ABSTRACT

GRODSKY, STEVEN MARK. How Good is Downed Wood? Avian and Invertebrate Use of Harvest Residues and the Implications of Forest-Based Bioenergy. (Under the direction of Dr. Christopher E. Moorman).

Increased market viability of harvest residues gleaned for forest bioenergy feedstocks may intensify downed wood removal, particularly in intensively managed forests of the Southeast. Meanwhile, downed wood serves important ecological functions, such as providing food and cover for many wildlife species, including birds and invertebrates. Few studies have investigated avian or invertebrate use of downed wood following timber harvests. As such, our objectives were to: (1) evaluate effects of varying intensities of woody biomass harvest on breeding and winter birds and invertebrates, and (2) document ecological relationships between birds and invertebrates and harvest residues. From 2012 – 2014, we surveyed breeding and winter birds and invertebrates in six woody biomass removal treatments with regenerating stands in North Carolina (*n* = 4), and Georgia (*n* = 4), USA. Treatments included clearcut harvest followed by: (1) traditional woody biomass harvest with no biomass harvesting guidelines; (2) 15% retention with harvest residues dispersed; (3) 15% retention with harvest residues clustered; (4) 30% retention with harvest residues dispersed; (5) 30% retention with harvest residues clustered; and (6) no woody biomass harvest (i.e., reference site). We tested for treatment-level effects on winter bird relative abundance (overall and individual species), breeding bird territory density, avian species diversity and richness, counts of birds detected near, in, or on branches of downed wood piles. Additionally, we tested for both large- and local-scale responses of invertebrates to harvest residue retention in the woody biomass removal treatments. We detected few treatment effects on any breeding or winter bird metrics. Our results suggest woody biomass harvests in regenerating stands had little effect on the avian communities therein. Vegetation structure and composition, rather than availability of harvest residues, primarily influenced both breeding and winter bird use of regenerating stands. Most invertebrate taxonomic groups showed no response to harvest residue removal. However, we found strong evidence of positive correlations between fungivore, granivore, and saprophage relative abundances and harvest residue availability, including fine and coarse woody debris, at multiple spatial scales. Retention of harvest residues following timber and woody biomass harvests could benefit several ecologically significant invertebrate functional groups and taxa. Specifically, harvest residues may mediate "bottom-up" interactions between invertebrates and fungi, detritus, and plants, potentially affecting downed-wood decay, site productivity, and seed dispersal in regenerating stands.

How Good is Downed Wood? Avian and Invertebrate Use of Harvest Residues and the Implications of Forest-Based Bioenergy

by
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DEDICATION

To Dr. Leonard H. Grodsky

BIOGRAPHY

During the peak of the northeastern white-tailed deer rut and under a full moon, Steve Grodsky was born on 6 November 1985 in Newton, NJ. He earned a Bachelor of Science degree in Conservation and Applied Ecology from Rutgers, the State University of New Jersey in 2008 and a Master of Science degree in Wildlife Ecology from the University of Wisconsin – Madison in 2010. Currently, Steve is a Postdoctoral Research Scholar in the Department of Entomology at North Carolina State University.

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CHAPTER 1

Winter bird use of downed wood and the implications of forest bioenergy harvest

ABSTRACT

Increased market viability of harvest residues gleaned for forest bioenergy feedstocks may intensify downed wood removal, particularly in intensively managed forests of the Southeast. Meanwhile, downed wood serves important ecological functions, such as providing food and cover for many wildlife species, including birds. Resident and migrant winter birds ubiquitously occur in intensively managed forests, yet we are aware of no study that has examined winter bird response to experimentally manipulated, operational-scale woody biomass harvests. Further, few studies have investigated avian use of downed wood following timber harvests. As such, our objectives were to: (1) evaluate effects of varying intensities of woody biomass harvest on the winter bird community, and (2) document spatial associations between winter bird species and available habitat structure, including downed wood, in regenerating stands. In January and February of 2012-2014, we surveyed birds using a modified version of spot-mapping and quantified vegetation structure and composition (2013 and 2014) in six woody biomass removal treatments in North Carolina, USA ($n = 4$). Treatments included clearcut harvest followed by: (1) traditional woody biomass harvest with no biomass harvesting guidelines; (2) 15% retention with harvest residues dispersed; (3) 15% retention with harvest residues clustered; (4) 30% retention with harvest residues dispersed; (5) 30% retention with harvest residues clustered; and (6) no woody biomass harvest (i.e., reference site). We tested for treatment-level effects on avian relative abundance (overall and individual species), species diversity and richness, counts of winter birds detected near, in, or on branches of downed wood piles, and vegetation composition and structure. In 69 visits over three winters, we observed 3,352 birds in treatments. With the exception of mourning dove (*Zenaida macroura*) and field sparrow (*Spizella pusilla*), we detected no treatment effects on winter bird relative abundance nor on species diversity and richness. Relative abundance of winter birds increased over time as vegetative cover established in regenerating stands. Our results suggest woody biomass harvests in intensively managed forests had no effect on the winter bird community. Further, vegetation structure and composition, rather than availability of harvest residues, primarily influenced winter bird use of regenerating stands.

INTRODUCTION

Renewable energy development has increased worldwide in response to sociopolitical interests in alternative energy production, economics, and policy (Pimentel 2008, IPCC 2011, Creutzig et al. 2014, Erakhrumen 2014). Forest bioenergy is an expanding renewable energy technology of interest (Milbrandt 2005, Mayfield et al. 2013). Intensively managed forests can produce vast amounts of woody biomass (e.g., harvest residues), which in turn may be used as a feedstock for forest bioenergy production to generate heat, electricity, and biofuels (Parikka 2004). Currently, woody biomass is an important feedstock for production of 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 transportation biofuels [United States Department of Agriculture (USDA) 2007, Forisk Consulting 2013].

In the southeastern United States (herein “Southeast”), approximately 22% of timberland is planted forest (Oswalt et al. 2014), much of which is comprised of intensively managed forests, making the “wood basket of the world” a nexus of forest bioenergy development (Mayfield et al. 2013). The Southeast currently is the largest exporter of wood pellets in the world (Evans et al. 2013), and wood pellet production in the region is predicted to increase to meet growing market demands driven by European Union renewable energy mandates (Forisk Consulting 2013, Goh et al. 2013, Galik and Abt 2015). Indeed, burning wood pellets to generate electricity is predicted to emit up to 85% less greenhouse gases than coal-based electricity in the European Union (Wang et al. 2015). The Southeast also is experiencing more rapid development of forest bioenergy-production facilities (e.g., woody biomass power plants) than anywhere else in the world (Mendell and Lang 2012, REN21

2013). Additionally, the USDA has predicted nearly 50% of second generation biofuels required to meet United States biofuel mandates by 2022 will be supplied by forests of the Southeast (USDA 2010).

Reductions of downed wood via gleaning of harvest residues following woody biomass harvests could affect forest ecosystems and wildlife communities (Perschel et al. 2012, Evans et al. 2013). Downed wood plays critical roles in forest ecosystem function and integrity (Harmon et al. 1986, Janowiak and Webster 2010, Riffell et al. 2011). Specifically, downed wood influences nutrient retention and water dynamics (Harmon et al. 1986, Fraver et al. 2002) and provides food and cover for wildlife (Lanham and Guynn 1996, Whiles and Grubaugh 1996) in forests. Following regeneration harvests, harvest residues are gleaned when volumes of downed wood are high (i.e., immediately following a major disturbance like clearcutting; Harmon et al. 1986). Therefore, woody biomass harvests may diminish food and cover resources for wildlife dependent on downed wood that typically occur following clearcutting.

Concerns regarding potential effects of woody biomass harvests on forest ecosystems and sustainability have led to development of non-regulatory biomass harvesting guidelines (BHGs) by state agencies and non-government organizations (Perschel et al. 2012). BHGs specify target volumes of downed wood to be retained on the forest floor for wildlife habitat, nutrient cycling, and erosion control to maintain biological diversity and site productivity (Ranius and Fahrig 2006, Perschel et al. 2012). In general, BHGs are based on the assumption that wildlife universally respond positively to increased volumes of downed wood (i.e., more downed wood is better than less; Harmon and Hua 1991). However, responses to downed wood may differ among wildlife species, suggested volumes and spatial arrangements of downed wood vary among regional BHGs, and BHGs have limited technical underpinnings from a paucity of empirical support. Therefore, research is needed to determine effects of woody biomass harvests and implementation of BHGs on forest ecosystem sustainability and wildlife habitat.

Our study was part of an interdisciplinary research project that assessed sustainability of woody biomass harvests and efficacy of BHGs. We aimed to complement concurrent studies of breeding bird (*see* Grodsky 2016) and herpetofauna, shrew, and small mammal (*see* Fritts 2014, Fritts et al. 2015, Fritts et al. 2016) response to woody biomass harvests in intensively managed forests of the Southeast by using winter birds as study organisms. The Southeast supports a diversity of winter birds, including residents and short-distance winter migrants (Hamel 1992). Yet, winter birds represent an integral but often overlooked component of the bird community of the Southeast, especially in intensively managed forests. Winter bird habitat use is a relevant issue when addressing year-round avian conservation. For example, evidence suggests that successful breeding of resident birds is affected by availability of winter vegetation structure (DellaSala et al. 1996) and winter can be the critical, limiting season influencing avian survival (Chambers and McComb 1997).

In the Southeast, some winter birds use downed wood (Hamel 1992, Lohr et al. 2002), especially coarse woody debris (CWD; debris ≥ 7.62 cm in diameter for a length of at least 0.914 m; Woodall and Monleon 2008). CWD may trap seeds dispersed by surface flooding or wind and subsequently provide locally abundant food resources for granivores (Loeb 1996, Sharitz 1996), potentially including granivorous birds. CWD also harbors high densities of invertebrate prey (Hanula et al. 2006, Castro and Wise 2010). Thus, insectivorous winter birds may center their foraging around CWD when winter temperatures are warm enough for invertebrate activity (i.e., > 40° F). CWD piles maintain a relatively stable thermal environment (Loeb 1996), and winter birds may use CWD as thermal cover, in addition to escape cover (Lima 1993).

Few studies have addressed relationships between winter birds and downed wood, avian response to experimental manipulations of harvest residues, or winter bird use of recent clearcuts (herein “regenerating stands”; Lanham and Guynn 1996, Riffell et al. 2011). The dearth of research on winter bird use of harvest residues, coupled with the lack of empirical data guiding BHGs, indicate that studies of winter bird response to harvest residue removal following woody biomass harvests are warranted. Thus, our primary objectives were to: (1) evaluate effects of varying intensities of woody biomass harvest on the winter bird community; and (2) document spatial associations between winter bird species and available habitat structure, including downed wood, in regenerating stands.

METHODS

Study area and design

We examined winter birds in four replicate, regenerating stands (herein “replicates”) in Beaufort County, North Carolina (-077°0′0″W to -076°53′50″ and 35°34′0″N to 35°38′20″N) within the Coastal Plain Physiographic Region of the Southeast. All four replicates [70.5 ± 6.1 (mean ± SE) ha] were intensively managed forests planted in loblolly pine (*Pinus taeda*) and managed by Weyerhaeuser Company. Replicates were managed for sawtimber production, commercially thinned twice before final harvest at 32-39 years old. Soils were predominantly loam and silt loam.

Following clearcut harvest in November 2010 through February 2011, we implemented woody biomass removal treatments (herein “treatments”) at each replicate. We used a randomized complete-block experimental design, dividing each replicate into the following six treatments [area = 11.7 ± 0.5 (mean ± SE) ha; range = 8.4-16.3 ha]: (1) clearcut with a traditional woody biomass harvest and no BHGs implemented (NOBHGS); (2) clearcut with 15% retention of harvest residues evenly dispersed throughout the treatment (15DISP); (3) clearcut with 15% retention of harvest residues clustered in large piles throughout the treatment (15CLUS); (4) clearcut with 30% retention of harvest residues evenly dispersed throughout the treatment (30DISP); (5) clearcut with 30% retention of harvest residues clustered in large piles throughout the treatment (30CLUS); and (6) clearcut with no woody biomass harvest (i.e., clearcut only; NOBIOHARV), which served as a reference site.

In each treatment, all standing pines merchantable as roundwood were cut and transported to a logging deck with a grapple skidder. For the NOBHG treatments, we instructed loggers to glean all harvest residues they deemed merchantable as woody biomass. For the NOBIOHARV treatments, pine roundwood was harvested; however, we instructed loggers to fell and leave all harvest residues (i.e., primarily midstory hardwoods) not harvested as roundwood.

To implement the four treatments emulating BHGs, we used ArcGIS (ESRI, Redlands, California, USA) to delineate retention areas that represented either 15% or 30% of the total treatment area. Prior to clearcut harvest, we located retention areas using a hand-held Garmin Rino global positioning system (Olathe, Kansas, USA) and flagged boundaries. We retained all hardwoods not merchantable as roundwood in retention areas. Retention areas were clearcut after loggers harvested 85% or 70% of the non-retention treatment areas, and harvest residues were redistributed throughout the treatment unit with a grapple skidder.

Harvest residues from the non-retention areas and the entire NOBHG treatment were chipped at the logging deck during harvest. In retention treatments, loggers used a grapple skidder to spread retained harvest residues from retention areas evenly throughout the DISP treatments or randomly placed piles of harvest residues throughout the CLUS treatments. Because we created treatments by distributing harvest residues with a grapple skidder, individual piles of harvest residues in the CLUS and NOBIOHARV treatments were approximately the size of one grapple load (volume ≈ 36.19 m^3ha^{-1}; Fritts et al. 2014).

In the winter of 2010-2011, site preparation followed clearcut harvest and treatment implementation. Replicates were sheared using a V-shaped blade, bedded into continuous, mounded strips of soil approximately 3 m wide and < 1 m tall, and planted with loblolly pine seedlings during the fall-winter of 2011-2012 at a density of ≈1100 trees ha^{-1}. Shearing moved retained woody biomass into the 3-m space between pine beds (i.e., interbeds). Consequently, woody biomass was rearranged following shearing into long, linear rows in interbeds parallel to pine beds. However, volume of woody biomass in treatments was largely unaltered by site preparation. Replicates were treated with the following two post-harvest herbicide applications of Chopper© (BASF, Raleigh, North Carolina, USA) for herbaceous weed control: (1) a broadcast application (applied by helicopter) one year after harvest; and (2) a banded application (applied only to pine seedlings in bedded rows) two years after harvest. Replicates and treatments were bordered by drainage ditches (~1 m wide) containing vegetation which was unaffected by site preparation and thus more developed than vegetation growing in treatments. A logging road (~3.7 m wide) separated each side of most sites and adjacent forest stands, which typically fell into two age classes: 1) young (~10 years old); and 2) mature (~30 years old). Snags were rare on all replicates.

Avian sampling and habitat use

We surveyed winter birds using a modified version of spot-mapping (Bibby et al. 1992, Lohr et al. 2002) along uniformly distributed, continuous strip transects in treatments from 1 January – 28 February, 2012 – 2014. Transects were 25 m from all replicate edges, 50 m apart from one another, and ran the entire length of the replicates. During each winter field season, one experienced observer continuously walked along transects and counted the number of winter birds within each treatment, in drainage ditches (see *Study area and design*), and ~10 m into adjacent forest stands (herein "adjacent forest edge"). The observer recorded the spatial location, movements (i.e., with directional arrows), and species of each detected winter bird on maps of treatments. For each detection, the observer also recorded (when applicable) whether the winter bird was on the ground within ~1 m of a downed wood pile (herein "near pile"), within a downed wood pile (herein "in pile"), or on branches protruding from a downed wood pile (herein "on branch of pile"). For each detection, we estimated distance to the nearest drainage ditch and assigned one of three classes: 1) 0 – 25 m; (2) 25 – 50 m; and (3) and ≥ 50 m.

A single observer sampled each of the four replicates and treatments therein 3 times in 2012, 6 times in 2013, and 8 times in 2014. The observer conducted one survey of all treatments in one entire replicate between sunrise and 1000 hours on mornings with no precipitation and winds < 25 km/hour. The observer started each survey route at a random corner of each replicate and alternated the order in which replicates were surveyed to eliminate potential temporal and directional biases. Because we surveyed winter birds 25 m to either side of transect lines in relatively open areas consisting primarily of low-lying, grasses (when vegetation was present), we assumed detection probability in treatments was near 100% (Diefenbach et al. 2003, Plush et al. 2013). Additionally, use of spot mapping allowed us to track winter bird movements (e.g., flushes) after initial detections, which minimized double-counting of individuals.

Quantifying harvest residues

During a concurrent study, Fritts et al. (2014) measured scattered and piled downed wood in each treatment plot in 2012 using the line-intersect sampling (LIS) technique (Van Wagner 1968) and a visual encounter method, respectively (*see* Fritts et al. 2014 for detailed methods). To generate total volume of downed wood (m^3/ha) for each treatment plot, they summed the volume of piled downed wood estimated from the visual encounter method and volume of scattered downed wood estimated using the LIS method.

Quantifying vegetation

We did not characterize vegetation in 2012 because replicates had minimal vegetation due to intensive site preparation and young stand age. In February of 2013 and 2014, when vegetation was well-established in regenerating stands, we characterized vertical vegetation structure, maximum vegetation height, groundcover (i.e., cover < 1 dm off the forest floor), and horizontal vegetation cover (i.e., cover ≥ 1 dm off the forest floor) at three (2013) and six (2014) systematically distributed vegetation plots in each treatment. At each vegetation plot, we established three, 10-m transects along which we measured vegetation at 10, 1-m increments (i.e., 30 total sampling points/vegetation plot). We oriented the first transect based on a random bearing and oriented the remaining two transects 120° to either side (USDA 2007). As an index of vertical structure, we counted the number of times any vegetation type (forb, grass, woody shrubs and vines) touched any decimeter increment along a 2-m tall, 4.8-cm diameter rod at 30 sampling points (Moorman and Guynn 2001). We considered maximum vegetation height for each vegetation plot to be the maximum decimeter increment (up to 2 m) at which we recorded a vegetative hit for each of the 30 sampling points. We recorded groundcover types (bare ground, coarse woody debris, grass, and litter) that touched anywhere from the bottom through the first 1-dm increment of the rod. We recorded horizontal vegetation cover types (forb, grass, and woody shrubs and vines) that touched anywhere above the 1-dm increment of the rod. We calculated percent cover of each groundcover and horizontal vegetation type at each vegetation plot by dividing the number of sampling points where the rod touched each ground or horizontal vegetation type by 30.

Statistical analyses

We calculated yearly relative abundance as the count per treatment in each replicate divided by the number of visits to replicates for each year for all winter bird species combined, each species with ≥ 30 detections per year, and two wren species, [Carolina wren (*Thryothorus ludovicianus*) and house wren (*Troglodytes aedon*)], that have documented relationships with downed wood (Hamel 1992). With the exception of wrens, we chose minimum sample size based on natural breaks in the distribution of species counts. For each treatment plot, we also calculated species richness and derived the Shannon-Weaver index of diversity (herein “species diversity”; Shannon & Weaver 1949) for the entire winter bird community using the *diversity* function in the R package “vegan” (Oksanen et al. 2012) and used each as response variables. We also divided species diversity and richness by number of visits to each replicate for each year to account for variation in survey effort among years. To avoid biases induced by edge effects, we only included winter bird detections recorded ≥ 25 m from all drainage ditches and adjacent forest edges. We excluded winter birds recorded within logging decks because logging decks were not included in implementation of treatments.

To test for treatment-level effects on winter birds, we ran generalized linear models (GLMs) with a Gamma distribution, winter bird (i.e., all winter birds and each species) relative abundance, species diversity, and species richness as each response variable, and treatment, replicate, and year as independent, explanatory variables. Because datasets for relative abundance, species diversity, and species richness all contained at least one value of 0 and the Gamma distribution requires positive values, we added half the value of the smallest positive observation to each data point with an original value of 0 among each dataset for each response variable. To generate a standardized metric demonstrative of the spatial associations winter birds maintained with piles of downed wood in treatments, we divided the count of all winter birds detected near, in, or on branches of piles, respectively, by the number of visits to each replicate for each year. We then used these relative counts of winters birds detected near, in, or on branches of piles as response variables and treatment and replicate as independent, explanatory variables in Poisson regression models for each year. We assumed overdispersion when the residual deviance divided by the residual degrees of freedom was >1.5. When we detected overdispersion, we corrected for it by applying a negative binomial regression model (Venables and Ripley 2002). For the categorical variables treatment and year, we performed *post-hoc* Tukey's pair-wise comparisons of means for all models using general linear hypothesis testing (*glht* function; single-step method) in the R package "multcomp" (Hothorn et al. 2013).

To gain a more holistic understanding of winter bird use of available habitat structure in intensively managed forests, we calculated the relative, spatial use of available habitat structure (i.e., downed wood piles versus vegetation) by commonly encountered winter bird groups and determined winter bird distribution across a gradient of edge proximity spanning from adjacent forest edges and drainage ditches inwards to the interior of regenerating stands. Specifically, we calculated relative habitat use of commonly encountered winter bird groups, including wrens (Carolina wren and house wren), mourning dove (*Zenaida macroura*), and sparrows [savannah sparrow (*Passerculus sandwichensis*), song sparrow (*Melospiza melodia*), and swamp sparrow (*Melospiza georgiana*), as the count of detections near, in, or on branches of downed wood piles or in vegetation per group divided by the total count per group. For each year, we also compared total winter bird counts among adjacent forest edge, drainage ditches (see *Study area and design*), and distance classes away from drainage ditches (i.e., 0 – 25 m, 25 – 50 m, and >50 m) using Pearson's Chi Squared Goodness of Fit Tests. We summarized our findings for these portions of the analysis descriptively.

We compared yearly vegetation structure and composition among treatments using randomized complete block design analysis of variances (ANOVAs). After confirming normality and homogeneity among variances using Shapiro-Wilks and Bartlett tests, respectively, we ran ANOVAs using percent of each groundcover type (i.e., bare ground, coarse woody debris, grass, and litter), percent of each horizontal vegetation cover type (i.e., forb, grass, and woody shrubs and vines), vertical vegetation structure, and maximum vegetation height for each treatment plot in each year as dependent variables, replicate as the blocking factor, and treatment as a fixed effect. We arcsine square-root transformed percentile variables, but only untransformed means and standard errors are reported. We conducted all analyses using statistical software program R (version 3.1.0; R Core Team 2014). We set $\alpha = 0.05$.

RESULTS

In the winters of 2012-2014, we counted 9,618 birds representing 52 species, of which 3,352 (35%) occurred in treatments ≥ 25 m from drainage ditches and adjacent forest edge (*see* Appendix A). Winter bird counts differed among distance to edge categories in 2012 ($\chi^2 = 114.19$, DF = 3, P = <0.01), 2013 ($\chi^2 = 619.04$, DF = 3, P = <0.01), and 2014 ($\chi^2 = 1303.59$, DF = 3, P = <0.01). Each year, we counted more winter birds in adjacent forest edge, drainage ditches, and ≤ 25 m from drainage ditches than in treatment interiors (i.e., ≥ 25 m from drainage ditches; Fig. 1). In 2012, mourning dove was the most commonly encountered species (37%; Table 1). Sparrows, including savannah sparrow, song sparrow, and swamp sparrow, collectively comprised 67% and 88% of winter bird counts in 2013 and 2014, respectively (Table 1).

There were few treatment effects on any winter bird metrics (Table 1). Neither species diversity nor richness differed among treatments in any year. Mourning dove relative abundance (2012 and 2013 combined) was greater in the NOBIOHARV treatments than in the 15DISP treatments. In 2014, field sparrow relative abundance was greater in the NOBHGS treatments than in all other treatments, with the exception of the 30CLUS treatments. Apart from mourning dove in 2012 and field sparrow in 2014, we detected no treatment effects on relative abundance of the winter bird community and or individual species. However, winter bird relative abundances typically increased from 2012 to 2013, whereas differences in winter bird relative abundances between 2013 and 2014 were less dramatic (Table 1). Sparrow species were rare in 2012, relative abundance of swamp sparrow increased from 2013 to 2014, and relative abundance of Carolina wren, species richness, and species diversity all peaked in 2013 (Table 1).

In general, counts of winter birds near, in, or on branches of downed wood piles did not differ among treatments (Table 2). In 2013, counts of winter birds detected in piles were greater in the NOBIOHARV and 30CLUS treatments than in the NOBHGS treatments. We detected fewer winter birds in piles than near piles or on branches of piles in all years (Table 2; *see also* Discussion). Among the most commonly encountered winter bird groups, wrens and sparrows more frequently used vegetation than downed wood in regenerating stands, while doves were more often detected on the ground within 1 m of downed wood piles than in or among vegetation (Fig. 2). We also noted several species-specific patterns in relative use of downed wood piles (*see* Appendix B). For all years, we frequently detected Carolina wren and house wren in piles. Relative to other winter bird species in regenerating stands, we recorded a high number of counts near piles for the following species: dark-eyed junco (*Junco hyemalis*), mourning dove, and palm warbler (*Setophaga palmarum*) in 2012; chipping sparrow (*Spizella passerina*) and mourning dove in 2013; and mourning dove and northern bobwhite (*Colinus virginianus*) in 2014. In 2012, we most often detected eastern bluebird (*Sialia sialis*) and song sparrow on branches of piles.

Volume of harvest residues in treatment plots was shown to accurately match that of our original experimental design (Fritts et al. 2014). Most vegetation structure and composition metrics did not differ among treatments in either year (Table 3). Grass ground cover was greater in the 15CLUS treatments than in the 15DISP treatments in 2013 and in the 30CLUS treatments than in the 30DISP or NOBIOHARV treatments in 2014. In 2013, vegetative cover of grass was greater in the NOBHGS and 15CLUS treatments than in the 15DISP treatments. Although results of ANOVAs indicated differences in vertical vegetative structure among treatments for both years, pair-wise comparisons of treatment means revealed no significant differences. In 2013, ground cover was mostly comprised of bare ground and grass, whereas grass alone was the most dominant ground cover in 2014. Additionally, grass comprised most of the horizontal vegetation cover in both 2013 and 2014.

DISCUSSION

Our results suggest current levels of woody biomass harvests in regenerating stands within intensively managed forests of the Southeast had little effect on the winter bird community. After testing response of winter birds to experimental removal of downed wood in mature (between 40 and 50 years old) loblolly pine forests of the Southeast, Lohr et al. (2002) also found downed wood removal had no effect on the winter bird community. In contrast, Rost et al. (2010) documented a significant, positive relationship between constructed piles of downed wood and abundance of seed-dispersing, winter birds in harvested and burned Mediterranean pine forests, but no winter bird response to dispersed woody biomass. Although the winter bird community in our study was unaffected by volume and distribution of retained harvest residues, we demonstrated that downed wood may play an ecological role as winter bird habitat complementary to that of vegetation in regenerating stands. However, vegetation structure and composition, rather than availability of downed wood, primarily influenced winter bird abundance in and use of regenerating stands.

Operational and economic realities affecting forest industry at the time our experiment was implemented may have resulted in relatively high volumes of retained harvest residues following woody biomass harvest. Specifically, intensities of woody biomass harvests at the sites may have been restricted due to technological limitations of harvest equipment. Recent studies in the Southeast have shown that even the most intensive, unrestricted experimental woody biomass harvests leave relatively large volumes of harvest residues on the landscape (Homyack et al 2013, Fritts et al. 2014). For example, a concurrent study at the replicates showed that the minimum volume of harvest residues retained in a treatment plot was $16.28 m^3 ha^{-1}$ (7.81 tons ha^{-1}; Fritts et al. 2014**a**), which exceeds by over three-fold the Forest Guild's BHGs for the Southeast, which recommend at least 2.24 tons ha^{-1} of retained downed wood in pine forests of the Coastal Plain physiographic region (Perschel et al. 2012). Therefore, current levels of woody biomass harvest in the Southeast may retain volumes of harvest residues above the threshold needed to sustain winter bird populations, if a threshold even exists.

Some previous studies suggested breeding birds negatively responded to experimental decreases in downed wood (e.g., Lohr et al. 2002), and our finding of minimal winter bird response to harvest residue removal relative to that of breeding birds coincides with results from other studies (*see* Riffell et al. 2011). Differences between breeding and winter bird response to downed wood removal may be related to the suite of species occurring in each season or differences in the amount of downed wood necessary to meet foraging versus nesting requirements (Hutto and Gallo 2006, Riffell et al. 2011). Additionally, birds typically are non-territorial during winter and thus are unlikely to be as strongly tied to a particular habitat element (Lohr et al. 2002). However, Carolina wrens are territorial year-round (Simpson 1985, Strain and Mumme 1988), and we detected no response to woody biomass removal treatments by this species.

Knowledge of avian use of downed wood remains severely underdeveloped (Lanham and Guynn 1996, Seibold et al. 2015), yet our records of spatially explicit, winter bird counts recorded near, in, or on braches of downed wood piles, coupled with field observations, indicate that several winter bird species use downed wood extensively during winter. Based mainly on anecdotal information on breeding birds and natural history studies in the Southeast, Hamel (1992) cited nine species of birds associated with downed wood. We commonly recorded Carolina wren and house wren in piles of downed wood, verifying observations by Hamel (1992) and Lanham and Guynn (1996) that wrens are closely associated with downed wood. Indeed, greater counts of winter birds detected in piles within treatments maintaining higher volumes of harvest residues in 2013 coincided with peak relative abundance of Carolina wren among years. Additionally, we recorded many other bird species associated with downed wood previously unlisted by Hamel [(1992); *see* Appendix B]. We notably recorded several sparrow species (e.g., savannah sparrow, song sparrow, and swamp sparrow) using downed wood, indicating that downed wood may provide habitat structure in regenerating stands for some overwintering sparrows. However, sparrows used vegetation structure far more than downed wood in regenerating stands.

