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Variable responses of non-native and native ants to coarse woody debris removal following forest bioenergy harvests

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ABSTRACT

Timber harvests may facilitate ant invasions of forested landscapes, fostering interactions between non-native and native ants. Harvests that include removal of low-value woody biomass as forest bioenergy feedstock may reduce residual coarse woody debris, thereby altering food and cover resources for ant species. We manipulated: (1) volume and distribution of coarse woody debris in stand-scale treatments ranging from intensive coarse woody debris removal to no coarse woody debris removal; and (2) coarse woody debris availability at microsite locations within stand-scale treatments, including piles of hardwood stems, piles of conifer stems, and no pile locations in North Carolina, USA and windrows (i.e., long, linear piles of harvest residues) and no windrows in Georgia, USA, in recently clearcut pine plantations ($n = 4$ per state). We captured ants in regenerating stands and tested treatment- and location-level effects on non-native and native ant relative abundances. Invasive ants represented 19% of ant taxa richness, but comprised 94% of total ant captures. Red imported fire ant (*Solenopsis invicta* Buren, hereafter "RIFA") dominated the ant community in young plantations. RIFA avoided windrows, but its relative abundance did not differ among stand-scale treatments. Coarse woody debris retention in stand-scale treatments and at microsite locations favored non-RIFA ants, including Asian needle ant (*Brachyponera chinensis* Emery) and several native ant species. Dual invasions of RIFA and Asian needle ant in young plantations of the eastern United States may commonly occur because the two species may not compete for resources on the forest floor. Reduction of coarse woody debris via intensified woody biomass harvesting may negatively affect non-RIFA ant species and promote RIFA colonization, thereby indirectly increasing deleterious effects of RIFA on other wildlife.

1. Introduction

Globally, ants are among the most dominant and detrimental invasive species (Holway et al., 2002; Tsutsui and Suarez, 2002). Invasive ants may pose human health risks associated with medical complications from stings and inflict costly damage to agroecosystems (e.g., interference with integrated pest management practices, crop damage) and property (e.g., ground disturbance from mounds) (DeShazo et al., 1990; Pimentel et al., 2005). Non-native ants may cause significant decreases in biodiversity and disturb ecological networks germane to ecosystem function and integrity (Ness et al., 2004). In addition to displacing some native ants, non-native ants may negatively affect soil biota, other invertebrates, and vertebrates via soil disturbance, competition for resources, and predation (Lessard et al., 2009; Lach and Hooper-Bui, 2010). Non-native ants are difficult to control and nearly impossible to eradicate once established, so their management often is a conservation priority (Holway et al., 2002).

Successful colonization and relatively high abundances of non-native ant species are often linked to anthropogenic disturbance (King and Tschinkel, 2008). For example, timber harvests in intensively managed plantations of the southeastern United States create conditions conducive to disturbance-mediated colonization of non-native ants (Zettler et al., 2004; Todd et al., 2008). These harvests create widely distributed patches of disturbed forest over large land areas, which likely facilitates

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range expansions of non-native ants in the region (Zettler et al., 2004). Approximately 22% of all timberland in the southeastern United States is plantation forest in the Coastal Plain and Piedmont Physiographic Regions; most of these plantations are harvested via clearcutting (Siry, 2002; Oswalt et al., 2014). Red imported fire ant (*Solenopsis invicta*; hereafter "RIFA") are well-known invaders of disturbed forests in the Coastal Plain and Piedmont Physiographic Regions of the southeastern United States. RIFA is a notorious invasive species throughout most of the southern United States, especially in areas with frequent anthropogenic distrubance, and has well-documented, deleterious effects on other wildlife (e.g., displacement, mortality) in the region (*see* Allen et al., 2004). Meanwhile, Asian needle ant (*Brachyponera chinensis* Emery) is known to have invaded relatively undisturbed, mature forests in the southeastern United States (Canter, 1981; Guénard and Dunn, 2010). Most studies of Asian needle ant were conducted in mature forests of the eastern United States; these studies reported localized reductions in abundances of native ants caused by competitive displacement from Asian needle ant invasions (Guénard and Dunn, 2010). Current literature suggests that RIFA is a more noxious invasive species than Asian needle ant in the eastern United States because it has larger colony sizes and it can rapidly exploit disturbed areas. However, studies on ecosystem effects of RIFA invasions currently far outnumber those on Asian needle ant.

