

Invertebrate community response to coarse woody debris removal for bioenergy production from intensively managed forests

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Abstract. Increased market viability of harvest residues as forest bioenergy feedstock may escalate removal of coarse woody debris in managed forests. Meanwhile, many forest invertebrates use coarse woody debris for cover, food, and reproduction. Few studies have explicitly addressed effects of operational-scale woody biomass harvesting on invertebrates following clearcutting. Therefore, we measured invertebrate community response to large-scale harvest residue removal and micro-site manipulations of harvest residue availability in recently clear-cut, intensively managed loblolly pine (*Pinus taeda*) forests in North Carolina (NC; $n = 4$) and Georgia (GA; $n = 4$), USA. We captured 39,794 surface-active invertebrates representing 171 taxonomic groups using pitfall traps situated among micro-site locations (i.e., purposefully retained piles of hardwood stems and piles of conifer stems and areas without coarse woody debris in NC; windrows and no windrows in GA). Micro-site locations were located within six, large-scale treatments (7.16–14.3 ha) in clearcuts. Large-scale treatments represented intensive harvest residue removal, 15% and 30% harvest residue retention, and no harvest residue removal. In NC, ground beetles (Coleoptera: Carabidae) and crickets (Orthoptera: Gryllidae) were three times more abundant in treatments with no harvest residue removal than those with the most intensive harvest residue removal and were reduced in treatments that retained 15% or 30% of harvest residues, although not significantly. Invertebrate taxa richness was greater at micro-site locations with retained hardwood and pine (*Pinus* spp.) harvest residues than those with minimal amounts of coarse woody debris. In both states, relative abundances of several invertebrate taxa, including cave crickets (Orthoptera: Rhaphidophoridae), fungus gnats (Diptera: Mycetophilidae and Sciaridae), millipedes (Diplopoda), and wood roaches (Blattodea: Ectobiidae), were greater at micro-site locations with retained harvest residues than those with minimal coarse woody debris. Intensified woody biomass harvesting without retention of $\geq 15\%$ of harvest residue volume may reduce invertebrate taxa richness and abundances of some key invertebrate taxa in regenerating stands. Further, harvest residue management during and after woody biomass harvesting may be an important consideration for maintaining invertebrate diversity and conserving invertebrates that are influential in the maintenance of ecosystem function and integrity in young forests.

Key words: bioenergy; clearcuts; coarse woody debris; downed wood; Georgia, USA; harvest residues; intensively managed forests; invertebrates; North Carolina, USA; renewable energy; woody biomass harvesting.

INTRODUCTION

Coarse woody debris provides food and cover for forest wildlife; hence management of coarse woody debris may affect biodiversity in forest ecosystems (Harmon 1986, Huston 1996, Hagan and Grove 1999). Additionally, coarse woody debris plays critical roles in

forest ecosystem function and integrity by acting as a carbon sink, retaining nutrients, and influencing water dynamics (Fraver et al. 2002, Woodbury et al. 2007, Zhou et al. 2007). Early forest ecologists recognized coarse woody debris as one of the most important resources for animal species in forests (Elton 1966), and management of coarse woody debris is an increasingly relevant consideration for intensively managed forests (Jones et al. 2009, Janowiak and Webster 2010).

Timber harvests can be large-scale, anthropogenic disturbances that lead to substantial increases in coarse woody debris in the form of harvest residues (Grodsky et al. 2016b). However, increases in the market viability

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of harvest residues as forest bioenergy feedstock may lead to intensified levels of coarse woody debris removal (i.e., woody biomass harvest), particularly in intensively managed forests (Rudolphi and Gustafsson 2005, Riffell et al. 2011). Forest bioenergy is an expanding renewable energy technology capable of generating heat, electricity, and biofuels from woody biomass (Parikka 2004). Harvest residues specifically comprise a potential feedstock for producing wood pellets (Sikkema et al. 2011), co-generated electricity (i.e., coal and woody biomass simultaneously burned; Annamalai and Wooldridge 2001), and, to a lesser extent, liquid biofuels (United States Department of Agriculture 2007, Forisk Consulting 2013).

Given the known and potential ecological relationships between coarse woody debris and animals, removal of harvest residues via woody biomass harvesting could affect wildlife communities, including invertebrates (Evans et al. 2013, Eräjää et al. 2010). Indeed, concerns regarding potential effects of woody biomass harvesting on forest ecosystem sustainability and biodiversity have led to non-regulatory biomass harvesting guidelines, such as those developed in the United States (see Perschel et al. 2012). In general, biomass harvesting guidelines are based on the assumption that wildlife universally responds positively to increased volumes of coarse woody debris (i.e., more coarse woody debris is better than coarse woody debris; Harmon and Hua 1991). Yet, wildlife responses to harvest residue removal may differ among species or vary regionally, and biomass harvesting guidelines currently have limited technical underpinnings and a paucity of empirical support. Further, knowledge regarding ecological relationships between wildlife, especially invertebrates, and coarse woody debris in young, intensively managed forests remains limited, especially in the United States (McMinn and Crossley 1996, Riffell et al. 2011).

Many woody biomass harvests concurrently occur with clearcut harvesting of intensively managed forests, which entails overstory tree removal in a single entry (hereafter “regenerating stands”; Riffell et al. 2011). Yet, understanding invertebrate responses to harvest residue reduction in regenerating forest generally is lacking (Nittérus et al. 2007). Harvest residues generated by timber harvests in intensively managed forests differ in volume and spatial distribution from coarse woody debris created by natural disturbance and senescence (Hanula et al. 2006, Grodsky et al. 2016b). Harvest residues in intensively managed forests typically include both coniferous and deciduous tree species, potentially supporting different invertebrate groups (Jonsell et al. 2007).

Coarse woody debris is an important resource for many forest invertebrates (Harmon 1986, Landis and Werling 2010), and its management may play a pivotal role in conservation of invertebrate biodiversity in forested ecosystems (Castro and Wise 2010). Invertebrates may use coarse woody debris for foraging, refugia from variable temperature and moisture conditions, oviposition sites, and, in the case of saproxylic (i.e., dead-wood dependent)

insects, a food resource (Hanula et al. 2006, Bouget et al. 2013). Relationships between saproxylic insects and coarse woody debris have been extensively studied (Grove 2002, Ulyshen et al. 2004). Further, some studies have specifically addressed saproxylic insect response to harvest residue removal and stump harvesting. For example, Lassaue et al. (2012) determined that harvest residue retention favored saproxylic beetles in temperate forests in France. In comparison to saproxylic invertebrates, relationships between non-saproxylic invertebrates and coarse woody debris are less represented in the current literature (Hanula et al. 2006).

Non-saproxylic invertebrate responses to experimentally manipulated coarse woody debris have varied among previous studies (Bengtsson et al. 1997, Ulyshen and Hanula 2009a, Castro and Wise 2010). Kataja-Aho et al. (2016) measured invertebrate response to experimental stump removal and showed that several invertebrate groups, including ground beetles, spiders, and springtails, were affected by stump harvesting for biofuel. Two large-scale experiments with variable coarse woody debris retention were conducted in mature, loblolly pine (*Pinus taeda*) forests in South Carolina, USA (Hanula et al. 2006, Ulyshen and Hanula 2009a). Hanula et al. (2006) reported that coarse woody debris removal decreased overall invertebrate diversity and activity of several invertebrate taxa and thus affected community composition, whereas a later study at the same site documented no effect of coarse woody debris removal on the invertebrate community (Ulyshen and Hanula 2009a). Castro and Wise (2009) manipulated availability of fine woody debris (i.e., downed woody debris with a diameter ≤ 7.62 cm in diameter for a length of at least 0.914 m) in an undisturbed, mature forest in Kentucky, USA, and documented no effect on spider diversity.

Other research has addressed facultative use of coarse woody debris by invertebrates, albeit primarily through observational studies, by testing for differences in taxon composition and abundance in areas directly near and farther from coarse woody debris piles (Jabin et al. 2004, Castro and Wise 2010). In general, areas directly adjacent to coarse woody debris piles maintain a deeper litter layer (Marra and Edmonds 1998), higher concentrations of fine woody debris (Evans et al. 2003), and more stable microclimatic conditions (Spears et al. 2003, Remsburg and Turner 2006). In some cases, litter adjacent to coarse woody debris had greater densities of invertebrate taxa (Jabin et al. 2007, Kappes et al. 2007, Ulyshen and Hanula 2009b). Coarse woody debris often supports high abundances of arthropod prey and thus provides food resources for predatory invertebrates, including carabids (Ulyshen and Hanula 2009a) and spiders (Varadi-Szabo and Buddle 2006). Despite apparent positive relationships between invertebrates and coarse woody debris, some studies reported no difference in invertebrate diversity between sites near and far from coarse woody debris (Marra and Edmonds 1998, Andrew et al. 2000, Buddle 2001). Differences among studies may be

attributable to variation in responses by diverse invertebrate groups or variable sampling methods (Evans et al. 2003, Varadi-Szabo and Buddle 2006).