Although no studies have directly addressed mechanisms behind winter bird use of downed wood, our results support previous studies that inferred downed wood is used by winter birds for perching and cover (Shackleford and Conner 1997, Lavan and Mac Nally 1998, Hagan and Grove 1999, Lohr et al. 2002). Prior to vegetation establishment, we frequently detected eastern bluebird perching on branches of downed wood piles, and observed this species pouncing on grounded prey [e.g., crickets (Gryllidae)] from these vantage points (S. Grodsky, *pers. obs.*). Similar inter-relationships between downed wood perches and foraging have been recorded for European robin (*Erithacus rubecula*; Rost et al. 2010) and several Australian robins (*Petroica* spp.; Mac Nally et al. 2001). Winter bird use of downed wood perches decreased as maximum vegetation height increased from 2013 to 2014, potentially indicating structural height more so than perch type (i.e., downed wood versus vegetation) dictates winter bird perch selection. Yet, at least during early stand development, perches provided by retained harvest residues may have facilitated predator vigilance among winter birds in regenerating stands (Lohr et al. 2002). Additionally, we frequently observed winter birds, including sparrows, flush into piles of downed wood rather than nearby clumps of grasses when vegetation was present (S. Grodsky*, pers. obs.*), potentially supporting the hypothesis that some passerines prefer woody cover when threatened (Lima 1993). However, our ability to account for birds using downed wood as cover was limited by 2014 because developing vegetation in interbeds made it nearly impossible to decipher whether a bird flushed into or out of piles of downed wood.

Our results also indicate winter birds may have used downed wood for the abundant insect prey and seeds it harbored (Jabin et al. 2004, Ulyshen and Hanula 2009, Castro and Wise 2010). During each year of our study, we commonly detected ground-gleaning, granivores (e.g., mourning dove) near piles. In this case, granivorous birds may be concentrating their feeding around piles of downed wood, which may in turn be damming seeds during pre- (seeds sourced from adjacent stands) and post-vegetation establishment (seeds sourced within stands). Loeb (1996) hypothesized that seed-damming capabilities of downed wood may attract mammalian granivores to downed wood structure for feeding. Based on our results, the same idea may apply to some granivorous winter birds, especially mourning dove. We detected mourning dove near piles more often than in vegetation, potentially suggesting that seed availability near downed wood heavily influenced habitat use by this species. Further, granivorous birds concentrating their attention downward while feeding also could benefit from the cover downed wood provides from diurnal raptors overhead (Mac Nally et al. 2001). In 2012, we frequently detected palm warbler, an insectivore, on the ground near piles, and, for most detections, this species was actively foraging (S. Grodsky, *unpublished data*). Therefore, some ground-foraging insectivores may take advantage of highly abundant and easily accessed invertebrate prey resources associated with downed wood, especially prior to vegetation establishment (Lohr et al. 2002). Unlike in more northern latitudes, winter temperatures in the Southeast often are mild enough to support invertebrate activity (i.e., > 40 F).

Most woody biomass harvests in the Southeast are predicted to occur on private, intensively managed forests following clearcutting (Riffell et al. 2011), which has implications for avian use of regenerating stands beyond woody biomass harvest alone. Dynamic, successional trajectories of vegetation in regenerating stands and spatiotemporal implications of managed forest landscapes (i.e., a mosaic of variably aged stands) inevitably will affect winter birds in conjunction with woody biomass harvests. Birds frequently associate with vertical structure in the form of vegetation (MacArthur and MacArthur 1961) and snags (Fisher and McClelland 1983, Lanham and Guynn 1996). We detected more birds each year in and within 25 m of drainage ditches and adjacent forest edge likely because edge maintained greater vegetative complexity than the interiors of regenerating stands for the duration of our study. Further, many winter birds likely moved between adjacent forest stands and regenerating stands, taking advantage of the resources available in each. In contrast, sparrows most often used the interior of regenerating stands, but only after grasses were present as early successional, vegetation cover. Considering these points and the fact that winter bird relative abundance markedly increased from pre- to post-vegetation establishment, vegetation in and surrounding the sites likely had a marked effect on winter bird use of regenerating stands. In most cases involving woody biomass harvests following clearcutting in intensively managed forests, we suggest the relationship between birds and vegetation structure and composition may outweigh any effects of harvest residue retention in regenerating stands.

CONCLUSION

Winter birds apparently were unaffected by current levels of woody biomass harvest in intensively managed forests, suggesting that current BHGs are adequate or potentially unnecessary with respect to winter birds. Winter birds responded to successional changes in vegetation structure and composition more so than availability of downed wood. Yet, many winter bird species used harvest residues, indicating that downed wood is a valuable habitat component following clearcutting. Although current levels of woody biomass harvest in the Southeast leave considerable volumes of harvest residues on the landscape, technological advances in harvest machinery or increases in the market value of woody biomass could result in intensified removal of downed wood. If future woody biomass harvests intensify, leading to a substantial decrease in harvest residue retention relative to current levels on our study sites, we recommend that winter bird response to woody biomass harvests be re-evaluated to inform and update BHGs, if necessary.

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Table 1. Mean±SE of Shannon-Weaver index of diversity and species richness, and relative abundance (counts/# visits per replicate each year) of winter birds recorded in six woody biomass removal treatments within regenerating stands (*n* = 4), January and February, 2012 – 2014, Beaufort County, North Carolina. With the exception of Carolina Wren and House Wren, we only included winter bird species with ≥ 30 detections per year in our species-specific analyses. Treatments included: (1) no Biomass Harvesting Guidelines (NOBHGS); (2) 15% woody biomass retention distributed evenly throughout the treatment unit (15DISP); (3) 15% woody biomass retention in piles (15CLUS); (4) 30% woody biomass retention distributed evenly throughout the treatment unit (30DISP); (5) 30% woody biomass retention in piles (30CLUS); and (6) no woody biomass harvest (NOBIOHARV). Different letters indicate significant differences among treatments or years; years were pooled for analyses. Scientific names of winter bird species available in appendices.

Community metric	Year	Woody biomass removal treatment					
		NOBHGS	15DISP	15CLUS	30DISP	30CLUS	NOBIOHARV
Shannon-Weaver (H)	2012^{a}	0.13±0.09	0.23±0.08	0.33±0.06	0.35±0.06	0.12±0.12	0.17±0.12
	2013^{a}	0.30±0.02	0.29±0.01	0.30±0.01	0.30±0.03	0.30±0.02	0.29±0.02
	2014^{b}	0.14±0.02	0.13±0.02	0.15±0.03	0.12±0.03	0.13±0.01	0.15±0.01
Species richness (N)	2012^{b}	0.67±0.24	0.75±0.25	1.00±0.19	1.25±0.21	0.67±0.33	0.75±0.32
	2013^{a}	1.43±0.17	1.57±0.06	1.51±0.21	1.57±0.33	1.62±0.20	1.40±0.11
	2014^{b}	0.78±0.16	0.69±0.17	0.75±0.05	0.75±0.17	0.56±0.15	0.78±0.08
Relative abundance							
All birds	2012^{b}	2.42±1.24	1.42±0.70	2.00±0.56	3.42±0.96	2.83±1.08	3.08±1.16
	2013^{a}	6.30±1.47	8.37±1.03	7.13±0.73	7.22±0.65	10.84±4.41	6.99±0.93
	2014^{a}	9.28±1.15	10.84±3.29	11.50±2.22	9.19±0.96	11.72±4.73	9.81±1.42
Carolina wren	2012^{b}	0.17±0.17	0	0.42±0.32	0.17±0.17	0.33 ±0.33	0.17±0.17
	2013^{a}	0.32±0.07	0.28±0.08	0.32±0.12	0.58±0.17	0.43±0.12	0.42±0.17
	2014^{c}	0.03±0.03	0.06±0.04	0	0.06±0.04	0.06±0.06	0.09±0.06
House wren	2012^{ab}	0	0.08±0.08	0	0.08±0.08	0	0.17±0.17
	2013^{a}	0.04±0.04	0.08±0.04	0.08±0.04	0.08±0.04	0.12±0.04	0.12±0.04
	2014^{a}	0.13±0.05	0.09±0.06	0.16±0.08	0.31±0.17	0.09±0.09	0.16±0.06
Field sparrow	2012	N/A	N/A	N/A	N/A	N/A	N/A
	2013	N/A	N/A	N/A	N/A	N/A	N/A

Table 1 (continued)

	2014	1.19±0.58^{a}	0.22±0.15^{b}	0.03±0.03^{b}	0.09±0.06^{b}	0.78±0.51^{a}	0.22±0.11^{b}
Mourning dove	2012^{a}	0.75±0.55^{ab}	0.17±0.10^{b}	0.17±0.10^{ab}	0.92±0.57^{ab}	1.42±1.20^{ab}	2.33±1.31^{a}
	2013^{b}	0.16±0.07^{ab}	0^{b}	0.42±0.21^{ab}	0.04±0.04^{ab}	0.16±0.12^{ab}	0.17±0.10^{a}
	2014	N/A	N/A	N/A	N/A	N/A	N/A
Savannah sparrow	2012	N/A	N/A	N/A	N/A	N/A	N/A
	2013	1.14±0.41	1.39±0.44	1.05±0.10	0.82±0.45	0.80±0.28	0.61±0.12
	2014	0.22±0.18	2.59±2.51	1.03±0.78	0.22±0.22	2.94±2.85	0.88±0.60
Song sparrow	2012	N/A	N/A	N/A	N/A	N/A	N/A
	2013	1.34±0.30	2.06±0.37	1.34±0.36	1.62±0.20	2.21±0.44	1.96±0.30
	2014	1.66±0.24	1.88±0.37	2.09±0.54	1.53±0.42	1.59±0.39	2.25±0.30
Swamp sparrow	2012	N/A	N/A	N/A	N/A	N/A	N/A
	2013^{b}	0.73±0.18	1.28±0.04	0.92±0.24	0.76±0.08	1.39±0.44	0.82±0.25
	2014^{a}	5.19±0.97	5.25±1.06	6.94±1.00	6.22±0.96	6.03±1.87	5.44±0.87
Yellow-rumped warbler	2012	N/A	N/A	N/A	N/A	N/A	N/A
	2013	0.17±0.12	0.56±0.16	0.15±0.06	0.32±0.14	0.27±0.12	0.42±0.22
	2014	N/A	N/A	N/A	N/A	N/A	N/A

Table 2. Counts of all winter bird detections near, in, or on branches of piles of downed wood per visit (mean±SE) recorded in six woody biomass removal treatments within regenerating stands (*n* = 4), January and February, 2012 – 2014, Beaufort County, North Carolina. Treatments included: (1) no Biomass Harvesting Guidelines (NOBHGS); (2) 15% woody biomass retention in piles (15CLUS); (3) 15% woody biomass retention distributed evenly throughout the treatment unit (15DISP); (4) 30% woody biomass retention in piles (30CLUS); (5) 30% woody biomass retention distributed evenly throughout the treatment unit (30DISP); and (6) no woody biomass harvest (NOBIOHARV). We analyzed counts from each year independently. Different letters indicate significant differences among treatments.

Location	Year	Woody biomass removal treatment					
		NOBHGS	15DISP	15CLUS	30DISP	30CLUS	NOBIOHARV
Near pile	2012	3.00±1.35	3.25±0.63	4.50±0.96	4.00±0.58	4.00±1.47	3.75±1.31
	2013	8.00±1.08	5.25±1.11	6.50±1.55	4.00±0.91	5.25±1.70	8.00±1.78
	2014	3.50±1.50	1.75±0.48	3.75±1.80	2.00±0.71	3.25±1.38	4.75±1.44
In pile	2012	0.75±0.48	0.50±0.29	1.00±0.41	1.25±0.25	1.25±0.63	2.75±1.03
	2013	0.50±0.29$^{\mathbf{b}}$	1.00±1.00$^{\mathbf{ab}}$	1.75±0.75$^{\mathbf{ab}}$	1.75±0.48$^{\mathbf{ab}}$	4.50±1.32$^{\mathbf{a}}$	4.50±1.04$^{\mathbf{a}}$
	2014[1]	N/A	N/A	N/A	N/A	N/A	N/A
On branches of pile	2012	2.00±0.91	1.75±0.48	3.00±0.58	3.75±0.75	1.00±0.41	4.25±2.21
	2013	9.00±2.27	8.50±3.20	11.25±2.56	7.00±2.45	14.25±1.93	11.25±3.42
	2014	0.50±0.29	1.00±0.71	1.00±0.41	2.25±1.03	1.25±0.48	2.75±1.55

[1] Our ability to detect birds in piles was severely limited by 2014 because developing vegetation in interbeds made it difficult to decipher whether a bird flushed into or out of piles of downed wood.

Table 3. Winter habitat covariates[1] (mean ± SE) estimated in six woody biomass removal treatments within regenerating stands (*n* = 4) in February, 2013 and 2014, Beaufort County, North Carolina. Treatments included: (1) no Biomass Harvesting Guidelines (NOBHGS); (2) 15% woody biomass retention in piles (15CLUS); (3) 15% woody biomass retention distributed evenly throughout the treatment unit (15DISP); (4) 30% woody biomass retention in piles (30CLUS); (5) 30% woody biomass retention distributed evenly throughout the treatment unit (30DISP); and (6) no woody biomass harvest (NOBIOHARV). Winter habitat covariates for each treatment in each site were compared using randomized complete block design ANOVAs with replicate as a blocking factor and treatment as a fixed effect. Different letters indicate significant differences among treatments.

Covariate	Woody biomass removal treatments						Treatment		Replicate	
	NOBHGS	15DISP	15CLUS	30DISP	30CLUS	NOBIOHARV	$F_{5,16}$	P_{trt}	$F_{3,16}$	P_{rep}
Ground cover (%)										
Bare ground (2013)	39.17±6.24	45.00±2.44	33.33±3.58	38.89±1.71	35.00±4.46	40.56±4.11	1.18	0.37	3.92	0.03
Bare ground (2014)	26.81±5.91	28.06±4.01	26.67±4.50	30.00±2.97	25.83±5.49	27.08±3.49	0.35	0.87	16.26	<0.01
Litter (2013)	10.56±2.80	17.22±45.28	13.06±2.65	7.50±1.82	15.28±2.37	13.06±3.82	2.42	0.09	13.40	<0.01
Litter (2014)	11.25±2.07	16.67±3.25	16.11±1.50	17.92±4.22	10.83±1.82	18.19±2.39	1.19	0.36	1.46	0.27
Grass (2013)	37.78±4.21^{ab}	24.44±4.73^{b}	43.06±2.13^{a}	34.72±6.03^{ab}	35.28±4.93^{ab}	27.50±3.82^{ab}	3.14	0.04	5.59	<0.01
Grass (2014)	52.78±6.52^{ab}	46.67±5.56^{ab}	50.42±5.35^{ab}	40.97±6.23^{b}	55.00±6.87^{a}	41.39±3.68^{b}	4.93	<0.01	32.67	<0.01
CWD (2013)	6.67±1.52	7.50±0.72	7.50±1.49	12.50±2.43	8.06±2.50	13.61±3.41	1.98	0.14	3.78	0.03
CWD (2014)	8.06±1.25	7.36±1.01	7.08±0.80	9.31±41.20	7.08±1.20	11.11±1.95	1.05	0.43	1.63	0.23
Vegetative cover (%)										

Table 3 (continued)

Forb (2013)	9.94±2.68	11.11±4.55	3.61±1.64	11.39±3.43	10.28±1.86	11.67±1.00	2.03	0.13	3.55	0.04
Forb (2014)	16.11±4.68	16.67±5.60	12.92±2.65	20.00±5.00	10.83±3.40	21.81±4.05	2.23	0.11	14.30	<0.01
Grass (2013)	58.06±5.86^{a}	34.17±7.84^{b}	63.89±3.96^{a}	55.56±6.07^{ab}	54.72±5.87^{ab}	44.44±7.87^{ab}	4.43	0.01	7.25	<0.01
Grass (2014)	75.14±4.30	73.33±4.45	73.33±4.24	70.00±7.28	81.53±4.28	67.36±4.39	2.40	0.09	15.02	<0.01
WSV (2013)	3.89±0.62	2.78±1.15	3.33±1.04	3.89±0.28	5.56±0.40	6.11±1.78	1.78	0.18	2.86	0.07
WSV (2014)	22.08±1.46	20.14±3.43	19.03±1.65	24.72±3.61	22.92±2.15	30.83±4.39	1.39	0.28	0.66	0.59
VVS (2013)	4.28±0.53	2.63±0.48	4.20±0.12	4.43±0.71	4.09±0.57	2.99±0.42	2.93	0.05	5.35	0.01
VVS (2014)	4.35±0.25	3.89±0.28	3.91±0.26	3.58±0.33	4.47±0.39	3.55±0.18	3.43	0.03	10.66	<0.01
MVH (2013)	5.31±0.52	3.44±0.65	5.22±0.12	5.75±0.62	5.30±0.68	3.92±0.53	3.28	0.04	4.58	0.02
MVH (2014)	7.39±0.39	7.02±0.06	6.88±0.48	7.21±0.35	7.52±0.16	7.08±0.27	0.40	0.84	0.67	0.58

[1] CWD = Coarse woody debris; WSV = Woody shrub/vine; VVS = vertical vegetative structure; MVH = maximum vegetation height

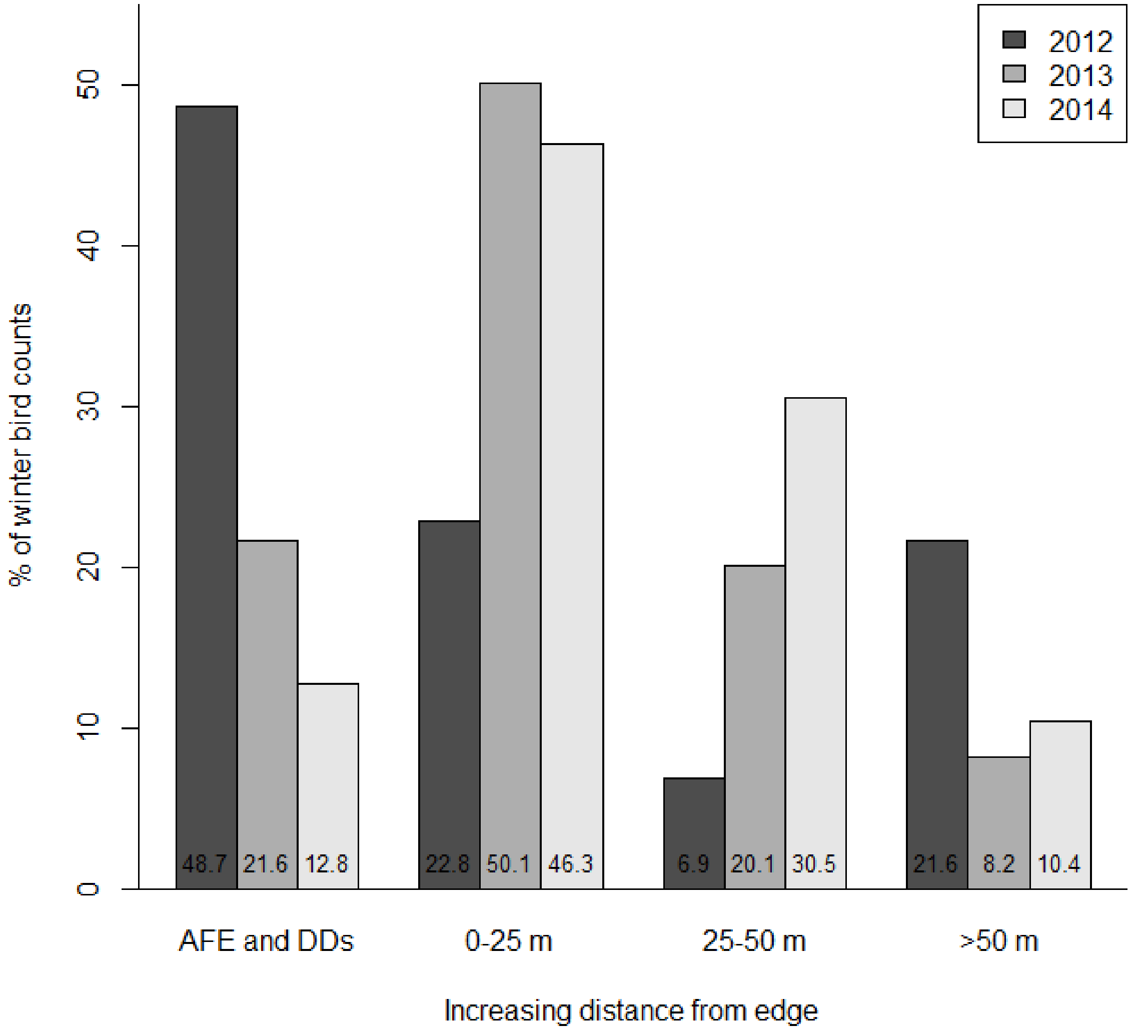

Figure 1. Yearly variation in percentage of winter bird counts in adjacent forest edge (AFE; up to ~10 m into stands) and drainage ditches (DDs), and distance classes away from drainage ditches (0 – 25 m, 25 – 50 m, and ≥ 50 m) in intensively managed pine plantations, January and February, 2012 – 2014, Beaufort County, North Carolina.

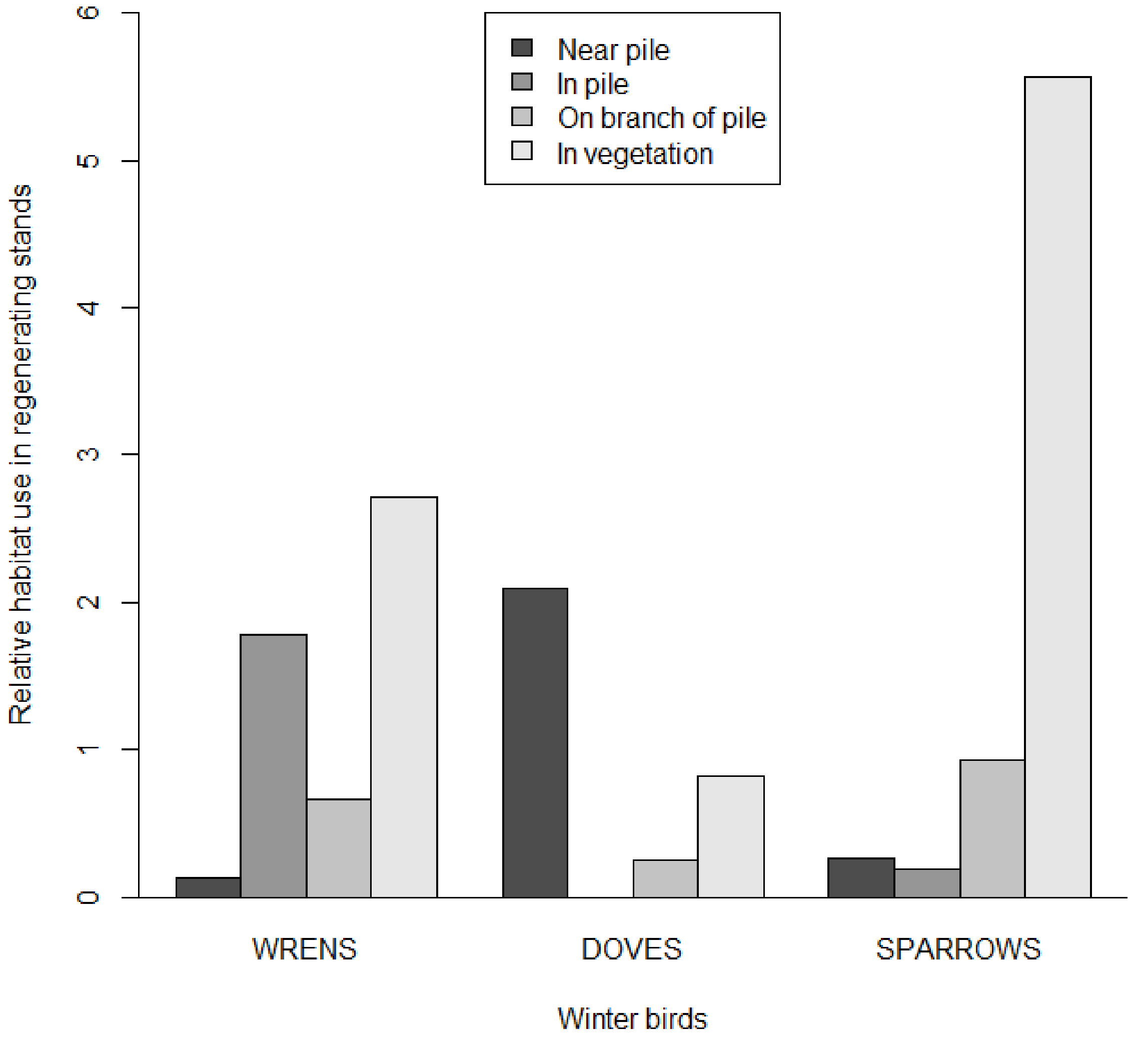

Figure 2. Relative habitat use (i.e., count of detections near (within ~ 1m) piles of downed wood, in piles of downed wood, or on branches of piles of downed wood or in vegetation/total count) of wrens, mourning dove, and sparrows in regenerating stands (*n* = 4), January and February, 2012 – 2014, Beaufort County, North Carolina. WRENS = Carolina wren and house wren (2012-2014); DOVES = mourning dove (2012 and 2013 only); SPARROWS included savannah sparrow, song sparrow, and swamp sparrow (2013 and 2014). Only detections recorded ≥25 m from edge were included. Scientific names of winter bird species available in appendices.

CHAPTER 2

Breeding, early-successional bird response to forest harvests for renewable bioenergy

ABSTRACT

Forest regeneration following timber harvest is a principal anthropogenic source of habitat for early-successional birds and characterized not only by influxes in early-successional vegetation, but also harvest residues. Early-successional birds may use downed wood for communication, cover, foraging, and nesting. Meanwhile, increased market viability of harvest residues as a forest bioenergy feedstock may intensify downed wood removal, particularly in intensively managed forests of the Southeast. Yet, few studies have investigated avian use of downed wood following timber harvests and not study to date has examined early-successional bird response to experimentally manipulated, operational-scale woody biomass harvests. As such, our objectives were to: 1) evaluate effects of varying intensities of woody biomass harvest on the early-successional bird community; and (2) document early-successional bird use of downed wood in regenerating stands. We spot-mapped birds from 15 April – 15 July, 2012 – 2014, and quantified vegetation composition and structure in six woody biomass removal treatments within regenerating stands in North Carolina (*n* = 4) and Georgia (*n* = 4), USA. Treatments included clearcut harvest followed by: (1) traditional woody biomass harvest with no biomass harvesting guidelines; (2) 15% retention with harvest residues dispersed; (3) 15% retention with harvest residues clustered; (4) 30% retention with harvest residues dispersed; (5) 30% retention with harvest residues clustered; and (6) no woody biomass harvest (i.e., reference site). We tested for treatment-level effects on avian species diversity and richness, early-successional focal species territory density (combined and individual species), counts of winter birds detected near, in, or on branches of downed wood piles/windrows, avian behaviors, and vegetation composition and structure. Across three breeding seasons, we delineated 536 and 654 territories and counted 2,489 and 4,204 in the North Carolina and Georgia treatments, respectively. Harvest residue removal had little effect on the early-successional, breeding bird community. The successional trajectory of vegetation structure, rather than availability of harvest residues, primarily drove avian use of regenerating stands. However, many breeding bird species associated with downed wood, in addition to vegetation. Further, results indicated harvest residues may provide important habitat for early-successional birds in regenerating stands when vegetation largely is absent due to young stand age coupled with high intensity site preparation.

INTRODUCTION

Early-successional vegetation is ephemeral, briefly occurring on the changing timeline of forest succession, and precipitously declining in extent in North America due to changes in natural and anthropogenic disturbance regimes (King and Schlossberg 2014). As such, conservation of disturbance-dependent plant and animal species specifically adapted to early-successional vegetation has become high priority (Hunter et al. 2001, Litvaitis 2001, Wagner et al. 2003, Elliott et al. 2011). Indeed, many early-successional species are listed under or candidates for the United States Endangered Species Act, such as the Karner blue butterfly (*Lycaeides melissa samuelis*) and the New England cottontail rabbit (*Sylvilagus transitionalis*). Birds especially are useful ecological indicators of land use change for early-successional communities and the species therein because numerous bird species are restricted to particular stages of forest stand development, sensitive to disturbance, and exhibit responses to disturbance indicative of general patterns for most other organisms (DeGraaf 1991, King and Schlossberg 2014).

Early-successional (i.e., disturbance-dependent) birds are among the most threatened avian habitat specialists (Brawn et al. 2001, Hunter et al. 2001). North American breeding bird survey data indicate 44% of 160 early-successional bird species show declining population trends, whereas only 9% are increasing (Sauer et al. 2013). Many early-successional bird species also rank highly by composite conservation scores based on measures of vulnerability assigned by Partners in Flight, an international consortium of ornithologists concerned with bird conservation (Partners in Flight Science Committee 2012). Early-successional birds are adapted to open-canopy conditions created by natural or anthropogenic disturbances, including fire (Pyne 1982, Haney et al. 2008) and silvicultural practices (e.g., clearcutting – Thompson and DeGraaf 2001). Fire suppression, dwindling active timber harvest, and urbanization all have led to significant declines in disturbances that create favorable habitat conditions for early-successional birds (Bessinger et al. 2000, Trani et al. 2001, King and Schlossberg 2014).

Currently, forest regeneration following timber harvest is a principal anthropogenic source of habitat for early-successional birds (King and Schlossberg 2014), especially in regions supporting forest industry like the southeastern United States (hereafter "Southeast"; Brawn et al. 2001). Indeed, pine (*Pinus* spp.) plantations account for 20% of forest cover in the Southeast, with 13.4 million ha in loblolly pine (*Pinus taeda*) production alone (Schultz 1997, US Forest Service 2008). In ecological terms, overstory tree removal following a clearcut harvest increases light levels reaching the forest floor, which in turn stimulates development of a dense layer of herbaceous and, soon after, woody, early-successional vegetation (DeGraaf and Yamasaki 2003, Tozer et al. 2010, Haché et al. 2013). Importantly, clearcutting also results in habitat patches large enough to accommodate area-sensitive, early-successional bird species (Annand and Thompson 1997, King and DeGraaf 2000). The positive relationship between vegetation structure and composition following clearcutting and early-successional birds has been well-studied, and young, industrial forests have been shown to provide habitat for early-successional birds prior to canopy closure (Thompson et al. 1993, Dickson et al. 1995, Brawn et al. 2001, Keller et al. 2003).

Following timber harvest, the influx of early-successional vegetation is inevitably accompanied by drastic increases in downed wood from harvest residues (Harmon et al. 1986). Specifically, volume of downed wood follows a U-shaped timeline, with large volumes created immediately following a disturbance, ensued by a steady decrease in volume as downed wood decays, and then a slow increase in volume as mature trees senesce and die

(Grodsky et al. 2016). Downed wood plays a major role in forest ecosystem function and integrity (Harmon et al. 1986, Janowiak and Webster 2010, Riffell et al. 2011). In particular, downed wood influences nutrient retention and water dynamics in forests (Harmon et al. 1986, Fraver et al. 2002) and also provides important food and cover for wildlife, including early-successional birds (Lanham and Guynn Jr. 1996, Whiles and Grubaugh 1996).

