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# Ground Beetle (Coleoptera: Carabidae) Response to Harvest Residue Retention: Implications for Sustainable Forest Bioenergy Production

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**Abstract:** Research Highlights: Our study adds to the scant literature on the effects of forest bioenergy on ground beetles (Coleoptera: Carabidae) and contributes new insights into the responses of ground beetle species and functional groups to operational harvest residue retention. We discovered that count of Harpalus pensylvanicus (DeGeer)—a habitat generalist—increased owing to clear-cut harvests but decreased due to harvest residue reductions; these observations uniquely allowed us to separate effects of additive forest disturbances to demonstrate that, contrarily to predictions, a generalist species considered to be adapted to disturbance may be negatively affected by altered habitat elements associated with disturbances from renewable energy development. Background and Objectives: Despite the potential environmental benefits of forest bioenergy, woody biomass harvests raise forest sustainability concerns for some stakeholders. Ground beetles are well established ecological indicators of forest ecosystem health and their life history characteristics are connected to habitat elements that are altered by forest harvesting. Thus, we evaluated the effects of harvest residue retention following woody biomass harvest for forest bioenergy on ground beetles in an operational field experiment. Materials and Methods: We sampled ground beetles using pitfall traps in harvest residue removal treatments representing variable woody biomass retention prescriptions, ranging from no retention to complete retention of all merchantable woody biomass. We replicated treatments in eight clear-cut stands in intensively managed loblolly pine (*Pinus taeda* L.) forests in North Carolina and Georgia. Results: Harvest residue retention had no effect on ground beetle richness and diversity. However, counts of *H. pensylvanicus*, *Anisodactylus* spp., and "burrower" and "fast runner" functional groups, among others, were greater in treatments with no woody biomass harvest than those with no harvest residue retention; all of these ground beetles may confer ecosystem services in forests. We suggest that *H. pensylvanicus* is a useful indicator species for burrowing and granivorous ground beetle response to harvest residue reductions in recently harvested stands. Lastly, we propose that retaining 15% retention of total harvest residues or more, depending on regional and operational variables, may support beneficial ground beetle populations.

## 1. Introduction

Managed forests present opportunities for sustainable development of renewable energy on a global scale. While *Homo erectus* burned wood for energy ~1.5 million years ago, today's market demand for woody biomass as a feedstock for renewable forest bioenergy is driven by a booming renewable energy industry and concerns regarding energy crises and climate change. Forest-based biomass is increasingly used for wood pellet production, electricity generation, and liquid transportation fuels [1]. Renewable energy mandates in the European Union have been a boon to wood pellet production from the "wood basket" of the southeastern United States (hereafter "Southeast"), a region that has increased wood pellet exportation to Europe by over 5 million green metric tons from 2000 to 2015 alone [2]. Forest bioenergy typically is produced as a byproduct of commercial harvesting operations (e.g., harvest residues or low value stems) and silvicultural practices (e.g., thinning) in managed forests; thus, it does not compete with lands for food production and provides additional markets for forest-based natural resources [1]. Given its high available wood volume and active forest industry, the Southeast has the greatest potential for forest bioenergy development in the United States [1,3]. Forest bioenergy feedstock from the Southeast is predominantly sourced from harvest residues, also known as logging residuals, comprised of pulpwood and pine tops and limbs from planted and naturally regenerated softwood stands [4].

Despite the potential environmental benefits of forest bioenergy, woody biomass harvests for renewable energy production elicit sustainability concerns. Forest-based biomass harvests may negatively affect soils and degrade food and cover resources for wildlife by reducing the volume and cover of downed wood, including coarse woody debris [5]. Coarse woody debris is a critical component of forest ecosystems that acts as a carbon sink, retains nutrients, and influences water dynamics [6,7]. Coarse woody debris also may be used by a variety of wildlife for food and cover, including birds [8,9], small mammals [10,11], amphibians [12,13], and especially invertebrates [14–17]. For example, invertebrates use coarse woody debris for refugia, foraging, oviposition sites, and, in the case of saproxylic insects, food [18,19]. A recent metanalysis of results from field experiments testing the response of wildlife to woody biomass harvesting suggested that operational woody biomass harvests may have minimal impacts of the abundance and diversity of many taxa; yet, the same metanalysis also revealed that studies on the effects of woody biomass harvests on invertebrates are lacking relative to those on other taxa [1].

Management of coarse woody debris may play a pivotal role in conservation of invertebrates in forested ecosystems [16,17,20,21]. While relationships between saproxylic insects and coarse woody debris have been extensively studied (e.g., [22,23]), research on facultative interactions between epigaeic invertebrates and coarse woody debris historically has been lacking and has yielded mixed results [18]. For example, researchers conducted two temporally explicit experiments with variable coarse woody debris retention in the same mature loblolly pine (*Pinus taeda* L.) forests in South Carolina (USA). The first study determined that coarse woody debris removal decreased overall invertebrate diversity and invertebrate activity [18], whereas the later study documented no effect of coarse woody debris removal on invertebrate richness, diversity, and composition [24]. Nevertheless, observational studies have documented greater densities of invertebrates in litter adjacent to coarse woody debris compared to other areas of the forest floor [25–27]. The high concentration of invertebrate prey near coarse woody debris may provide food resources for predatory invertebrates [16]. In general, field experiments that manipulate varying volumes of coarse woody debris, especially in the context of woody biomass harvesting, are needed to determine effective coarse woody debris management for forest invertebrates [20].