Our project goals centered on filling gaps of knowledge pertaining to (1) facultative, ecological relationships between non-saproxyllic invertebrates and harvest residues; and (2) implications of operational woody biomass harvesting for forest invertebrate conservation, specifically in intensively managed forests. We aimed to determine effects of coarse woody debris availability following woody biomass harvesting on community-level invertebrate metrics, including richness and relative abundances of common invertebrate families, at two spatial scales. Within this multi-scale experimental framework, our objectives were to test (1) micro-scale invertebrate responses to presence or absence of harvest residue piles, harvest residue pile type (i.e., coniferous versus hardwood), and localized ground-cover of fine woody debris and vegetation to improve understanding of ecological relationships between invertebrates and coarse woody debris at the micro-scale; and (2) stand-scale invertebrate responses to operational woody biomass removal treatments to inform downed wood management when woody biomass harvesting is incorporated into management plans.

METHODS

Study area and design

We studied forest invertebrates in eight replicate clearcuts (hereafter “blocks”) in intensively managed loblolly pine forests within the Coastal Plain physiographic region of the southeastern United States. Our study included four blocks (70.5 ± 6.1 [mean \pm SE] ha) in Beaufort County, North Carolina (NC) and four blocks (64.64 ± 3.1 ha) in Georgia (GA): three in Glynn County and one in Chatham County. Blocks were in the temperate/subtropical biogeographic regions; fire was the historical forest disturbance in the region, but has since been predominantly replaced with anthropogenic disturbance via timber harvest (see Grodsky et al. [2016a] for management history and site descriptions).

Following clearcut harvest in 2010–2011, we implemented stand-scale, harvest residue removal treatments (hereafter “treatments”) at each block. We used a randomized complete-block experimental design, dividing each block into the following six, large-scale treatments: (1) clearcut with intensive downed wood removal (NOBHGs); (2) clearcut with 15% retention of downed wood evenly dispersed throughout the treatment (15DISP); (3) clearcut with 15% retention of downed wood clustered in large piles throughout the treatment (15CLUS); (4) clearcut with 30% retention of downed wood evenly dispersed throughout the treatment (30DISP); (5) clearcut with 30% retention of downed wood clustered in large piles throughout the treatment (30CLUS); and (6) clearcut with no downed wood removal (i.e., clearcut only; NOBIOHARV), which

served as a reference site (see Fritts et al. [2014] and Grodsky et al. [2016a] for detailed methods on large-scale treatment implementation; Fig. S1). In NC, treatment area averaged 11.7 ± 0.5 (mean \pm SE) ha and ranged from 8.4 to 16.3 ha, In GA, treatment area averaged 10.7 ± 0.4 ha and ranged from 7.6 to 14.3 ha. We defined harvest residues as non-roundwood stems and pine tops and limbs traditionally considered non-merchantable prior to the advent of forest bioenergy-driven woody biomass markets.

Although treatment implementation was similar in NC and GA, preparation of harvested sites for replanting differed between states. In NC, site preparation occurred following clearcut harvest and implementation of treatments in the winter of 2010–2011. Blocks were sheared using a V-shaped blade, bedded into continuous, mounded strips of soil (i.e., beds) approximately 3 m wide and <1 m tall, and planted with loblolly pine during the fall–winter of 2011–2012 at a density of ≈ 1100 trees/ha (Fig. 1). Prior to revegetation, pine beds essentially consisted of bare soil and pine seedlings. Shearing moved retained coarse woody debris into the 3-m space between pine beds (hereafter “interbeds”). Consequently, coarse woody debris was rearranged following shearing into long, linear rows in interbeds parallel to pine beds; however, volume of coarse woody debris was largely unaltered by shearing (Fritts et al. 2014). Blocks were treated with the following two post-harvest herbicide applications of imazapyr (Chopper; BASF, Raleigh, North Carolina, USA) for herbaceous weed control: (1) a broadcast application (applied by helicopter) one year after clearcut harvest; and (2) a banded application (applied only to pine trees in bedded rows) two years after clearcut harvest.

In GA, most coarse woody debris in treatments was concentrated into large, linear piles (hereafter “windrows”) extending the entire length of treatments or into large, conical piles ($1\text{--}100\text{ m}^3$) within treatments (Fig. 2). As such, few individual stems and no small coarse woody debris piles ($<1\text{ m}^3$) occurred between windrows ($\sim 30\text{--}50$ m apart) in treatments. In Glynn County (GA), two blocks were bedded in the summer of 2011 and the remaining block was bedded in fall 2011. All Glynn County (GA) blocks were planted in winter 2012 at a density of $\approx 1,495$ trees/ha and treated with imazapyr (Arsenal; BASF) and sulfometuron methyl for herbaceous weed control one year after clearcut harvest. In 2012, the Chatham County (GA) block was bedded and planted at a density of ≈ 726 trees/ha and received a broadcast treatment of Chopper one year after clearcut harvest.

Following site preparation and planting, we identified micro-scale locations within treatment blocks that emulated harvest residue removal or lack thereof (hereafter “locations”). To accomplish this, we randomly located clusters of locations in each treatment in each block. In NC, locations included (1) hardwood pile; (2) pine pile; and (3) no pile (i.e., no coarse woody debris, control). The NOBHGs treatments had all hardwood harvest



FIG. 1. A site 2-yr post-harvest in North Carolina, with uniformly intermittent interbeds containing coarse woody debris (1) and bedded rows containing planted pine seedlings (2). Three pitfall trap arrays representing micro-site locations (hardwood pile, pine pile, and no pile) were clustered within each of the six, large-scale harvest residue removal treatments. Each array was oriented perpendicular to interbeds and beds (A; hardwood pile shown). Pitfall traps (black dots) were 1 m apart, resulting in a total array length of 3 m. Two pitfall traps were situated immediately adjacent to either side of harvest residues piles, when present, and two pitfall traps were situated in bedded rows on either side of the interbed. We maintained the same array design and inter-trap spacing for no-pile locations, despite the fact that no CWD was present in interbeds. Photo by Sarah Fritts. Drawing by Steve Grodsky. [Color figure can be viewed at wileyonlinelibrary.com]

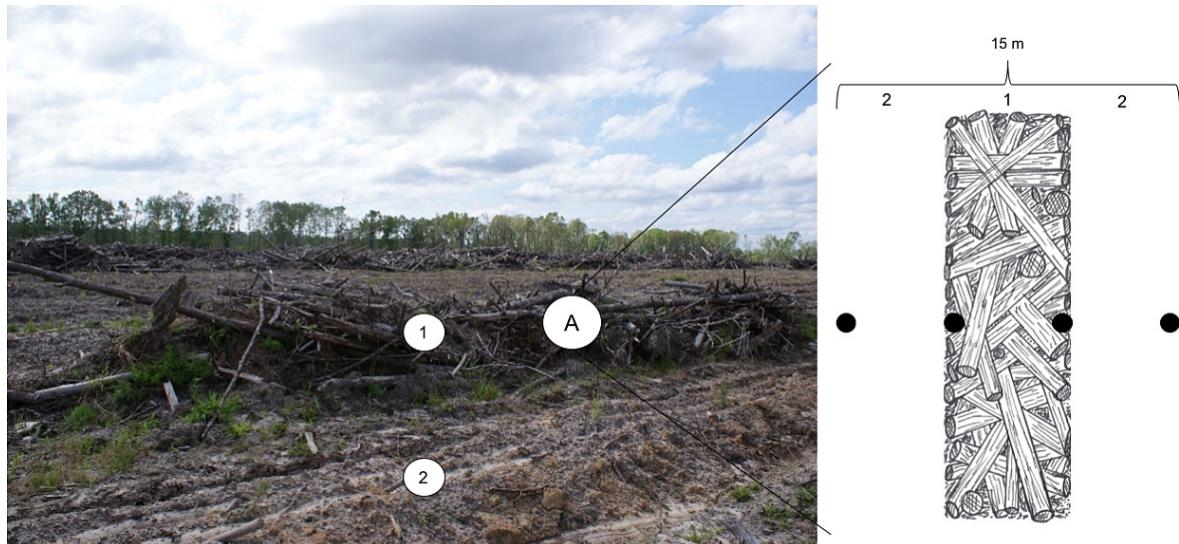


FIG. 2. A site 1-yr post-harvest in Georgia, with windrows (1) separated by large expanses of bare ground (2). Two pitfall trap arrays representing micro-site locations (windrow, no windrow) were clustered within each of the six, large-scale harvest residue removal treatments. Each array was oriented perpendicular to windrows (A). To accommodate the width of windrows, pitfall traps (black dots) were 5 m apart, resulting in a total array length of 15 m. Two pitfall traps were situated immediately adjacent to either side of windrows, when present, and two pitfall traps were situated in bedded rows on either side of the windrow. We maintained the same array design and inter-trap spacing for no windrow locations, despite the fact that no windrows were present. Photo and drawing by Steve Grodsky. [Color figure can be viewed at wileyonlinelibrary.com]

residues removed and thus did not include hardwood pile locations. In GA, harvest residues consisted of pine in windrows exclusively; as such, locations in GA included (1) windrow and (2) no windrow (i.e., no coarse woody debris, control).