In regenerating stands, early-successional birds may use downed wood for communication, cover, foraging, and nesting (Hamel 1992, Lanham and Guynn 1993, Lohr et al. 2002). Downed wood can trap seeds moved by flooding events and wind dispersal ("seed damming"; Loeb 1996), which in turn may provide food for granivorous birds. Similarly, downed wood harbors high densities of invertebrate prey (Hanula et al. 2006, Castro and Wise 2010, Grodsky et al. 2016). As such, insectivorous birds may center their foraging on downed wood. Birds also may use downed wood as escape cover. Indeed, most Passeriformes are known to seek woody cover when under attack by a predator (Lima 1993). Perching platforms provided by downed wood also may provide a home base for avian territory defense (Hamel 1992).

Although large amounts of harvest residues created by clearcutting, including treetops, limbs, slash, foliage, and felled non-crop and small-diameter trees, traditionally were left at harvest sites because cost of removal outweighed market values (Gan and Smith 2006), current increases in the market viability of woody biomass as a forest bioenergy feedstock may lead to intensified levels of harvest residue removal (Riffell et al. 2011). Forest bioenergy is an expanding renewable energy technology of interest (Milbrandt 2005, Mayfield et al. 2013). Forests are capable of producing vast amounts of woody biomass (e.g., harvest residues), which in turn may be used in forest bioenergy production to generate heat, electricity, and biofuels (Parikka 2004). Currently, harvest residues are an important feedstock for production of wood pellets (Sikkema et al. 2011), co-generated electricty (i.e., coal and woody biomass simultaneously burned; Annamalai and Wooldridge 2001), and, to a lesser extent, liquid transportation biofuels (United States Department of Agriculture (USDA) 2007, Forisk Consulting 2013).

Woody biomass harvests are especially prominent following clearcutting in intensively managed forests of the Southeast (Riffell et al. 2011). The Southeast currently is the largest exporter of wood pellets in the world (Evans et al. 2013), and wood pellet production in the region is predicted to increase (Forisk Consulting 2013). In particular, shipping ports in the Southeast are strategically positioned to export wood pellets to Europe, meeting increased market demands driven by European Union renewable energy mandates (Goh et al. 2013, Galik and Abt 2015). The Southeast also is experiencing more rapid development of forest bioenergy-production facilities (e.g., woody biomass power plants) than anywhere else in the world (Mendell and Lang 2012, REN21 2013). Additionally, nearly 50% of second generation biofuels required to meet United States biofuel mandates by 2022 will be supplied by forests of the Southeast (USDA 2010).

Concerns regarding potential effects of woody biomass harvests on forest ecosystems have led to development of non-regulatory biomass harvesting guidelines (BHGs) by state agencies and non-profit organizations in regions supporting woody biomass harvests (*see* Perschel et al. 2012 for Southeast BHGs). In an effort to maintain biological diversity and site productivity, BHGs specify target volumes of downed wood to be retained on the forest floor for wildlife habitat, nutrient cycling, and erosion control (Ranius and Fahrig 2006, Perschel et al. 2012). In general, BHGs are based on the assumption that “more” downed wood is better than “less” downed wood (Harmon and Hua 1991). However, suggested volumes and spatial arrangements of downed wood vary among regional BHGs, and BHGs have limited technical underpinnings due to a paucity of empirical support. Furthermore, BHGs will need to be better justified for practitioners based on scientific literature to offset stakeholder perceptions that they create unnecessary costs (Fielding et al. 2012). Therefore, research is needed to determine effects of woody biomass harvests and implementation of BHGs on forest ecosystem sustainability and wildlife habitat.

Few studies specifically have addressed relationships between birds and downed wood and no study to date that we are aware of has addressed early-successional, breeding bird response to operational-scale woody biomass harvests (Lanham and Guynn 1996 Jr., Riffell et al. 2011). The dearth of research on relationships between early-successional birds and downed wood, coupled with the lack of empirical data guiding BHGs, suggest that studies of early-successional bird response to harvest residue retention following woody biomass harvests are warranted. Thus, our primary objectives were to: (1) evaluate effects of varying intensities of woody biomass harvest on the early-successional bird community; and (2) document early-successional bird use of downed wood in regenerating stands.

METHODS

Study area and design

We examined breeding birds in eight replicate regenerating stands (herein “replicates”) in intensively managed loblolly pine (*Pinus taeda*) plantations within the Coastal Plain Physiographic Region of the Southeast. Our study included four replicates [70.5±6.1 (mean ± SE) ha] in Beaufort County, North Carolina (NC; -077°0′0″W to -076°53′50″ and 35°34′0″N to 35°38′20″N) and four replicates (64.64±3.1 ha) in Georgia

(GA): three in Glynn County, GA (-081°44′40″W to -081°40′42″W and 31°07′31″N to 31°11′14″N) and one in Chatham County, GA (-081°11′26″W to -081°10′37″W and 32°18′46″N to 32°19′21″N). In NC, replicates were managed for sawtimber production, commercially thinned twice prior to harvest, and 32-39 years old at time of clearcut harvest. In GA, replicates were managed for chip-and-saw and pulpwood production, commercially thinned once at each Glynn County replicate and twice at the Chatham County replicate prior to harvest, and 25-33 years old at time of clearcut harvest. Soils at the NC replicates predominantly were loam and silt loam, while soils at the GA replicates mainly were loam, clay loam, and fine sandy loam.

Following clearcut harvest in 2010-2011, we implemented woody biomass removal treatments (herein “treatments”) at each replicate. We used a randomized complete-block experimental design, dividing each replicate into the following six treatments [NC – area = 11.7±0.5 (mean ± SE) ha, range = 8.4-16.3 ha; GA – area = 10.7±0.4 ha, range = 7.6-14.3 ha]: (1) clearcut with a traditional woody biomass harvest and no biomass harvesting guidelines implemented (NOBHG); (2) clearcut with 15% retention of harvest residues evenly dispersed throughout the treatment (15DISP); (3) clearcut with 15% retention of harvest residues clustered in large piles throughout the treatment (15CLUS); (4) clearcut with 30% retention of harvest residues evenly dispersed throughout the treatment (30DISP); (5) clearcut with 30% retention of harvest residues clustered in large piles throughout the treatment (30CLUS); and (6) clearcut with no woody biomass harvest (i.e., clearcut only; NOBIOHARV), which served as a reference site.

In each treatment, all standing pines merchantable as roundwood were cut and transported to a logging deck with a grapple skidder. For the NOBHG treatments, we instructed loggers to glean all harvest residues they deemed merchantable as woody biomass. For the NOBIOHARV treatments, pine roundwood was harvested; however, we instructed loggers to fell and leave all harvest residues (almost entirely midstory hardwoods) not harvested as roundwood.

To implement the four treatments emulating BHGs, we used ArcGIS (ESRI, Redlands, California, USA) to delineate retention areas that represented either 15% or 30% of the total treatment area. Prior to clearcut harvest, we located retention areas using a hand-held Garmin Rino global positioning system (Olathe, Kansas, USA) and flagged the boundaries. Retention areas were clearcut after loggers harvested 85% or 70% of the non-retention treatment areas. We retained all hardwoods not merchantable as roundwood in retention areas. Following clearcut harvest, harvest residues were redistributed throughout treatments with a grapple skidder.

Harvest residues from the non-retention areas and NOBHG treatment were chipped at the logging deck during woody biomass harvest. Loggers used a grapple skidder to spread retained harvest residues evenly throughout the DISP treatments or randomly placed piles throughout the CLUS treatments. Because we created treatments by distributing harvest residues with a grapple skidder, individual piles of harvest residues in the CLUS and NOBIOHARV treatments were approximately the size of one grapple load (volume ≈ 36.19 m^3ha^{-1}; Fritts et al. 2014).

Although treatment implementation was identical in NC and GA, site preparation differed between states. In NC, site preparation occurred following clearcut harvest and implementation of treatments in the winter of 2010-2011. Replicates 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^{-1}. Shearing moved retained harvest residues into the 3-m space between pine beds (i.e., interbeds). Consequently, woody biomass was rearranged following shearing into long, linear rows in interbeds parallel to pine beds. Replicates were treated with the following two post-harvest herbicide applications of 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 harvest residues in treatments were concentrated into large, linear piles (i.e., windrows) extending for the entire length of treatments or into large, conical piles (1-100 m^3) within treatments. As such, few individual stems and no small downed wood piles (<1m^3) occurred between windrows (~30-50 m apart) in treatments. In Glynn County (GA), two replicates were double-bedded in the summer of 2011 and the remaining replicate was double-bedded in fall 2011. All Glynn County (GA) replicates were planted in winter 2012 at a density of ≈1495 trees ha^{-1} and treated with Arsenal© (BASF, Raleigh, North Carolina, USA) and Sulfometuron methyl for herbaceous weed control one year after clearcut harvest. In 2012, the Chatham County (GA) replicate was bedded and planted at a density of ≈726 trees ha^{-1} and received a broadcast treatment of Chopper© on year after clearcut harvest.

In NC, replicates and treatments therein were bordered by drainage ditches (~1 m wide) containing vegetation which was unaffected by site preparation and thus more developed than vegetation growing in treatments per se. In both states, logging road (~3.7 m wide) separated most replicates from adjacent forest stands, which typically fell into two age classes: 1) young loblolly pine stands (~10 years old); and 2) mature loblolly pine stands

(~30 years old). Snags were virtually absent from all NC replicates and occurred sporadically throughout GA replicates. In GA, replicates contained some retained, riparian forests (e.g., stringers) that were left unharvested during clearcutting.

Avian sampling

In NC and GA, we surveyed early-successional birds from 15 April – 15 July during the 2012-2014 breeding seasons by spot-mapping (Bibby et al. 1992, Lohr et al. 2002). Replicates were traversed along uniformly distributed, continuous strip transects in each treatment plot. Transects were 25 m from all replicate boundaries, 50 m apart from one another, and ran the entire length of the replicates and the treatments therein. Therefore, we surveyed birds no further than 25 m to either side of transect lines throughout treatments. For each survey, one experienced observer continuously walked along transects within each treatment and recorded the spatial location of each bird heard or seen on maps of treatments. For each bird detected, the observer recorded the following information: 1) discernable behavior (e.g., counter-singing, perching, foraging); 2) movement after initial detection (i.e., with directional arrows on maps), which aided in minimizing double-counting of individuals; 3) whether the bird was on the ground within ~1 m of a downed wood pile or windrow (herein “near pile”), within a downed wood pile or windrow (herein “in pile”), on branches protruding from a downed wood pile or windrow (herein “on branch of pile”), or in vegetation; and 4) estimated distance to the nearest drainage ditch (i.e., edge) based on one of three classes: 1) 0 – 25 m; (2) 25 – 50 m; and (3) and ≥ 50 m.

Observers conducted one survey of all treatments in one entire replicate between sunrise and 1000 hours on mornings with no precipitation and winds ≤25 km/hour. Observers started each survey route at a random corner of each replicate and alternated the order in which each replicate was surveyed to eliminate potential temporal and directional biases. In NC, two observers independently surveyed replicates and the treatments therein at the following annual frequencies: 1) two replicates 13 times and two replicates 12 times in 2012; 2) two replicates 9 times, one replicate 8 times, and one replicate 7 times in 2013; and 3) all replicates 8 times in 2014. In GA, two observers independently surveyed replicates and the treatments therein at the following annual frequencies: 1) three replicates 12 times and one replicate 5 times in 2012; 2) one replicate 22 times, two replicates 21 times, and one replicate 10 times in 2013; and 3) one replicate 16 times, two replicates 15 times, and one replicate 5 times in 2014.

We used spatiotemporally explicit locations of signing, male birds derived from our spot-mapping surveys to delineate territories in treatments. Our method of territory mapping early-successional passerines was appropriate because most species consistently sing and conspicuously maintain and defend territories throughout the breeding season (Bibby et al. 1992). We defined a territory as a cluster of at least three detections recorded during independent visits throughout an individual breeding season. We used observed movements and counter-signing to more accurately delineate territories. We calculated territory density in each treatment as the total number of individual territories divided by the treatment area (ha) and converted these densities to territories per 40 ha to facilitate interpretation. In a small number of cases, individual territories spanned across two treatment boundaries. When these cases arose, we calculated the proportion of the territory in each treatment based on the number of detections recorded in each treatment (e.g., two detections in treatment = 0.66, one detection in adjacent treatment = 0.33) and incorporated these proportions into our territory density calculations (Gram et al. 2003).

Quantifying harvest residues

We measured scattered and piled downed wood in each treatment at the NC and GA replicates using the line-intersect sampling (LIS) technique (Van Wagner 1968) and a visual encounter method (*see* Fritts et al. 2014 for detailed methods). In NC, we located each pile of downed wood in each treatment, measured its length, width, and height, and visually estimated its packing ratio (i.e., density of wood in pile; 0 – 100%). In the GA treatments, we measured the width, 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). For both states, we summed volume of piled downed wood estimated from the visual encounter method and volume of scattered downed wood estimated using the LIS method to generate total volume of downed wood (m^3/ha) for each treatment in each replicate. Volume of downed wood in the NC treatments was shown to accurately match that of our original experimental design (Fritts et al. 2014). However, the efficacy of treatment implementation in GA was influenced by higher intensity site preparation relative to NC (i.e., windrowing in GA versus shearing in NC) and, as such, treatments may not have matched intended outcomes.

Quantifying vegetation

We quantified vegetation composition and structure in regenerating stands in NC in July, 2012 – 2014 and in GA in July, 2013 and 2014. We characterized vertical vegetation structure, maximum vegetation height, groundcover (i.e., cover less than 1 dm off the forest floor), and horizontal vegetation cover (i.e., cover 1 dm or greater off the forest floor) at systematically distributed vegetation plots in each treatment. In NC, we sampled nine plots/treatment in 2012 and 2013 and six plots/treatment in 2014. In GA, we sampled nine plots/ treatment in 2013 and eight plots/treatment in 2014. At each vegetation plot, we established three, 10-m transects along which vegetation was measured at 10, 1-m increments (i.e., 30 total sampling points/vegetation plot). We oriented the first transect based on a random bearing and oriented the remaining two transects 120° to either side of the first transect (USDA 2007). As an index of vertical structure, we counted the number of times any vegetation (forb, grass, woody shrub/vine) touched any decimeter increment along a 2-m tall, 4.8-cm diameter rod at 30 sampling points (Moorman and Guynn 2001). We considered maximum vegetation height for each vegetation plot to be the average maximum decimeter increment (up to 2 m) at which we recorded a vegetative hit over the 30 sampling points. We recorded all groundcover types (bare ground, coarse woody debris, grass, and litter) that touched anywhere from the bottom through the first 1-dm increment of the rod. We recorded horizontal vegetation cover types (forb, grass, and woody shrub/vine) that touched anywhere above the 1-dm increment of the rod. We calculated percent cover of each groundcover and horizontal vegetation cover type at each vegetation plot by dividing the number of sampling points where the rod touched each groundcover or horizontal vegetation cover type by 30.

Statistical analysis

We used the most commonly detected species of breeding, early successional birds as focal species in our analysis, with cutoffs based on natural breaks in the distribution of number of species' territories per year. Focal species included: 1) blue grosbeak (*Passerina caerulea*); 2) common yellowthroat (*Geothlypis trichas*); 3) eastern towhee (*Pipilo erythrophthalmus*); 4) field sparrow (*Spizella pusilla*); 5) indigo bunting (*Passerina cyanea*); 6) prairie warbler (*Setophaga discolor*); and 7) yellow-breasted chat (*Icteria virens*). We also considered Carolina wren (*Thryothorus ludovicianus*) a focal species because of documented relationships between this species and downed wood (Hamel 1992). Of these focal species, we only included in analyses those with greater than 10 territories per breeding season in a single state. Among focal species, we also included northern bobwhite (*Colinus virginianus*), a regionally important early-successional gamebird with declining population trends (Brennan 1991). Because northern bobwhite maintains loose territories that are difficult to determine (Dickson 2001), we did not delineate territories for the species and instead set our cutoff for analysis at ≥30 northern bobwhite detections per breeding season in a single state. We chose this cutoff based on natural breaks in the distribution of northern bobwhite counts. To avoid biases induced by edge effects, we only included in our analyses detections and resultant territories recorded ≥25 m from all drainage ditches and adjacent forest edges. We also excluded detections recorded within logging decks in both states and in forested, wetland-retention areas (e.g., stringers) within the GA treatments.

We used territory density of each focal species and all focal species combined, species richness, and the Shannon-Weaver index of diversity (Shannon and Weaver 1949; herein “species diversity”), the latter of which we derived using the *diversity* function in the R package “vegan” (Oksanen et al. 2012), as response variables to determine effects of harvest residue removal on focal bird species and the overall bird community. We accounted for potential biases induced by variable treatment areas by defining territory densities as the number of territories per 40 ha (see *Avian Sampling*). We included relative abundance (i.e., count per treatment per year) as a response variable for northern bobwhite. To account for variation in survey effort, we standardized species richness, species diversity, and northern bobwhite relative abundance by dividing each by the number of visits to each replicate per breeding season.

We tested for effects of harvest residue removal on each aforementioned avian response variables using generalized linear models (GLMs). For the NC data, we first included a year x treatment interaction term and replicate as explanatory variables in each model. If we detected a significant year x treatment interaction, we consequently ran a model for each year separately and included treatment and replicate as independent, explanatory variables. Otherwise, we pooled data amongst years and included treatment, year, and replicate as independent, explanatory variables. We followed the same procedure for the GA avian analyses as we did for NC, but included volume of harvest residues (m^3/ha^{-1}) per treatment rather than treatment as an explanatory variable because windrowing at the GA replicates altered the distribution of downed wood in treatments (*see* Discussion). For GLMs, we assumed overdispersion when the residual deviance divided by the residual degrees of freedom was >1.0. If we detected overdispersion, we corrected for it by applying a negative binomial regression model (Venables and Ripley 2002). We performed *post-hoc*, Tukey's pair-wise comparisons of means among treatments and years using general linear hypothesis testing (*glht* function; single-step method) in the R package "multcomp" (Hothorn et al. 2013).

We also examined effects of harvest residue removal on spatial and behavioral use of downed wood in treatments by the overall, breeding bird community and focal species. Specifically, we included the count of detections near, in, or on branches of piles and the count of birds recorded foraging on the ground (i.e., not in vertical vegetation structure) and perching (excluding perching on vegetation) as response variables in the same models outlined above for the territory density analysis. Prior to analysis, we standardized counts of detections near, in, or on branches of piles and birds recorded foraging on the ground by dividing each by the number of visits to each replicate per year. We also described proportional use of available habitat structure (i.e., downed wood versus vegetation) by focal species in regenerating stands in NC and GA by documenting the proportion of detections recorded near, in, or on branches of piles or among vegetation for each focal species for all years combined. We summarized these data descriptively.

We tested for effects of downed wood removal on the following vegetation characteristics for each state and year: 1) percent of each groundcover type (i.e., bare ground, coarse woody debris, grass, and litter); 2) percent of each horizontal vegetation cover type (i.e., forb, grass, and woody shrub/vine); 3) vertical vegetation structure; and 4) maximum vegetation height. For NC, we ran randomized complete block design analysis of variances (ANOVAs) with each aforementioned vegetation characteristic as a response variable, treatment (NC), and replicate as a blocking factor. For GA, we ran GLMs with each aforementioned vegetation characteristic as a response variable, volume of harvest residues (m^3ha^{-1}), and replicate as a blocking factor. We arcsine square-root transformed percentile variables, but only untransformed means and standard errors are reported. We performed *post-hoc*, pair-wise comparisons among treatments using Tukey's Honest Significant Difference tests. We conducted all aforementioned analyses using statistical software program R (version 3.1.0; R Core Team 2014). We set $\alpha = 0.05$.

RESULTS

Across three breeding seasons, we delineated 536 territories and counted 2,489 birds and 40 species in treatments (i.e., ≥25 m from edge) in NC (*see* Appendix A) and 654 territories, 4,024 birds and 63 species in treatments in GA (*see* Appendix B). In NC, the following focal species met the minimum territory number for inclusion in analyses: 1) blue grosbeak [(*Passerina caerulea*); NC = 2012/2013, GA = 2013/2014]; 2) Carolina wren (NC = 2012/2013, GA = 2013/2014); 3) common yellowthroat [(*Geothlypis trichas*); NC and GA = 2013/2014]; 4) eastern towhee [(*Pipilo erythrophthalmus*); NC and GA = 2013/2014]; 5) field sparrow [(*Spizella pusilla*); NC = 2013/2014]; 6) indigo bunting [(*Passerina cyanea*); NC = 2013/2014, GA = 2012-2014]; 7) prairie warbler [(*Setophaga discolor*); NC and GA = 2014]; 8) northern bobwhite (NC and GA = 2013/2014); and 9) yellow-breasted chat [(*Icteria virens*); NC = 2014, GA = 2013/2014]. Focal species accounted for 83% and 59% of total bird detections in the NC and GA treatments, respectively. Generalist species were abundant in GA than NC. For example, northern cardinal (*Cardinalis cardinalis*) and northern mockingbird (*Mimus polyglottos*) collectively comprised approximately 15% of total bird detections in GA treatments. We identified 536 and 653 focal species territories in the NC and GA treatments, respectively.

In NC, harvest residue removal had little effect on the early-successional bird community in regenerating stands (Table 1). Species diversity and territory density of all focal species combined did not differ among treatments. In 2012, Carolina wren territory density was greater in the NOBIOHARV treatment than in all other treatments but 30CLUS. In 2013, common yellowthroat territory density was greater in the NOBIOHARV and 30DISP treatments than in the 15CLUS and 15DISP treatments. In 2014, species richness was lower in the NOBHG treatment than in the 15DISP treatment. Northern bobwhite relative abundance was greater in the NOBHG treatment than in the 15CLUS treatment. Territory density was greater in 2013 than in 2014 for indigo bunting and field sparrow.

Count of individual birds detected on branches of piles was greater in 2012 than 2013. Count of individual birds actively foraging on the ground (i.e., not foraging in vegetation) and perching on branches of piles was greater in 2012 than 2013 and 2014.

In GA, harvest residue removal also had little overall effect on the early-successional bird community in regenerating stands (Table 2). However, territory density of all focal species combined increased with increasing volume of harvest residues in treatments. Additionally, relative abundance of northern bobwhite and territory density of yellow-breasted chat both increased with increasing volume of harvest residues in treatments. Species diversity and richness for all bird species was unaffected by volume of downed wood. Indigo bunting territory density was lower in 2012 than in 2013 and 2014. Territory density was lower in 2013 than in 2014 for common yellowthroat, Carolina wren, eastern towhee, and yellow-breasted chat. Conversely, territory density for blue grosbeak decreased from 2013 to 2014. Relative abundance of northern bobwhite was lower in 2013 than 2014. Count of individual birds detected in piles increased with increasing volume of harvest residues in treatments and was increased from 2012 to 2013. Count of individual birds actively foraging on the ground was greater in 2012 and 2014 than in 2013.

In both states, most focal species used vegetation disproportionately to piles of downed wood (Fig. 1**a**, **b**). In NC, over 50% blue grosbeak and Carolina wren detections were recorded near, in, or on branches of piles, but all other focal species were more frequently recorded using vegetation than downed wood piles. In GA, all focal species were more frequently recorded using vegetation than downed wood piles. We documented more focal species using downed wood and recorded more individuals of focal species in piles of downed wood in GA than in NC. In NC, Carolina wren and field sparrow were detected near, on branches of, and especially in piles downed wood more frequently than other focal species. In NC and GA, northern bobwhite was detected near windows far more than any other focal species. Apart from focal species, we documented many early successional, breeding bird species associating with piles of downed wood (*see* Appendices C and D).

In NC, we detected minimal effects of harvest residue removal on habitat characteristics, although some vegetation measures varied by treatments (Table 3). In 2012, woody shrub and vine cover was greater in the 30DSIP treatments than the 15DISP treatments. In 2013, vertical vegetation structure was greater in the 30CLUS treatments than the NOBIOHARV treatments. In 2014, grass cover was greater in the 30CLUS treatments than in the NOBIOHARV treatments, woody shrub/vine cover was greater in the NOBIOHARV and 30DISP treatments than in the 15CLUS treatment, and maximum vegetation height was greater in treatments with higher volumes of harvest residues than those with less.

In GA, most habitat characteristics were unaffected by harvest residue removal (Table 4). Grass groundcover (2013) decreased with increasing volume of harvest residues, whereas litter groundcover (2014) increased with increasing volume of harvest residues. In both 2013 and 2014, grass cover decreased with increasing volume of harvest residues. In 2014, woody shrubs and vines increased with increasing volume of harvest residues.

For both states, vegetation composition and structure increased through time, following typical successional trajectories for regenerating stands (e.g., Table 3).

DISCUSSION

Our results suggest that the successional trajectory of vegetation structure and composition rather than volume of residual harvest residues following timber harvest is the primary driver of breeding, early successional bird use of regenerating stands. Indeed, the early-successional bird community showed minimal response to woody biomass removal treatments or volume of retained harvest residues. However, many breeding bird species associated with downed wood, in addition to vegetation, in regenerating stands (*see also* Appendices C and D). Further, harvest residues may provide important habitat for breeding birds in regenerating stands when vegetation largely is absent due to young stand age coupled with high intensity site preparation.

The paucity of literature on early-successional bird use of downed wood restricted interpretation of our results in relation to other studies. In their recent review of biodiversity and wood-based bioenergy, Riffell et al. (2011) identified only one study that addressed avian response to downed wood removal. Lohr et al. (2002) showed that weak excavating and secondary-cavity-nesting species, Neotropical migrants, and eastern towhee all had fewer breeding territories on plots where downed wood was experimentally removed in mature (between 40 and 50 years old) loblolly pine forests of the Southeast. Similarly, we found species-specific, positive responses to harvest residue retention by some Neotropical migrants (i.e., common yellowthroat and yellow-breasted chat) in young, loblolly pine forests of the Southeast. However, we documented no relationship between harvest residue removal and territory densities of eastern towhee. Overall, Lohr et al. (2002) documented a greater avian response to downed wood removal in mature pine stands than we did in young, regenerating stands, which may be attributable to their analysis of guilds rather than species-specific metrics or inherent differences in the relationship between birds, downed wood, and understory vegetation at different successional stages. For example, mature, commercial pine trees often limit (i.e., shade-out) understory vegetation (Hill 1979, Jennings et al. 1999), potentially making downed wood a more prominent habitat component on the forest floor in older pine forests.

Current levels of woody biomass harvest in the Southeast may retain volumes of downed wood above the threshold needed to sustain breeding, early successional bird populations, if a threshold even exists. Importantly, the woody biomass removal treatments implemented in our study were operational, reflecting current woody biomass extraction trends directly related to market values, rather than purely experimental, which typically entails removal of all downed wood (*see* Lohr et al. 2002). Indeed, stumpage price of woody biomass was found to be far more important to BHG stakeholders in the Southeast (n = 718) than wildlife habitat quality (Serenari et al. 2015). Recent studies in the Southeast have shown that even the most intensive, unrestricted operational woody biomass harvests leave relatively large volumes of downed wood on the landscape (Homyack et al 2013, Fritts et al. 2014). For example, a concurrent study at the replicates showed that the minimum volume of downed wood retained in the NOBHG treatments exceeded by over three-fold the Forest Guild's BHGs for the Southeast, which recommend at least 2.24 tons ha^{-1} of retained downed wood in pine forests of the Coastal Plain (Perschel et al. 2012, Fritts et al. 2014).

Despite the fact that the early-successional bird community was largely unaffected by downed wood removal, our results indicate downed wood was an important structural characteristic for some resident species. Although northern bobwhite was present in GA only when in-stand vegetation was well established (i.e., 2013 and 2014), relative abundance of the species increased with increasing volumes of downed wood. In terms of documented associations with downed wood, northern bobwhite has only been listed as a "log rooster" (Lanham and Guynn Jr. 1996). In NC, Carolina wren territory density was greater in treatments with more downed wood retention than those with less, albeit when vegetation structure was minimal (2012), and commonly associated with downed wood piles, verifying observations by Hamel (1992) and Lanham and Guynn Jr. (1996) that this species is heavily associated with downed wood.

Downed wood also was an important habitat component for some Neotropical migrant, early-successional species. In NC, common yellowthroat territory density was greater in treatments with more downed wood than those with less. Common yellowthroat is previously undocumented as being downed-wood associated; this species may use downed wood in regenerating stands as nesting cover, as do other ground- or near ground-nesting birds (Lanham and Guynn Jr. 1996). In GA, yellow-breasted chat territory density increased with increasing volumes of downed wood. Yellow-breasted chat also is previously undocumented as being associated with downed wood. Yellow-breasted chat is an insectivore (Eckerle and Thompson 2001) and, as such, may have responded to the high abundance of invertebrate prey associated with higher volumes of downed wood (Ulyshen and Hanula 2009). Additionally, downed wood piles may have served as perching platforms for territorial, common yellowthroat and/or yellow-breasted chat males

Breeding birds responded to harvest residue removal more so than winter birds studied at some of the same research sites (*see* Grodsky 2016). Lohr et al. (2002) recorded similar disparities between breeding and winter bird responses to down wood removal in mature, loblolly pine forests of the Southeast. Differences between breeding and winter bird response to downed wood removal may be related to the suite of species occurring in each season or differences in the amount of downed wood necessary to meet foraging versus nesting requirements (Hutto and Gallo 2006, Riffell et al. 2011). Additionally, winter birds typically are non-territorial, and thus may be less likely to be as strongly tied to particular habitat elements (Lohr et al. 2002).