Ground beetles (Coleoptera: Carabidae) are well established ecological indicators of forest ecosystem health (e.g., [28–30]) and therefore, are suitable invertebrate study organisms to address the sustainability of harvest residue removal from intensively managed forests. Observations from previous studies have identified positive associations between ground beetles and coarse woody debris in mature forests of northern Wisconsin (USA) and northwestern Ontario, Canada [31,32]. In South Carolina (USA), ground beetles in mature pine forests were more species rich and diverse in plots with high densities of coarse woody debris than those with lower densities, potentially due to their attraction to increased prey availability associated with coarse woody debris [24]. Further, ground beetles may positively associate with coarse woody debris in clear-cut stands [31,33].

Our objective was to determine the effects of harvest residue retention treatments in the context of operational woody biomass harvests for forest bioenergy on ground beetle richness, diversity, functional groups, genera, and species in recently clear-cut stands. The results on invertebrate family-level responses to the same harvest residue retention treatments from a concurrent study indicated that, as a family, carabid beetles were less abundant in areas with less harvest residue retention than in areas with no biomass harvest [16]. We hypothesized that species richness and diversity of ground beetles would be greater in areas with more harvest residues than those with less harvest residues and that predatory and burrowing ground beetles would positively respond to harvest residue retention due to increased prey availability and soil moisture, respectively.

## 2. Materials and Methods

### 2.1. Study Area

We sampled ground beetles in eight replicate clear-cut stands (hereafter "blocks") in intensively managed loblolly pine forests within the Coastal Plain Physiographic Region of the Southeastern United States. Prior to harvest, the blocks were comprised of a planted loblolly pine (*P. taeda*) overstory and a hardwood midstory (e.g., red maple (*Acer rubrum* L.), American sweetgum (*Liquidambar styraciflua* L.)). Our study included four blocks (70.5 ± 6.1 (mean ± SE) ha) in Beaufort County, North Carolina (NC) and four blocks (64.64 ± 3.1 ha) in Georgia (GA): three in Glynn County and one in Chatham County. The blocks were in the temperate/subtropical biogeographic region. Frequent, low-intensity fire caused by humans and lightning was the historical forest disturbance in the area, but fire has since been suppressed in most managed forests of the Southeast (see [8] for detailed management history and site descriptions).

### 2.2. Study Design

Following clear-cut harvests in 2010–2011, we implemented woody biomass retention treatments (hereafter "treatments") in each block. Woody biomass was low value stems (i.e., not sawtimber) and pine tops and limbs traditionally considered non-merchantable prior to the advent of bioenergy-driven woody biomass markets. Our experiment was a randomized complete block design; we divided each block into the following six stand-scale treatments: (1) clear-cut with intensive woody biomass harvest (NOBHGs); (2) clear-cut with 15% retention of harvest residues evenly dispersed throughout the treatment unit (15DISP); (3) clear-cut with 15% retention of harvest residues clustered in large piles throughout the treatment unit (15CLUS); (4) clear-cut with 30% retention of harvest residues evenly dispersed throughout the treatment unit (30DISP); (5) clear-cut with 30% retention of harvest residues clustered in large piles throughout the treatment unit (30CLUS); and (6) clear-cut with no woody biomass harvest (i.e., clear-cut only; NOBIOHARV), which served as a control (see [17,34] for detailed methods on treatment implementation and maps of treatments). We designed harvest residue percent retention and distribution treatments to emulate prescriptions recommended in preexisting biomass harvesting guidelines for the Southeast (see [35]). In NC, treatment unit areas averaged 11.7 ± 0.5 ha. In GA, treatment unit areas averaged 10.7 ± 0.4 ha. Researchers published estimates

of pre-harvest standing volume ($m^3$ $ha^{-1}$) of non-roundwood stems and coarse woody debris and estimates of post-harvest volume ($m^3$ $ha^{-1}$) of harvest residues in each treatment in NC [34].

We implemented treatments similarly in NC and GA, but managers prepared the harvested sites for replanting differently between states. In NC, site preparation occurred following clear-cut harvests, and we implemented the treatments in the winter of 2010–2011. Managers sheared the blocks using a V-shaped blade and a bedding plow, creating continuous, mounded strips of soil (hereafter "beds") approximately 3 m wide and <1 m tall, and planted stands with loblolly pine during the fall/winter of 2011–2012 at a density of ≈1100 trees $ha^{-1}$. Prior to revegetation, pine beds consisted of bare soil and pine seedlings. Shearing moved retained harvest residues into the 3 m space between pine beds (hereafter "interbeds"). Consequently, harvest residues were rearranged following shearing into long, linear rows in interbeds parallel to pine beds (Figure 1). However, volume of harvest residues was unaltered by shearing [34]. Managers treated the blocks with the following two post-harvest herbicide applications of imazapyr (Chopper®; BASF, Raleigh, NC, USA) for herbaceous weed control: (1) a broadcast application (applied by helicopter) one year after clear-cut harvests; and (2) a banded application (applied only to pine trees in beds) two years after clear-cut harvests.