Invertebrate sampling, identification, and measures

In 2012 and 2013, we sampled invertebrates in NC and GA using pitfall trapping. We specifically targeted surface-active invertebrates because they occupy niches on the forest floor (e.g., Pearce and Venier 2006), where coarse woody debris provides habitat structure. Pitfall traps (Spence and Niemelä 1994) were 0.47-L plastic containers with a diameter of ~8.5 cm filled with equal amounts of propylene glycol and water and a drop of liquid dish soap to reduce surface tension. We placed the lip of each container at or slightly below ground-level (e.g., Murkin et al. 1994, Ausden 1996). We removed vegetation (when present) immediately surrounding pitfall traps (i.e., ≤5 cm from trap lips) to improve trapping efficiency (Greenslade 1964; but see *Quantifying stand- and micro-scale habitat characteristics*). Four pitfall traps comprised a pitfall trap array (hereafter “array”). To control for edge effects, we situated all arrays ≥100 m from treatment and block edges.

In NC, we established 3 m long arrays (four pitfall traps per array) with 1-m inter-trap spacing at each location (Fig. 1). Each array was oriented in a straight line perpendicular to interbeds and bedded rows. For hardwood and pine pile locations, we situated two pitfall traps immediately adjacent to each side of harvest residue piles within interbeds and one pitfall trap in bedded rows on either side of interbeds. We maintained the same inter-trap spacing for the no pile location, despite the fact that no harvest residue pile was present. We sampled each location monthly for a 48-h period, June–September 2012 and June, July, and September, 2013.

In GA, we established 15 m long arrays (four pitfall traps per array) with 5-m inter-trap spacing at each location; the width of windrows in GA precluded replication of array design in NC (i.e., 1-m inter-trap spacing; Fig. 2). For the windrow location, we situated two pitfall traps immediately adjacent to each side of windrows and one pitfall trap in bedded rows 5 m from either side of windrows. We maintained the same inter-trap spacing for the no windrow location, despite the fact that no windrow was present. We sampled each location once for a 48-h period in August 2012 and 2013.

At the conclusion of each sampling period, we strained invertebrates from each pitfall trap and stored specimens in 60 mL Nalgene bottles filled with 70% ethanol and labeled with trap locality data. We identified most specimens to family using taxonomic keys and confirmation for type specimens representative of each invertebrate group. In rare cases when family-level identification was infeasible, we identified invertebrate specimens at coarser taxonomic resolutions (e.g., Diptera: Schizophora,

Chilopoda, Diplopoda). We also identified highly abundant cricket (Gryllidae) nymphs. We sorted, pinned, and labeled with location and sampling date information type specimens representative of captured invertebrate families to serve as voucher specimens in the North Carolina State University Insect Museum collections.

We plotted relative abundances for all invertebrate groups per state and visually binned them into one of the following three abundance levels: (1) superabundant, (2) abundant, and (3) rare. We set the cutoff for inclusion of individual invertebrate families in analyses at the break between abundant and rare invertebrate groups, thereby excluding all rare invertebrate groups with relatively low relative abundances. For example, the cutoff between abundant and rare invertebrate groups for micro-sites in NC was $n = 84$ because counts of invertebrate captures dropped from $n = 84$ to $n \leq 20$ at that point on the plot. Given differences in scale and consequent levels of inference between micro-scale and stand-scale analyses, sample size cutoffs for invertebrate taxa in stand-scale analyses were larger and therefore differed from cutoffs assigned to micro-scale analyses.

Quantifying stand- and micro-scale habitat characteristics

We measured scattered and piled harvest residues in each treatment at NC and GA blocks using the line-intersect sampling (LIS) technique (Van Wagner 1968) and a visual encounter method. For the visual encounter method in NC, we located each harvest residue pile in each treatment, measured its length (cm), width (cm), and height (cm), and visually estimated its packing ratio (i.e., density of wood in pile; 0–100%). For the visual encounter method in GA, we measured width and height and visually estimated packing ratio every 50 m along each windrow and at each spot-pile. Because windrows often ran the entire length of treatments, we measured the length of each windrow in ArcGIS using post-harvest aerial imagery (Google Maps, Mountain View, California, USA). For both states, we summed the volume of harvest residue piles estimated from the visual encounter method and volume of scattered harvest residues estimated using the LIS method to generate total volume of harvest residues (m^3/ha) for each treatment plot. Volume (m^3/ha) and spatial distribution of harvest residues in treatment plots in NC was shown to accurately match that of our original experimental design; Fritts et al. (2014) calculated the following volumes of harvest residues in each treatment in NC: NOBHG = 20.65 ± 1.45 ; 15DISP = 40.80 ± 13.11 ; 15CLUS = 37.76 ± 9.42 ; 30DISP = 55.75 ± 12.49 ; 30CLUS = 55.17 ± 12.49 ; NOBIOHARV = 108.20 ± 20.05 . Efficacy of treatment implementation in GA was less clear because windrowing greatly altered spatial arrangement of harvest residues from that in the original experimental design.

We visually estimated decay class of hardwood piles, pine piles, and windrows following Forest Inventory and Analysis (FIA) protocols (United States Department of

Agriculture 2007). Hardwood and pine piles and windrows ranked as Decay Class 2 in 2012 and Decay Class 3 in 2013 (see FIA protocol for definitions; United States Department of Agriculture 2007). In NC and GA, July 2012 and 2013, we quantified micro-site groundcover at each pitfall trap by placing a 1- by 1-m Daubenmire frame centered over each pitfall trap and visually estimating percent groundcover (total = 100%) for the following categories: (1) bare ground, (2) fine woody debris, and (3) vegetation (included all living grasses, forbs, and woody shrubs and vines).

Statistical framework and analysis

We conducted Poisson generalized linear models (GLMs) with number of captured individuals for each invertebrate group as dependent variables to test response of the invertebrate community to harvest residue removal at the stand-scale and micro-scale locations in NC and GA. For all models, we tested for correlation among covariates and assumed overdispersion when the residual deviance divided by the residual degrees of freedom was >1.0 ; we used quasipoisson GLMs when we detected overdispersion. To account for variation in effort, we also included average number of active traps per treatment plot and average number of active traps per array as an additive effect (*sensu* relative abundance) in all stand- and micro-scale models, respectively. For categorical covariates in all stand- and micro-scale models, we performed post-hoc Tukey's pairwise comparisons of means using general linear hypothesis testing (*glht* function; single-step method) in the R package *multcomp* (Hothorn et al. 2013). We set $\alpha = 0.05$.

For stand-scale analyses, we used treatment plot as the experimental unit and number of captured individuals of each invertebrate group pooled over all arrays at each treatment plot in each state as dependent variables. We first included year, treatment, a year \times treatment interaction term, block, and effort as explanatory variables in each model. If we detected a significant year \times treatment interaction, we consequently developed a model for each year separately and included treatment, block, and effort as explanatory variables. Otherwise, we included treatment, year, block, and effort as explanatory variables. For GA sites, we replaced the categorical, fixed effect for treatment with volume (m^3/ha) of harvest residues in windrows in each treatment (see *Quantifying stand- and micro-scale habitat characteristics*) and first tested for harvest residue volume \times year interactions.