Our results support the notion inferred by previous studies that downed wood is used by birds for food and cover (Hagan and Grove 1999, Lohr et al. 2002). Furthermore, we recorded several early successional bird species using downed wood that were previously unlisted as doing so in the Southeast (*see* Hamel 1992, Lanham and Guynn Jr. 1996; Appendices 1 and 2). In GA, we detected more birds in piles (i.e., windrows) in areas with more overall harvest residue retention. Birds detected in windrows may have been using downed wood therein as cover, potentially in response to observer presence, and/or for gleaning invertebrate prey contained within windrows (Lima 1993, Hagan and Grove 1999). For example, we often recorded Carolina wren in piles, and the species not only uses downed wood for nesting and cover (Hamel 1992), but also for the highly abundant arthropod prey base it maintains (Hagerty and Morton 1995). In GA, ground-foraging, insectivores (e.g., eastern towhee) likely took advantage of abundant, downed-wood associated invertebrate prey near piles (Jabin et al. 2004, Ulyshen and Hanula 2009, Castro and Wise 2010). Ground-foraging, granivores (e.g., mourning dove, northern bobwhite) were more frequently detected near piles of downed wood than insectivorous focal species, potentially suggesting that the significant ground-foraging response to increasing volume of harvest residues in GA is related to locally abundant seeds resources dispersed by flooding or wind “damming up” against windrows (Loeb 1996). Ground-foraging birds concentrating their attention downward while feeding could benefit from cover downed wood provides for protection from predators (e.g., diurnal raptors; Mac Nally et al. 2001).

Downed wood may be especially important as habitat structure for early-successional birds in regenerating stands prior to significant revegetation (i.e., 0 – 1 year post-harvest). In 2012, territory density of all focal species combined was positively correlated with increasing harvest residue volumes in the GA treatments, which exhibited lower vegetation structure and composition relative other years due to young stand age coupled with high intensity site preparation (e.g., windrowing, herbicide treatments). In 2012, the NC replicates maintained the least vegetation structure compared to subsequent years; meanwhile, count of detections of birds on branches of piles, ground-foraging, and perching were all greater in 2012 relative to later years. Downed wood is known to be used as perching platforms by birds (Shackleford and Conner 1997, Hagan and Grove 1999). Our findings suggest that birds in regenerating stands may select perching platforms based on height rather than substrate, using branches of downed wood until vegetation becomes the tallest available structure. Furthermore, availability of perches on branches of downed wood in the absence of other structure may facilitate predator vigilance among breeding birds (Lohr et al. 2002). Similarly, availability of downed wood during early stand development may influence foraging opportunities for early-successional birds. For instance, insectivorous birds with flexible foraging strategies may center their feeding on ground-dwelling invertebrates harbored by downed wood in the absence of other structure during pre-vegetation establishment, and then shift to foliage-gleaning of phytophagous insects once vegetation becomes established in regenerating stands.

Differences in site preparation between states allowed us the unique opportunity to explore potential variability in harvest residue retention and consequential avian response to woody biomass harvests following common silvicultural practices, namely shearing (NC) and windrowing (GA). Importantly, woody biomass harvests are predicted to predominantly occur in industrial pine plantations (Riffell et al. 2011), where implementation of site preparation practices facilitating commercial tree growth is nearly ubiquitous. In GA, windrowing had profound effects on the spatial arrangement of downed wood, and to a lesser extent, the intended, proportional volumes of downed wood originally assigned to treatments in our experimental design. Meanwhile, shearing in NC left volumes and spatial arrangements of downed wood that still left our original experimental design intact (Fritts et al. 2014). Piles of downed wood were much smaller in NC compared to windrows in GA, which likely is why we detected far more birds “in piles” in GA. This finding may indicate that larger piles of downed wood are more often used by birds, likely for food and cover, compared to smaller ones in regenerating stands.

Most of the focal species established territories only after vegetation structure and composition (e.g., woody vegetation for shrub/scrub nesters) was well-established. Given that vegetation in replicates was largely unaffected by treatments, most early-successional birds are likely to somewhat predictably respond to successional changes in vegetation structure and composition in regenerating stands (e.g., Conner and Adkisson 1975), regardless of whether or not woody biomass harvests occur. However, we did record greater vegetation height and prevalence of woody vegetation in treatments with more harvest residue retention than those with less in NC during the final year of the study. These findings suggest that, in some cases, woody shrubs used by many early-successional species for nesting may benefit from harvest residue retention, potentially because of the nutrient-rich growing substrate it provides (Harmon et al. 1986, Takahashi et al. 2000). Studies spanning further along the successional timeline could shed new light on the interplay between harvest residues and vegetation and consequential avian response but most early-successional birds are excluded from stands after canopy-closure, when harvest residues availability is concurrently reduced due to decay (Hill 1979, Keller et al. 2003, Loftis et al. 2011, Grodsky et al. 2016).

CONCLUSION

Early-successional, breeding birds mostly were unaffected by current levels of woody biomass harvest in intensively managed forests of the Southeast, suggesting that existing BHGs are adequate or potentially unnecessary with respect to breeding birds in the region. Furthermore, early-successional birds appeared to respond to successional changes in vegetation structure and composition more so than availability of harvest residues. However, several early successional bird species used harvest residues, many of which were previously undocumented as doing so. As such, downed wood may be a valuable habitat component following timber harvest in intensively managed forests. Although current levels of woody biomass harvest in the Southeast leave considerable volumes of downed wood on the landscape, technological advances in harvest machinery or increases in the market value of woody biomass could result in intensified removal of downed wood. If future woody biomass harvests intensify leading to a substantial decrease in downed wood retention relative to current levels recorded in our study, we recommend that breeding, early-successional bird response to woody biomass harvests be re-evaluated to inform and update BHGs.

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Table 1. Mean (SE) species diversity, species richness, focal species territory density per 40 ha, count of birds detected near, in, or on branches of piles, and count of birds foraging on the ground (i.e., not in vegetation) and perching (excluding perching on vegetation) in six woody biomass removal treatments in regenerating pine plantations, North Carolina (*n* = 4), 15 April – 15 July, 2012–2014. Treatments included: (1) no Biomass Harvesting Guidelines (NOBHGS); (2) 15% woody biomass retention in piles (15CLUS); (3) 15% woody biomass retention distributed evenly throughout the treatment unit (15DISP); (4) 30% woody biomass retention in piles (30CLUS); (5) 30% woody biomass retention distributed evenly throughout the treatment unit (30DISP); and (6) no woody biomass harvest (NOBIOHARV). We only included detections and resultant territories recorded ≥25 m from all drainage ditches and adjacent forest edge. We tested for treatment-level effects on response variables using GLMs with treatment, year, and replicate (blocking factor) as independent, explanatory variables. Different letters indicate significantly different, pair-wise comparisons of treatment means at α = 0.05 level.

	Woody biomass removal treatments					
	NOBHGS	15CLUS	15DISP	30CLUS	30DISP	NOBIOHARV
Species diversity	0.21 (0.02)	0.19 (0.02)	0.20 (0.02)	0.18 (0.02)	0.20 (0.01)	0.19 (0.02)
Species richness ϒ						
2012	0.52 (0.09)	0.46 (0.13)	0.44 (0.10)	0.38 (0.06)	0.56 (0.07)	0.48 (0.10)
2013	1.06 (0.11)	0.93 (0.08)	1.18 (0.15)	0.90 (0.09)	1.05 (0.08)	0.96 (0.17)
2014	1.09^{b} (0.08)	1.25^{ab} (0.07)	1.44^{a} (0.08)	1.25^{ab} (0.15)	1.31^{ab} (0.06)	1.12^{ab} (0.09)
All focal species ζ						
2012/2013/2014	19.96 (4.17)	22.65 (5.68)	26.46 (5.77)	28.13 (5.74)	31.49 (6.53)	31.14 (5.63)
Blue grosbeak						
2012/2013	2.38 (1.00)	2.93 (0.59)	4.27 (0.77)	3.75 (0.73)	3.50 (0.97)	2.82 (0.68)
Carolina wren ϒ						
2012	0^{b}	0.80^{b} (0.80)	0.95^{b} (0.95)	2.33^{ab} (1.48)	0.80^{b} (0.80)	6.93^{a} (2.67)
2013	0.92 (0.92)	0.26 (0.26)	0.95 (0.95)	0.77 (0.77)	2.94 (2.25)	3.02 (1.82)
2014	N/A	N/A	N/A	N/A	N/A	N/A
Common yellowthroat ϒ						
2012	N/A	N/A	N/A	N/A	N/A	N/A
2013	11.15^{ab} (2.33)	8.64^{b} (2.16)	9.51^{b} (2.73)	11.64^{ab} (3.14)	16.13^{a} (2.32)	15.65^{a} (3.54)
2014	8.54 (1.29)	9.31 (2.60)	11.67 (2.58)	10.44 (2.90)	11.64 (0.97)	8.99 (1.80)
Eastern towhee ϒ						

Table 1 (continued)

2012	N/A	N/A	N/A	N/A	N/A	N/A
2013	2.60 (0.92)	1.83 (1.83)	1.80 (1.04)	1.54 (0.89)	3.44 (1.41)	2.50 (1.54)
2014	1.30 (0.75)	1.57 (0.91)	4.11 (2.06)	5.89 (2.35)	1.80 (1.04)	7.51 (4.13)
Field sparrow ζ						
2013/2014	5.54 (1.85)	5.74 (1.41)	5.00 (1.37)	4.73 (0.99)	4.88 (1.07)	6.43 (1.55)
Indigo bunting ζ						
2013/2014	4.48 (1.09)	4.85 (2.31)	4.89 (1.42)	7.53 (1.01)	8.27 (2.08)	7.27 (1.52)
Northern bobwhite[1]						
2013/2014	0.34^{a} (0.10)	0.04^{b} (0.03)	0.20^{ab} (0.08)	0.26^{ab} (0.08)	0.20^{ab} (0.07)	0.26^{ab} (0.08)
Prairie warbler						
2014	4.75 (1.64)	7.98 (4.08)	6.75 (1.52)	9.48 (1.96)	7.81 (2.24)	6.36 (1.81)
Yellow-breasted chat						
2014	3.97 (1.32)	7.56 (2.39)	11.48 (3.06)	7.08 (1.84)	11.21 (1.09)	8.79 (0.90)
Near pile	0.51 (0.11)	0.55 (0.11)	0.34 (0.11)	0.38 (0.10)	0.30 (0.06)	0.40 (0.06)
In pile	0.06 (0.03)	0.08 (0.03)	0.11 (0.06)	0.22 (0.07)	0.17 (0.05)	0.20 (0.07)
On branch of pile ζ	0.97 (0.26)	0.93 (0.19)	0.79 (0.11)	0.93 (0.23)	0.89 (0.19)	1.32 (0.11)
Foraging ζ	0.09 (0.04)	0.04 (0.03)	0.06 (0.04)	0.08 (0.04)	0.06 (0.02)	0.13 (0.04)
Perching ζ	1.10 (0.19)	1.11 (0.20)	1.31 (0.19)	1.29 (0.18)	1.32 (0.18)	1.29 (0.15)

[1] Relative abundance rather than territory density used as response variable

ϒ = years analyzed separately when there was a significant year x treatment interaction

ζ = significant year effect

Table 2. Mean (SE) species diversity, species richness, focal species territory density per 40 ha, count of birds detected near, in, or on branches of piles, and count of birds foraging on the ground (i.e., not in vegetation) and perching (excluding perching on vegetation) in six woody biomass removal treatments in regenerating pine plantations, Glynn County (*n* = 3) and Chatham County (*n* = 1), Georgia, 15 April – 15 July, 2012–2014. Treatments included: (1) no Biomass Harvesting Guidelines (NOBHG); (2) 15% woody biomass retention in piles (15CLUS); (3) 15% woody biomass retention distributed evenly throughout the treatment unit (15DISP); (4) 30% woody biomass retention in piles (30CLUS); (5) 30% woody biomass retention distributed evenly throughout the treatment unit (30DISP); and (6) no woody biomass harvest (NOBIOHARV). We only included detections and resultant territories recorded ≥25 m from adjacent forest edge. We tested for effects of harvest residue removal using GLMs with harvest residue volume, year, and replicate (blocking factor) as independent, explanatory variables. Different letters indicate significantly different, pair-wise comparisons of treatment means at α = 0.05 level.

	Woody biomass removal treatments						Harvest residue volume (m^3/ha^{-1})		
	NOBHGS	15CLUS	15DISP	30CLUS	30DISP	NOBIOHARV	β	t	P
Species diversity ϒ									
2012	0.13 (0.04)	0.11 (0.04)	0.11 (0.04)	0.17 (0.05)	0.12 (0.02)	0.15 (0.03)	0.0002	1.35	0.19
2013	0.11 (0.01)	0.11 (0.01)	0.12 (0.02)	0.11 (0.02)	0.12 (0.01)	0.12 (0.02)	0.00007	1.50	0.15
2014	0.23 (0.07)	0.24 (0.07)	0.24 (0.08)	0.24 (0.08)	0.24 (0.07)	0.24 (0.08)	0.00002	0.81	0.43
Species richness ϒ									
2012	0.51 (0.10)	0.56 (0.24)	0.61 (0.21)	0.63 (0.19)	0.40 (0.07)	0.55 (0.14)	0.001	1.08	0.29
2013	0.47 (0.06)	0.62 (0.20)	0.69 (0.16)	0.59 (0.12)	0.62 (0.12)	0.60 (0.07)	0.001	2.00	0.06
2014	1.43 (0.33)	1.51 (0.26)	1.66 (0.45)	1.58 (0.41)	1.62 (0.41)	1.52 (0.43)	0.0008	1.22	0.24
All focal species ϒ									
2012	5.26 (2.25)	6.19 (2.30)	5.86 (2.59)	5.12 (2.12)	3.96 (2.27)	4.83 (1.37)	0.006	2.25	0.04

Table 2 (continued)

2013	36.07 (2.76)	35.21 (2.29)	36.10 (10.65)	38.38 (6.89)	41.77 (6.61)	36.18 (3.24)	0.014	1.89	0.07
2014	55.77 (3.55)	60.97 (6.81)	60.05 (9.35)	58.02 (10.35)	67.71 (1.78)	52.08 (4.85)	0.013	1.62	0.12
Blue grosbeak ζ							0.0002	0.11	0.91
2013/2014	4.06 (1.27)	4.74 (1.47)	3.29 (1.08)	5.45 (1.36)	5.87 (1.04)	4.95 (0.85)			
Carolina wren ζ							0.001	0.62	0.53
2013/2014	2.33 (0.69)	3.20 (1.05)	2.52 (0.83)	3.42 (1.25)	4.22 (1.31)	4.33 (1.06)			
Common yellowthroat ζ							0.001	0.48	0.63
2013/2014	8.00 (1.40)	6.73 (1.51)	6.03 (1.24)	6.63 (1.43)	11.70 (2.32)	7.48 (1.19)			
Eastern towhee ζ							-0.001	-0.47	0.64
2013/2014	6.32 (1.58)	8.70 (1.80)	8.43 (1.71)	8.13 (1.93)	7.26 (2.54)	5.37 (1.82)			
Indigo bunting ζ							0.002	1.53	0.13
2012/2013/2014	9.56 (1.63)	10.15 (1.61)	10.16 (1.80)	7.90 (1.48)	10.52 (2.02)	7.35 (1.34)			
Northern bobwhite[1] ζ	0.40 (0.13)	0.46 (0.15)	0.43 (0.13)	0.43 (0.17)	0.48 (0.20)	0.47 (0.20)	0.002	3.63	<0.01
Prairie warbler							0.002	0.81	0.43
2014	5.04 (3.52)	5.07 (3.54)	5.84 (3.40)	5.90 (4.35)	3.79 (2.16)	4.96 (3.00)			
Yellow-breasted chat ζ							0.003	2.01	0.05
2013/2014	7.63 (1.01)	6.79 (1.76)	8.21 (2.02)	8.10 (1.31)	6.49 (1.13)	7.10 (1.13)			

Table 2 (continued)

Near pile	0.26 (0.15)	0.34 (0.09)	0.26 (0.06)	0.34 (0.17)	0.18 (0.06)	0.20 (0.07)	0.0005	1.02	0.31
In pile ζ	0.34 (0.13)	0.33 (0.12)	0.35 (0.13)	0.43 (0.16)	0.47 (0.20)	0.45 (0.11)	0.001	2.87	<0.01
On branch of pile ϒ									
2012	1.63 (0.38)	1.34 (0.41)	1.53 (0.35)	1.36 (0.55)	1.25 (0.34)	1.33 (0.48)	0.003	1.55	0.14
2013	1.75 (0.24)	1.66 (0.34)	1.36 (0.09)	1.71 (0.23)	2.62 (0.91)	1.63 (0.29)	0.0007	0.31	0.76
Foraging ζ	0.19 (0.04)	0.25 (0.07)	0.18 (0.04)	0.17 (0.06)	0.22 (0.09)	0.24 (0.06)	0.0007	2.42	0.02
Perching ϒ									
2012	2.37 (0.42)	2.74 (0.57)	2.38 (0.46)	2.28 (0.69)	1.59 (0.39)	2.23 (0.53)	0.005	1.81	0.09
2013	3.00 (0.25)	3.96 (1.34)	3.66 (0.80)	3.75 (0.33)	4.35 (1.03)	3.40 (0.44)	0.009	2.30	0.03
2014	0.69 (0.12)	0.74 (0.21)	0.60 (0.08)	0.70 (0.16)	0.89 (0.18)	0.93 (0.38)	0.001	1.52	0.14

[1] Relative abundance rather than territory density used as metric

ϒ = years were analyzed separately when there was a significant year x volume interaction

ζ = significant year effect

Table 3. Mean (SE) of habitat characteristics in six woody biomass removal treatments in regenerating pine plantations, North Carolina (*n* = 4), July, 2012–2014. Treatments included: (1) no Biomass Harvesting Guidelines (NOBHG); (2) 15% woody biomass retention in piles (15CLUS); (3) 15% woody biomass retention distributed evenly throughout the treatment unit (15DISP); (4) 30% woody biomass retention in piles (30CLUS); (5) 30% woody biomass retention distributed evenly throughout the treatment unit (30DISP); and (6) no woody biomass harvest (NOBIOHARV). We tested for treatment-level effects using randomized complete block design ANOVAs with each habitat characteristic as a response variable, treatment as an explanatory variable, and replicate as a blocking factor. Different letters indicate significantly different, pair-wise comparisons of treatment means at α = 0.05 level.

	Woody biomass removal treatments					
Habitat characteristics	NOBHGS	15CLUS	15DISP	30CLUS	30DISP	NOBIOHARV
Groundcover (%)						
Bare ground						
2012	53.24 (4.12)	53.24 (1.96)	53.43 (1.94)	50.28 (1.44)	49.26 (3.62)	47.50 (5.38)
2013	37.22 (3.51)	31.76 (4.97)	33.36 (2.71)	29.63 (3.85)	31.96 (4.13)	30.19 (4.66)
2014	35.39 (6.20)	28.50 (2.75)	21.86 (3.12)	29.17 (5.51)	30.72 (2.93)	24.72 (0.86)
Grass						
2012	5.74 (2.35)	6.57 (1.46)	4.54 (2.45)	5.37 (1.79)	8.24 (3.07)	4.26 (1.37)
2013	37.59 (2.96)	33.24 (2.05)	31.82 (4.68)	39.17 (3.21)	33.96 (5.54)	27.84 (3.56)
2014	15.39 (1.93)	18.17 (1.22)	13.60 (2.13)	17.08 (1.72)	14.28 (1.67)	13.50 (1.76)
Litter						
2012	21.94 (3.18)	21.11 (2.87)	24.26 (3.50)	22.13 (4.45)	20.19 (2.19)	27.04 (2.37)
2013	13.61 (1.84)	19.54 (1.74)	19.14 (2.94)	14.91 (4.02)	15.01 (3.73)	25.43 (2.25)
2014	39.61 (5.94)	42.78 (3.12)	54.61 (1.31)	47.64 (4.36)	45.33 (3.59)	46.86 (2.46)
Vegetation cover (%)						
Forb						
2012	5.46 (1.77)	3.52 (1.59)	5.00 (1.80)	5.83 (1.96)	5.37 (1.36)	5.19 (1.74)
2013	18.98 (3.81)	17.78 (1.87)	20.56 (4.16)	17.41 (3.54)	19.93 (2.03)	23.78 (0.99)
2014	18.28 (2.77)	16.69 (1.47)	19.01 (3.01)	13.47 (2.76)	18.86 (3.52)	17.83 (3.82)
Grass						
2012	7.96 (3.53)	7.69 (1.67)	6.02 (3.06)	7.78 (2.41)	11.20 (3.68)	6.11 (1.69)
2013	56.11 (5.22)	54.26 (4.26)	54.41 (12.73)	60.65 (10.42)	54.84 (8.63)	46.82 (5.97)

Table 3 (continued)

2014	63.86^{ab} (4.35)	65.03^{ab} (5.30)	57.04^{ab} (8.89)	66.67^{a} (2.05)	61.81^{ab} (8.40)	47.11^{b} (4.59)
Woody shrub/vine						
2012	5.37^{ab} (1.07)	3.89^{ab} (1.11)	2.87^{b} (1.18)	4.35^{ab} (1.32)	6.57^{a} (1.65)	6.20^{ab} (1.07)
2013	25.37 (1.96)	22.59 (5.09)	31.83 (9.52)	32.22 (8.23)	35.32 (7.33)	35.10 (7.33)
2014	45.56^{ab} (3.18)	36.75^{b} (6.04)	48.43^{ab} (9.86)	54.31^{ab} (8.22)	57.25^{ab} (8.08)	63.42^{a} (5.15)
Vertical vegetation structure						
2012	0.49 (0.14)	0.51 (0.16)	0.34 (0.10)	0.55 (0.17)	0.48 (0.09)	0.52 (0.18)
2013	4.08^{ab} (0.29)	4.03^{ab} (0.35)	3.80^{ab} (0.41)	4.59^{a} (0.58)	4.46^{ab} (0.44)	3.67^{b} (0.38)
2014	3.67 (0.18)	3.79 (0.09)	3.58 (0.36)	4.01 (0.28)	4.16 (0.24)	4.14 (0.13)
Maximum vegetation height						
2012	0.59 (0.13)	0.57 (0.17)	0.40 (0.12)	0.65 (0.18)	0.61 (0.08)	0.61 (0.22)
2013	5.57 (0.38)	5.70 (0.50)	5.24 (0.58)	6.23 (0.74)	6.20 (0.58)	5.46 (0.56)
2014	7.39^{bc} (0.35)	6.91^{c} (0.14)	7.00^{bc} (0.45)	7.86^{abc} (0.39)	7.96^{ab} (0.51)	8.57^{a} (0.49)

Table 4. Effects of harvest residue removal on habitat characteristics in regenerating pine plantations, Glynn County (*n* = 3) and Chatham County (*n* = 1), Georgia, July, 2013 and 2014. We tested for effects of harvest residue removal using GLMs with each habitat characteristic as a response variable and harvest residue volume (m^3/ha^{-1}) and replicate as independent, explanatory variables. We set $\alpha = 0.05$.

	Harvest residue volume (m^3/ha^{-1})		
Habitat characteristics	β	t	P
Groundcover (%)			
Bare ground			
2013	-0.001	-0.58	0.57
2014	-0.001	-0.44	0.66
Grass			
2013	-0.001	-2.30	0.03
2014	-0.001	-1.79	0.09
Litter			
2013	-0.001	-0.67	0.51
2014	0.001	2.58	0.02
Vegetative cover (%)			
Forb			
2013	0.001	0.12	0.91
2014	0.001	0.77	0.45
Grass			
2013	-0.001	-2.29	0.03
2014	-0.001	-2.38	0.03
Woody shrub/vine			
2013	0.001	1.53	0.14
2014	0.001	2.60	0.02
Vertical vegetation structure			
2013	0.001	0.79	0.44
2014	-0.001	-0.87	0.40
Maximum vegetation height			
2013	0.001	0.40	0.70
2014	-0.001	-0.33	0.74

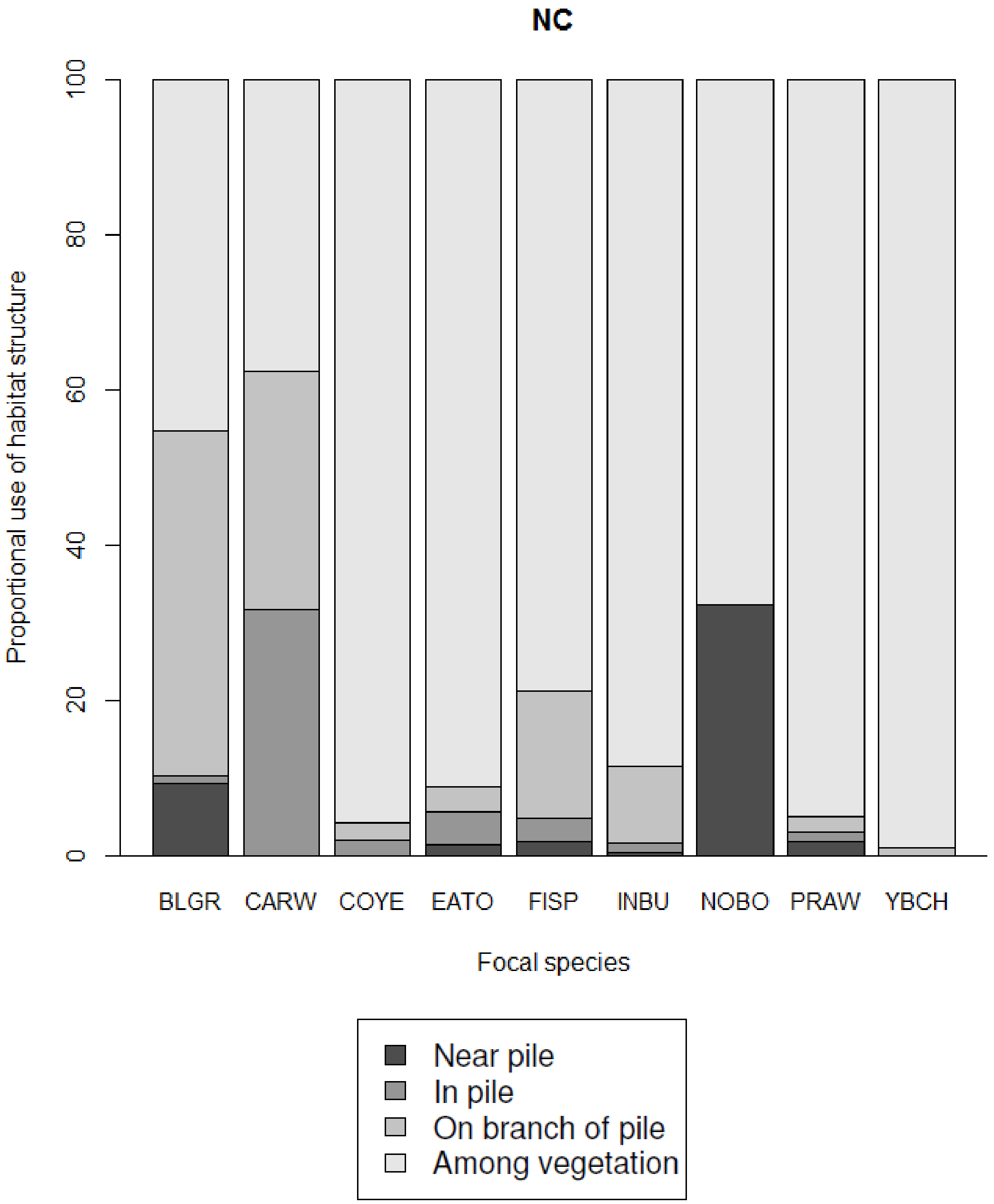
NC
Proportional use of habitat structure
0
20
40
60
80
100
BLGR
CARW
COYE
EATO
FISP
INBU
NOBO
PRAW
YBCH
Focal species
Near pile
In pile
On branch of pile
Among vegetation

Figure 1 (continued)

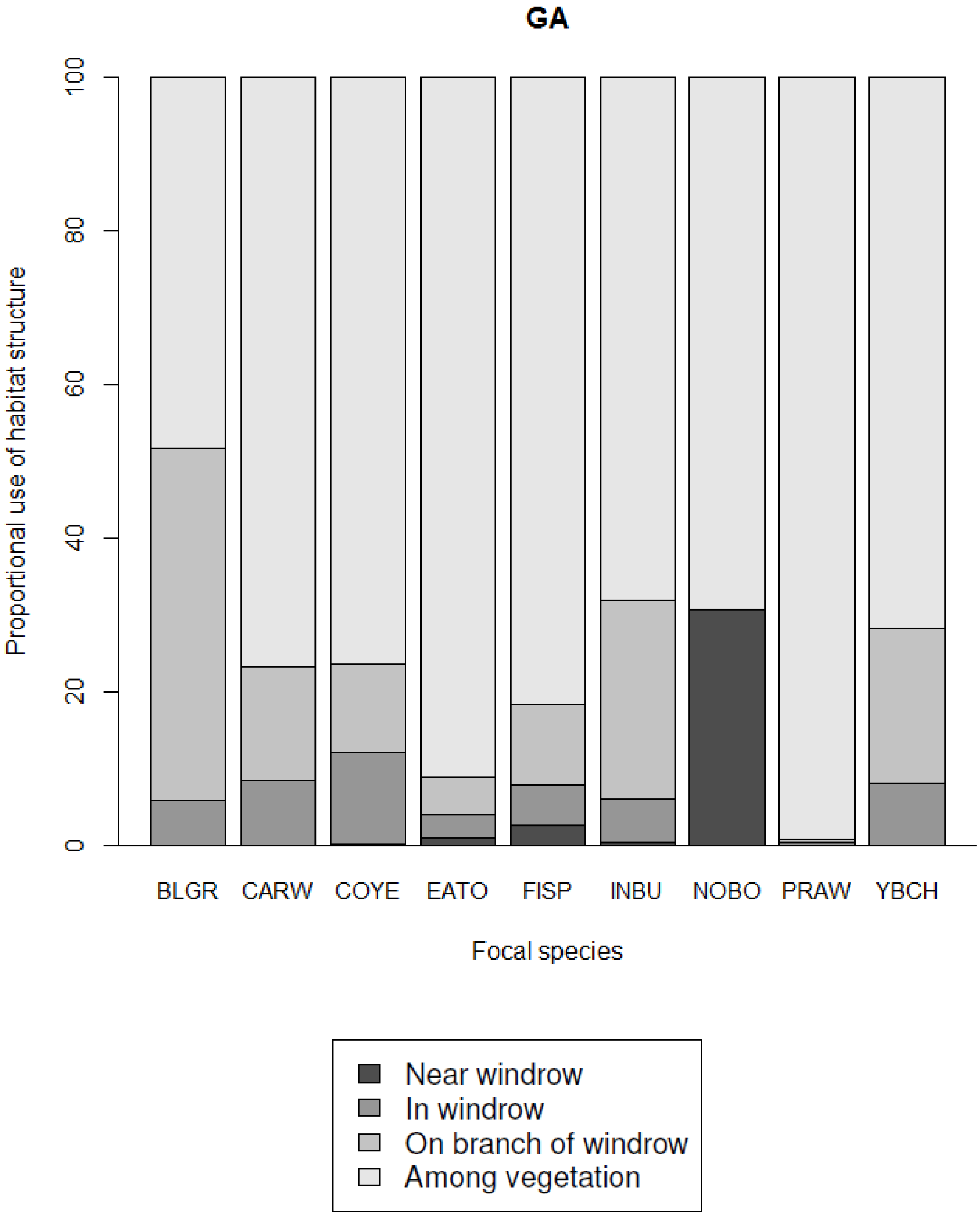

Figure 1. Proportional use of habitat structure in NC (**a**) and GA (**b**), including harvest residue piles [i.e., downed wood; near, in, and on branches of piles (NC) or windrows (GA)] and vegetation, by focal species in regenerating pine plantations, North Carolina (*n* = 4) and Georgia (*n* = 4), 15 April – 15 July, 2012–2014. BLGR = blue grosbeak; CARW = Carolina wren; COYE = common yellowthroat; EATO = eastern towhee; FISP = field sparrow; INBU = indigo bunting; NOBO = northern bobwhite; PRAW = prairie warbler; and YBCH = yellow-breasted chat. See Appendices for scientific names of focal species.