Although non-native ant colonization of young plantations often is attributable to anthropogenic disturbance (e.g., timber harvest and site preparation for replanting; *see* Zettler et al., 2004), species' success may also be linked to their ability to exploit available habitat structure following timber harvests, including coarse woody debris (e.g., harvest residues) and colonizing pioneer plant species. As such, studies explicitly addressing response of non-native (and native) ants to experimental manipulations of habitat structure in young plantations are warranted. Importantly, both coarse woody debris and vegetation could be managed, especially in production forests, to reduce persistence of non-native ants, should studies suggest that relationships between non-native ants and habitat structure in young plantations indeed exist.

Recent interest in woody biomass as forest bioenergy feedstock may lead to increased extraction of low-value woody material following clearcutting, which may, in turn, affect availability of food and cover resources for ants associated with coarse woody debris (Riffell et al., 2011). Some ant species use coarse woody debris for nesting, while others (e.g., RIFA) nest in bare ground (Harmon et al., 1986, Higgins and Lindgren, 2006). Areas directly adjacent to coarse woody debris piles often provide favorable microhabitat conditions for nesting ants, including a deep litter layer, high concentrations of fine woody debris, and stable microclimate conditions (Spears et al., 2003; Higgins and Lindgren, 2006; Remsburg and Turner, 2006). Additionally, coarse woody debris may support arthropod prey consumed by predatory and omnivorous ant species (Holway et al., 2002; Castro and Wise, 2010). Despite accumulated knowledge of relationships between ants and coarse woody debris in forests, little is known about effects of woody biomass harvesting on interactions between non-native and native ants.

We hypothesized that reduced volume and distribution of coarse woody debris in young plantations would lead to increased RIFA relative abundance because it often nests in bare ground. We also hypothesized that relative abundance of native ants would be greater in areas with greater coarse woody debris availability because they may be competitively excluded from areas with less coarse woody debris by RIFA and because coarse woody debris provides food and cover for several native ant species in the southeastern United States. To test these hypotheses, we quantified ant response to stand-scale, manipulative coarse woody debris removal treatments and microsite manipulations of coarse woody debris availability at locations in recently clearcut stands. Our objectives were to: (1) measure effects of coarse woody debris removal treatments on ant relative abundances in young plantations; and (2) measure effects of groundcover and coarse woody debris availability and pile type (i.e., conifer or hardwood) on ant relative abundances at microsite locations. The goals of this study were to inform broad forest and coarse woody debris management geared towards native ant conservation and non-native ant management and to improve understanding of local, ecological relationships and interactions among non-native ants, native ants, and coarse woody debris.

2. Methods

2.1. Study area and design

We studied ants in eight replicate clearcuts (hereafter "blocks") in intensively managed loblolly pine (*Pinus taeda*) forests within the Coastal Plain Physiographic Region of the southeastern United States. Prior to harvest, blocks were comprised of a planted loblolly pine overstory and a hardwood midstory [e.g., red maple (*Acer rubrum*), American sweetgum (*Liquidambar styraciflua*]. 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. Blocks were in the temperate/subtropical biogeographic regions. Frequent, low-intensity, human- and lightning-caused fire was the historical forest disturbance in the southeastern United States, but fire is suppressed in most managed industrial forests of the region (*see* Grodsky et al., 2016a for management history and site descriptions).

Following clearcut harvests in 2010–2011, we implemented coarse woody debris (i.e., operational harvest residue) removal treatments (hereafter "treatments") in each block. We used a randomized complete-block experimental design, dividing each block into the following six, stand-scale treatments: (1) clearcut with intensive harvest residue removal (INTREM); (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 harvest residue removal (i.e., clearcut only; NOREM), which served as a reference (*see* Fritts et al., 2014; Grodsky et al., 2016b; Grodsky et al., 2018 for detailed methods on and maps of stand-scale treatment implementation). We designed harvest residue percent retention and distribution treatments to emulate prescriptions recommended in pre-existing biomass harvesting guidelines for the southeastern United States (*see* Perschel et al., 2012). In NC, treatment areas averaged 11.7 ± 0.5 ha. In GA, treatment areas averaged 10.7 ± 0.4 ha. We defined harvest residues as non-roundwood stems (i.e., stems unused for pulpwood or sawtimber) and pine tops and limbs traditionally considered non-merchantable prior to the advent of forest bioenergy-driven woody biomass markets. Fritts et al., 2014 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 (*see* Quantifying stand- and micro-scale habitat characteristics).