We used each array as the experimental unit in NC ($n = 68$) and GA ($n = 48$) for micro-scale location analyses, and number of captured individuals of each invertebrate group pooled over all traps at each array in each state as dependent variables. We first included percent groundcover of FWD and vegetation and effort as continuous, fixed effects, and year, location, and a year \times location interaction term as explanatory variables in each model. If we detected a significant year \times location

interaction, we consequently developed a model for each year separately and included location, groundcover of fine woody debris and vegetation, and effort as explanatory variables. Otherwise, we included location, groundcover of fine woody debris, and vegetation, year, and effort as explanatory variables. For both NC and GA, bare ground was inversely correlated with vegetation groundcover; therefore, we excluded bare ground as a covariate in all micro-scale location models.

RESULTS

We captured 39,794 invertebrate specimens representing 171 individual taxonomic groups, and most ($n = 147$; 86%) were identified to family (see Appendix S1). In NC, we set the cutoff for inclusion of individual taxonomic groups in stand- and micro-scale analyses at $n = 410$ and $n = 84$ per year, respectively. In GA, we set the cutoff for inclusion of individual taxonomic groups in stand- and micro-scale analyses at $n = 110$ and $n = 44$ captures per year, respectively. Collembolans were ubiquitous in samples (S. M. Grodsky, *unpublished data*), and we opted not to include them in analyses.

Stand-scale models

Invertebrate taxa richness did not differ among treatments in NC and was unaffected by volume of harvest residues in the GA treatments. In NC, carabid beetles, gryllids, and gryllid nymphs were more abundant in NOBIOHARV treatments than in NOBHG treatments, but had similar abundances in 15% and 30% harvest residue retention treatments (Table 1). Carabid beetles, formicids (ants), and gryllid nymphs increased in abundance from 2012 to 2013, whereas sciarids decreased in abundance from 2012 to 2013. In GA, invertebrate taxa were unaffected by volume of harvest residues in treatments, and both gryllids and lycosids decreased in abundance from 2012 to 2013 (Table S1).

Micro-scale models

Invertebrate taxa richness was greater at hardwood and pine pile locations than in no pile locations in NC, but did not differ among windrow and no windrow locations in GA (Fig. 3). In NC, relative abundance of most invertebrate taxa did not differ among locations, but several groups positively responded to presence of harvest residue piles (Table 2). Relative abundances of diplopods (2012), ectobiids (2013), erotyliids (2013), mycetophilids (2012), and sciarids (2013) were greater in hardwood and pine pile locations than in no pile locations. Relative abundance of mycetophilids (2013) was greater in hardwood pile locations than in no pile locations. Relative abundance of sphaerocerids (2013) was greater in pine pile locations than in no pile locations. Relative abundance of sciarids (2012) was greater in pine pile locations than in no pile and hardwood pile locations. In GA,

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TABLE 1. Mean (SE in parentheses) number of captured individuals per 100 array nights for invertebrate taxa captured at 68 pitfall traps arrays situated within six downed wood removal treatments in regenerating stands ($n = 4$), North Carolina, pooled among 2012 and 2013.

Invertebrate taxa	Harvest residue removal treatment					
	NOBHGs	15DISP	15CLUS	30DISP	30CLUS	NOBIOHARV
Araneae†	233.27 (23.41)	456.67 (34.78)	378.28 (79.10)	435.70 (51.71)	401.74 (51.05)	352.58 (52.49)
Lycosidae	716.80 (130.81)	1145.66 (134.93)	1160.74 (268.75)	917.41 (88.67)	819.60 (107.38)	1024.07 (149.22)
Coleoptera						
Carabidae	263.77^b (90.89)	663.24^{ab} (220.00)	510.40^{ab} (157.00)	456.93^b (167.11)	427.19^{ab} (96.81)	784.57^a (233.00)
Staphylinidae*						
2012	358.66 (176.73)	242.88 (78.19)	234.41 (44.97)	218.47 (57.83)	229.36 (51.50)	147.33 (23.50)
2013	277.27 (32.46)	226.14 (66.42)	715.44 (257.02)	459.51 (63.79)	515.03 (155.53)	311.68 (67.96)
Diptera						
Sciariidae	301.39 (109.91)	372.56 (123.29)	249.42 (127.11)	160.07 (49.64)	441.66 (222.44)	246.79 (45.46)
Hymenoptera						
Formicidae	10572.37 (1119.87)	13224.41 (2930.21)	16316.49 (2802.05)	17303.55 (4556.60)	15456.07 (3188.12)	12767.54 (3042.93)
Orthoptera						
Gryllidae	968.94^b (200.59)	1920.18^{ab} (452.51)	1170.95^b (224.11)	1617.14^{ab} (265.96)	1922.62^{ab} (442.20)	2610.55^a (361.00)
Gryllidae (nymphs)‡	545.04^b (164.50)	1098.90^{ab} (306.92)	602.17^b (229.81)	848.20^{ab} (267.14)	986.71^{ab} (240.01)	1323.41^a (425.63)

Notes: Treatments included (1) intensive downed wood removal (NOBHGs); (2) 15% downed wood retention distributed evenly throughout the treatment unit (15DISP); (3) 15% downed wood retention in piles (15CLUS); (4) 30% downed wood retention distributed evenly throughout the treatment unit (30DISP); (5) 30% downed wood retention in piles (30CLUS); and (6) no downed wood removal (NOBIOHARV). Only taxa meeting cutoff requirements were included in analyses. Different letters indicate significantly different, pair-wise comparisons of treatment means. We set $\alpha = 0.05$. Rows in bold signify detection of significant differences among treatments.

*Significant year \times location interaction ($P \leq 0.05$), in which case years were analyzed separately.

†Includes all spiders not in Lycosidae.

‡Gryllid nymphs.

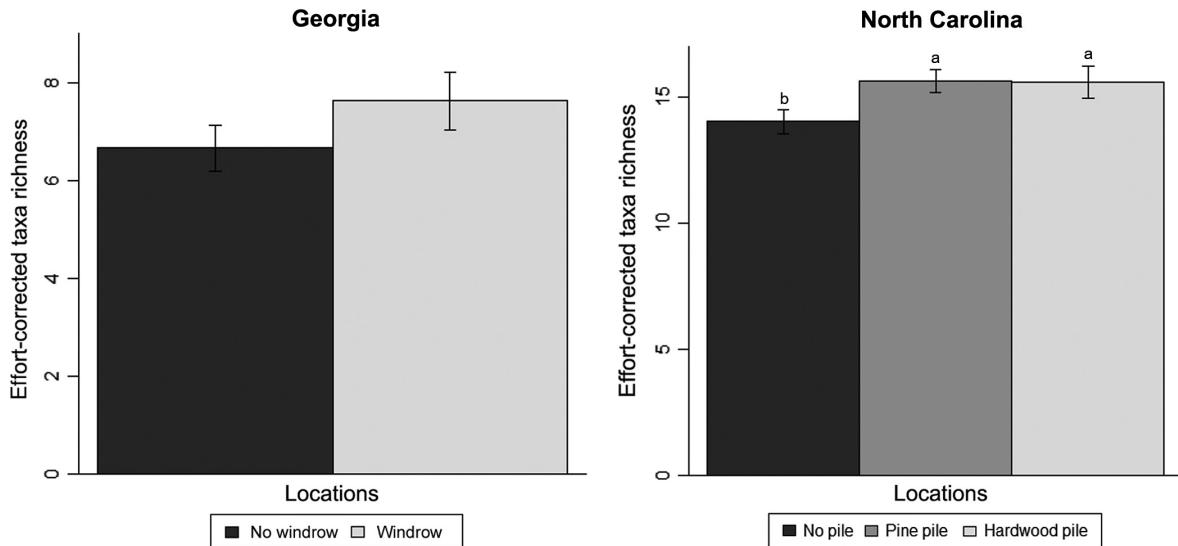


FIG. 3. Effects of no pile, pine pile, and hardwood pile locations in North Carolina and no windrow and windrow locations in Georgia on invertebrate taxa richness following woody biomass harvesting in regenerating stands. Different letters over bars indicate significantly different, pairwise comparisons of location means at $\alpha = 0.05$ level. Error bars show SE.

relative abundance of ectobiids (2012), formicids (2013), and rhabdophorids (2012) was greater in windrow locations than in no windrow locations (Table 3). In 2012, relative abundance of formicids and lycosids was greater in no windrow locations than in windrow locations. In both states, most invertebrate taxa were unaffected by array-level groundcover (Tables 2, 3).