CHAPTER 3

Multi-scale invertebrate response to harvest residue removal in intensively managed forests: implications for downed wood management and renewable energy development

SUMMARY

1. Increased market viability of harvest residues as a forest bioenergy feedstock may intensify downed wood removal, particularly in intensively managed forests of the Southeast. Invertebrates may use downed wood for cover, food, and reproduction, but knowledge of facultative, ecological relationships between invertebrates and downed wood in the Southeast is lacking. Further, no study to date has addressed effects of operational-scale woody biomass harvests on invertebrates in the early successional conditions inherent to regenerating stands.

2. As such, we aimed to measure invertebrate response to harvest residue removal following woody biomass harvesting in early successional pine plantations, North Carolina (NC; *n* = 4) and Georgia (GA; *n* = 4), USA. We captured surface-active invertebrates using 272 pitfall traps situated in 68 arrays at hardwood, pine, and no pile treatments in NC and 192 pitfall traps situated in 48 arrays at windrow and no windrow treatments in GA. We tested effects of downed wood availability in regenerating stands on community-level metrics, including richness and relative abundance of functional and taxonomic groups, at local- and landscape-levels.

3. We found strong evidence of positive correlations between fungivore, granivore, and saprophage relative abundances and harvest residue availability, including fine and coarse woody debris, at multiple spatial scales.

4. Most taxonomic groups showed no response to harvest residue removal. However, several invertebrate taxa, including blattids, mycetophilids, rhaphidophorids, sciarids, positively associated with harvest residues at micro- and macro-scales.

5. *Synthesis and applications*: Retention of harvest residues following timber and woody biomass harvests could benefit several ecologically significant invertebrate functional groups and taxa. Specifically, harvest residues may mediate “bottom-up” interactions between invertebrates and fungi, detritus, and plants, potentially affecting downed-wood decay, site productivity, and seed dispersal in regenerating stands. In comparison to vertebrate taxa at the same sites, invertebrates proved to be powerful ecological indicators of sustainable forest management.

INTRODUCTION

Downed wood provides food and cover for forest wildlife and, in turn, greatly impacts biodiversity as a manageable forest-habitat component (Harmon et al. 1986, Huston 1996, Hagan and Grove 1999). Additionally, downed wood 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 downed wood as one of the most important resources for animal species in natural forests (Elton 1966), and management of downed wood is an increasingly relevant consideration for intensively managed forests (IMFs; Jones et al. 2009, Janowiak and Webster 2010).

Timber harvests in IMFs are large-scale, anthropogenic disturbances that lead to drastic increases in downed wood from harvest residues (Grodsky et al. 2016). Increases in the market viability of harvest residues as a forest bioenergy feedstock may lead to intensified levels of downed wood removal (i.e., woody biomass harvest), particularly in IMFs (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 an important feedstock for the production of 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 (USDA) 2007, Forisk Consulting 2013].

In the southeastern United States (herein “Southeast”), approximately 22% of timberland is planted forest (Oswalt et al. 2014) and much of this area is comprised of IMFs, which has facilitated the growth of a burgeoning forest bioenergy industry in the region

(Mayfield et al. 2013). The Southeast currently is one of the largest exporter of wood pellets in the world (Evans et al. 2013). Further, wood pellet production in the Southeast is predicted to increase to meet growing market demands driven by European Union renewable energy mandates (Goh et al. 2013, Galik and Abt 2015). Additionally, the Southeast is experiencing rapid development of forest bioenergy-production facilities (e.g., woody biomass power plants; Mendell and Lang 2012, REN21 2013), and nearly 50% of second generation biofuels required to meet United States biofuel mandates by 2022 will be supplied by forests of the Southeast (USDA 2010).

Given the known and potential wildlife-value of downed wood, removal of harvest residues following woody biomass harvesting could affect wildlife communities (Evans et al. 2013). Concerns regarding potential effects on forest ecosystem sustainability, including biodiversity, have led to development of non-regulatory biomass harvesting guidelines (BHGs; Perchel et al. 2012). In general, BHGs are based on the assumption that wildlife universally respond positively to increased volumes of downed wood (i.e., more downed wood is better than less; Harmon and Hua 1991). Yet, wildlife response to woody biomass harvests may differ among species or vary regionally, and BHGs currently have limited technical underpinnings from a paucity of empirical support. Further, knowledge regarding the ecological relationships between wildlife and downed wood remains severely underdeveloped in the Southeast, especially in IMFs (Riffell et al. 2011) and in comparison to other regions (e.g., the Pacific Northwest), since the issue was first raised 20 years ago (i.e., McMinn and Crossley 1996).

Invertebrates are well-known as valuable bioindicators (Kremen et al. 1993, McGeouch 1998, Hodkinson and Jackson 2005). Invertebrates have proven to be useful ecological indicators of ecosystem-wide effects of anthropogenic disturbance and land use change in forests, including IMFs (Pearce and Venier 2006, Iglay et al. 2012). Additionally, invertebrates have been identified as suitable study organisms for assessing fine- and large-scale response to local and landscape-level changes in habitat structure (Grodsky et al. 2015). “Bottom-up” trophic interactions between invertebrates and vertebrates often drive ecosystem function (Loreau et al. 2001), making invertebrate responses to harvest residue removal following woody biomass harvesting potentially applicable to vertebrates in IMFs.

Downed wood is an important resource for many forest invertebrates (Harmon et al. 1986, Landis and Werling 2010). Consequently, downed wood management may play a pivotal role in the conservation of invertebrate biodiversity in forested systems (Castro and Wise 2010). Invertebrates may use downed wood for foraging, refugia from thermal and moisture variability, 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). While the relationship between obligate, saproxylic organisms and downed wood has been extensively studied (Grove 2002, Ulyshen et al. 2004), how downed wood influences the composition of invertebrate communities not solely dependent on it as food is not well-understood (Hanula et al. 2006) and still underrepresented in the current literature.

Few studies have experimentally manipulated downed wood and measured invertebrate response, and those that have been conducted yielded variable results (Bengtsson et al. 1997, Ulyshen and Hanula 2009a, Castro and Wise 2010). For example, two large-scale experiments with variable coarse woody debris (CWD) retention were conducted in mature, loblolly pine (*Pinus taeda*) forests in South Carolina., USA. Hanula et al. (2006) found CWD removal decreased overall arthropod diversity and activity of several arthropod taxa, and affected community composition, while a later study at the same site found no effect of CWD removal on the invertebrate community (Ulyshen and Hanula 2009**a**). Castro and Wise (2009) manipulated availability of fine woody debris (FWD) in an undisturbed, mature forest and found no effect on spider diversity.

Some research has addressed facultative use of downed wood by invertebrates, albeit primarily through observational studies, by testing for differences in taxa composition and abundance in areas directly near and father from piles of CWD (Jabin et al. 2004, Castro and Wise 2010). In general, areas directly adjacent to piles of CWD maintain a deeper litter layer (Marra and Edwards 1998), higher concentrations of FWD (Evans et al. 2003), and specific microclimate conditions (Spears et al. 2003, Remsburg and Turner 2006). Some studies have shown litter adjacent to CWD has higher densities of invertebrate taxa (Jabin et al. 2007, Kappes et al. 2007, Ulyshen and Hanula 2009b). Favorable environmental conditions leading to high abundances of arthropod prey near downed wood also may lead to positive associations between predatory invertebrates, including carabids (Ulyshen and Hanula 2009**a**) and spiders (Varadi-Szabo and Buddle 2006), and CWD. Conversely, other studies found no difference in the diversity of invertebrate taxa between sites near and far from CWD (Marra and Edmonds 1998, Andrew et al. 2000, Buddle 2001). Differences among studies may be attributable to variation in responses by diverse invertebrate groups (Evans et al. 2003) or sampling methods (Varadi-Szabo and Buddle 2006).

Overall, little is known about how downed wood removal from forest stands affects insect communities (McKinley et al. 2011). Most woody biomass harvests in the Southeast are expected to occur in recent clearcuts (herein “regenerating stands”) within IMFs (Riffell et al. 2011), yet little is known about invertebrate response to reduction of downed wood in the early successional conditions inherent to regenerating stands. Additionally, downed wood generated by timber harvests in IMFs differs in volume and distribution from that generated by natural branch fall or tree death (Hanula et al. 2006, Grodsky et al. 2016) and may include both coniferous and deciduous harvest residues, which, in turn, may support different invertebrate groups (Jonsell 2007). Last, we are aware of no studies that have experimentally addressed invertebrate response to downed wood removal in the explicit context of operational-scale woody biomass harvesting.

Our project goals centered on filling in gaps of knowledge pertaining to: 1) facultative, ecological relationships between invertebrates and harvest residues; and 2) implications of operational, woody biomass harvesting for forest invertebrate conservation, specifically in IMFs of the Southeast. We aimed to determine effects of downed wood availability following woody biomass harvesting on community-level invertebrate metrics, including richness and relative abundances of functional and taxonomic groups, at two, spatially and experimentally explicit scales. Within this multi-scale, experimental framework, our objectives were to test: 1) micro-scale invertebrate responses to localized groundcover of FWD and vegetation at variable distances from areas with and without downed wood to inform ecological relationships between invertebrates and downed wood at micro-sites; and 2) macro-scale invertebrate responses to presence or absence of harvest residue piles, harvest residue pile type (i.e., pine versus hardwood), and operational-scale, woody biomass removal treatments to inform larger-scale, forest and downed wood management in light of woody biomass harvesting.

METHODS

Study area and design

We conducted our study on eight replicate regenerating stands (herein “replicates”) in loblolly pine plantations within the Coastal Plain Physiographic Region of the Southeast. Our study included four replicates [70.5±6.1 (mean ± SE) ha] in Beaufort County, North Carolina (NC; -077°0′0″W to -076°53′50″ and 35°34′0″N to 35°38′20″N) and four replicates (64.64±3.1 ha) in Georgia (GA): three in Glynn County, GA (-081°44′40″W to -081°40′42″W and 31°07′31″N to 31°11′14″N) and one in Chatham County, GA (-081°11′26″W to -081°10′37″W and 32°18′46″N to 32°19′21″N). In NC, replicates were managed for sawtimber production, commercially thinned twice prior to final harvest at 32-39 years old. In GA, replicates were managed for chip-and-saw and pulpwood production, commercially thinned once at each Glynn County replicate and twice at the Chatham County replicate prior to final harvest at 25-33 years old. Soils predominantly were loam and silt loam in NC and loam, clay loam, and fine sandy loam in GA.

Following clearcut harvest in 2010-2011, we implemented woody biomass removal treatments (herein WBRTs) at each replicate. We used a randomized complete-block experimental design, dividing each replicate into the following six treatments [NC – area = 11.7±0.5 (mean ± SE) ha, range = 8.4-16.3 ha; GA – area = 10.7±0.4 ha, range = 7.6-14.3 ha]: (1) clearcut with a traditional woody biomass harvest and no biomass harvesting guidelines implemented (NOBHG); (2) clearcut with 15% retention of harvest residues evenly dispersed throughout the treatment (15DISP); (3) clearcut with 15% retention of harvest residues clustered in large piles throughout the treatment (15CLUS); (4) clearcut with 30% retention of harvest residues evenly dispersed throughout the treatment (30DISP); (5) clearcut with 30% retention of harvest residues clustered in large piles throughout the treatment (30CLUS); and (6) clearcut with no woody biomass harvest (i.e., clearcut only; NOBIOHARV), which served as a reference site.

In each treatment, all standing pines merchantable as roundwood were cut and transported to a logging deck with a grapple skidder. For the NOBHG treatments, we instructed loggers to glean all harvest residues they deemed merchantable as woody biomass. For the NOBIOHARV treatments, pine roundwood was harvested; however, we instructed loggers to fell and leave all harvest residues (i.e., primarily midstory hardwoods) not harvested as roundwood.

To implement the four treatments emulating BHGs, we used ArcGIS (ESRI, Redlands, California, USA) to delineate retention areas that represented either 15% or 30% of the total treatment area. Prior to clearcut harvest, we located retention areas using a hand-held Garmin Rino global positioning system (Olathe, Kansas, USA) and flagged boundaries. We retained all hardwoods not merchantable as roundwood in retention areas. Retention areas were clearcut after loggers harvested 85% or 70% of the non-retention treatment areas, and harvest residues were redistributed throughout the treatment unit with a grapple skidder.

Harvest residues from the non-retention areas and the entire NOBHG treatment were chipped at the logging deck during harvest. In retention treatments, loggers used a grapple skidder to spread retained harvest residues from retention areas evenly throughout the DISP treatments or randomly placed piles throughout the CLUS treatments. Because we created treatments by distributing harvest residues with a grapple skidder, individual piles of harvest residues in the CLUS and NOBIOHARV treatments were approximately the size of one grapple load (volume $\approx$ 36.19 m^3ha^{-1}; Fritts et al. 2014).

Although WBRT implementation was identical in NC and GA, site preparation differed between states. In NC, site preparation followed clearcut harvest and implementation of WBRTs in the winter of 2010-2011. Replicates 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 seedlings during the fall-winter of 2011-2012 at a density of ≈1100 trees ha-1. Shearing moved retained harvest residues into the 3-m space between pine beds (i.e., interbeds). Consequently, woody biomass was rearranged following shearing into long, linear rows in interbeds parallel to pine beds, which essentially consisted of bare soil and pine seedlings. Replicates were treated with the following two post-harvest herbicide applications of 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 harvest residues in treatments were concentrated into large, linear piles (i.e., windrows) extending for the entire length of treatments or into large, conical piles (1-100 m^3) within treatments. As such, few individual stems and no small downed wood piles (<$1m^3$) occurred between windrows (~30-50 m apart) in treatments (Fig. 1**b**). In Glynn County (GA), two replicates were double-bedded in the summer of 2011 and the remaining replicate was double-bedded in fall 2011. All Glynn County (GA) replicates were planted in winter 2012 at a density of ≈1495 trees ha^{-1} and treated with Arsenal© (BASF, Raleigh, North Carolina, USA) and Sulfometuron methyl for herbaceous weed control one year after clearcut harvest. In 2012, the Chatham County (GA) replicate was bedded and planted at a density of ≈726 trees ha^{-1} and received a broadcast treatment of Chopper© on year after clearcut harvest.

Following establishment of WBRTs, site preparation, and planting, we identified finer scale harvest residue removal treatments (herein treatments) within WBRTs. We randomly located clusters of treatments in each large-scale, WBRT at each replicate. In NC, treatments included 1) hardwood pile; 2) pine pile; and 3) no pile (i.e., no coarse woody debris; control). In GA, harvest residues consisted of pine in windrows exclusively; as such, treatments in GA included: 1) windrow; and 2) no windrow (i.e., no coarse woody debris; control). We visually estimated decay class of hardwood piles, pine piles, and windrows following Forest Inventory and Analysis (FIA) protocols (USDA 2007).

In NC, replicates and WBRTs therein were bordered by drainage ditches (~1 m wide) containing vegetation which was unaffected by site preparation and thus more developed than vegetation growing in treatments per se. In both states, a logging road (~3.7 m wide) separated most replicates from adjacent forest stands, which typically fell into two age classes: 1) young loblolly pine stands (~10 years old); and 2) mature loblolly pine stands (~30 years old). Snags were rare on all NC replicates and occurred sporadically throughout GA replicates. In GA, replicates contained some retained, riparian forests (e.g., stringers) that were left unharvested during clearcutting following Best Management Practices for forest harvest near wetlands (R. Hicks, pers. comm.).

Invertebrate sampling, identification, and measures

In 2012 and 2013, we sampled invertebrates using pitfall trapping. We specifically targeted surface-active invertebrates because they occupy niches on the forest floor (e.g., Pearce and Venier 2006), which in turn contains harvest residues as habitat structure. Pitfall trapping is one of the most commonly used methods to capture a wide range of surface-active invertebrates (Spence and Niemalä 1994). Pitfall traps were 0.47-L containers with a diameter of ~8.5 cm filled with equal amounts of propylene glycol and water and a drop of liquid dish soap. 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 large- and local-scale habitat characteristics). Four pitfall traps comprised a pitfall trap array (herein array). To control for edge effects, we situated all arrays ≥ 100 m from drainage ditches and replicate edges.

In NC, we established 4-m long arrays with 1-m inter-trap spacing in each treatment. Each array was oriented in a straight line perpendicular to interbeds and bedded rows. For the hardwood and pine pile treatments, 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 treatment, despite the fact that no harvest residue pile was present. We sampled each treatment monthly for a 48-hour period, June – September, 2012 and June, July, and September, 2013.

In GA, we established 15-m long arrays with 5-m inter-trap spacing in each treatment to accommodate the width of windrows. For the windrow treatment, 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 treatment, despite the fact that no windrow was present. We sampled each treatment once for a 48-hour 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 labelled with trap locality data. With the exception of highly abundant cricket nymphs, we (SG and JC) identified all adult specimens (i.e., juveniles excluded) to family or, in rare cases, division (e.g., Diptera) or order (e.g., Chilopoda, Diplopoda) using taxonomic keys and confirmation for type specimens representative of each taxonomic group from expert taxonomists, including Matt Bertone (Entomologist, North Carolina State University Plant Disease and Insect Clinic, Raleigh, NC, USA) and David Stephan [Entomologist (retired), North Carolina State University Plant Disease and Insect Clinic, Raleigh, NC, USA]. Additionally, we sorted, pinned, and labelled with trap locality data type specimens representative of captured, invertebrate families to serve as voucher specimens, which we submitted to the North Carolina State University Insect Museum.

Based on pooled count data from pitfall traps recorded in each state and year, we indexed the following hierarchical, ecological and taxonomic invertebrate measures based on catch-per-unit effort (CPUE; number of captures/number of active traps): 1) overall richness; 2) abundance of functional groups; and 3) abundance of orders, divisions, families (most common), or subfamilies (Ludwig and Reynolds 1988, Iglay et al. 2012; *but see* Statistical Analysis). We accounted for CPUE because external factors out of our control, namely localized surface-flooding from rain events, led to some inactive pitfall traps during some sampling periods. Specifically, we defined invertebrate metrics as follows: 1) overall richness = total count of individual taxonomic groups/number of active traps per pitfall trap and array; 2) relative abundance of each functional group = count of individual taxa falling into each functional group/number of active traps per pitfall trap and array; and 3) relative abundance of taxonomic groups at each pitfall trap = total count of captures of each taxonomic group/number of active traps per pitfall trap; and 4) relative abundance of taxonomic groups at each array = pooled count of captures among pitfall traps of each taxonomic group/number of active traps per array.

We (MB) assigned up to two primary, adult functional groups and, if applicable, one juvenile functional group (holometabolous insects with larva filling different niches than adults only) to each captured taxon. As such, some invertebrate taxa with diverse life histories contributed to the relative abundance of more than one functional group. However, we did not assign functional groups to taxa exhibiting extremely variable life histories and thus falling into >2 primary, functional groups (e.g., Formicidae, *see* Appendix A). Functional groups included: 1) fungivores; 2) granivores; 3) herbivores; 4) pollinators; 5) parasitoids; 6) predators; and 7) saprophages. We set the cutoff for inclusion of functional groups in our paper based on natural breaks in the distribution of the total number of captures for each functional group. We also excluded functional groups only represented by taxa already being analyzed as individual taxonomic groups. We plotted the distribution of relative abundances for all taxonomic groups per year and state and binned all taxa into one of the following three abundance levels: 1) superabundant; 2) abundant; and 3) rare. We set the cutoff for inclusion of individual taxonomic groups in our paper as the lowest relative abundance at the break between abundant and rare taxa, thereby excluding all rare taxa with relatively low relative abundances.

Quantifying local- and large-scale habitat characteristics

During a concurrent study, we measured scattered and piled harvest residues in each treatment at the NC and GA replicates 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 pile of downed wood in each treatment, measured its length, width, and height, and visually estimated its packing ratio (i.e., density of wood in pile; 0 – 100%). For the visual encounter method in GA, we measured the width, 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). For both states, we summed volume of piled downed wood estimated from the visual encounter method and volume of scattered downed wood estimated using the LIS method to generate total volume of downed wood (m^3ha^{-1}) for each WBRT plot. Volume of downed wood in the NC treatments was shown to accurately match that of our original experimental design (Fritts et al. 2014). However, the efficacy of treatment implementation in GA was influenced by greater intensity site preparation relative to NC (i.e., windrowing in GA versus shearing in NC) and, as such, treatments may not have matched intended outcomes.

In NC and GA, July 2012 and 2013, we quantified local-scale habitat characteristics at each pitfall trap by placing a 1- by 1-m Daubenmire frame over each pitfall trap such that the pitfall trap was centered in the frame and visually estimating percent groundcover (total = 100%) for the following categories: 1) bare ground; 2) FWD; and 3) vegetation (included all living grasses, forbs, and woody shrubs and vines).

Statistical framework and analysis

For each year in NC and GA, we ran Poisson generalized linear models (GLMs) to test community-level response of surface-active invertebrates to harvest residue removal at the micro- and macro-scale. We opted to forego analyses including random effects to account for sampling biases because we believe our standardized approach to pitfall trap and array design sufficiently accounted for such variation. 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 ran quasipoisson GLMs when we detected overdispersion. To account for variation in effort (i.e., CPUE), we also included number of active traps and number of active arrays as an additive, fixed effect (*sensu* relative abundance) in all micro- and macro-scale models, respectively. For categorical covariates in all micro- and macro-models, we performed *post-hoc* Tukey's pair-wise 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 our micro-scale analyses, we used each pitfall trap as the experimental unit (n = 272 in NC; n = 192 in GA), count of overall richness and number of captures of functional and taxonomic groups as response variables, percent cover of FWD and vegetation and effort as continuous, fixed effects, and trap location [Bed or Interbed (NC); Far from windrow, In bedded rows near windrow, or In interbeds near windrow (GA)] as categorical, fixed effects. For both years in NC and GA, bare ground was inversely correlated with vegetation groundcover and consequently was excluded as a covariate in all micro-scale models.

For our macro-scale analyses in NC, we used array as the experimental unit (n = 68), count of overall richness and number of captures of functional and taxonomic groups pooled over all pitfall traps at each array as response variables, treatment, WBRT, and replicate (blocking factor) as categorical, fixed effects, and effort as a continuous, fixed effect. For macro-scale analyses in GA, we used array as the experimental unit (n = 48) and followed the same modelling framework outlined for NC, but replaced the categorical, fixed effect for

WBRT with the volume (m^3ha^{-1}) of harvest residues in windrows in each WBRT (*see* Quantifying large- and local-scale habitat characteristics).

RESULTS

We captured 39,794 adult specimens representing 171 individual taxonomic groups, most of which (n = 147; 86%) we identified to family (*see* Appendix A). In NC, we set the cutoff for inclusion of individual taxonomic and functional groups at 45 and 100 captures per year, respectively, included 22 individual taxon and 5 functional groups in our analyses for 2012, and included 24 individual taxon and 7 functional groups in our analyses for 2013. In GA, we set the cutoff for inclusion of individual taxonomic groups and functional groups 25 captures per year, included 10 individual taxon and 4 functional groups in our analyses for 2012, and included 18 individual taxon and 6 functional groups in our analyses for 2013. Collembolans were ubiquitous in samples (S. Grodsky, *pers. obs.*), so we opted not to include them in analyses. Hardwood and pine piles and windrows ranked as Decay Class 1 in 2012 and Decay Class 2 in 2013 [*see* FIA protocol for definitions; USDA (2007)], indicating increased decay through time.

Micro-scale results (NC)

In 2012, overall richness increased with increasing vegetation groundcover, and fungivore, herbivore, and saprophage relative abundance was greater in interbeds than beds (Table 1). Over half (n = 12; 60%) of invertebrate taxa responded to groundcover of FWD, groundcover of vegetation, or distance from harvest residue piles (Table 1). Mycetophilid relative abundance increased with increasing FWD and vegetation groundcover. Centipede, dolichopodid, and sciarid relative abundance increased with increasing FWD groundcover, whereas millipede, phorid, and scarabaeid relative abundance decreased with increasing

FWD groundcover. Ant, carabid, cicadellid, and the dipteran division Schizophora relative abundance increased with increasing vegetation groundcover. Chrysomelid and Blattid relative abundance was greater in interbeds than beds.

In 2013, overall richness was unaffected by groundcover or trap location, granivore relative abundance increased with increasing FWD groundcover, and fungivore and saprophage relative abundance was greater in interbeds than beds (Table 1). Nearly a quarter (n = 7; 26%) of invertebrate taxa responded to groundcover of vegetation, groundcover of FWD, or distance from harvest residue piles (Table 1). Carabid relative abundance increased with increasing FWD and vegetation groundcover. Blattid relative abundance increased with increasing FWD groundcover. The cricket subfamily Nemobiinae and paradoxosomatid relative abundance decreased with increasing vegetation groundcover. Chloropid, sciarid, and staphylinid relative abundance was greater in interbeds than beds.

Micro-scale results (GA)

In 2012, overall richness was unaffected by groundcover or trap location, fungivore relative abundance was greater in interbeds adjacent to windrows than far from windrows, and saprophage relative abundance was greater in interbeds and beds adjacent to windrows than far from windrows (Table 1). Approximately one-third (n = 3; 30%) of invertebrate taxa responded to groundcover of vegetation, groundcover of FWD, or distance from harvest residue piles (Table 1). We found no relationship between any invertebrate taxa and FWD. Acridid relative abundance increased with increasing vegetation groundcover. Rhapidophorid relative abundance also increased with increasing vegetation groundcover and was greater in interbeds adjacent to windrows than far from windrows. Blattid relative abundance was greater in interbeds and beds adjacent to windrows than far from windrows and gryllid relative abundance was greater in interbeds adjacent to windrows than far from windrows, whereas ant relative abundance was greater far from windrows than in interbeds adjacent to windrows.

In 2013, overall richness was unaffected by groundcover or trap location, pollinator relative abundance increased with increasing FWD and vegetation groundcover, and herbivore and saprophage relative abundance increased with increasing vegetation groundcover (Table 1). One-third (n = 6, 33%) of invertebrate taxa responded to groundcover of vegetation, groundcover of FWD, or distance from harvest residue piles (Table 1). Ceratopogoniid and sacrophagid relative abundance increased with increasing FWD and vegetation groundcover. Additionally, ceratopogoniid relative abundance was greater in beds adjacent to windrows than far from windrows, and sacrophagid relative abundance was greater in interbeds and beds adjacent to windrows that far from windrows. Cydnid relative abundance increased with increasing FWD groundcover, whereas mycetophilid, the cricket subfamily Nemobiinae, and scelionid relative abundance decreased with increasing FWD groundcover.

Macro-scale results (NC)

In 2012, neither treatments nor WBRTs affected overall richness, and fungivore and saprophage relative abundance was greater at pine pile treatments than no pile treatments (Fig. 2**a**). Fewer invertebrate taxa responded to treatments (n = 4; < 20%; Table 2) or WBRTs (n = 6; 30%; Table 3) than for the micro-scale analyses (*see* Table 1). Mycetophilid and sciarid relative abundance was greater at pine pile treatments than no pile treatments. Schizophoran relative abundance was greater at pine pile treatments than hardwood pile treatments. Scarabaeid relative abundance was greater at no pile treatments than pine pile treatment, but not hardwood pile treatments. Millipede, gryllid, and gryllid nymph relative abundance differed among WBRTs, but showed no clear response to harvest residue removal along the WBRT gradient. However, ant, phorid, and staphylinid relative abundance all were greater in the NOBHGS WBRT than the NOBIOHARV WBRT, indicating a positive association with decreased harvest residue volumes for these taxa.

In 2013, overall richness and relative abundance and diversity of functional groups (Fig. 1**a**, **b**) and relative abundances of most taxa increased relative to 2012 (Tables 2; Table 3). Neither treatments nor WBRTs affected overall richness, granivore relative abundance was greater at pine pile treatments than no pile treatments, and saprophage relative abundance was greater at pine and hardwood pile treatments than no pile treatment (Fig. 1**b**). Approximately 20% of invertebrate taxa responded to treatments (n = 4; 17%; Table 2) and WBRTs (n = 5; 21%; Table 3) in 2013. Blattid relative abundance was greater in both the pine and hardwood pile treatments than the no pile treatment. As in 2012, sciarid relative abundance was greater in the pine pile treatment than the no pile treatment. Chrysomelid relative abundance was greater in the no pile treatment than the hardwood pile treatment, and staphylinid relative abundance was greater in the no pile treatment than both the pine and hardwood pile treatments. Dolichopodid relative abundance was lesser in the NOBIOHARV WBRT relative to all other WBRTs. Gryllid and gryllid nymphs responded similarly to WBRTs in 2013 as they did in 2012, with differences in relative abundance occurring among WBRTs but with no clear pattern in relation to harvest residue removal. Paradoxosomatid relative abundance was greater in the NOBIOHARV WBRT than in the 15DISP and 15CLUS WBRTs, but not the NOBHGS WBRT.

