greenberg and others 2016); our short-term study would not detect potential longer term changes in macroarthropod activity-abundance.

Within upland hardwood ecosystems, inconsistent results among studies could be due to differences in elevation, topographic position, site quality, or weather that affect movement or abundance. For example, Healy (1985) reported three times more invertebrates in productive, forested mixed-hardwood and yellow-poplar stands than red oak-scarlet oak stands with lower site quality. In contrast, Dress and Boerner (2004) documented greater abundance of oribatid mites on drier than intermediate or mesic topographic positions in an Ohio hardwood forest. In our study, higher CWD levels (Perry and Herms 2016) from logging slash and an intermediate site quality promoted rapid shrub recovery and associated shade, which may have mitigated effects of reduced post-harvest leaf litter cover and depth in the SW treatment.

Despite their ecological importance, and the potential of some taxa as indicators of forest conditions (Pearce and Venier 2006), ground-dwelling macroarthropods in the Central Hardwood Region rarely are considered in forest management or restoration planning (Grodsky and others 2015). For most orders or families in our study, order- and family-level richness and abundance and dry biomass of total macroarthropods were unaffected in the short term by shelterwood harvests despite substantial post-harvest reductions in tree density, canopy cover, and leaf litter cover and depth. Among taxa, abundance and dry biomass of Opiliones (all Phalangiidae) and Lepidoptera (mostly larvae) were greater in shelterwoods than controls, whereas abundance and dry biomass of Orthoptera (predominantly Rhaphidophoridae) were greater in forested controls. Abundance and dry biomass of Carabidae and Araneae, both considered indicators of environmental change (Pearce and Venier 2006), did not differ between shelterwoods and controls. Our results suggest that use of ground-dwelling macroarthropod taxa as indicators of forest disturbance be tempered with consideration of other environmental and siterelated factors potentially affecting forest floor conditions and activity-abundance, such as forest type, site quality, elevation, topographic position, and weather.

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Abstract: Macroarthropods rarely are considered in forest management decisions, despite their ecological importance as decomposers, herbivores, pollinators, predators, and nutrient cyclers, and potential of some taxa as indicators of forest condition. We used a replicated design to experimentally determine if, and how, community composition, richness, and biomass of terrestrial macroarthropods differed between recent shelterwood harvests and unharvested controls in an intermediate quality upland hardwood forest. Richness of orders or families did not differ between treatments. Abundance and dry biomass of total macroarthropods and most orders or families were unaffected by shelterwood harvests despite substantial post-harvest reductions in tree density, canopy cover, and leaf litter cover and depth, at least in the short term. Among taxa, abundance and dry biomass of Opiliones (all Phalangiidae) and Lepidoptera (mostly larvae) were greater in shelterwoods than controls, whereas abundance and dry biomass of Orthoptera (predominantly Rhaphidophoridae) were greater in controls. Our results suggest that use of ground-dwelling macroarthropod taxa as indicators of forest disturbance be tempered with consideration of other site-related factors potentially affecting forest floor conditions and activity-abundance of macroarthropods, such as forest type, site quality, elevation, topographic position, and weather.

Keywords: Ground-dwelling macroarthropods; shelterwood harvest; southern Appalachians; upland hardwood forest.



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