DISCUSSION

Our results indicate that coarse woody debris is an important, local-scale habitat component influencing the pattern of surface-active invertebrate diversity in regenerating pine plantations. Specifically, the pattern of coarse woody debris availability within harvested stands following woody biomass harvesting had important implications for the pattern of invertebrate community richness in regenerating stands, echoing similar studies conducted in mature forests. For example, experimentally reduced volumes of coarse woody debris negatively affected invertebrate community composition in mature pine forests in the southeastern United States (Hanula et al. 2006), and Grove (2002) documented a positive correlation between beetle richness and volume of coarse woody debris in mature forests of Australia.

We documented evidence of positive relationships between fungus-associated invertebrates, including erotylid beetles and mycetophilid and sciarid flies, and harvest residue availability, suggesting that harvest residue removal may affect “bottom-up” interactions between fungi and some fungivorous invertebrates. Species richness of wood-decaying fungi typically increases with the amount of available coarse woody debris (Berg et al. 1994, Allen et al. 2000, Lonsdale et al. 2008). Küffer and

Senn-Irlet (2005) postulated coarse woody debris may provide refugia for many wood-inhabiting fungi that specifically occur in intensively managed forests. As such, greater relative abundance of erotylids, mycetophilids, and sciarids at harvest residue pile locations than at no pile locations may be linked to availability of coarse woody debris-associated fungi and associated breeding substrate for these taxa. In turn, invertebrate fungivores may influence fungal community structure via grazing pressure and act as dispersal agents for fungal spores (Shaw 1992). Many studies of mycetophilid and other dipteran fungivores have been conducted in mature, European forests (e.g., Komonen 2001), where it has been estimated that 417 mycetophilid species may be associated with over 600 species of fungi (Jakovlev 2012). However, the amount of dead wood has been positively correlated with mycetophilid diversity in both harvested and unharvested forests in Norway (Økland 1994, 1996). Our results suggest that coarse woody debris also is an important habitat component for mycetophilids and some other fungivores in early-successional, regenerating stands of the United States and that intensive harvest residue removal may compromise habitat availability for some invertebrate fungivores.

Retention of coarse woody debris favored crickets and wood roaches. Given their active foraging habits and typically high abundance, crickets are integral components of many forest food webs (Ponsard and Ardit 2000). Additionally, crickets act as detritivores, aiding in decomposition of organic matter and nutrient cycling in soil (Dangles et al. 2005). Similarly, wood roaches are consumers of plant debris and litter in the detrital trophic chain and provide food resources for forest wildlife (Crossley 1977, Horn and Hanula 2002). Relative abundance of

TABLE 2. Mean (SE in parentheses) number of captured individuals per 100 trap nights and response to groundcover for invertebrate taxa captured at 68 pitfall trap arrays situated among no pile, pine pile, and hardwood pile locations (herein "locations") following woody biomass harvesting in regenerating stands ($n = 4$), North Carolina, pooled among 2012 and 2013.

Invertebrate taxa	Location			Percent groundcover	
	No pile	Pine pile	Hardwood pile	Fine woody debris	Vegetation
Araneae †	30.72^{ab} (2.88)	41.02^a (3.77)	28.18^b (2.82)	Ø	Ø
Lycosidae	86.67 (7.44)	94.01 (8.39)	75.65 (7.58)	Ø	Ø
Blattodea					
Ectobiidae *					
2012	4.80 (1.23)	5.38 (2.30)	4.43 (1.72)	Ø	+
2013	3.64^b (1.15)	28.24^a (6.28)	15.70^a (3.28)	Ø	Ø
Chilopoda	15.48 (2.66)	11.10 (2.20)	10.47 (1.92)	Ø	Ø
Coleoptera					
Carabidae‡	44.32 (8.31)	42.59 (6.24)	50.72 (6.48)	Ø	Ø
Cicindellinae	6.02 (1.34)	4.81 (1.19)	5.92 (1.80)	Ø	Ø
Erotylidae (2013)	2.88^b (1.11)	4.46^a (1.39)	11.10^a (3.24)	–	Ø
Galerucinae (2013)	98.67 (26.37)	123.29 (26.75)	152.07 (43.69)	Ø	Ø
Nitidulidae (2013)	6.65 (2.13)	5.92 (2.07)	4.83 (2.22)	Ø	Ø
Scarabaeidae	11.60 (2.91)	5.32 (1.07)	9.17 (2.42)	Ø	Ø
Scolytinae (2012)	7.92 (2.98)	5.09 (1.89)	8.56 (4.15)	Ø	Ø
Staphylinidae	28.40 (3.94)	31.42 (6.81)	26.87 (3.51)	–	Ø
Diplopoda § (2012)	61.89^b (21.39)	103.11^a (28.49)	51.97^b (12.43)	–	Ø
Paradoxosomatidae (2013)	305.39 (82.13)	330.40 (90.05)	356.45 (104.58)	Ø	Ø
Diptera					
Ceratopogoniidae (2013)	9.48 (2.46)	16.29 (4.09)	14.86 (5.04)	Ø	Ø
Chloropidae (2013)	11.19 (2.71)	10.66 (2.59)	12.49 (3.27)	Ø	Ø
Dolichopodidae	14.32 (2.12)	11.90 (2.04)	14.95 (3.25)	Ø	Ø
Mycetophilidae *					
2012	1.65^b (0.68)	8.57^a (3.61)	5.88^a (1.78)	Ø	Ø
2013	2.11^b (0.91)	5.92^{ab} (1.28)	8.46^a (2.20)	Ø	Ø
Phoridae	5.46 (1.32)	5.82 (1.25)	5.62 (1.22)	Ø	–
Sciaridae *					
2012	22.18^b (5.48)	45.72^a (11.66)	22.19^b (6.59)	Ø	Ø
2013	7.54^b (2.31)	27.60^a (9.13)	31.82^a (12.80)	Ø	Ø
Schizophora¶ (2012)	14.61 (2.93)	18.02 (3.90)	12.08 (2.52)	Ø	Ø
Sphaeroceridae (2013)	3.36^b (1.27)	17.28^a (10.44)	9.97^{ab} (3.41)	–	Ø
Tipulidae (2013)	3.85 (1.59)	4.65 (1.27)	8.01 (4.36)	Ø	+
Hemiptera					
Acrididae	7.30 (1.62)	5.12 (1.22)	9.02 (1.93)	Ø	Ø
Aphididae	5.26 (1.22)	9.25 (2.97)	6.58 (1.54)	Ø	Ø
Cicadellidae	12.81 (1.75)	12.98 (2.17)	11.81 (1.63)	Ø	Ø
Cydnidae (2013)	5.30 (2.10)	10.30 (4.41)	15.30 (5.40)	Ø	Ø
Delphacidae (2012)	3.68 (1.67)	6.28 (2.25)	5.76 (2.22)	–	Ø
Reduviidae (2013)	6.80 (2.02)	5.97 (1.98)	8.16 (2.59)	Ø	Ø
Hymenoptera					
Formicidae	1328.33 (123.46)	1215.83 (104.16)	1246.32 (145.87)	Ø	Ø
Scelionidae (2013)	14.20 (2.85)	7.40 (1.60)	8.91 (2.01)	Ø	–
Orthoptera					
Gryllidae#	136.98 (12.71)	143.74 (15.66)	172.89 (18.62)	Ø	Ø
Gryllidae (nymph)	73.79 (10.48)	75.10 (9.62)	92.62 (15.24)	Ø	Ø
Nemobiinae (2013)	7.85 (2.94)	9.96 (4.36)	9.64 (4.35)	Ø	Ø

Notes: Only taxa meeting cutoff requirements were included in analyses. Different letters indicate significantly different, pair-wise comparisons of location means. + or – indicates positive or negative response, respectively. Ø indicates no response. We set $\alpha = 0.05$. Rows in bold signify detection of significant differences among locations.

*Indicates significant year \times location interaction ($P \leq 0.05$), in which case years were analyzed separately.

†Includes all spiders not in Lycosidae.

‡Cicindellinae split from total count of Carabidae.

§Pooled all diplopod families.

¶Sphaeroceridae excluded from total count of Schizophorans.

#Nemobiinae excluded from total count of Gryllidae.

TABLE 3. Mean (SE in parentheses) number of captured individuals per 100 trap nights and response to groundcover for invertebrate taxa captured at 48 pitfall trap arrays situated among no windrow and windrow locations (herein "locations") following woody biomass harvesting in regenerating stands ($n = 4$), Georgia, pooled among 2012 and 2013.