Macro-scale results (GA)

In 2012, overall richness was unaffected by treatment or harvest residue volume, and saprophage relative abundance was greater at windrow treatments than no windrow treatments (Fig 1**c**). Herbivore relative abundance increased with increasing harvest residue volume. Nearly half (n = 4; 40%) of invertebrate taxa responded to treatments but relatively few (n = 2; 20%) responded to WBRT harvest residue volumes. Blattid relative abundance was greater at windrow treatments than no windrows treatments and increased with increasing WBRT harvest residue volumes. Rhaphidophorid relative abundance also was greater at windrow treatments than no windrow treatments, whereas ant and lycosid relative abundance was greater at no windrow treatments than windrow treatments. Gryllid relative abundance decreased with increasing WBRT harvest residue volumes. Overall richness and relative abundance and diversity of functional groups were greater in 2013 than 2012 (Fig. 1**d)**, and no invertebrate metrics were affected by treatments or WBRT harvest residue volumes (Table 4).

DISCUSSION

Results suggested that some invertebrates positively responded to availability of downed wood at the local and/or landscape-level in early successional IMFs following several major, environmental perturbations, including clearcutting, woody biomass harvesting, and site preparation. Yet, many invertebrates showed no response to harvest residue removal (i.e., treatment- and WBRT-level effects) in any given year or state. Several common invertebrate groups, including herbivores and some predators, likely responded to the successional trajectory of vegetation composition and structure rather than harvest residue availability in regenerating stands. However, several ecologically significant functional groups, including fungivores, granivores, and saprophages, positively associated with harvest residues, indicating that downed wood management in IMFs may be an important consideration for these invertebrate guilds.

We found strong evidence of positive correlations between fungivore relative abundances and harvest residues at multiple spatial scales, demonstrating that “bottom-up” interactions between fungi and fungivores may be mediated by downed wood in regenerating stands. Invertebrate fungivores influence fungal community structure via grazing pressure and act as dispersal agents for fungal spores (Shaw 1992). In turn, fungi significantly contribute to wood decay, which is fundamental to the formation of ecological niches and creation of different substrates in forests (Odling-Smee et al. 2003, Lonsdale et al. 2008). We captured more fungivores in pitfall traps closer to than farther from downed wood (e.g., interbeds > beds) and at pine pile treatments than no pile treatments, supporting the theory that species richness of wood-decaying fungi typically increases with the amount of available downed wood (Berg et al. 1994, Allen et al. 2000, Lonsdale et al. 2008). Additionally, we documented strong affiliations between the fungivorous fly families Mycetophilidae and Sciaridae and downed wood at treatments, specifically pine piles, suggesting that availability of downed wood and thereby fungi in IMFs may affect these Dipterans. Økland (1996) also found a strong relationship between mycetophilids and downed wood in unharvested forests of Norway. Additionally, both mycetophilids and sciarids positively responded to FWD at micro-sites, which supports findings from Küffer and Senn-Irlet (2005) that demonstrated FWD can provide important refuges for many wood-inhabiting fungi in IMFs.

Granivores were positively linked to FWD, captured closer to than farther from windrows, and had greater relative abundance at hardwood pile treatments than no pile treatments, all of which supports previously established “seed-damming” hypotheses at multiple, spatial scales. Specifically, piles of downed wood may trap seeds dispersed by surface flooding or wind and subsequently provide locally abundant food resources for granivores (Loeb 1996, Sharitz 1996). While “seed-damming” is typically associated with CWD (e.g. Sharitz 1996), our results indicate FWD may trap seeds as well. In addition to granivores as a functional group, granivorous families, including Carabidae and Cydnidae, positively responded to FWD, providing further support that FWD may play a more important role in “seed-damming” than previously recognized. Granivory significantly affects the regeneration, colonization ability, and spatial distribution of plants (Hulme and Benkman 2002), so population-level effects of downed wood removal on granivores could affect plant communities in IMFs.

In general, saprophages were positively influenced by availability and proximity of harvest residues and showed the most sensitivity to harvest residue removal (e.g., treatment-level effects) of any functional group. Saprophagous invertebrates are important consumers of plant debris and litter in the detrital trophic chain, and may influence site productivity in IMFs by accelerating decomposition and affecting soil fertility and nutrient cycling (Crossley Jr. 1977). Saprophages did not respond to availability of FWD at the micro-scale, but had greater relative abundance in interbeds (NC) and near windrows (GA), both of which exclusively maintained continuous, linear rows of FWD and piles of CWD at the stand-level (Fritts et al. 2014). Woodroaches in the saprophagous family Blattelidae, most of which were in the genus *Parcoblatta* (SMG, *unpublished data*), mirrored the response of saprophages as a functional group, but additionally showed positive associations with FWD in NC and landscape-level responses to harvest residue volumes in GA. As such, *Parcoblatta* may be especially affected by harvest residue removal in IMFs. Previous studies in pine forests of the

Southeast have shown that CWD provides important habitat for *Parcoblatta* species, many of which are eaten by forest birds (Horn and Hanula 2002, Hanula et al. 2006).

Lack of response to harvest residue removal for remaining functional groups may have reflected the life histories of commonly captured invertebrates or low numbers of captures for some guilds. For example, many hemimetabolous herbivores exclusively use vegetation. Herbivores were largely comprised of hemimatabolous Homopteran families (e.g., Aphididae, Cicadellidae) that spend their entire lives on host plants, unlike holometabolous insects that may fill different juvenile and adult niches (Mitchell 1981). Additionally, predators are highly diverse and exhibit a variety of hunting strategies. Lycosid spiders were a common, surface-active predator that showed no response to downed wood availability or vegetation in regenerating stands, possibly because bare ground accommodates the hunting behavior of some lycosid species (i.e., active hunting based on visual cues; Kuusk and Ekbom 2012). On the other hand, carabids, centipedes, and dolichopodids were all surface-active predators that positively responded to FWD at micro-sites in IMFs and have been shown to associate with downed wood in other forest systems, presumably for cover and food (Summers and Uetz 1979, Braccia and Batzer 2001, Hanula et al. 2009). Although parasitoids and pollinators met the minimum requirements for analysis in some cases, number of captures were much lower in comparison to other functional groups and thus may have limited our ability to detect responses to harvest residue removal among these groups.

Results indicated that harvest residue decay dynamics affected invertebrate response to harvest residue availability. Increased relative abundances of downed wood-associated invertebrates from 2012 to 2013 likely were driven by downed wood decay, which facilitates the creation of different substrates and consequently, ecological niches in forests through time (Odling-Smee et al. 2003, Lonsdale et al. 2008; *see also* section on vegetation). For example, more decayed harvest residues in 2013 may have led to greater relative abundance of fungivores in the NOBIOHARV and 30CLUS WBRTs than the NOBHGS WBRT, whereas no landscape-level differences between these WBRTs occurred in 2012 when downed wood was less decayed.

Several invertebrate groups responded to harvest residue pile type (i.e., pine versus hardwood), possibly due to the interplay between pile type and decay rates and/or fungal community composition. In NC, pine piles contained smaller diameter CWD and more FWD in comparison to hardwood piles (Fritts et al. 2014), which likely lead to increased rates of decay (Harmon et al. 1986, Hagan and Grove 1999). Further, dead wood consisting of pine typically decays at faster rates than that consisting of hardwood in the Southeast (Moorman et al. 1999). Although we found no difference in decay class between hardwood and pine piles, we believe the FIA ranking system lacked the resolution to decipher variation in decay rate between the two. Fungivores, including mycetophilids and sciarids, heavily selected pine pile treatments over hardwood and no pile treatments, which may indicate this functional group positively responded to more decayed harvest residues and/or the distinct fungal communities prominently or exclusively found on dead pine (e.g., Visser 1995, Gardes and Bruns 1996). Saprophage relative abundance was greater at pine pile treatments than both hardwood and no pile treatments in 2012 but greater in both pine and hardwood pile treatments than no pile treatments in 2013, possibly because harvest residues comprised of hardwoods took longer to reach a suitable decay state. Understanding differences in invertebrate responses to pine compared to hardwood harvest residue removal may be important in the context of woody biomass harvesting because of the dynamic marketability of different woody biomass feedstocks.

Following timber harvest, the influx of harvest residues is inevitably accompanied by drastic increases in early successional vegetation (White and Jentsch 2001, Grodsky et al. 2016), which in turn may have acted independently of or in conjunction with decay to drive invertebrate use of regenerating stands. Indeed, relative abundance of nearly all invertebrates in both states increased from 2012 to 2013, which coincided with a drastic increase in vegetation from one to two years post-harvest (Grodsky 2016). Further, overall invertebrate richness was linked to fine-scale availability of vegetation, albeit only in NC (2012). In GA (2013), we detected no invertebrate response to harvest residue removal, possibly because the influx of vegetation during the same year trumped any effects of availability of downed wood. Several families positively responded to both FWD and vegetation, providing evidence that availability of groundcover in general, regardless of type, may have driven some invertebrate use of micro-sites in regenerating stands.

Site preparation is a silvicultural practice inextricably linked to IMFs, regardless of whether woody biomass harvesting occurs, and influences the spatial distribution of harvest residues and vegetation in regenerating stands (Grodsky et al. 2016). Therefore, effects of site preparation on wildlife use of regenerating stands should be concurrently considered when addressing wildlife response to harvest residue removal in IMFs (e.g., Fritts et al. 2015; Fritts et al. 2016). For example, relative abundance of herbivores in NC (2012) was greater in interbeds than beds most likely because spot-applications of herbicides during the same year precluded vegetative growth in beds, rather than the exclusive availability of downed wood in interbeds relative to beds. Despite our reduced sampling effort in GA relative to NC, a similar number of invertebrate groups responded to downed wood availability in windrows and interbeds in GA and NC, respectively, at the micro-scale (2012 & 2013) and treatment-level (2012). Proportionally amplified invertebrate responses to downed wood retention in windrows relative to interbeds likely reflected the highly polarized distribution of harvest residues caused by windrowing, which restricted invertebrate access to downed wood to windrows, in contrast to the more uniform distribution of harvest residues throughout regenerating stands caused by shearing.

The taxonomic resolution at which we addressed invertebrate response to harvest residue removal may have limited levels of inference for highly diverse families or families represented by a small number of exceedingly abundant species. For example, many ants are well known to associate with dead wood, particularly for nesting (Hagan and Grove 1999, Higgins and Lindgren 2006). Yet, results from both states indicated ants positively responded to harvest residue removal at the landscape-level and were more frequently captured in pitfall traps farther from than closer to downed wood. Red imported fire ants (*Solenopsis invicta*) were by far the most common ant species in regenerating stands (SMG, *unpublished data*), and this species likely drove the overall ant response to harvest residue removal. Although large-scale disturbances like clearcutting create favorable conditions for fire ant invasions (i.e., lack of overstory, prevalent bare ground; Zettler et al. 2004), Todd et al. (2008) demonstrated that fire ants may be deterred by CWD retention in clearcuts in the Southeast.

The results of this study pertain to the response of invertebrates to harvest residue removal in regenerating, early successional stands, and therefore inform post-harvest downed wood management and implications of woody biomass harvesting for invertebrates in young, IMFs. Effects of clearcutting on forest invertebrate communities are well understood (e.g., Seastedt and Crossley Jr. 1981, Grove 2002), and the transition from mature to early successional forest is less experimentally relevant in the context of this study because harvest residue removal via woody biomass harvesting occurred after timber harvests. Invertebrate response to harvest residue removal in regenerating stands may change through time, but we sampled the invertebrate community during a successional window in which both downed wood and vegetation were concurrently available. As regenerating stands age, vegetation cover and structure increases and downed wood volumes decrease via decay (i.e., U-shaped chronosequence; Harmon et al. 1986, Grodsky et al. 2016).

Invertebrates proved to be powerful ecological indicators in early successional IMFs, reinforcing the notion that invertebrates can be useful bioindicators of sustainable forest management (Taylor and Doran 2001, Pearce and Venier 2006, Iglay et al. 2012). Specifically, concurrent studies at the replicates with similar experimental designs and objectives found a lack of consistent response to harvest residue removal for all vertebrate taxa that were sampled, including amphibians and reptiles (Fritts et al. 2016), breeding and wintering birds (Grodsky 2016), shrews (Fritts et al. 2015), and rodents (Fritts 2016). Meanwhile, we detected both local- and large-scale invertebrate responses to all available habitat structure (i.e., CWD, FWD, and vegetation) in regenerating stands following timber and woody biomass harvest.

MANAGEMENT IMPLICATIONS

We documented positive responses to downed wood availability by several, ecologically important invertebrate functional groups and families, suggesting that these invertebrates would benefit from harvest residue retention in IMFs following timber harvest. Recent studies in the Southeast have shown that even the most intensive and unrestricted operational, woody biomass harvests left relatively large volumes of downed wood on the landscape (Homyack et al. 2013, Fritts et al. 2014). As such, current levels of woody biomass harvesting in the Southeast may leave enough downed wood on the landscape to support downed-wood associated, surface-active invertebrates in IMFs. However, technological advances in woody biomass harvest machinery or increases in the market value of woody biomass feedstock could result in intensified harvest residue removal. If woody biomass harvesting intensifies in the Southeast, we recommend that the response of invertebrates, especially those groups we identified as being downed-wood associated in this paper, to harvest residue removal via woody biomass harvesting be re-addressed to inform downed wood management in IMFs.

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Table 1. Micro-scale invertebrate community response to groundcover and location of pitfall traps in North Carolina (NC; n = 272) and Georgia (GA; n = 192) following woody biomass harvesting in regenerating stands, 2012 and 2013. Groundcover measures included percent (total = 100%) groundcover of fine woody debris (FWD) and vegetation (all living grasses, forbs, and woody shrubs and vines). In NC, trap locations included interbeds (I) and beds (B), the former of which almost exclusively contained downed wood. In GA, trap locations included far from windrows (F; downed wood not present and inaccessible), in bedded rows adjacent to windrows (BW; downed wood not present but highly accessible), and in interbeds adjacent to windrows (IW; downed wood present and highly accessible). We ran Poisson or quasipoisson GLMs with count of overall richness and number of captures of functional and taxonomic groups as response variables and percent cover of FWD and vegetation, trap location, and effort as fixed effects. + or − indicates positive or negative response, respectively. Ø indicates no response. We set α = 0.05. N/A indicates insufficient number of captures for inclusion in the analysis, when cutoffs were met for at least one year in one state.

	North Carolina			Georgia		
Invertebrate group[1]	FWD	Vegetation	Trap location	FWD	Vegetation	Trap location
Overall richness						
2012	Ø	+	Ø	Ø	Ø	Ø
2013	Ø	Ø	Ø	Ø	Ø	Ø
Fungivores						
2012	Ø	Ø	I > B	Ø	Ø	IW > F
2013	Ø	Ø	I > B	Ø	Ø	Ø
Granivores						
2013	+	Ø	Ø	N/A	N/A	N/A
Herbivores						
2012	Ø	Ø	I > B	Ø	Ø	Ø
2013	Ø	Ø	Ø	Ø	+	Ø
Parasitoids						
2013	Ø	Ø	Ø	N/A	N/A	N/A
Pollinators						
2012	Ø	Ø	Ø	N/A	N/A	N/A
2013	Ø	Ø	Ø	+	+	Ø
Predators						
2012	Ø	Ø	Ø	Ø	Ø	Ø
2013	Ø	Ø	Ø	Ø	Ø	Ø
Saprophages						
2012	Ø	Ø	I > B	Ø	Ø	IW > F; BW > F
2013	Ø	Ø	I > B	Ø	+	Ø
Acrididae						
2012	N/A	N/A	N/A	Ø	+	Ø
2013	Ø	Ø	Ø	N/A	N/A	N/A
Aphididae						

Table 1 (continued)

2012	Ø	Ø	Ø	N/A	N/A	N/A
Araneae[2]						
2012	Ø	Ø	Ø	Ø	Ø	Ø
2013	Ø	Ø	Ø	Ø	Ø	Ø
Armadillidiidae						
2013	N/A	N/A	N/A	Ø	Ø	Ø
Blattidae						
2012	Ø	Ø	I > B	Ø	Ø	IW > F; BW > F
2013	+	Ø	Ø	N/A	N/A	N/A
Carabidae						
2012	Ø	+	Ø	Ø	Ø	Ø
2013	+	+	Ø	Ø	Ø	Ø
Ceratopogoniidae						
2013	N/A	N/A	N/A	+	+	BW > F
Chliopoda						
2012	+	Ø	Ø	N/A	N/A	N/A
2013	Ø	Ø	Ø	N/A	N/A	N/A
Chloropidae						
2013	Ø	Ø	I > B	N/A	N/A	N/A
Chrysomelidae						
2012	Ø	Ø	I > B	N/A	N/A	N/A
2013[3]	N/A	N/A	N/A	N/A	N/A	N/A
Cicadellidae						
2012	Ø	+	Ø	N/A	N/A	N/A
2013	Ø	Ø	Ø	N/A	N/A	N/A
Cicindelinae						
2012	Ø	Ø	Ø	N/A	N/A	N/A
Cydnidae						
2013	Ø	Ø	Ø	+	Ø	BW > F
Delphacidae						
2012	Ø	Ø	Ø	N/A	N/A	N/A
Diplopoda						
2012[4]	−	Ø	Ø	N/A	N/A	N/A
2013	N/A	N/A	N/A	N/A	N/A	N/A
Dolichopodidae						
2012	+	Ø	Ø	N/A	N/A	N/A
2013	Ø	Ø	Ø	N/A	N/A	N/A
Formicidae						
2012	Ø	+	Ø	Ø	Ø	F > IW
2013	Ø	Ø	Ø	Ø	Ø	Ø
Galerucinae						
2013	Ø	Ø	Ø	Ø	Ø	Ø
Gryllidae						

Table 1 (continued)

2012	Ø	Ø	Ø	Ø	−	IW > F
2013	Ø	Ø	Ø	Ø	Ø	Ø
Gryllidae (nymph)						
2012	Ø	Ø	Ø	N/A	N/A	N/A
2013	Ø	Ø	Ø	Ø	Ø	Ø
Lycosidae						
2012	Ø	Ø	Ø	Ø	Ø	Ø
2013	Ø	Ø	Ø	Ø	Ø	Ø
Mycetophilidae						
2012	+	+	Ø	N/A	N/A	N/A
2013	N/A	N/A	N/A	−	Ø	IW > F
Nemobiinae						
2013	Ø	−	Ø	−	Ø	Ø
Nitidulidae						
2013	N/A	N/A	N/A	Ø	Ø	Ø
Paradoxosomatidae						
2013	Ø	−	Ø	N/A	N/A	N/A
Phoridae						
2012	−	Ø	Ø	N/A	N/A	N/A
Reduviidae						
2013	Ø	Ø	Ø	N/A	N/A	N/A
Rhapidophoridae						
2012	N/A	N/A	N/A	Ø	+	IW > F
Sacrophagidae						
2013	N/A	N/A	N/A	+	+	IW > F; BW > F
Scarabaeidae						
2012	−	Ø	Ø	Ø	Ø	Ø
2013	Ø	Ø	Ø	N/A	N/A	N/A
Scelionidae						
2013	Ø	Ø	Ø	−	Ø	Ø
Schizophora						
2012	Ø	+	Ø	N/A	N/A	N/A
Sciaridae						
2012	+	Ø	Ø	N/A	N/A	N/A
2013	Ø	Ø	I > B	N/A	N/A	N/A
Scolytidae						
2012	Ø	Ø	Ø	N/A	N/A	N/A
Sphaeroceridae						
2013	Ø	Ø	Ø	N/A	N/A	N/A
Staphylinidae						
2012	Ø	Ø	Ø	N/A	N/A	N/A
2013	Ø	Ø	I > B	Ø	Ø	Ø

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[1] Includes divisions, orders, families, and subfamilies

[2] Includes all spiders not in Lycosidae

[3] Galerucinae split from other chrysomelids
[4] Pooled all diplopod families

Table 2. Mean (SE) of invertebrate taxon captured at pitfall trap arrays (n = 68) situated amongst no pile, pine pile, and hardwood pile treatments (herein “treatments”) following woody biomass harvesting in regenerating stands (n = 4), North Carolina, 2012 and 2013. Only taxa meeting cutoff requirements were included in the analysis. We ran Poisson or quasipoisson GLMs with number of captures of taxonomic groups as response variables and treatment, woody biomass removal treatment, replicate (blocking factor), and effort as fixed effects. Different letters indicate significantly different, pair-wise comparisons of treatment means at α = 0.05 level.

		Treatment [mean (SE)]		
Taxa[1]	# of captures	No pile	Pine pile	Hardwood pile
Acrididae				
2013	73	0.42 (0.11)	0.36 (0.08)	0.50 (0.13)
Aphididae				
2012	71	0.31 (0.08)	0.54 (0.22)	0.21 (0.08)
Araneae[2]				
2012	264	1.18 (0.12)	1.56 (0.17)	1.10 (0.14)
2013	290	1.50 (0.21)	1.86 (0.30)	1.37 (0.20)
Carabidae				
2012	205	0.81 (0.12)	0.77 (0.22)	1.11 (0.25)
2013	492	2.48 (0.50)	2.63 (0.36)	3.26 (0.50)
Ceratopogonidae				
2013	100	0.44 (0.17)	0.56 (0.11)	0.67 (0.21)
Chilopoda				
2012	72	0.44 (0.08)	0.24 (0.07)	0.28 (0.06)
2013	117	0.83 (0.19)	0.63 (0.15)	0.54 (0.14)
Chloropidae				
2013	85	0.38 (0.11)	0.48 (0.10)	0.50 (0.14)
Chrysomelidae				
2012	386	1.46 (0.28)	2.50 (0.50)	1.75 (0.32)
2013[3]	46	0.44$^{\mathbf{a}}$ (0.21)	0.27$^{\mathbf{ab}}$ (0.08)	0.05$^{\mathbf{b}}$ (0.03)
Cicadellidae				
2012	64	0.31 (0.06)	0.26 (0.08)	0.38 (0.08)
2013	132	0.77 (0.13)	0.73 (0.13)	0.59 (0.10)
Cicindelinae				
2012	58	0.26 (0.06)	0.30 (0.08)	0.34 (0.12)
Delphacidae				
2012	47	0.15 (0.07)	0.25 (0.09)	0.23 (0.09)
Diplopoda				
2012[4]	592	2.48 (0.86)	3.32 (1.14)	2.08 (0.50)
Dolichopodidae				
2012	62	0.32 (0.09)	0.32 (0.08)	0.26 (0.08)
2013	139	0.71 (0.12)	0.66 (0.14)	1.03 (0.23)
Blattidae				
2012	46	0.19 (0.05)	0.22 (0.09)	0.18 (0.07)

Table 2 (continued)

2013	111	0.15^{b} (0.05)	1.17^{a} (0.25)	0.57^{a} (0.13)
Formicidae				
2012	6037	30.98 (4.46)	29.94 (4.35)	25.22 (3.08)
2013	12875	70.77 (5.35)	71.03 (5.39)	75.34 (8.07)
Galerucinae				
2013	831	4.23 (1.14)	4.31 (0.92)	6.50 (1.78)
Gryllidae				
2012	1470	6.57 (0.70)	5.85 (0.87)	7.52 (0.93)
2013	963	4.33 (0.68)	5.66 (0.92)	6.23 (1.18)
Gryllidae (ny.)				
2012	316	1.12 (0.35)	1.19 (0.33)	1.68 (0.52)
2013	910	4.81 (0.56)	4.72 (0.45)	5.82 (0.90)
Lycosidae				
2012	849	3.84 (0.44)	4.81 (0.55)	3.26 (0.48)
2013	515	2.97 (0.33)	2.78 (0.33)	2.88 (0.40)
Mycetophilidae				
2012	49	0.07^{b} (0.03)	0.34^{a} (0.14)	0.24^{ab} (0.07)
Nemobiinae				
2013	63	0.33 (0.12)	0.38 (0.18)	0.39 (0.17)
Paradoxosomatidae				
2013	2431	12.87 (3.44)	13.43 (3.78)	13.19 (4.07)
Phoridae				
2012	52	0.27 (0.08)	0.24 (0.07)	0.20 (0.06)
Reduviidae				
2013	49	0.29 (0.08)	0.24 (0.08)	0.31 (0.10)
Scarabaeidae				
2012	69	0.39^{a} (0.11)	0.10^{b} (0.04)	0.37^{ab} (0.10)
2013	77	0.41 (.12)	0.46 (0.17)	0.37 (0.17)
Scelionidae				
2013	75	0.50 (0.11)	0.34 (0.07)	0.37 (0.08)
Schizophora				
2012	69	0.58^{ab} (0.12)	0.72^{a} (0.16)	0.48^{b} (0.10)
Sciaridae				
2012	279	0.89^{b} (0.22)	1.83^{a} (0.47)	0.89^{ab} (0.26)
2013	131	0.38^{b} (0.10)	1.06^{a} (0.37)	1.24^{ab} (0.51)
Scolytidae				
2012	60	0.32 (0.12)	0.20 (0.08)	0.34 (0.17)
Sphaeroceridae				
2013	75	0.65 (0.50)	0.26 (0.11)	0.40 (0.14)
Staphylinidae				
2012	185	0.83 (0.24)	1.04 (0.19)	0.67 (0.09)
2013	275	2.01^{a} (0.60)	1.00^{b} (0.16)	1.48a^{b} (0.24)

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[1] Includes divisions, orders, families, and subfamilies

[2] Includes all spiders not in Lycosidae

[3] Galerucinae split from other chrysomelids

4 Pooled all diplopod families

Table 3. Mean (SE) of invertebrate taxon captured at pitfall trap arrays (n = 68) situated within six woody biomass removal treatments (WBRTs) following woody biomass harvesting in regenerating stands (n = 4), North Carolina, 2012 and 2013. WBRTs included: (1) no Biomass Harvesting Guidelines (NOBHGS); (2) 15% woody biomass retention distributed evenly throughout the treatment unit (15DISP); (3) 15% woody biomass retention in piles (15CLUS); (4) 30% woody biomass retention distributed evenly throughout the treatment unit (30DISP); (5) 30% woody biomass retention in piles (30CLUS); and (6) no woody biomass harvest (NOBIOHARV). Only taxa meeting cutoff requirements were included in the analysis. We ran Poisson or quasipoisson GLMs with number of captures of taxonomic groups as response variables and treatment, woody biomass removal treatment, replicate (blocking factor), and effort as fixed effects. Different letters indicate significantly different, pair-wise comparisons of treatment means at α = 0.05 level.