**Figure 1.** A harvest residue pile in a clear-cut stand two-years post-harvest in North Carolina. Stands consisted of uniformly dispersed interbeds containing harvest residues (1) and bedded rows containing planted pine seedlings (2). We set pitfall traps immediately adjacent to either side of harvest residues piles, when present, and two pitfall traps were situated in bedded rows on either side of the interbed (A). Photo by Sarah Fritts. Drawing by Steve Grodsky.

In GA, most harvest residues in treatments were concentrated into large, linear piles (i.e., windrows) extending the entire length of treatments or into large, conical piles (1–100 $m^3$) within treatments (Figure 2). As such, few individual stems and no small harvest residue piles (<1 $m^3$) occurred between windrows (~30–50 m apart) in treatments. In Glynn County (GA), managers bedded two blocks in the summer of 2011 and bedded the remaining block in fall 2011. Managers planted all Glynn County (GA) blocks in the winter of 2012 at a density of ≈1495 trees $ha^{-1}$ and treated stands with imazapyr (Arsenal®; BASF, Raleigh, NC, USA) and sulfometuron methyl for herbaceous weed control one year after clear-cut harvest. In 2012, managers bedded the Chatham County (GA) block and planted the stand at a density of ≈726 trees $ha^{-1}$; the stand received a broadcast treatment of Chopper® one year after clear-cut harvest.

**Figure 2.** (A) Windrow in a clear-cut stand one-year post-harvest in Georgia. (1) Windrows were separated by (2) large expanses of bare ground. To accommodate the width of windrows, we set pitfall traps (black dots) 5 m apart, resulting in a total array length of 15 m. Two pitfall traps were situated immediately adjacently to either side of windrows, when present, and two pitfall traps were situated in bedded rows on either side of the windrow. Photo and drawing by Steve Grodsky.

*2.3. Ground Beetle Sampling*

We pitfall trapped ground beetles in NC and GA in 2012 and 2013. Many studies have singularly employed pitfall traps to assess arthropod diversity and abundance under variable forest management schemes [16,17,24,29,36]. We created pitfall traps with 0.47 L plastic containers (diameter ~8.5 cm) filled with equal amounts of propylene glycol and water and a drop of liquid dish soap to reduce surface tension [37]. We placed the lip of each container at or slightly below ground level (e.g., [38,39]). We removed vegetation (when present) immediately surrounding pitfall traps (i.e., ≤5 cm from trap lips) to improve trapping efficiency [40]. We set four pitfall traps at each pitfall trap array (hereafter "array"). To control for edge effects, we situated all arrays ≥100 m from treatment and block edges.

In NC, we established 3 m-long arrays (four pitfall traps per array) with 1-m inter-trap spacing. We sampled each location monthly for a 48-h period, June–September 2012 and June, July, and September 2013. In GA, we established 15 m-long arrays (four pitfall traps per array) with 5 m inter-trap spacing; the width of windrows in GA precluded replication of array design in NC (i.e., 1 m inter-trap spacing; Figure 2). We sampled each location once for a 48-h period in August 2012 and 2013. At the conclusion of each sampling period, we strained ground beetles from each pitfall trap and stored specimens in 60-mL Nalgene® bottles filled with 70% ethanol and labeled with trap locality data. Kevin Hinson identified all the specimens to species using taxonomic keys (e.g., [41]) and confirmed identifications using museum-type specimens representative of each ground beetle species. We submitted all ground beetles as voucher specimens to the North Carolina State University Insect Museum (NCSU).

*2.4. Analysis*

We developed generalized linear models (GLMs) to test the response of ground beetles to treatments in NC and GA (see also [16,17]). We used the count of each ground beetle genus, species, and functional group (Poisson distribution) and species richness and Shannon–Weaver diversity index of ground beetles (Gamma distribution) captured at each pitfall trap array in each treatment as dependent variables. We based functional group assignments for each species on accounts in "A Natural History of the Ground-beetles (Coleoptera: Carabidae) of America" [42]; the book uses standardized categories for functional traits (Table 1). In our models, we first included a treatment × year interaction term, treatment, year, and block as explanatory variables in each model. If we detected a significant

treatment × year interaction, we consequently developed a model for each year separately and included treatment and block as explanatory variables. Otherwise, we included treatment, year, and block as explanatory variables. For GA sites, we replaced the categorical variable for treatment with volume ($m^3$ $ha^{-1}$) of harvest residues in windrows in each treatment, which was calculated during a concurrent study (see [16,34] for detailed methods regarding quantification of harvest residue volume) and tested for treatment effects following the same procedure outlined for NC. For GA models, we used only species richness and Shannon–Weaver diversity index as dependent variables due to insufficient sample sizes for individual beetle species. Similarly, we only analyzed ground beetle species in NC for 2013 due to relatively low sample sizes for individual genera and species in 2012. For all the models, we assumed overdispersion when the residual deviance divided by the residual degrees of freedom was >1.0. We conducted quasi-poisson GLMs when we detected overdispersion. We performed likelihood ratio tests on all GLMs to determine significant treatment effects. We conducted post hoc Tukey's pairwise comparisons of treatment means using general linear hypothesis testing (glht function; single-step method) in the R package "multcomp" [43]. We set $\alpha = 0.05$.