Invertebrate taxa	Location		Percent groundcover	
	No windrow	Windrow	Fine woody debris	Vegetation
Araneae†	50.57 (10.23)	67.97 (11.62)	Ø	Ø
Lycosidae*				
2012	224.33^a (66.18)	123.33^b (27.58)	Ø	Ø
2013	81.25 (14.53)	119.79 (19.50)	Ø	Ø
Blattodea				
Ectobiidae (2012)	29.93^b (10.68)	233.43^a (106.06)	Ø	Ø
Coleoptera				
Carabidae	41.30 (10.02)	46.44 (8.54)	Ø	Ø
Diptera				
Ceratopogoniidae (2013)	25.00 (8.24)	53.13 (16.71)	+	+
Hymenoptera				
Formicidae*				
2012	2165.11^a (652.80)	904.33^b (225.50)	Ø	Ø
2013	933.33^b (149.73)	1487.50^a (185.66)	Ø	Ø
Orthoptera				
Gryllidae	125.58 (22.61)	179.12 (29.94)	Ø	Ø
Gryllidae [nymph (2013)]	54.17 (14.95)	89.58 (30.17)	Ø	Ø
Rhaphidophoridae (2012)	18.06^b (9.14)	86.87^a (26.39)	–	Ø

Notes: Only taxa meeting cutoff requirements were included in analyses. Different letters indicate significantly different, pair-wise comparisons of location means. + or – indicates positive or negative response, respectively. Ø indicates no response. We set $\alpha = 0.05$. Rows in bold signify detection of significant differences among locations.

*Indicates significant year \times treatment interaction ($P \leq 0.05$), in which case years were analyzed separately.

†Includes all spiders not in Lycosidae.

both gryllid adults and nymphs were greater in NOBIOHARV than in NOBHGs, which indicates that intensive harvest residue removal in regenerating stands without $\geq 15\%$ retention of harvest residue volume could decrease prey resources and ecosystem services provided by multiple life stages of gryllids at stand levels. Rhaphidophorids had greater relative abundance in windrow locations than in no windrow locations, potentially providing locally abundant prey resources for other invertebrates and vertebrates already using windrows for cover. Wood roaches were primarily represented by the ectobiid genus *Parcoblatta* (S. M. Grodsky, unpublished data); given the apparent positive association between ectobiids and coarse woody debris, *Parcoblatta* may be especially susceptible to harvest residue removal in regenerating stands. Previous studies in pine forests of the southeastern United States have demonstrated that coarse woody debris provides cover for *Parcoblatta* species, many of which are eaten by forest birds (Horn and Hanula 2002, Hanula et al. 2006).

Carabid beetles are well-established ecological indicators for forest ecosystem health (Taylor and Doran 2001, Pearce and Venier 2006, Iglay et al. 2012, Grodsky et al. 2015), and the beetle family demonstrated a positive, stand-level response to harvest residue retention in NC. Nittérus et al. (2007) addressed carabid beetle response to harvest residue removal in the context of woody biomass harvesting and found that harvest residue removal caused a shift in community composition in the form of increasing generalist species and decreasing forest species.

Additionally, previous forest management studies showed that coarse woody debris may be an important habitat component for carabid beetles in recent clearcuts and mature forests alike (Pearce et al. 2003, Latty et al. 2006). Many carabid beetles are ground predators of other invertebrates (Tolonen 1995); some predatory carabid beetles may have been more abundant in NOBIOHARV than in NOBHGs because more harvest residues in NOBIOHARV supported greater arthropod prey resources (e.g., Ulyshen and Hanula 2009a). Greater relative abundance granivorous carabids in NOBIOHARV than in NOBHGs may be explained by the "seed-damming" hypothesis, which postulates that piles of coarse woody debris may trap seeds dispersed by surface water flow or wind and subsequently provide locally abundant food resources for granivores (Loeb 1996, Sharitz 1996).

Given the dynamic marketability of different woody biomass feedstocks, understanding differences in invertebrate responses to pine compared to hardwood harvest residue removal may be important. Invertebrate responses for a few taxa differed between pine and hardwood pile locations, possibly due to differences in tree species composition (e.g., Jonsell 2008), decay rates, and/or fungal community composition. For example, the relative abundance of diplopods was greater at pine pile locations than no pile and hardwood pile locations. Diplopods at high risk for desiccation in exposed regenerating stands may have selected pine piles over hardwood piles because pine piles may have been more

decayed and therefore moist, which in turn may have facilitated water replacement via cuticular and gut water exchange in diplopods (O'Neill 1969). Sciarid flies selected pine pile locations over hardwood and no pile locations in 2012, but selected both pine and hardwood pile locations over no pile locations in 2013. This result may indicate that hardwood piles were not sufficiently decayed to support fungal communities for this fungivore in 2012, but supported sufficient fungi in 2013 after another year of decay. As fungivores, both diplopods and sciarids may have associated with the distinct fungal communities predominantly or exclusively found on dead pine (e.g., Visser 1995, Gardes and Bruns 1996).

Following timber harvest, the influx of harvest residues is accompanied by increases in early successional vegetation (White and Jenstch 2001, Grodsky et al. 2016b), which may have acted independently of, or in conjunction with, mechanisms like harvest residue decay to drive invertebrate use of regenerating stands. Several common invertebrate groups, including many herbivores and their predators, likely responded to the successional trajectory of vegetation composition and structure rather than harvest residue availability in regenerating stands. In NC, several invertebrate groups increased at micro- and stand-scales from 2012 to 2013, which may have been related to increased vegetative cover and/or coarse woody debris decay. Nevertheless, vegetation composition and structure was similar among treatments and locations (Grodsky 2016), so observed differences in invertebrate abundance were most likely related to coarse woody debris and its dynamics.

Lack of apparent responses of some invertebrates (e.g., ants, spiders) to harvest residue removal may have been a function of taxonomic resolution, and if we had identified highly diverse invertebrate groups, for instance, to genus or species, different patterns may have emerged. For example, many ant species use coarse woody debris for nesting (Hagan and Grove 1999, Higgins and Lindgren 2006). Yet, recent clearcuts provide favorable conditions, including lack of overstory and prevalent bare ground, for red imported fire ant (*Solenopsis invicta*) invasions (Zettler et al. 2004). Todd et al. (2008) reported that colonization of red imported fire ants in the southeastern United States may be deterred by retention of coarse woody debris in clearcuts. The red imported fire ant exemplifies a highly abundant ant species that may have avoided areas with coarse woody debris, and, in turn, may have offset the family-level ant response to coarse woody debris removal in regenerating stands. In this case, understanding fire ant response to coarse woody debris removal, in contrast with that of native, downed-wood-associated ant species, may have informed implications of woody biomass harvesting on ecosystem integrity. Specifically, fire ants are considered detrimental, noxious invaders of young forests that negatively affect forest communities, whereas native, downed-wood associated ants often facilitate ecosystem services in forests (Zettler et al. 2004).

Many individual invertebrate groups did not respond to harvest residue removal at the family level. However, invertebrate taxa richness and relative abundance of several key invertebrate groups were positively linked to harvest residue availability in young, intensively managed forests. Further, we demonstrated positive, invertebrate-coarse-woody-debris relationships at both micro and stand scales in the operational context of woody biomass harvests. As such, intensified woody biomass harvesting without retention of $\geq 15\%$ of harvest residue volume may adversely affect invertebrate diversity and some key invertebrate taxa. Harvest residue management during and after woody biomass harvesting may be an important consideration for conserving invertebrates that play major roles in maintenance of ecosystem function and integrity in young forests. We suggest future entomological studies regarding woody biomass harvesting in regenerating stands specifically focus on invertebrate families we identified as positively responding to harvest residue retention to determine ecological responses of species to harvest residue removal in regenerating stands. Further, studies extending beyond the stand level to investigate landscape-scale availability of coarse woody debris in managed pine forests may facilitate understanding of invertebrate use of downed wood resources in intensively managed forest landscapes.

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LITERATURE CITED

- Allen, R. B., P. K. Buchanan, P. W. Clinton, and A. J. Cone. 2000. Composition and diversity of fungi on decaying logs in a New Zealand temperate beech (*Nothofagus*) forest. *Canadian Journal of Forest Research* 30:1025–1033.
- Andrew, N., L. Rodgerson, and A. York. 2000. Frequent fuel-reduction burning: the role of logs and associated leaf-litter in the conservation of ant biodiversity. *Austral Ecology* 25:99–107.
- Annamalai, M. S., and M. Wooldridge. 2001. Co-firing of coal and biomass fuel blends. *Progress in Energy and Combustion Science* 27:171–214.
- Ausden, M. 1996. Invertebrates. Pages 139–177 in W. J. Sutherland, editor. *Ecological census techniques. A handbook*. Cambridge University Press, Avon, UK.
- Bengtsson, J., T. Persson, and H. Lundkvist. 1997. Long-term effects of logging residue addition and removal on macroarthropods and enchytraeids. *Journal of Applied Ecology* 34: 1014–1022.