		Woody biomass removal treatment [mean (SE)]					
Taxa[1]	# of captures	NOBHGS	15DISP	15CLUS	30DISP	30CLUS	NOBIOHARV
Acrididae							
2013	73	0.13 (0.06)	0.46 (0.14)	0.55 (0.14)	0.43 (0.19)	0.31 (0.13)	0.55 (0.17)
Aphididae							
2012	71	0.13 (0.06)	0.46 (0.14)	0.55 (0.14)	0.43 (0.19)	0.31 (0.13)	0.55 (0.17)
Araneae[2]							
2012	264	1.29 (0.21)	1.43 (0.23)	1.07 (0.15)	1.45 (0.28)	1.45 (0.26)	1.07 (0.09)
2013	290	1.15 (0.20)	1.56 (0.33)	1.87 (0.39)	1.75 (0.48)	1.53 (0.27)	1.52 (0.32)
Carabidae							
2012	205	1.09 (0.59)	1.05 (0.22)	0.61 (0.18)	0.75 (0.32)	0.74 (0.16)	1.14 (0.27)
2013	492	1.57 (0.47)	3.23 (0.83)	2.94 (0.48)	2.30 (0.63)	2.08 (0.38)	4.06 (0.73)
Ceratopogonidae							
2013	100	0.55 (0.23)	0.53 (0.17)	0.73 (0.31)	0.60 (0.29)	0.41 (0.15)	0.47 (0.22)
Chilopoda							
2012	72	0.49 (0.14)	0.26 (0.11)	0.19 (0.08)	0.46 (0.11)	0.46 (0.10)	0.14 (0.06)
2013	117	0.76 (0.40)	0.68 (0.18)	0.69 (0.18)	0.71 (0.26)	0.49 (0.22)	0.75 (0.24)
Chloropidae							
2013	85	0.38 (0.21)	0.51 (0.14)	0.57 (0.19)	0.30 (0.14)	0.36 (0.14)	0.59 (0.18)
Chrysomelidae							
2012	386	1.89 (0.44)	2.11 (0.48)	2.17 (0.73)	1.39 (0.28)	1.67 (0.77)	2.23 (0.46)
2013[3]	46	0.21 (0.09)	0.15 (0.07)	0.22 (0.09)	0.54 (0.42)	0.14 (0.09)	0.30 (0.14)

Table 3 (continued)

Cicadellidae							
2012	64	0.38 (0.11)	0.17 (0.09)	0.12 (0.06)	0.18 (0.06)	0.59 (0.12)	0.44 (0.10)
2013	132	0.71 (0.20)	0.96 (0.17)	0.62 (0.21)	0.73 (0.11)	0.43 (0.15)	0.75 (0.17)
Cicindelinae							
2012	58	0.32 (0.12)	0.27 (0.09)	0.26 (0.10)	0.29 (0.13)	0.35 (0.20)	0.31 (0.10)
Delphacidae							
2012	47	0.39 (0.18)	0.33 (0.15)	0.09 (0.05)	0.05 (0.04)	0.33 (0.16)	0.12 (0.05)
Diplopoda							
2012[4]	592	4.99^{a} (3.22)	4.15^{ab} (1.07)	0.55^{c} (0.22)	1.79^{bc} (0.63)	3.41^{ab} (1.38)	1.85^{bc} (0.58)
Dolichopodidae							
2012	62	0.20 (0.08)	0.39 (0.14)	0.41 (0.13)	0.18 (0.11)	0.30 (0.09)	0.31 (0.09)
2013	139	0.67^{ab} (0.24)	1.03^{a} (0.21)	1.02^{a} (0.23)	0.92^{a} (0.26)	0.88^{a} (0.23)	0.18^{b} (0.07)
Blattidae							
2012	46	0.34 (0.21)	0.04 (0.04)	0.12 (0.09)	0.20 (0.07)	0.41 (0.12)	0.11 (0.05)
2013	111	0.95 (0.68)	0.37 (0.20)	0.48 (0.14)	0.35 (0.12)	0.76 (0.24)	1.00 (0.20)
Formicidae							
2012	6037	43.88^{a} (8.50)	28.56^{ab} (8.04)	35.94^{ab} (4.82)	25.60^{ab} (4.04)	24.76^{ab} (3.99)	19.78^{b} (3.70)
2013	12875	63.38 (5.90)	68.03 (9.81)	66.18 (6.62)	89.18 (11.41)	77.39 (6.42)	66.14 (7.93)
Galerucinae							
2013	831	3.51 (1.07)	4.82 (1.61)	2.92 (0.87)	4.47 (2.24)	5.29 (2.07)	8.07 (2.02)
Gryllidae							
2012	1470	5.40^{ab} (1.25)	6.86^{ab} (1.27)	4.15^{b} (0.80)	6.06^{ab} (0.87)	8.11^{a} (1.40)	8.58^{ab} (1.04)
2013	963	4.14^{ab} (1.04)	5.58^{ab} (1.37)	3.90^{b} (0.70)	4.83^{ab} (1.14)	4.70^{ab} (1.16)	8.60^{a} (1.74)
Gryllidae (ny.)							
2012	316	1.18^{ab} (0.59)	1.29^{ab} (0.43)	0.38^{b} (0.19)	1.79^{a} (0.72)	1.40^{ab} (0.63)	1.76^{ab} (0.58)
2013	910	4.28^{ab} (0.69)	6.11^{ab} (0.67)	3.54^{b} (0.55)	3.92^{b} (0.71)	5.23^{ab} (0.67)	7.10^{a} (1.37)
Lycosidae							
2012	849	4.05 (0.94)	4.88 (0.68)	4.12 (0.99)	3.12 (0.58)	3.31 (0.52)	4.59 (0.56)
2013	515	3.11 (0.37)	3.63 (0.62)	3.03 (0.57)	3.05 (0.44)	2.31 (0.33)	2.21 (0.39)
Mycetophilidae							

Table 3 (continued)

2012	49	0.40 (0.19)	0.16 (0.07)	0.21 (0.11)	0.16 (0.06)	0.36 (0.26)	0.05 (0.03)
Nemobiinae							
2013	63	0.45 (0.36)	0.90 (0.26)	0.47 (0.26)	0.08 (0.05)	0.28 (0.17)	0.03 (0.03)
Paradoxosoma.[5]							
2013	2431	12.8^{ab} (5.59)	8.71^{b} (3.58)	9.91^{b} (3.65)	10.91^{ab} (4.10)	10.00^{b} (3.79)	26.52^{a} (8.12)
Phoridae							
2012	52	0.56^{a} (0.16)	0.29^{ab} (0.13)	0.07^{b} (0.05)	0.24^{ab} (0.09)	0.21^{ab} (0.08)	0.17^{b} (0.06)
Reduviidae							
2013	49	0.25 (0.08)	0.15 (0.12)	0.43 (0.13)	0.21 (0.13)	0.33 (0.15)	0.27 (0.10)
Scarabaeidae							
2012	69	0.55 (0.28)	0.21 (0.08)	0.43 (0.09)	0.19 (0.14)	0.17 (0.06)	0.21 (0.14)
2013	77	0.18 (0.10)	0.67 (0.41)	0.51 (0.18)	0.40 (0.15)	0.33 (0.09)	0.31 (0.12)
Scelionidae							
2013	75	0.52 (0.14)	0.62 (0.20)	0.35 (0.12)	0.37 (0.09)	0.27 (0.09)	0.35 (0.10)
Schizophora							
2012	69	0.98 (0.33)	0.48 (0.15)	0.43 (0.09)	0.76 (0.15)	0.73 (0.23)	0.36 (0.13)
Sciaridae							
2012	279	2.67 (0.98)	1.41 (0.42)	1.14 (0.65)	0.67 (0.24)	0.99 (0.39)	0.92 (0.18)
2013	131	0.42 (0.24)	0.98 (0.37)	0.55 (0.18)	0.36 (0.16)	2.02 (0.99)	0.75 (0.25)
Scolytidae							
2012	60	0.13 (0.07)	0.36 (0.14)	0.38 (0.19)	0.38 (0.27)	0.33 (0.16)	0.07 (0.05)
Sphaeroceridae							
2013	75	0.43^{ab} (0.29)	0.12^{ab} (0.05)	1.31^{a} (0.98)	0.43^{ab} (0.20)	0.22^{b} (0.07)	0.12^{ab} (0.05)
Staphylinidae							
2012	185	1.82^{a} (0.72)	0.82^{ab} (0.17)	0.77^{b} (0.15)	0.77^{ab} (0.18)	0.79^{ab} (0.18)	0.49^{b} (0.11)
2013	275	1.38 (0.23)	0.79 (0.17)	2.51 (1.17)	1.52 (0.36)	1.70 (0.33)	1.04 (0.24)

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[1] Includes divisions, orders, families, and subfamilies

[2] Includes all spiders not in Lycosidae

[3] Galerucinae split from other chrysomelids

[4] Pooled all diplopod families

[5] Abbreviation for Diplopod family Paradoxosomatidae

Table 4. Mean (SE) of invertebrate taxon captured at pitfall trap arrays (n = 48) situated amongst no windrow and windrow treatments (herein “treatments”) within woody biomass removal treatments with variable retained harvest residue volumes (m^{3}ha^{-1}) following woody biomass harvesting in regenerating stands (n = 4), Georgia, 2012 and 2013. Only taxa meeting cutoff requirements were included in the analysis. We ran Poisson or quasipoisson GLMs with number of captures of taxonomic groups as response variables and treatment, woody biomass removal treatment volume, replicate (blocking factor), and effort as fixed effects. Different letters indicate significantly different, pair-wise comparisons of treatment means at $\alpha = 0.05$ level.

		Treatment [mean (SE)]		Woody biomass removal treatment volume (m^{3}ha^{-1})		
Taxa[1]	# of captures	No windrow	Windrow	β	t	P
Acrididae						
2012	32	0.34 (0.12)	0.35 (0.13)	0.004	0.91	0.36
Araneae[2]				0.004	1.29	0.21
2012	65	0.79 (0.17)	0.88 (0.17)	-0.001	-0.51	0.61
2013	67	0.88 (0.29)	1.92 (0.60)			
Armadillidiidae						
2013	31	0.92 (0.59)	0.38 (0.18)	-0.02	-1.72	0.09
Carabidae						
2012	38	0.37 (0.14)	0.64 (0.14)	0.005	1.74	0.09
2013	72	1.83 (0.58)	1.17 (0.37)	-0.002	-0.66	0.51
Ceratopogoniidae						
2013	75	1.00 (0.33)	2.13 (0.67)	0.004	1.11	0.27
Cydnidae						
2013	27	0.29 (0.11)	0.83 (0.28)	0.007	1.77	0.08
Diplopoda						
2013	49	0.54 (0.28)	1.50 (0.58)	-0.003	-0.70	0.49
Dolichopodidae						
2013	38	0.38 (0.22)	1.21 (0.42)	0.001	0.19	0.85
Blattidae						
2012	117	$0.39^{\mathbf{b}}$ (0.11)	$2.33^{\mathbf{a}}$ (1.06)	0.009	2.50	0.02
Formicidae						

Table 4 (continued)

2012	1230	21.65^{a} (6.53)	9.04^{b} (2.26)	-0.004	-1.38	0.17
2013	2324	37.33 (5.99)	59.5 (7.43)	-0.001	-0.29	0.77
Galerucinae						
2013	105	2.58 (0.84)	1.79 (0.53)	0.007	1.87	0.07
Gryllidae						
2012	206	2.16 (0.35)	2.95 (0.47)	-0.003	-2.56	0.01
2013	95	1.42 (0.49)	2.54 (0.72)	0.004	1.20	0.24
Gryllidae (nymph)						
2013	138	2.17 (0.60)	3.58 (1.21)	-0.003	-0.77	0.44
Lycosidae						
2012	144	2.24^{a} (0.66)	1.23^{b} (0.28)	0.001	0.56	0.57
2013	193	3.25 (0.58)	4.79 (0.78)	0.002	1.01	0.32
Mycetophilidae						
2013	39	0.58 (0.38)	1.04 (0.40)	0.001	0.22	0.83
Nemobiinae						
2013	42	0.79 (0.26)	0.96 (0.38)	0.001	0.10	0.92
Nitidulidae						
2013	38	1.13 (0.54)	0.46 (0.20)	0.002	0.48	0.64
Rhaphidophoridae						
2012	44	0.18^{b} (0.09)	0.87^{a} (0.26)	-0.004	-1.39	0.17
Sacrophagidae						
2013	29	0.46 (0.19)	0.75 (0.28)	0.003	0.69	0.50
Scarabaeidae						
2012	28	0.69 (0.54)	0.20 (0.10)	0.001	0.21	0.83
Staphylinidae						
2013	161	3.50 (0.86)	3.21 (0.67)	0.001	0.16	0.88

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[1] Includes divisions, orders, families, and subfamilies

[2] Includes all spiders not in Lycosidae

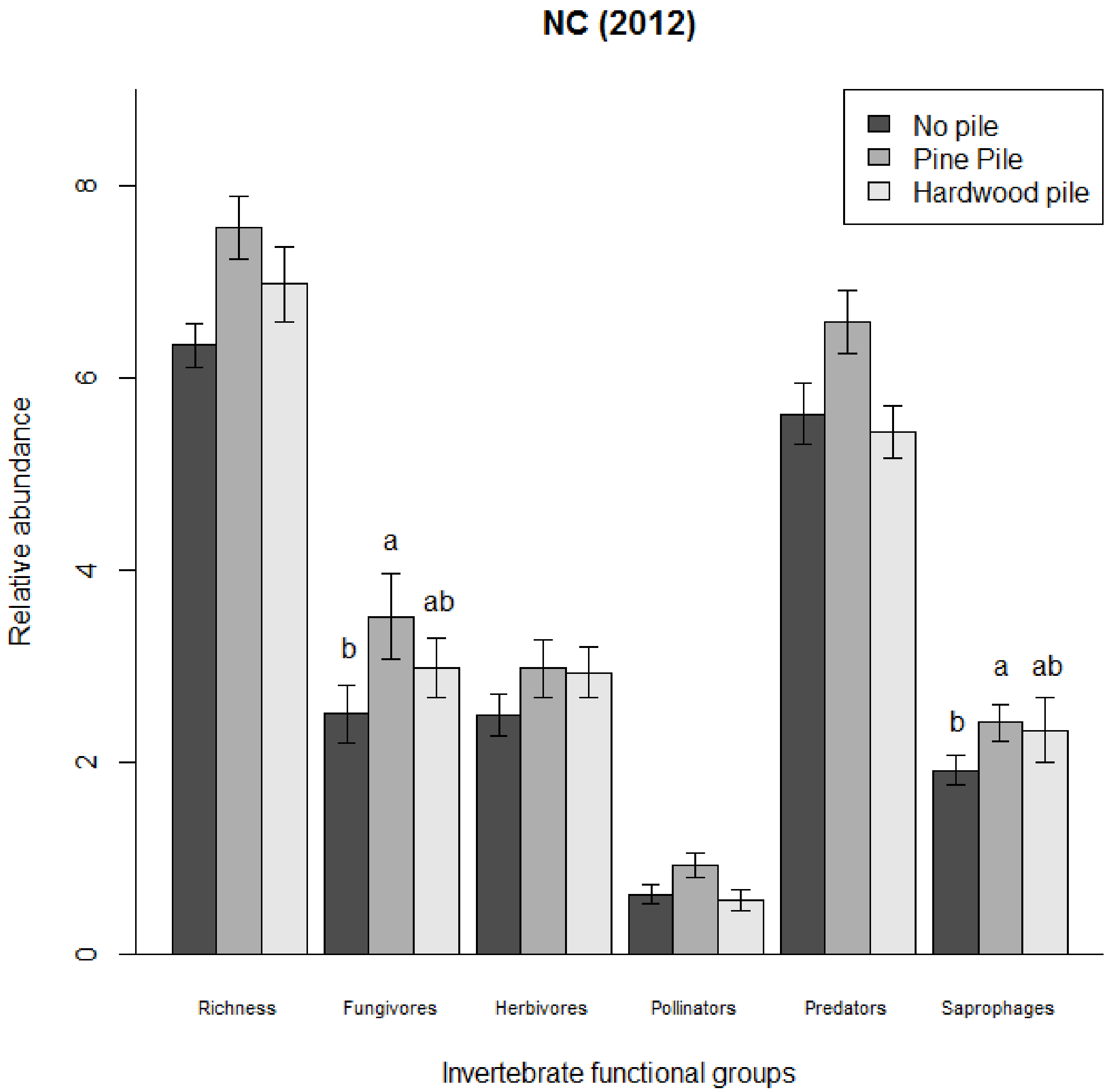
NC (2012)
No pile
Pine Pile
Hardwood pile
Relative abundance
0
2
4
6
8
a
ab
b
a
ab
b
Richness
Fungivores
Herbivores
Pollinators
Predators
Saprophages
Invertebrate functional groups

Figure 1 (continued)

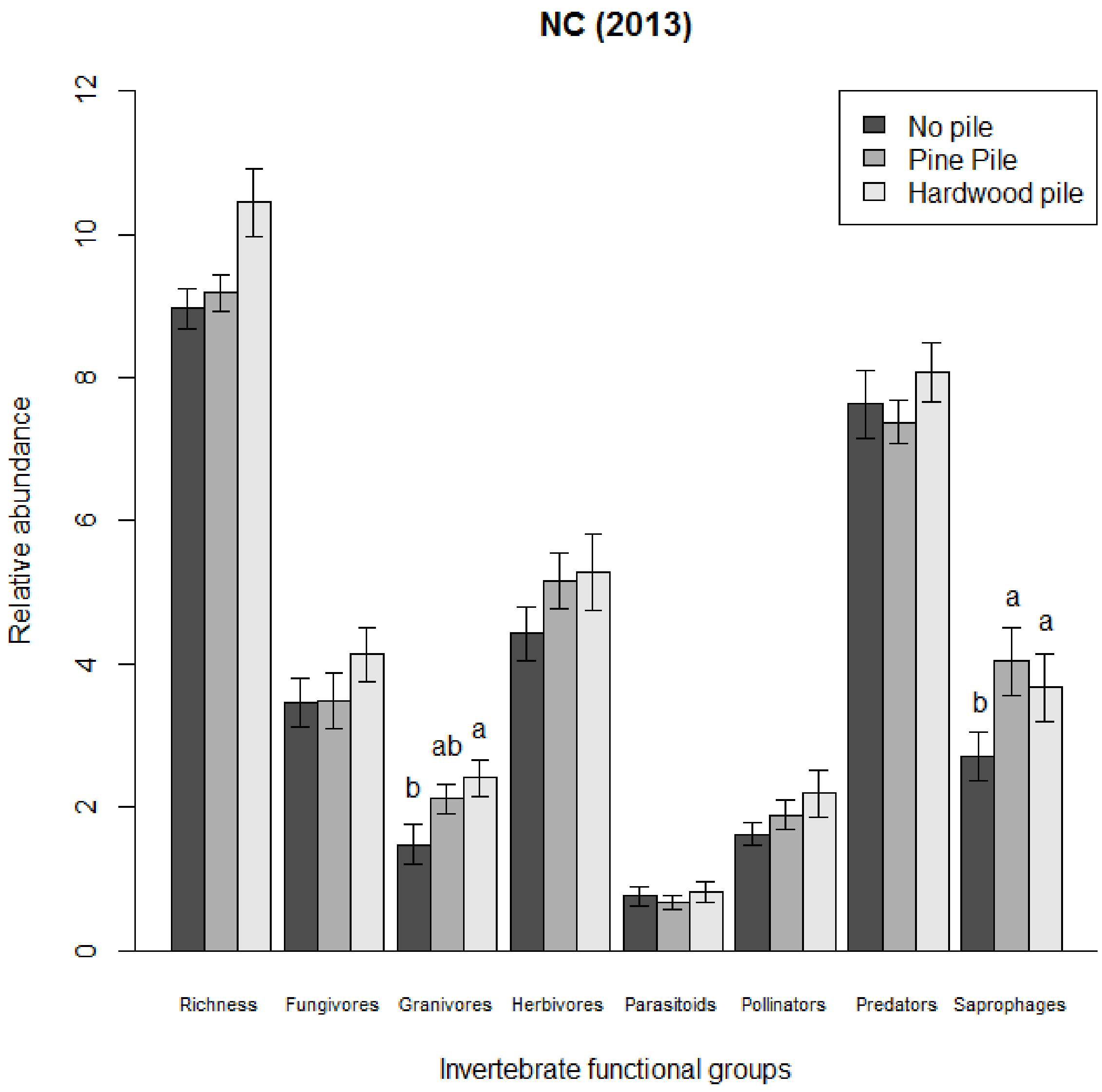

Figure 1 (continued)

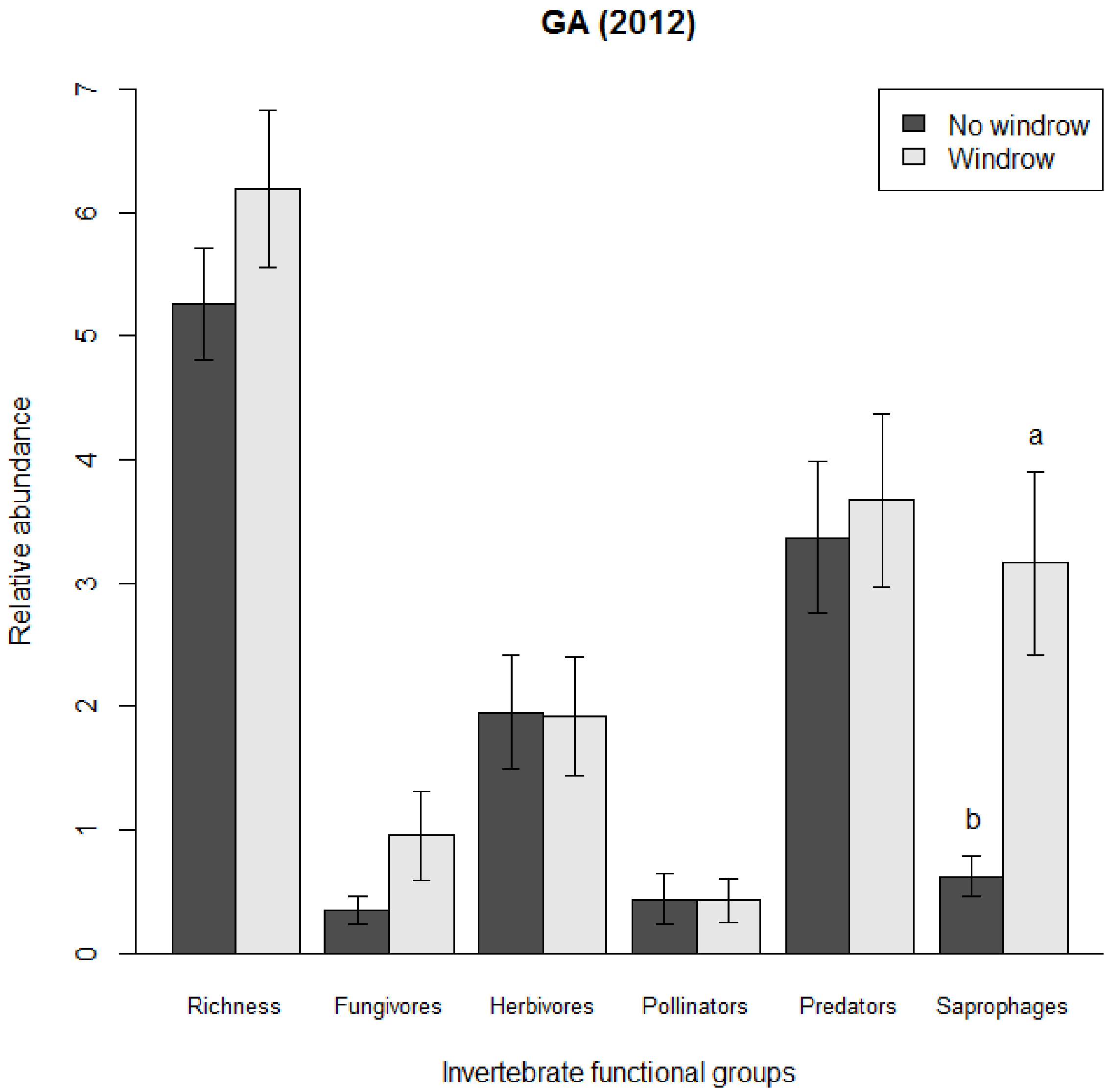

Figure 1 (continued)

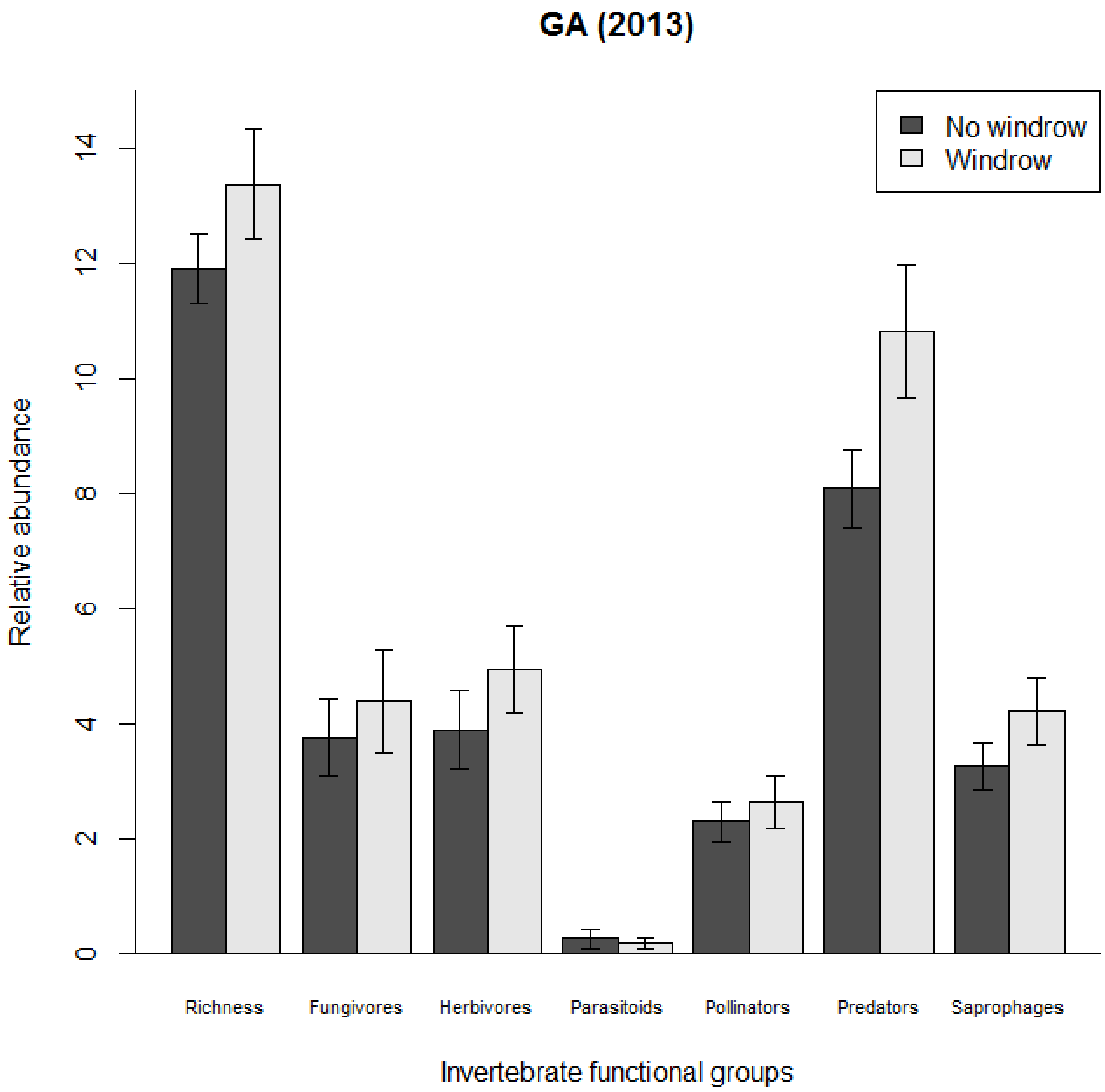

Figure 1. Effects of no pile, pine pile, and hardwood pile treatments in North Carolina, 2012 (**a**) and 2013 (**b**) and no windrow and windrow treatments in Georgia, 2012 (**c**) and 2013 (**d**) on invertebrate richness and functional guilds following woody biomass harvesting in regenerating stands. Different letters indicate significantly different, pair-wise comparisons of treatment means at α = 0.05 level. Error bars = SE.

APPENDIX

LIST OF APPENDICES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 1 – Appendix A. Number and location of winter birds observed in regenerating stands ($n = 4$) and surrounding edge, January and February, 2012–2014, Beaufort County, North Carolina.

Winter bird species		Number of detections in regenerating stands and edge						
Common name	Scientific name	Interior	Moderate	Short	Drainage ditch	AFE (mature)	AFE (young)	Total
American crow	*Corvus brachyrhynchos*	0	0	0	0	15	15	30
American goldfinch	*Spinus tristis*	4	1	6	4	0	41	56
American kestrel	*Falco sparverius*	2	1	0	1	0	0	4
American robin	*Turdus migratorius*	2	9	0	0	6	1	18
Bluejay	*Cyanocitta cristata*	0	0	0	0	1	7	8
Brown creeper	*Certhia americana*	0	0	0	0	1	0	1
Brown-headed nuthatch	*Sitta pusilla*	0	0	0	0	3	0	3
Brown thrasher	*Toxostoma rufum*	0	0	0	0	2	0	2
Carolina chickadee	*Poecile carolinensis*	1	4	3	1	33	11	53
Carolina wren	*Thryothorus ludovicianus*	34	49	114	36	61	18	312
Chipping sparrow	*Spizella passerina*	0	84	411	48	4	2	549
Cooper's hawk	*Accipiter cooperii*	1	0	0	2	0	0	3
Dark-eyed junco	*Junco hyemalis*	35	37	91	44	2	4	222
Downy woodpecker	*Picoides pubescens*	0	0	0	0	3	0	3
Eastern bluebird	*Sialia sialis*	18	25	47	24	5	2	123
Eastern phoebe	*Sayornis phoebe*	6	8	6	11	0	1	32

Appendix A (continued)

Eastern towhee	*Pipilo erythrophthalmus*	8	7	35	23	78	58	209
Field sparrow	*Spizella pusilla*	22	79	141	107	5	13	367
Fox sparrow	*Passerella iliaca*	0	0	0	0	5	0	5
Golden-crowned kinglet	*Zonotrichia atricapilla*	0	0	0	0	2	3	5
Gray catbird	*Dumetella carolinensis*	0	0	2	1	1	4	8
Great blue heron	*Ardea herodias*	0	0	0	2	0	0	2
Great horned owl	*Bubo virginianus*	0	0	0	0	1	0	1
Hairy woodpecker	*Leuconotopicus villosus*	0	0	0	0	10	0	10
Hermit thrush	*Catharus guttatus*	0	0	1	2	9	2	14
Henslow's sparrow	*Ammodramus henslowii*	0	0	1	0	0	0	1
House wren	*Troglodytes aedon*	16	31	74	9	0	0	130
Killdeer	*Charadrius vociferus*	11	0	0	0	0	0	11
Marsh wren	*Cistothorus palustris*	0	0	1	0	0	0	1
Merlin	*Falco columbarius*	0	0	1	0	0	0	1
Mourning dove	*Zenaida macroura*	72	44	138	20	3	13	291
Northern bobwhite	*Colinus virginianus*	0	45	122	0	0	0	167
Northern cardinal	*Cardinalis cardinalis*	0	0	15	11	15	9	50
Northern flicker	*Colaptes auratus*	0	0	0	2	14	4	20
Northern mockingbird	*Mimus polyglottos*	0	0	1	9	4	6	20

Appendix A (continued)

Palm warbler	*Setophaga palmarum*	8	18	26	11	4	4	71
Pileated woodpecker	*Hylatomus pileatus*	0	0	0	0	11	3	14
Pine warbler	*Setophaga pinus*	0	0	0	0	33	1	34
Red-bellied woodpecker	*Melanerpes carolinus*	0	0	0	0	13	0	13
Red-shouldered hawk	*Buteo lineatus*	0	0	0	0	0	1	1
Red-tailed hawk	*Buteo jamaicensis*	0	0	0	0	1	2	3
Red-winged blackbird	*Agelaius phoeniceus*	17	7	32	0	0	0	86
Ruby-crowned kinglet	*Regulus calendula*	0	0	4	1	4	4	13
Savannah sparrow	*Passerculus sandwichensis*	98	300	349	68	0	0	815
Song Sparrow	*Melospiza melodia*	201	417	849	314	9	21	1811
Sparrow spp.	n/a	64	217	423	26	0	45	775
Swamp sparrow	*Melospiza georgiana*	341	930	1462	129	7	6	2875
Tufted titmouse	*Baeolophus bicolor*	0	0	0	0	16	0	16
Wilson’s snipe	*Gallinago delicata*	4	3	2	0	0	0	9
Winter wren	*Troglodytes hiemalis*	0	1	4	0	1	0	6
White-crowned sparrow	*Zonotrichia leucophrys*	0	1	1	4	0	0	6
White-throated sparrow	*Zonotrichia albicollis*	3	4	26	38	14	11	96
Yellow-rumped warbler	*Setophaga coronata*	9	40	90	69	33	21	262

Appendix A (continued)

Unknown shorebird	n/a	3	2	0	0	0	0	5
Unknown wren	n/a	1	3	4	1	0	0	9
Total		984	2368	4485	1019	429	333	9618

CHAPTER 1 – Appendix B. Total counts of winter birds detected near, in, or on branches of piles of downed wood in regenerating stands ($n = 4$), January and February, 2012–2014, Beaufort County, North Carolina. * indicates bird species previously listed as downed-wood associated by Hamel (1992).