**Table 1.** Count and functional group assignments of ground beetles (*n* = 480) captured in clear-cut stands within intensively managed pine plantations, North Carolina, 2012 and 2013. We assigned functional groups to each species per accounts in Larochelle and Lariviere 2003.

| Species | Count | | Functional Group Assignments | | | | | | | |
| | 2012 | 2013 | Habitat Type | Soil Type | Diel Activity | Dispersal Power | Locomotion | Climbing | Digging | Human Activity |
|---|---|---|---|---|---|---|---|---|---|---|
| *Acupalpus pauperculus* Dejean | 0 | 4 | Open ground | Wet | Mostly nocturnal | Frequent flyer | Slow runner | Occasional | Non-burrower | Negative |
| *Acupalpus testaceus* Dejean | 6 | 9 | Open ground | Wet | Nocturnal | Frequent flyer | Slow runner | N/A | Non-burrower | Negative |
| *Agonum octopunctatum* (Fabricius) | 1 | 0 | Open ground | Wet | Mostly nocturnal | Frequent flyer | Moderate runner | Occasional | Non-burrower | Neutral |
| *Agonum punctiforme* (Say) | 2 | 1 | Open ground | Moist | Mostly nocturnal | Frequent flyer | Moderate runner | Occasional | Non-burrower | Positive |
| *Amara aenea* (DeGeer) | 1 | 2 | Open ground | Dry | Diurnal | Frequent flyer | Moderate runner | Frequent | Non-burrower | Positive |
| *Anisodactylus dulcicollis* (LaFerté-Sénectère) | 0 | 1 | Open ground | Dry | Nocturnal | Frequent flyer | Fast runner | N/A | Non-burrower | Positive |
| *Anisodactylus haplomus* Chaudoir | 1 | 11 | Pine forest | Moist | Nocturnal | Frequent flyer | Fast runner | N/A | Non-burrower | Negative |
| *Anisodactylus nigerrimus* Dejean | 0 | 9 | Open ground | Dry | Mostly nocturnal | Frequent flyer | Moderate runner | N/A | Non-burrower | Positive |
| *Anisodactylus rusticus* (Say) | 0 | 16 | Open ground | Dry | Mostly nocturnal | Frequent flyer | Fast runner | Occasional | Non-burrower | Positive |
| *Bradycellus rupestris* (Say) | 0 | 1 | Open ground | Dry | Mostly nocturnal | Frequent flyer | Moderate runner | Occasional | Non-burrower | Positive |
| *Calosoma sayi* Dejean | 3 | 0 | Open ground | Moist | Crepuscular | Frequent flyer | Moderate runner | Occasional | Non-burrower | Positive |
| *Chlaenius emarginatus* Say | 5 | 1 | Shaded | Moist | Nocturnal | Frequent flyer | Moderate runner | N/A | Burrower | Negative |
| *Chlaenius pennsylvanicus pennsylvanicus* Say | 0 | 1 | Open ground | Wet | Mostly nocturnal | Frequent flyer | Moderate runner | Occasional | Non-burrower | Negative |

**Table 1.** *Cont.*

| Species | Count | | Functional Group Assignments | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 2012 | 2013 | Habitat Type | Soil Type | Diel Activity | Dispersal Power | Locomotion | Climbing | Digging | Human Activity |
| *Cicindela sexguttata* Fabricius | 0 | 3 | Open ground | Dry | Diurnal | Occasional flyer | Fast runner | N/A | Non-burrower | Negative |
| *Cicindelidia punctulata punctulata* Olivier | 3 | 8 | Open ground | Dry | Diurnal | Occasional flyer | Fast runner | N/A | Non-burrower | Negative |
| *Clivina* sp. | 0 | 1 | N/A | N/A | N/A | N/A | N/A | N/A | N/A | N/A |
| *Cyclotrachelus sigillatus* (Say) | 1 | 0 | Shaded | Moist | Nocturnal | Brachypterous | Moderate runner | N/A | Non-burrower | Negative |
| *Dicaelus dilatatus* Say | 3 | 0 | Shaded | Moist | Nocturnal | Brachypterous | Moderate runner | N/A | Non-burrower | Negative |
| *Dicaelus elongatus* Bonelli | 0 | 1 | Shaded | Moist | Nocturnal | Brachypterous | Moderate runner | Occasional | Non-burrower | Negative |
| *Dicaelus purpuratus* Bonelli | 0 | 1 | Shaded | Moist | Nocturnal | Brachypterous | Moderate runner | N/A | Non-burrower | Negative |
| *Dyschirius globosus* (Say) | 3 | 6 | Open ground | Moist | Mostly nocturnal | Occasional flyer | Slow runner | N/A | Burrower | Positive |
| *Harpalus erythropus* Dejean | 1 | 0 | Open ground | Dry | Nocturnal | Frequent flyer | Moderate runner | Occasional | Non-burrower | Positive |
| *Harpalus herbivagus* Say | 2 | 0 | Open ground | Dry | Mostly nocturnal | Frequent flyer | Moderate runner | Occasional | Non-burrower | Positive |
| *Harpalus pensylvanicus* (DeGeer) | 38 | 233 | Open ground | Dry | Mostly nocturnal | Frequent flyer | Moderate runner | Frequent | Burrower | Positive |
| *Loxandrus crenatus* LeConte | 10 | 5 | N/A | N/A | N/A | Occasional flyer | N/A | N/A | Non-burrower | Negative |
| *Notiobia nitidipennis* LeConte | 0 | 10 | Shaded | Moist | Nocturnal | Frequent flyer | Moderate runner | N/A | Non-burrower | Negative |
| *Notiobia terminata* (Say) | 1 | 0 | Open ground | Dry | Nocturnal | Frequent flyer | Moderate runner | Frequent | Non-burrower | Positive |