- Berg, Å., B. Ehnström, L. Gustasson, T. Hallingbäck, M. Jonsell, and J. Weslien. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology* 8:718–731.
- Bouget, C., L. Larrieu, B. Nusillard, and G. Parmian. 2013. In search of the best habitat drivers for saproxylic beetle diversity in temperate deciduous forests. *Biodiversity and Conservation* 22:2111–2130.
- Buddle, C. M. 2001. Spiders (Araneae) associated with downed woody material in a deciduous forest in central Alberta, Canada. *Agricultural and Forest Entomology* 3:241–251.
- Castro, A., and D. H. Wise. 2009. Influence of fine woody debris on spider diversity and community structure in forest leaf litter. *Biodiversity and Conservation* 18:3705–3731.
- Castro, A., and D. H. Wise. 2010. Influence of fallen coarse woody debris on the diversity and community structure of forest-floor spiders (Arachnida: Araneae). *Forest Ecology and Management* 260:2088–2101.
- Crossley Jr., D. A. 1977. The roles of terrestrial saprophagous arthropods in forest soils: current status and concepts. Pages 49–56 in W. J. Matteson, editor. *The role of arthropods in forest ecosystems*. Springer-Verlag, New York, New York, USA.
- Dangles, O., C. Magal, D. Pierre, A. Olivier, and J. Casas. 2005. Variation in morphology and performance of predator-sensing system in wild cricket populations. *Journal of Experimental Biology* 208:461–468.
- Elton, C. S. 1966. Dying and dead wood. Pages 279–305. *The pattern of animal communities*. Wiley, New York, New York, USA.
- Eräjää, S., P. Halme, J. S. Kotiaho, A. Markkanen, and T. Toivainen. 2010. The volume and composition of dead wood on traditional and forest fuel harvested clear-cuts. *Silva Fennica* 44:203–211.
- Evans, A. M., P. W. Clinton, R. B. Allen, and C. M. Frampton. 2003. The influence of logs on the spatial distribution of litter-dwelling invertebrates and forest floor processes in New Zealand forests. *Forest Ecology and Management* 184: 251–262.
- Evans, J. M., R. J. Fletcher Jr., J. R. R. Alavalapati, A. L. Smith, D. Geller, P. Lal, D. Vasudev, M. Acevedo, F. Calabria, and T. Upadhyay. 2013. Forestry bioenergy in the southeast United States. Pages 1–275. Implications for wildlife habitat and biodiversity. National Wildlife Federation, Merrifield, Virginia, USA.
- Forisk Consulting. 2013. Forisk news. <http://forsik.com/wordpress/wp-content/assets/Forisk-News-20131108.df>
- Fraver, S., R. G. Wagner, and M. Day. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, USA. *Canadian Journal of Forest Research* 32:2094–2105.
- Fritts, S. R., C. E. Moorman, D. W. Hazel, and B. D. Jackson. 2014. Biomass harvesting guidelines affect downed wood debris retention. *Biomass and Bioenergy* 70:382–391.
- Gardes, M., and T. D. Bruns. 1996. Community structure of ectomycorrhizal fungi in a *Pinus muricata* forest: above- and below-ground views. *Canadian Journal of Botany* 74:1572–1583.
- Greenslade, P. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* 33:301–310.
- Grodsky, S. M. 2016. How good is downed wood? Avian and invertebrate conservation and forest bioenergy in the southeastern United States. Dissertation. North Carolina State University, Raleigh, North Carolina, USA.
- Grodsky, S. M., R. B. Iglay, C. E. Sorenson, and C. E. Moorman. 2015. Should invertebrates receive greater inclusion in wildlife research journals? *Journal of Wildlife Management* 79:529–536.
- Grodsky, S. M., C. E. Moorman, S. R. Fritts, D. W. Hazel, J. A. Homyak, S. B. Castleberry, and T. B. Wigley. 2016a. Winter bird use of harvest residues in clearcuts and the implications of forest bioenergy harvest in the southeastern United States. *Forest Ecology and Management* 379:91–101.
- Grodsky, S. M., C. E. Moorman and K. R. Russell. 2016b. Forest wildlife management. Pages 47–85 in G. Larocque, editor. *Ecological forest management handbook*. Taylor and Francis Group, LLC/CRC Press, Boca Raton, Florida, USA.
- Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. *Annual Review of Ecology and Systematics* 33:1–23.
- Hagan, J. M., and S. L. Grove. 1999. Coarse woody debris. *Journal of Forestry* 97:6–11.
- Hanula, J. L., S. Horn and D. D. Wade. 2006. The role of dead wood in maintaining arthropod diversity on the forest floor. Pages 57–66 in S. J. Grove and J. L. Hanula, editors. *Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology, 15–24 August 2004*. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, USA.
- Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advanced Ecological Research* 15: 133–202.
- Harmon, M. E., and C. Hua. 1991. Coarse woody debris dynamics in two old-growth ecosystems. *BioScience* 41:604–610.
- Higgins, R. J. and B. S. Lindgren. 2006. Insect biodiversity and dead wood: proceedings of a symposium for the 22nd International Congress of Entomology. Pages 1–120 in S. J. Grove and J. L. Hanula, editors. *General Technical Report SRS-93*. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, North Carolina, USA.
- Horn, S., and J. Hanula. 2002. Life history and habitat associations of the broad wood cockroach (*Parcoblatta lata*) (Blattaria: Blattellidae) and other native cockroaches in the Coastal Plain of South Carolina. *Annals of the Entomological Society of America* 95:665–671.
- Hothorn, T., F. Bretz, P. Westfall, R. M. Heiberger and A. Schuetzenmeister. 2013. Package multcomp. <http://cran.r-project.org/web/packages/multcomp/multcomp.pdf>
- Huston, M. A. 1996. Modeling and management implications of coarse woody debris impacts on biodiversity. Pages 139–143 in J. McMinn and D. A. Crossley, editors. *Biodiversity and coarse woody debris in southern forests*. General Technical Report SE-94. USDA Forest Service, Athens, Georgia, USA.
- Iglay, R. B., D. A. Miller, B. D. Leopold, and G. Wang. 2012. Carabid beetle response to prescribed fire and herbicide in intensively managed, mid-rotation pine stands in Mississippi. *Forest Ecology and Management* 281:41–47.
- Jabin, M., D. Mohr, H. Kappes, and W. Topp. 2004. Influence of deadwood on density of soil macro-arthropods in a managed oak-beech forest. *Forest Ecology and Management* 194:61–69.
- Jabin, M., W. Topp, J. Kulfan, and P. Zach. 2007. The distribution pattern of centipedes in four primeval forests on central Slovakia. *Biodiversity and Conservation* 16:3437–3445.
- Jakovlev, J. 2012. Fungal hosts of mycetophilids (Diptera: Scarioidea excluding Sciaridae): a review. *Mycology* 3:11–23.
- Janowiak, M. K., and C. R. Webster. 2010. Promoting ecological sustainability in woody biomass harvesting. *Journal of Forestry* 108:16–23.
- Jones, P., B. Hanberry, and S. Demarias. 2009. Stand-level wildlife habitat features and biodiversity in southern pine forests: a review. *Journal of Forestry* 8:398–404.