Winter bird species		Number of detections near, in, or on branches of piles of downed wood			
Common name	Scientific name	Near pile	In pile	On branch of pile	Total
Carolina wren*	*Thryothorus ludovicianus*	5	23	18	46
Chipping sparrow	*Spizella passerina*	462	0	7	469
Dark-eyed junco	*Junco hyemalis*	102	13	29	144
Eastern bluebird	*Sialia sialis*	0	0	48	48
Eastern phoebe	*Sayornis phoebe*	0	0	11	11
Eastern towhee	*Pipilo erythrophthalmus*	1	2	6	9
Field sparrow	*Spizella pusilla*	1	0	13	14
House wren*	*Troglodytes aedon*	0	19	8	27
Killdeer	*Charadrius vociferus*	10	0	0	10
Mourning dove	*Zenaida macroura*	139	0	30	169
Northern bobwhite	*Colinus virginianus*	27	0	0	27
Northern cardinal	*Cardinalis cardinalis*	3	1	0	4
Northern mockingbird	*Mimus polyglottos*	0	0	1	1
Palm warbler	*Setophaga palmarum*	11	0	10	21
Savannah sparrow	*Passerculus sandwichensis*	36	0	55	91
Song Sparrow	*Melospiza melodia*	23	27	133	183
Swamp sparrow	*Melospiza georgiana*	9	18	60	87
Wilson’s snipe	*Gallinago delicata*	7	0	0	7
White-crowned sparrow	*Zonotrichia leucophrys*	1	0	2	3
White-throated sparrow	*Zonotrichia albicollis*	12	0	3	15

Appendix B (continued)

Yellow-rumped warbler	*Setophaga coronata*	53	0	14	67
Total		902	104	447	1453

CHAPTER 2 – Appendix A. Number and location of breeding birds observed in regenerating stands (*n* = 4) and surrounding edge, 15 April – 15 July, 2012–2014, Beaufort County, North Carolina.

Breeding bird species		Number of detections in regenerating stands and edge						
Common name	Scientific name	Interior	Moderate	Short	Drainage ditch	AFE (mature)	AFE (young)	Total
Acadian flycatcher	*Empidonax virescens*	0	0	0	0	4	4	8
American crow	*Corvus brachyrhynchos*	4	10	1	8	0	2	25
American goldfinch	*Spinus tristis*	2	1	1	9	1	3	17
American kestrel	*Falco sparverius*	2	0	2	0	0	1	5
Bald eagle	*Haliaeetus leucocephalus*	0	0	0	0	1	0	1
Barn swallow	*Hirundo rustica*	0	1	1	0	0	0	2
Black-and-white warbler	*Mniotilta varia*	0	0	0	0	6	1	7
Blue-gray gnatcatcher	*Polioptila caerulea*	0	1	0	5	35	1	41
Blue grosbeak	*Passerina caerulea*	73	95	128	172	7	30	505
Bluejay	*Cyanocitta cristata*	0	0	0	0	7	0	7
Brown thrasher	*Toxostoma rufum*	6	10	14	47	16	12	105
Brown-headed cowbird	*Molothrus ater*	11	19	28	22	7	23	110
Brown-headed nuthatch	*Sitta pusilla*	0	0	0	0	1	0	1
Carolina chickadee	*Poecile carolinensis*	2	2	0	9	13	2	28
Carolina wren	*Thryothorus ludovicianus*	33	32	64	35	124	74	358
Cedar waxwing	*Bombycilla cedrorum*	0	0	0	0	1	0	1
Chipping sparrow	*Spizella passerina*	0	0	1	0	2	2	5

Appendix A (continued)

Chuck-wills-widow	*Antrostomus carolinensis*	1	0	0	0	0	0	1
Common grackle	*Quiscalus quiscula*	0	0	0	8	1	2	11
Common nighthawk	*Chordeiles minor*	13	9	11	2	0	0	35
Common yellowthroat	*Geothlypis trichas*	318	181	187	206	42	94	1028
Cooper’s hawk	*Accipiter cooperii*	0	0	1	0	0	0	1
Downy woodpecker	*Picoides pubescens*	0	0	0	0	9	0	9
Eastern bluebird	*Sialia sialis*	13	16	23	17	0	8	77
Eastern kingbird	*Tyrannus tyrannus*	29	20	61	86	10	15	221
Eastern meadowlark	*Sturnella magna*	0	0	0	1	0	0	1
Eastern phoebe	*Sayornis phoebe*	0	0	1	0	1	0	2
Eastern towhee	*Pipilo erythrophthalmus*	117	58	41	228	82	163	689
Eastern wood-pewee	*Contopus virens*	0	0	1	1	29	2	33
Field sparrow	*Spizella pusilla*	189	117	126	111	2	25	570
Gray catbird	*Dumetella carolinensis*	0	2	9	94	102	104	311
Great-crested flycatcher	*Myiarchus crinitus*	1	4	4	22	80	15	126
Hairy woodpecker	*Leuconotopicus villosus*	0	0	0	1	1	0	2
Hooded warbler	*Setophaga citrina*	0	0	0	0	1	0	1
Indigo bunting	*Passerina cyanea*	183	104	116	282	56	66	807
Killdeer	*Charadrius vociferus*	3	1	1	0	0	0	5
Mallard	*Anas platyrhynchos*	0	0	12	0	0	0	12
Mourning dove	*Zenaida macroura*	60	67	116	91	16	18	368
Northern bobwhite	*Colinus virginianus*	56	33	37	14	7	37	184
Northern cardinal	*Cardinalis cardinalis*	4	4	8	17	25	18	76
Northern flicker	*Colaptes auratus*	1	0	5	13	19	2	40

Appendix A (continued)

Northern mockingbird	*Mimus polyglottos*	10	26	22	42	3	6	109
Orchard oriole	*Icterus spurius*	10	5	12	46	16	4	93
Ovenbird	*Seiurus aurocapilla*	0	0	0	0	5	2	7
Palm warbler	*Setophaga palmarum*	0	0	1	0	0	0	1
Pine warbler	*Setophaga pinus*	0	0	16	1	21	0	38
Pileated woodpecker	*Hylatomus pileatus*	0	0	0	0	10	0	10
Prairie warbler	*Setophaga discolor*	197	51	49	204	56	220	777
Purple martin	*Progne subis*	0	0	0	20	0	0	20
Red-bellied woodpecker	*Melanerpes carolinus*	0	1	0	1	13	1	16
Red-eyed vireo	*Vireo olivaceus*	0	0	0	0	10	0	10
Red-headed woodpecker	*Melanerpes erythrocephalus*	0	1	4	0	20	3	28
Red-tailed hawk	*Buteo jamaicensis*	0	0	0	1	4	0	5
Ruby-throated hummingbird	*Archilochus colubris*	0	1	0	0	1	0	2
Savannah sparrow	*Passerculus sandwichensis*	2	2	1	2	0	0	7
Song Sparrow	*Melospiza melodia*	0	1	2	1	0	0	4
Sparrow spp.	n/a	0	0	8	0	0	0	8
Summer tanager	*Piranga rubra*	4	4	13	13	31	1	66
Swamp sparrow	*Melospiza georgiana*	3	0	2	0	0	0	5
Tufted titmouse	*Baeolophus bicolor*	1	0	0	1	14	1	17
Turkey vulture	*Cathartes aura*	3	0	6	0	0	1	10
White-eyed vireo	*Vireo griseus*	4	3	9	50	71	70	207
Wild turkey	*Meleagris gallopavo*	7	9	5	2	4	0	27
Wood thrush	*Hylocichla mustelina*	0	0	0	0	6	1	7
White-throated sparrow	*Zonotrichia albicollis*	0	0	2	1	1	0	4

Appendix A (continued)

Yellow-breasted chat	*Icteria virens*	198	43	52	266	62	162	783
Yellow-rumped warbler	*Setophaga coronata*	0	0	0	2	5	0	7
Yellow-throated warbler	*Setophaga dominica*	0	0	0	4	6	0	10
Total		1558	931	1204	2160	1067	1194	8114

CHAPTER 2 – Appendix B. Number and location of breeding birds observed in regenerating stands ($n = 4$) and surrounding edge, 15 April – 15 July, 2012–2014, Glynn and Chatham counties, Georgia.

Breeding bird species		Number of detections in regenerating stands and edge					
Common name	Scientific name	Interior	Moderate	Short	Riparian forest edge	Mature forest edge	Total
Acadian flycatcher	*Empidonax virescens*	0	0	0	8	3	11
American crow	*Corvus brachyrhynchos*	2	4	9	4	7	26
American kestrel	*Falco sparverius*	0	3	0	0	0	3
American robin	*Turdus migratorius*	0	5	6	1	0	12
Barn owl	*Tyto alba*	0	0	1	0	0	1
Barn swallow	*Hirundo rustica*	8	4	1	0	0	13
Black-and-white warbler	*Mniotilta varia*	0	0	0	0	3	3
Blue-gray gnatcatcher	*Polioptila caerulea*	15	6	8	115	48	192
Blue grosbeak	*Passerina caerulea*	145	85	158	74	31	493
Bluejay	*Cyanocitta cristata*	3	2	6	32	22	65
Bobolink	*Dolichonyx oryzivorus*	2	3	58	0	0	63
Brown thrasher	*Toxostoma rufum*	27	26	80	75	20	228
Brown-headed cowbird	*Molothrus ater*	2	4	6	2	1	15
Carolina chickadee	*Poecile carolinensis*	0	8	21	15	14	58
Carolina wren	*Thryothorus ludovicianus*	57	37	120	140	110	464
Chipping sparrow	*Spizella passerina*	6	4	10	1	0	21
Chuck-wills-widow	*Antrostomus carolinensis*	1	0	0	0	2	3
Cliff Swallow	*Petrochelidon pyrrhonota*	0	0	3	0	0	3
Common grackle	*Quiscalus quiscula*	0	4	7	28	23	62
Common nighthawk	*Chordeiles minor*	0	1	1	2	0	4
Common yellowthroat	*Geothlypis trichas*	238	115	203	53	59	668
Dark-eyed junco	*Junco hyemalis*	0	1	0	0	0	1
Downy woodpecker	*Picoides pubescens*	0	0	3	24	16	43
Eastern bluebird	*Sialia sialis*	46	41	46	0	0	133
Eastern kingbird	*Tyrannus tyrannus*	70	62	100	32	8	272

Appendix B (continued)

Eastern towhee	*Pipilo erythrophthalmus*	268	51	102	177	71	669
Eastern wood-pewee	*Contopus virens*	1	0	6	18	20	45
Field sparrow	*Spizella pusilla*	12	13	13	1	0	39
Fish crow	*Corvus ossifragus*	0	0	0	1	1	2
Grasshopper sparrow	*Ammodramus savannarum*	0	0	1	0	0	1
Gray catbird	*Dumetella carolinensis*	24	12	21	16	4	77
Great-crested flycatcher	*Myiarchus crinitus*	18	11	39	151	53	272
Great egret	*Ardea alba*	4	0	1	1	0	6
Green heron	*Butorides virescens*	2	3	3	0	0	8
Hairy woodpecker	*Leuconotopicus villosus*	0	0	1	19	4	24
Hooded warbler	*Setophaga citrina*	3	1	5	6	8	23
Indigo bunting	*Passerina cyanea*	356	215	453	237	57	1318
Kentucky warbler	*Geothlypis formosa*	0	0	0	1	1	2
Killdeer	*Charadrius vociferus*	0	0	1	0	0	1
Little blue heron	*Egretta caerulea*	4	0	4	2	0	10
Loggerhead shrike	*Lanius ludovicianus*	0	1	0	0	0	1
Mourning dove	*Zenaida macroura*	115	84	191	77	28	495
Northern bobwhite	*Colinus virginianus*	93	62	122	24	2	303
Northern cardinal	*Cardinalis cardinalis*	212	101	314	319	130	1076
Northern flicker	*Colaptes auratus*	0	0	2	15	4	21
Northern mockingbird	*Mimus polyglottos*	157	143	285	142	10	737
Northern parula	*Setophaga americana*	8	15	45	110	67	245
Orchard oriole	*Icterus spurius*	16	6	17	40	2	81
Ovenbird	*Seiurus aurocapilla*	0	0	0	1	0	1
Painted bunting	*Passerina ciris*	1	3	2	4	4	14
Pine warbler	*Setophaga pinus*	3	8	10	45	61	127
Pileated woodpecker	*Hylatomus pileatus*	6	2	17	32	22	79
Prairie warbler	*Setophaga discolor*	179	75	128	9	5	396
Red-bellied woodpecker	*Melanerpes carolinus*	16	4	17	128	61	226

Appendix B (continued)

Red-eyed vireo	*Vireo olivaceus*	3	2	10	80	36	131
Red-headed woodpecker	*Melanerpes erythrocephalus*	11	7	35	20	4	77
Red-shouldered hawk	*Buteo lineatus*	1	0	1	1	1	4
Red-tailed hawk	*Buteo jamaicensis*	1	0	13	4	1	19
Red-winged blackbird	*Agelaius phoeniceus*	1	0	2	0	1	4
Ruby-throated hummingbird	*Archilochus colubris*	0	0	1	0	0	1
Savannah sparrow	*Passerculus sandwichensis*	7	7	13	0	0	27
Snowy egret	*Egretta thula*	0	1	0	0	0	1
Song Sparrow	*Melospiza melodia*	1	0	0	0	0	1
Spotted sandpiper	*Actitis macularius*	0	0	1	0	0	1
Summer tanager	*Piranga rubra*	8	13	42	38	21	122
Swamp sparrow	*Melospiza georgiana*	3	0	1	0	1	5
Tufted titmouse	*Baeolophus bicolor*	6	1	19	18	18	62
Turkey vulture	*Cathartes aura*	0	0	0	0	1	1
Veery	*Catharus fuscescens*	1	1	1	0	0	3
Eastern whip-por-will	*Caprimulgus vociferus*	0	1	1	0	0	2
White-eyed vireo	*Vireo griseus*	165	87	137	188	87	664
Wild turkey	*Meleagris gallopavo*	1	2	11	2	5	21
Wood duck	*Aix sponsa*	0	0	0	4	0	4
Wood stork	*Mycteria americana*	0	1	2	0	0	3
Wood thrush	*Hylocichla mustelina*	0	1	2	0	2	5
White-throated sparrow	*Zonotrichia albicollis*	0	0	1	0	0	1
Yellow warbler	*Setophaga petechia*	0	1	3	0	0	4
Yellow-billed cuckoo	*Coccyzus americanus*	1	1	0	26	11	39
Yellow-breasted chat	*Icteria virens*	267	74	143	113	23	620
Yellow-throated vireo	*Vireo flavifrons*	1	0	3	36	33	73
Yellow-throated warbler	*Setophaga dominica*	3	3	13	15	14	48

Appendix B (continued)

Total	2599	1425	3044	2727	1241	11036

CHAPTER 2 – Appendix C. Total counts of breeding birds detected near, in, or on branches of piles of downed wood in regenerating stands (*n* = 4), 15 April – 15 July, 2012–2014, Beaufort County, North Carolina.

Breeding bird species		Number of detections near, in, or on branches of piles of downed wood			
Common name	Scientific name	Near pile	In pile	On branch of pile	Total
American crow	*Corvus brachyrhynchos*	3	0	4	7
American kestrel	*Falco sparverius*	0	0	2	2
Barn swallow	*Hirundo rustica*	1	0	1	2
Blue grosbeak	*Passerina caerulea*	26	4	129	159
Brown thrasher	*Toxostoma rufum*	2	4	13	19
Brown-headed cowbird	*Molothrus ater*	16	0	28	44
Carolina wren	*Thryothorus ludovicianus*	0	48	41	89
Chipping sparrow	*Spizella passerina*	0	0	1	1
Chuck-wills-widow	*Antrostomus carolinensis*	0	0	1	1
Common grackle	*Quiscalus quiscula*	0	0	1	1
Common nighthawk	*Chordeiles minor*	16	0	4	20
Common yellowthroat	*Geothlypis trichas*	0	13	17	30
Eastern bluebird	*Sialia sialis*	4	0	44	48
Eastern kingbird	*Tyrannus tyrannus*	2	0	83	85
Eastern phoebe	*Sayornis phoebe*	0	0	1	1
Eastern towhee	*Pipilo erythrophthalmus*	3	9	9	21
Eastern wood-pewee	*Contopus virens*	0	0	1	1
Field sparrow	*Spizella pusilla*	8	13	72	93
Gray catbird	*Dumetella carolinensis*	4	0	6	10
Great-crested flycatcher	*Myiarchus crinitus*	1	0	9	10
Indigo bunting	*Passerina cyanea*	1	5	42	48
Mourning dove	*Zenaida macroura*	131	0	44	175
Northern bobwhite	*Colinus virginianus*	40	0	0	40
Northern cardinal	*Cardinalis cardinalis*	0	0	3	3

Appendix C (continued)

Northern flicker	*Colaptes auratus*	2	0	0	2
Northern mockingbird	*Mimus polyglottos*	1	2	36	39
Orchard oriole	*Icterus spurius*	0	1	6	7
Palm warbler	*Setophaga palmarum*	0	0	1	1
Pine warbler	*Setophaga pinus*	1	0	6	7
Prairie warbler	*Setophaga discolor*	5	4	6	15
Red-bellied woodpecker	*Melanerpes carolinus*	1	0	0	1
Red-headed woodpecker	*Melanerpes erythrocephalus*	4	0	5	9
Savannah sparrow	*Passerculus sandwichensis*	3	1	2	6
Song Sparrow	*Melospiza melodia*	0	0	2	2
Sparrow spp.	n/a	7	0	1	8
Summer tanager	*Piranga rubra*	1	0	9	10
Swamp sparrow	*Melospiza georgiana*	1	1	1	3
Turkey vulture	*Cathartes aura*	9	0	6	15
Wild turkey	*Meleagris gallopavo*	3	0	0	3
Yellow-breasted chat	*Icteria virens*	0	0	4	4
Total		296	105	641	1042

CHAPTER 2 – Appendix D. Total counts of breeding birds detected near, in, or on branches of windrows in regenerating stands (*n* = 4), 15 April – 15 July, 2012–2014, Glynn and Chatham counties, Georgia.

Breeding bird species		Number of detections near, in, or on branches of piles of windrows			
Common name	Scientific name	Near windrow	In windrow	On branch of windrow	Total
American robin	*Turdus migratorius*	0	0	1	1
Blue-gray gnatcatcher	*Polioptila caerulea*	0	2	0	2
Blue grosbeak	*Passerina caerulea*	4	23	183	210
Bluejay	*Cyanocitta cristata*	0	0	2	2
Bobolink		0	0	63	63
Brown thrasher	*Toxostoma rufum*	1	20	38	59
Brown-headed cowbird	*Molothrus ater*	3	0	1	4
Carolina chickadee	*Poecile carolinensis*	0	0	4	4
Carolina wren	*Thryothorus ludovicianus*	2	18	31	51
Common grackle	*Quiscalus quiscula*	2	0	3	5
Common nighthawk	*Chordeiles minor*	2	0	0	2
Common yellowthroat	*Geothlypis trichas*	1	66	67	134
Eastern bluebird	*Sialia sialis*	0	0	76	76
Eastern kingbird	*Tyrannus tyrannus*	0	1	49	50
Eastern towhee	*Pipilo erythrophthalmus*	7	13	21	41
Field sparrow	*Spizella pusilla*	1	2	4	7
Great-crested flycatcher	*Myiarchus crinitus*	0	0	9	9
Great egret	*Ardea alba*	3	0	1	4
Green heron	*Butorides virescens*	0	0	7	7
Hooded warbler	*Setophaga citrina*	0	0	1	1
Indigo bunting	*Passerina cyanea*	4	55	256	315
Little blue heron	*Egretta caerulea*	3	0	1	4
Mourning dove	*Zenaida macroura*	157	4	37	198
Northern bobwhite	*Colinus virginianus*	88	0	0	88
Northern cardinal	*Cardinalis cardinalis*	9	64	90	163
Northern mockingbird	*Mimus polyglottos*	14	36	273	323

Appendix D (continued)

Orchard oriole	*Icterus spurius*	1	7	17	25
Painted bunting	*Passerina ciris*	0	0	2	2
Prairie warbler	*Setophaga discolor*	0	1	2	3
Red-bellied woodpecker	*Melanerpes carolinus*	0	0	3	3
Red-eyed vireo	*Vireo olivaceus*	0	0	2	2
Red-headed woodpecker	*Melanerpes erythrocephalus*	0	1	2	3
Savannah sparrow	*Passerculus sandwichensis*	7	1	12	20
Snowy egret	*Egretta thula*	1	0	0	1
Spotted sandpiper	*Actitis macularius*	1	0	0	1
Summer tanager	*Piranga rubra*	1	4	28	33
Tufted titmouse	*Baeolophus bicolor*	0	2	1	3
White-eyed vireo	*Vireo griseus*	0	22	3	25
Wild turkey	*Meleagris gallopavo*	11	0	0	11
Wood stork	*Mycteria americana*	2	0	0	2
Yellow-breasted chat	*Icteria virens*	0	39	99	138
Yellow-billed cuckoo	*Coccyzus americanus*	0	1	0	1
Yellow-throated warbler	*Setophaga dominica*	0	1	7	8
Total		325	383	1396	2104

CHAPTER 3 – Appendix A. Number of captures of invertebrate taxonomic groups in regenerating stands, North Carolina and Georgia, 2012 – 2013, with geographic information and functional adult and juvenile functional group assignments. Functional groups included the following: FUNG = fungivores; GRAN = granivores; HERB = herbivores; PARA = parasitoids; POLL = pollinators; PRED = predators; SCAV = scavengers; and SAP = saprophages.

Taxonomic groups		# of captures			Functional groups[2]	
Order	Family[1]	GA	NC	Total	Adult	Juvenile
Araneae	n/a	134	554	688	PRED	n/a
	Lycosidae	337	1364	1701	PRED	n/a
	Salticidae	n/a	32	32	PRED	n/a
Archaeognatha	Machilidae	0	5	5	SCAV	n/a
Blattodea	Blattidae	129	157	286	SAP	n/a
Chilopoda	n/a	4	190	194	PRED	n/a
Coleoptera	Anobiidae	4	5	9	GRAN	n/a
	Anthribidae	0	1	1	n/a	n/a
	Bostrichidae	0	2	2	n/a	n/a
	Buprestidae	0	4	4	HERB/POLL	n/a
	Carabidae	110	697	807	GRAN/PRED	n/a
	Carabidae/Cicindelinae	9	84	93	PRED	n/a
	Cerambycidae	4	60	64	POLL	n/a
	Chrysomelidae	28	433	461	HERB	n/a
	Chrysomelidae/Galerucinae	105	831	936	HERB	n/a
	Cleridae	0	1	1	PRED	n/a
	Coccinellidae	0	2	2	PRED/HERB	n/a
	Cucujidae	2	13	15	n/a	n/a
	Curculionidae	8	27	35	GRAN/HERB	n/a
	Dytiscidae	0	2	2	PRED	n/a
	Elateridae	26	49	75	HERB	Pr.
	Elmidae	0	1	1	HERB/SAP	n/a
	Endomychidae	7	4	11	FUNG/POLL	n/a
	Erotylidae	2	46	48	FUNG/POLL	n/a

Appendix A (continued)

	Histeridae	0	4	4	PRED	n/a
	Hydrophilidae	1	0	1	SCAV	PRED
	Latridiidae	1	1	2	FUNG/SAP	n/a
	Mordellidae	6	28	34	POLL	HERB
	Nitidulidae	38	58	96	n/a	n/a
	Noteridae	1	0	1	PRED	n/a
	Scarabaeidae	48	139	187	HERB	n/a
	Scolytidae/Scolytinae	0	60	60	FUNG	n/a
	Silphidae	1	1	2	PRED	n/a
	Silvanidae	2	4	6	FUNG/SAP	n/a
	Staphylinidae	172	460	632	FUNG/PRED	n/a
	Staphylinidae/Pselaphinae	0	2	2	PRED	n/a
	Tenebrionidae	3	10	13	FUNG/SAP	n/a
	Trogossitidae	0	1	1	FUNG/PRED	n/a
	Unknown	3	39	42	n/a	n/a
	Zopheridae	0	3	3	FUNG/SAP	n/a
Decapoda	Cambaridae	1	0	1	SCAV	n/a
Dermaptera	Anisolabididae	0	1	1	PRED/SAP	n/a
	Labiduridae	1	0	1	PRED/SAP	n/a
Diplopoda	n/a	65	593	658	FUNG/SAP	n/a
	Cleidogonidae	n/a	1	1	FUNG/SAP	n/a
	Paradoxosomatidae	n/a	2431	2431	FUNG/SAP	n/a
	Polydesmidae	n/a	37	37	FUNG/SAP	n/a
Diptera	Brachycera	n/a	2	2	n/a	n/a
	Nematocera	n/a	2	2	n/a	n/a
	Schizophora	16	130	146	n/a	n/a
	Anthomyiidae	0	4	4	POLL/PRED	HERB
	Asilidae	1	9	10	PRED	n/a
	Bibionidae	1	0	1	POLL	SAP
	Cecidomyiidae	7	30	37	POLL	HERB

Appendix A (continued)

	Ceratopogonidae	75	101	176	PRED	n/a
	Chironomidae	5	25	30	n/a	n/a
	Chloropidae	16	86	102	POLL	HERB
	Culicidae	3	2	5	n/a	n/a
	Dolichopodidae	41	201	242	PRED	n/a
	Drosophilidae	0	20	20	n/a	n/a
	Empididae	2	9	11	PRED	n/a
	Ephydridae	4	1	5	n/a	n/a
	Lauxaniidae	1	0	1	n/a	SAP
	Lonchaeidae	0	1	1	POLL	SAP
	Muscidae	6	22	28	n/a	n/a
	Mycetophilidae	39	86	125	n/a	FUNG/PRED
	Phoridae	16	90	106	n/a	n/a
	Platystomatidae	4	0	4	n/a	n/a
	Psychodidae	1	3	4	n/a	n/a
	Sarcophagidae	33	9	42	n/a	n/a
	Scatopsidae	0	1	1	n/a	n/a
	Sciaridae	12	410	422	n/a	FUNG/SAP
	Sepsidae	0	1	1	n/a	n/a
	Simuliidae	15	0	15	n/a	n/a
	Sphaeroceridae	19	75	94	n/a	n/a
	Syrphidae	0	2	2	POLL	n/a
	Tachinidae	0	2	2	POLL	PARA
	Tephritidae	1	12	13	n/a	HERB
	Tipulidae	9	54	63	n/a	n/a
	Ulidiidae	0	9	9	n/a	SAP
	Unknown	0	15	15	n/a	n/a
Gastropoda	n/a	16	11	27	HERB/SAP	n/a
Hemiptera	Achilidae	0	1	1	HERB	FUNG
	Alydidae	10	2	12	HERB	n/a

Appendix A (continued)

	Anthicidae	3	1	4	FUNG/PRED	n/a
	Anthocoridae	0	1	1	PRED	n/a
	Aphididae	28	108	136	HERB	n/a
	Aradidae	3	4	7	FUNG	n/a
	Blissidae	0	1	1	HERB	n/a
	Caliscelidae	0	1	1	HERB	n/a
	Cercopidae	5	38	43	HERB	n/a
	Cicadellidae	35	196	231	HERB	n/a
	Cixiidae	0	1	1	HERB	n/a
	Cydnidae	34	78	112	GRAN/HERB	n/a
	Delphacidae	15	71	86	HERB	n/a
	Dictyopharidae	1	0	1	HERB	n/a
	Enicocephalidae	0	2	2	PRED	n/a
	Flatidae	1	0	1	HERB	n/a
	Geocoridae	2	0	2	PRED	n/a
	Lygaeidae	2	8	10	GRAN/HERB	n/a
	Membracidae	1	1	2	HERB	n/a
	Miridae	6	5	11	HERB/PRED	n/a
	Pentatomidae	4	1	5	HERB/PRED	n/a
	Psyllidae	0	1	1	HERB	n/a
	Reduviidae	23	52	75	PRED	n/a
	Saldidae	4	22	26	PRED	n/a
	Tingidae	0	1	1	HERB	n/a
	Unknown	5	8	13	n/a	n/a
Hymenoptera	Apidae	0	4	4	POLL	n/a
	Bethylidae	0	7	7	n/a	PARA
	Braconidae	0	9	9	POLL	PARA
	Crabronidae	1	3	4	POLL/PRED	n/a
	Diapriidae	0	5	5	POLL	PARA
	Dryinidae	1	10	11	n/a	PARA

Appendix A (continued)

	Formicidae	3554	18912	22,466	n/a	n/a
	Halictidae	0	3	3	POLL	n/a
	Ichneumonidae	0	9	9	POLL	PARA
	Megachilidae	0	2	2	POLL	n/a
	Mutillidae	1	8	9	n/a	PARA/PRED
	Pompillidae	1	16	17	POLL	PRED
	Rhopalosomatidae	0	4	4	n/a	PARA
	Scelionidae	30	96	126	n/a	PARA
	Scoliidae	0	1	1	POLL	PARA
	Sphecidae	4	3	7	POLL	PRED
	Tiphiidae	0	3	3	POLL	PARA
	Unknown	0	21	21	n/a	n/a
	Unknown parasitoid wasp	15	28	43	POLL	PARA
	Vespidae	2	3	5	PRED	n/a
Isopoda	Armadillidiidae	137	9	146	FUNG/SAP	n/a
Lepidoptera	n/a	2	6	8	POLL	n/a
	Hesperiidae	0	3	3	POLL	HERB
	Noctuidae	0	3	3	POLL	HERB
	Nymphalidae	0	1	1	POLL	HERB
Mantodea	Mantidae	0	1	1	PRED	n/a
Mecoptera	Panorpidae	0	1	1	PRED/SAP	n/a
Megadrilacea	n/a	8	27	35	SAP	n/a
Neuroptera	Chrysopidae	0	1	1	PRED	n/a
Opiliones	n/a	5	4	9	PRED	n/a
Oribatida	n/a	4	7	11	FUNG/SAP	n/a
Orthoptera	Acrididae	45	105	150	HERB	n/a
	Gryllidae	301	2468	2769	HERB/SCAV	n/a
	Gryllidae/Nemobiinae	42	63	105	HERB/SCAV	n/a
	Gryllidae/Oecanthinae	1	0	1	HERB/SCAV	n/a
	Gryllidae (nymph)	150	1226	1376	HERB/SCAV	n/a

Appendix A (continued)

	Gryllotalpidae	7	0	7	HERB/PRED	n/a
	Mogoplistidae	0	1	1	HERB/SCAV	n/a
	Rhaphidophoridae	56	1	57	SCAV/SAP	n/a
	Tetrigidae	0	6	6	FUNG/HERB	n/a
	Tettogoniidae	6	3	9	HERB	n/a
Pseudoscorpiones	n/a	0	1	1	PRED	n/a
Psocoptera	Psocidae	2	7	9	SCAV	n/a
Thysanura	n/a	0	1	1	n/a	n/a
Thysanoptera	Phlaeothripidae	0	1	1	FUNG/PRED	n/a
	Thripidae	0	1	1	HERB/POLL	n/a
Trichoptera	n/a	2	4	6	n/a	n/a
Total		6160	33634	39794		