**Table 1.** *Cont.*

| | Count | | | | | Functional Group Assignments | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 2012 | 2013 | Habitat Type | Soil Type | Diel Activity | Dispersal Power | Locomotion | Climbing | Digging | Human Activity |
| *Olisthopus parmatus* (Say) | 1 | 1 | Shaded | Moist | Nocturnal | Occasional flyer | Moderate runner | N/A | Non-burrower | Negative |
| *Paratachys columbiensis* Hayward | 0 | 1 | N/A | N/A | Nocturnal | Occasional flyer | Fast runner | N/A | Non-burrower | Negative |
| *Polyderis laeva* (Say) | 0 | 1 | Open ground | Dry | Mostly nocturnal | Frequent flyer | Moderate runner | N/A | Burrower | Positive |
| *Scarites quadriceps* Chaudoir | 0 | 3 | Open ground | Moist | Nocturnal | Frequent flyer | Slow runner | N/A | Burrower | Positive |
| *Scarites subterraneus* Fabricius | 0 | 2 | Open ground | Moist | Nocturnal | Frequent flyer | Slow runner | Frequent | Burrower | Positive |
| *Selenophorus fatuus* LeConte | 0 | 6 | Open ground | Dry | Nocturnal | Frequent flyer | Moderate runner | N/A | Burrower | Negative |
| *Selenophorus hylacis* (Say) | 0 | 2 | Shaded | N/A | Nocturnal | Frequent flyer | Moderate runner | Frequent | Non-burrower | Negative |
| *Selenophorus opalinus* (LeConte) | 2 | 2 | Open ground | Dry | Nocturnal | Frequent flyer | Moderate runner | Occasional | Non-burrower | Positive |
| *Stenolophus humidus* Hamilton | 0 | 1 | Open ground | Wet | Nocturnal | N/A | Moderate runner | N/A | Non-burrower | Negative |
| *Stenolophus infuscatus* Dejean | 0 | 1 | N/A | Moist | Nocturnal | Frequent flyer | Slow runner | Occasional | Burrower | Negative |
| *Stenolophus ochropezus* (Say) | 1 | 26 | Shaded | Wet | Nocturnal | Frequent flyer | Moderate runner | Occasional | Burrower | Negative |
| *Stenolophus plebejus* Dejean | 2 | 22 | Open ground | Wet | Nocturnal | Occasional flyer | Moderate runner | N/A | Burrower | Negative |
| *Tetracha carolina* (L.) | 0 | 1 | Open ground | Dry | Nocturnal | Occasional flyer | Fast runner | N/A | Non-burrower | Negative |
| Total | 87 | 393 | | | | | | | | |

## 3. Results

We captured and identified 579 individual ground beetles. In NC, we collected 480 ground beetle specimens comprised of 21 genera and 40 species (Table 1). In GA, we collected 99 ground beetle specimens comprised of 20 genera and 31 species (Table S1). *Harpalus pensylvanicus* (DeGeer) was the most abundant species in NC, constituting 44% and 60% of ground beetles captures in 2012 and 2013, respectively.

Species richness and diversity of ground beetles did not differ among treatments in NC, nor did they increase with an increasing volume of harvest residues in windrows at the GA sites (Table S2). We detected treatment effects for the following functional traits of ground beetles: 1) habitat type–open ground (2012 and 2013) and pine forest (2013); 2) soil type–dry (2013); 3) diel activity–mostly nocturnal (2012 and 2013); 4) dispersal power–frequent flyer (2013); 5) locomotion–fast runner (2013) and moderate runner (2012 and 2013); 6) climbing–frequent climber (2012 and 2013); 7) digging–burrower (2012 and 2013) and nonborrower (2013), and 8) response to human disturbance–positive (2012 and 2013) and negative (2013) (Table S3). We also found support for treatments effects on counts of *Anisodactylus* spp. (included *Anisodactylus haplomus* Chaudoir, *Anisodactylus nigerrimus* (Say), and *Anisodactylus rusticus* (Say)), *Anisodactylus haplomus*, and *H. pensylvanicus*.