- Jonsell, M. 2008. Saproxyllic beetle species in logging residues: which are they and which residues do they use? *Norwegian Journal of Entomology* 55:109–122.
- Jonsell, M., J. Hansson, and L. Wedmo. 2007. Diversity of saproxyllic beetle species in logging residues in Sweden – Comparisons between tree species and diameters. *Biological Conservation* 138:89–99.
- Kappes, H., C. Catalano, and W. Topp. 2007. Coarse woody debris ameliorates chemical and biotic parameters of acidified broad-leaf forests. *Applied Soil Ecology* 36:190–198.
- Kataja-Aho, S., P. Hannonen, T. Liukkonen, H. Rosten, M. J. Koivula, S. Koponen, et al. 2016. The arthropod community of boreal Norway spruce forests responds variably to stump harvesting. *Forest Ecology and Management* 371:75–83.
- Komonen, A. 2001. Structure of insect communities inhabiting old-growth forest specialist bracket fungi. *Ecological Entomology* 26:63–75.
- Küffer, N., and B. Senn-Irlet. 2005. Influence of forest management on the species-richness and composition of wood-inhabiting basidiomycetes in Swiss forests. *Biodiversity and Conservation* 14:2419–2435.
- Landis, D. A., and B. P. Werling. 2010. Arthropods and biofuel production systems in North America. *Insect Science* 17:220–236.
- Lassaue, A., F. Lieutier, and C. Bouget. 2012. Woodfuel harvesting and biodiversity conservation in temperate forests: effects of logging residue characteristics on saproxyllic beetle assemblages. *Biological Conservation* 147:204–212.
- Latty, E. F., S. M. Werner, D. J. Mladenoff, K. F. Raffa, and T. A. Sickley. 2006. Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood–hemlock forests. *Forest Ecology and Management* 222:335–347.
- Loeb, S. C. 1996. The role of coarse woody debris in the ecology of southeastern mammals. Pages 108–118 in J. W. McMinn and D. A. Crossley Jr., editors. *Biodiversity and coarse woody debris in southern forests*. Technical Report SE-94. U.S. Forest Service, Washington, D.C., USA.
- Lonsdale, D., M. Oautasso, and O. Holdenrieder. 2008. Wood-decaying fungi in the forest: conservation needs and management options. *European Journal of Forest Research* 127: 1–22.
- Marra, J. L., and R. L. Edmonds. 1998. Effects of coarse woody debris and soil depth on the density and diversity of soil invertebrates in clear-cut and forested sites on the Olympic Peninsula, Washington. *Environmental Entomology* 27: 1111–1124.
- McMinn, J. W. and D. A. Crossley, editors. 1996. *Biodiversity and coarse woody debris in southern forests*. Proceedings of the workshop on coarse woody debris in southern forests: effects on biodiversity. October 18–20, 1993, Athens, Georgia. General Technical Report SE-94. Department of Agriculture, Forest Service, Southern Research Station, Asheville, North Carolina, USA.
- Murkin, H. R., D. A. Wrubleski, and F. A. Reid. 1994. Sampling invertebrates in aquatic and terrestrial habitats. Pages 349–369 in T. A. Bookhout, editor. *Research and management techniques for wildlife and habitats*. Allan Press, Lawrence, Kansas, USA.
- Nittérus, K., M. Åström, and B. Gunnarson. 2007. Harvest of logging residue in clear-cuts affects the diversity and community composition of ground beetles (Coleoptera: Carabidae). *Scandinavian Journal of Forest Research* 22:231–240.
- Økland, B. 1994. Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. *Biological Conservation* 3:68–85.
- Økland, B. 1996. Unlogged forests: important site for preserving the diversity of mycetophilids (Diptera: Sciarioidea). *Biological Conservation* 76:297–310.
- O’Neill, R. V. 1969. Adaptive responses to desiccation in the millipede, *Narceus americanus* (Beauvois). *American Midland Naturalist* 81:578–583.
- Parikka, M. 2004. Global biomass fuel resources. *Biomass and Bioenergy* 27:613–620.
- Pearce, J. L., and L. A. Venier. 2006. The use of ground beetles (Coleoptera: Carabidae) and spiders (Araneae) as bioindicators of sustainable forest management: A review. *Ecological Indicators* 6:780–793.
- Pearce, J. L., L. A. Venier, J. McKee, J. Pedlar, and D. McKenney. 2003. Influence of habitat and microhabitat on carabid (Coleoptera: Carabidae) assemblages in four stand types. *Canadian Entomologist* 135:337–357.
- Perschel, B., A. Evans, and M. DeBonis. 2012. *Forest biomass retention and harvesting guidelines for the Southeast*. Forest Guild Southeast Biomass Working Group. Forest Guild, Sante Fe, New Mexico, USA.
- Ponsard, S., and R. Arditì. 2000. What can stable isotopes ($\delta^{15}\text{N}$ AND $\delta^{13}\text{C}$) tell about the food web of soil macro-invertebrates? *Ecology* 81:852–864.
- Remsburg, A. J., and M. G. Turner. 2006. Amount, position, and age of coarse wood influence litter decomposition in postfire *Pinus contorta* stands. *Canadian Journal of Forestry Research* 36:2112–2123.
- Riffell, S., J. Verschuyll, D. Miller, and T. B. Wigley. 2011. Biofuel harvests, coarse woody debris, and biodiversity – a meta-analysis. *Forest Ecology and Management* 261:878–887.
- Rudolph, J., and L. Gustafsson. 2005. Effects of forest-fuel harvesting on the amount of deadwood on clear cuts. *Scandinavian Journal of Forest Research* 20:235–242.
- Sharitz, P. 1996. Coarse woody debris and seedling recruitment in southeastern forests. Pages 29–34 in J. W. McMinn and D. A. Crossley Jr., editors. *Biodiversity and coarse woody debris in southern forests*. Technical Report SE-94. U.S. Forest Service, Washington, D.C., USA.
- Shaw, P. J. A. 1992. Fungi, fungivores, and fungal food webs. Pages 295–310 in G. Carroll and D. Wicklow, editors. *The fungal community: its organization and role in the ecosystem*. Second edition. Dekker, New York, New York, USA.
- Sikkema, R., M. Steiner, M. Junginger, W. Hiegl, M. T. Hansen, and A. Faaij. 2011. The European wood pellet market: current status and prospects for 2020. *Biofuels, Bioproducts, and Biorefining* 5:250–278.
- Spears, J. H. D., S. M. Holug, M. E. Harmon, and K. Lajtha. 2003. The influence of decomposing logs on soil biology and nutrient cycling in old-growth mixed coniferous forests in Oregon, USA. *Canadian Journal of Forestry Research* 33:2193–2201.
- Spence, J. R., and J. Niemelä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Canadian Entomologist* 126:881–894.
- Taylor, R. J., and N. Doran. 2001. Use of terrestrial invertebrates as indicators of the ecological sustainability of forest management under the Montreal Process. *Journal of Insect Conservation* 5:221–231.
- Todd, B. D., B. B. Rothermel, R. N. Reed, T. M. Lühring, K. Schlatter, L. Trenkamp, and J. W. Gibbons. 2008. Habitat alteration increases invasive fire ant abundance to the detriment of amphibians and reptiles. *Biological Invasions* 10: 539–546.
- Tolonen, T. 1995. Importance of generalist epigeal predator species in a cereal field: predation on baits. *Journal of Applied Entomology* 119:113–117.

- Ulyshen, M. D., and J. L. Hanula. 2009a. Responses of arthropods to large-scale manipulations of dead wood in loblolly pine stands of the southeastern United States. *Environmental Entomology* 38:1005–1012.
- Ulyshen, M. D., and J. L. Hanula. 2009b. Litter-dwelling arthropod abundance peaks near coarse woody debris in loblolly pine forests of the southeastern United States. *Florida Entomologist* 92:163–164.
- Ulyshen, M. D., J. L. Hanula, S. Horn, J. C. Kilgo, and C. E. Moorman. 2004. Spatial and temporal patterns of beetles associated with coarse woody debris in managed bottomland hardwood forests. *Forest Ecology and Management* 199: 259–272.
- United States Department of Agriculture. 2007. Phase 3 field guide—down woody material, version 4.0 . http://fia.fs.fed.us/library/field-guides-methods-proc/docs/2007/p3_4-0_sec14_10_2007.pdf
- Van Wagner, C. E. 1968. The line intersect method in forest fuel sampling. *Forest Science* 14:20–26.
- Varadi-Szabo, H., and C. M. Buddle. 2006. On the relationships between ground-dwelling spider (Araneae) assemblages and dead wood in a northern sugar maple forest. *Biodiversity and Conservation* 15:4119–4141.
- Visser, S. 1995. Ectomycorrhizal fungal succession in jack pine stands following wildfire. *New Phytologist* 129:389–401.
- White, P. S., and A. Jenstch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62:399–450.
- Woodbury, P. B., J. E. Smith, and L. S. Heath. 2007. Carbon sequestration in the U.S. forest sector from 1990 to 2010. *Forest Ecology and Management* 241:14–27.
- Zettler, J. A., M. D. Taylor, C. R. Allen, and T. P. Spira. 2004. Consequences of forest clear-cuts for native and nonindigenous ants (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 97:513–518.
- Zhou, L., L. Dai and L. Zhong. 2007. Review on the decomposition and influence factors of coarse woody debris in forest ecosystems. *Journal of Forestry Research* 18:48–54.

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