Treatment effects on ground beetle functional traits in 2012 largely were driven by relatively high abundances of common species in the 15DISP treatment of a particular block (Table S3). However, we detected treatment effects on ground beetle genera, species, and functional traits with discernable patterns in 2013; these patterns indicated positive associations between ground beetle functional traits and the availability of harvest residues and higher counts of ground beetles in the NOBIOHARV (i.e., complete harvest residue retention) treatment relative to the NOBHGs (i.e., no harvest residue retention) treatment (Table S3). Counts of ground beetles with the following functional traits were greater in the NOBIOHARV treatments than the NOBHGs treatments in 2013: open ground habitat type, dry soil, mostly nocturnal diel activity, frequent flyers, fast runners and moderate runners, frequent climbers, burrowers and non-burrowers, and positive and negative associations with human activity (Table S3, Figure 3).

Counts of *H. pensylvanicus* and *Anisodactylus* spp. were greater in the NOBIOHARV treatments than the NOBHGs treatments (Table S4, Figure 3). Given the high number of captures for *H. pensylvanicus*, this strongly influenced the results for the functional traits to which it was assigned. However, many other less abundant ground beetle species share some or all of the same functional traits as *H. pensylvanicus* (Table 1). Additionally, we determined that count of *H. pensylvanicus* and counts of most ground beetle functional groups were similar in the 15DISP retention treatments to those in the NOBIOHARV treatments (Table S4).
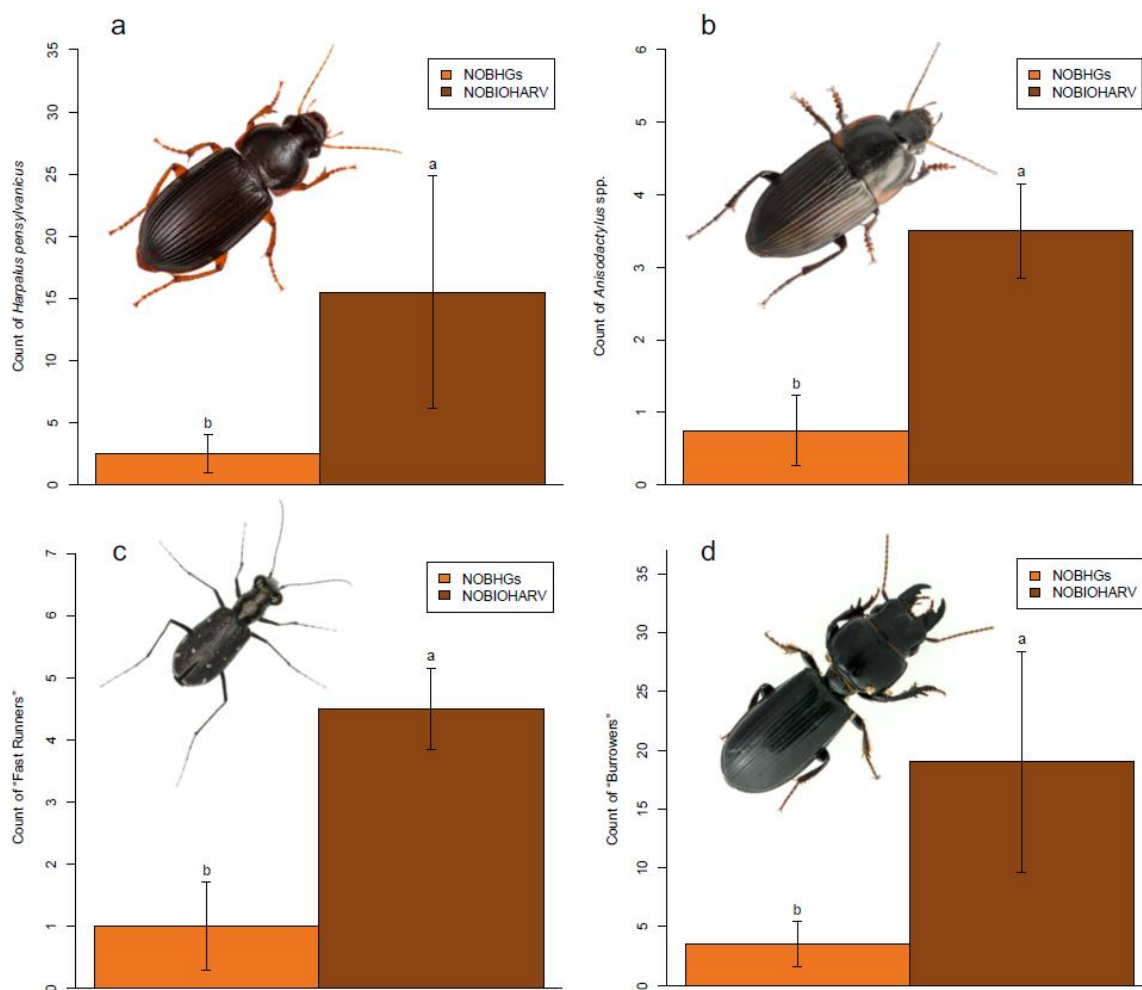
**Figure 3.** Response of (**a**) *Harpalus pensylvanicus* (Photo credit: Salvador Vintanza), (**b**) *Anisodactylus* spp.-*A. haplomus* pictured (Photo credit: Iustin Cret), (**c**) the "Fast Runner" functional trait-*Cicindelidia punctulata punctulata* pictured (Photo credit: Chris Wirth), and (**d**) the "Burrower" functional trait–*Scarites subterraneus* pictured (Photo credit: John and Kendra Abbot/Abbott Nature Photography) to no retention of harvest residues (NOBHGs) and complete retention of harvest residues (NOBIOHARV) treatments in clear-cut stands, North Carolina, 2013. Different letters indicate significantly different pairwise comparisons of treatment means. We set $\alpha = 0.05$. See Supplementary Materials for comparisons of all harvest reside retention treatment means.

## 4. Discussion

Our results indicate that response (or lack thereof) of the ground beetle community to harvest residue retention at the stand-scale does not necessarily reflect positive functional relationships between some ground beetles and the availability of harvest residues. On the one hand, our hypothesis that ground beetle richness and diversity would increase with greater harvest residue retention was rejected. As such, harvest residue reductions following woody biomass harvests for forest bioenergy from managed forests at the levels that occurred in our treatments may not affect ground beetle communities in the Southeast. However, we found evidence that burrowing and predatory ground beetle species were negatively affected by harvest residue reductions, indicating that woody biomass harvests may have consequences for ground beetles at functional levels and at local scales despite the lack of a community response in recently clear-cut stands in managed forests of the Southeast [1].

Our study adds to the scant literature on effects of forest bioenergy on ground beetles and contributes new insights into the response of ground beetles to forest bioenergy harvests in temperate/subtropical bioregions. Researchers determined that ground beetle assemblages were altered by intensive harvest residue removal in recently clear-cut jack-pine forests in western Quebec and specifically that populations of at least two species of forest ground beetles (*Agonum retractum* LeConte and *Calathus ingratus* Dejean) may have been depleted by successive, additive disturbances (i.e., clear-cut harvest and woody biomass harvest) [44]. A study in spruce forests in Sweden conducted 5–7 years after stands were clear-cut and harvested for woody biomass determined that harvest residue reductions increased generalist ground beetle species and decreased forest species [45]. Our results corroborate those of Nittérus et al. [45] that generalist ground beetle species increased following clear-cut harvests. Dynamics of coarse woody debris differ between northern latitudes and those closer to the equator. For example, coarse woody debris decays faster in the warmer, moister climactic conditions of the southeastern United States [14], whereas coarse woody debris in more northern climates with colder temperatures persists on the landscape for longer periods of time. Therefore, comparisons between studies addressing effects of harvest residue retention on ground beetles in different bioregions may be limited.

The response of *H. pensylvanicus*, a habitat generalist, to harvest residue retention in clearcut stands uniquely allowed us to separate effects of disturbance from clear-cut harvests from those of disturbance from woody biomass harvesting. Basic theory in forest ecology suggests that generalist species positively respond to disturbance [17,46]. The fact that *H. pensylvanicus* was the most abundant ground beetle species in clear-cut stands supports this theory. Although *H. pensylvanicus* benefited from clear-cut harvests, it was negatively affected by lack of harvest residue retention. *Harpalus pensylvanicus* is primarily granivorous and feeds on plant seeds [47]. Soils adjacent to harvest residues are fed by higher concentrations of fine woody debris and maintain stable microclimatic conditions [48,49]. Thus, soil conditions favorable to early successional vegetative growth located at micro-sites near harvest residues may have increased recruitment of seed-bearing grasses and forbs, providing increased food sources for *H. pensylvanicus*. *Harpalus pensylvanicus* forages and oviposits in fall, and individuals of the species overwinter in the soil as larvae and often times as adults [50]. Therefore, it is not unreasonable to presume that the population of *H. pensylvanicus* increased in regenerating stands from 2012 to 2013 due to the successional trajectory of seed-producing grasses and forbs, which, in turn, may have been locally promoted by harvest residues. Further, moist soils associated with harvest residues may increase seed imbibition rates, and imbibed seeds are consumed by *H. pensylvanicus* in greater amounts than ambient dry seeds [51].

The burrowing behavior of *H. pensylvanicus* also may have driven the species positive response to harvest residue retention, and, as such, *H. pensylvanicus* may serve as an indicator for other less common, burrowing ground beetle species. Soil moisture and chemical factors locally increase with increasing availability of coarse woody debris [26]. As such, burrowing ground beetles may overwinter as larvae and, for some species, engage in their fossorial lifestyles as adults in sites with more harvest residues than those with less harvest residues; the permeable soils associated with harvest residues may provide favorable conditions for digging and subterranean movement of ground beetles. Fossorial ground beetles herein classified as burrowers may be infrequently captured in pitfall traps because they spend much of their time underground or because they are rare in clear-cuts altogether. *H. pensylvanicus* is an active, epigaeic ground beetle species that burrows, so it may serve as a valuable indicator species for more cryptic and less abundant burrowing ground beetle species in regenerating stands of the Southeast.

Our results indicate that a positive relationship exists between predatory ground beetles and availability of harvest residues, specifically for a functional group known as the "fast runners" and the genus *Anisodactylus*, which may relate to previous hypotheses that coarse woody debris attracts invertebrate predators by harboring high densities of arthropod prey [16]. Of the ground beetles we documented, *Anisodactylus* spp., three species of tiger beetles (*Cicindela sexguttata* Fabricius, *Cicindelidia*

*punctulata punctulata* Olivier, and *Tetracha carolina* L.) and *Paratachys columbiensis* Hayward comprised the "fast runner" functional group, and all are considered cursorial. The response of these cursorial hunters to harvest residue removal may indicate that predatory ground beetles that can cover ground and search out arthropod prey harbored by individual harvest residues piles selected areas with greater concentrations of harvest residues, thereby potentially reducing energetic costs of prey searching. The concept of cursorial locomotion in areas with high volumes of debris of any kind may seem counterintuitive but one must consider the micro-landscape cursorial, predatory ground beetles encountered in intensively managed pine forests. The interbeds containing harvest residues were bordered on either side by bedded rows of pine trees, which received herbicidal treatment during both years of our study and thereby provided a proverbial "tiny highway" for cursorial, predatory ground beetles to hunt from. Indeed, we frequently observed *C. p. punctulata* running in or otherwise occupying bedded rows (S. M. Grodsky, *pers. observation*).

The ground beetle species and functional groups negatively affected by harvest residue removal all can confer ecosystem services in managed forests and may affect the ecological function of forests in general. For example, *H. pensylvanicus* is often used as a biocontrol agent in agroecosystems to combat weed populations by consuming weed seeds [52]. Given the potential for intercropping dedicated bioenergy crops like switchgrass (*Panicum virgatum*) in clear-cut stands following woody biomass harvests (e.g., [53]), biological weed control provided by *H. pensylvanicus* could limit weedy encroachment in bioenergy plots. Additionally, *H. pensylvanicus* is not only a seed predator but also a seed disperser; the larvae of *H. pensylvanicus* have been recorded caching seeds of native grasses in their burrows [54]. As ecosystem engineers, burrowing beetles may confer ecosystem services to forest managers by amending soils through mechanical manipulation of the soil matrix. For example, researchers determined that a burrowing dung beetle species conditioned soils such that growth in plants subjected to drought conditions was increased by 280% [55]. In the case of managed forests, burrowing ground beetles may similarly increase forest resiliency to drought, water inundation, and climate change via soil conditioning.

Although our results are specific to the Southeast, we suggest that general themes associated with effects of forest bioenergy harvests and associated reductions in harvest residues on ground beetle ecosystem services and prescribed percent harvest residue retention targets may be relevant to a variety of bioregions. Our study involved operational woody biomass harvests for which loggers harvested woody biomass that they deemed merchantable, resulting in substantial residual harvest residues following woody biomass harvests even in the no harvest residue retention treatments. Further, results from our group's previous studies on effects of harvest residue removal on wildlife suggest that species' responses likely vary by spatial scale and with regionally specific operational variables. Regardless, our results indicate that retaining a minimum of 15% retention of total harvest residues may maintain beneficial ground beetle populations in recently clear-cut stands.

## 5. Conclusions

The mixed results of our study exemplify the diversity of theoretical underpinnings and spatial scales that must be considered when interpreting effects of harvest residue removal on wildlife and, ultimately, the sustainability of forest bioenergy. Although the ground beetle community as a whole did not respond to harvest residue retention, we determined that individual ground beetle functional groups, genera, and species that may confer ecosystem services to forests were negatively impacted by harvest residue removal, at least in the short term. In general, our results indicate that a minimum of 15% retention of total harvest residues may maintain beneficial ground beetle populations in recently clear-cut stands. The common theory on the "winners" and "losers" of anthropogenic disturbance suggests that generalist species are better adapted to renewable energy development than specialist species [56,57]. As such, our study revealed a contradictory and novel result: *H. pensylvanicus*, a generalist species, positively responded to disturbance from clear-cut harvests but negatively responded to reductions in harvest residue. We suggest that *H. pensylvanicus* is a useful indicator

species for ground beetle response to amounts of harvest residue in recently harvested stands because it is readily abundant, represents functional traits of scarcer ground beetles, and provides ecosystem services as an ecosystem engineer of soils and weed-seed consumer. Ultimately, the sustainability of forest bioenergy development pertains not only to conservation of species but also to the maintenance of the ecosystem services conferred to people via positive inputs to managed forests (e.g., commercial plantations) provided by soils, plants, and animals.

**Supplementary Materials:** The following are available online at http://www.mdpi.com/1999-4907/11/1/48/s1, Table S1. Count of ground beetle species (no = 99) captured in harvest residue retention treatments in clearcut stands, Georgia, 2012 and 2013, Table S2. Results of likelihood ratio tests for treatment effects on species richness and species diversity of ground beetles in harvest residue retention treatments in clearcut stands, NC, 2012 and 2013, Table S3. Mean (±SE) number of functional trait assignments for ground beetle species in harvest residue retention treatments in clearcut stands, North Carolina, 2012 and 2013, Table S4. Mean (±SE) number of captured ground beetle genera and species in harvest residue retention treatments in clearcut stands, North Carolina, 2013.

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