Treatment implementation was similar in NC and GA, but preparation of the harvested sites for replanting differed between states. In NC, site preparation occurred following clearcut harvest and implementation of treatments in the winter of 2010–2011. Blocks were sheared using a V-shaped blade, bedded into continuous, mounded strips of soil (hereafter "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}. Prior to establishment of unplanted vegetation, pine beds consisted of bare soil and pine seedlings. Shearing moved retained coarse woody debris into the 3-m space between pine beds (hereafter "interbeds"). Consequently, coarse woody debris was rearranged following shearing into long, linear rows in interbeds parallel to pine beds (Fig. 1). However, volume of coarse woody debris largely was unaltered by shearing (Fritts et al., 2014). Blocks were

Fig. 1. A site 1-year post-harvest in North Carolina, with uniformly intermittent interbeds containing coarse woody debris (1) and bedded rows containing planted pine seedlings (2). Three pitfall trap arrays representing microsite locations (hardwood pile, pine pile, and no pile) were clustered within each of the six, large-scale harvest residue removal treatments. Each array was oriented perpendicular to interbeds and beds [(A) – hardwood pile shown]. Pitfall traps (black dots) were 1-m apart, resulting in a total array length of 3 m. Two pitfall traps were situated immediately adjacent to either side of harvest residues piles, when present, and two pitfall traps were situated in bedded rows on either side of the interbed. We maintained the same array design and inter-trap spacing for no pile locations, despite the fact that no CWD was present in interbeds. Photo by Sarah Fritts. Drawing from Grodsky et al. (2018) (used with permission).

treated with the following two post-harvest herbicide applications of imazapyr (Chopper®; BASF, Raleigh, North Carolina, USA) for herbaceous weed control: (1) a broadcast application (applied by helicopter) one year after clearcut harvest; and (2) a banded application (applied only to pine trees in beds) two years after clearcut harvest.

In GA, most coarse woody debris in treatments was 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 (Fig. 2). As such, few individual stems and no small coarse woody debris piles (< 1 m^3) occurred between windrows ($\sim$30–50 m apart) in treatments. In Glynn County (GA), two blocks were bedded in the summer of 2011 and the remaining block was bedded in fall 2011. All Glynn County (GA) blocks were planted in the winter of 2012 at a density of $\approx$1495 trees ha^{-1} and treated with imazapyr (Arsenal®; BASF, Raleigh, North Carolina, USA) and sulfometuron methyl for herbaceous weed control one year after clearcut harvest. In 2012, the Chatham County (GA) block was bedded and planted at a density of $\approx$726 trees ha^{-1} and received a broadcast treatment of Chopper® one year after clearcut harvest.

Following site preparation and planting, we established microsite locations that emulated coarse woody debris removal or lack thereof (hereafter "locations") within treatments. To accomplish this, we randomly selected one point $\geq$100 m from treatment and block edges at which to locate a cluster of locations in each stand-scale treatment in each block. In NC, locations included: (1) hardwood pile; (2) pine pile; and (3) no pile (i.e., no coarse woody debris = control). The INTREM treatments had all hardwood harvest residues removed and thus did not include hardwood pile locations. In GA, harvest residues consisted of pine in windrows exclusively, resulting in implementation of windrow and no windrow (i.e., no coarse woody debris = control) treatments in GA.

Fig. 2. A site 1-year post-harvest in Georgia, with windrows (1) separated by large expanses of bare ground (2). Two pitfall trap arrays representing microsite locations (windrow, no windrow) were clustered within each of the six, large-scale harvest residue removal treatments. Each array was oriented perpendicular to windrows (A). To accommodate the width of windrows, pitfall traps (black dots) were 5-m apart, resulting in a total array length of 15 m. Two pitfall traps were situated immediately adjacent to either side of windrows, when present, and two pitfall traps were situated in bedded rows on either side of the windrow. We maintained the same array design and inter-trap spacing for no windrow locations, despite the fact that no windrows were present. Photo by Steve Grodsky. Drawing from Grodsky et al. (2018) (used with permission).

2.2. Ant sampling, identification, and measures

We sampled ants in NC and GA using pitfall trapping in 2012 and 2013. We specifically targeted surface-active ants because they occupy niches on the forest floor (e.g., Pearce and Venier, 2006), which exclusively contains coarse woody debris that may provide habitat structure (and woody biomass feedstock). Pitfall trapping is a well-established method for capturing ground-dwelling invertebrates, including ants (Anderson et al., 1991). Many studies have singularly employed pitfall traps to assess arthropod diversity and abundance under variable forest management schemes (Greenberg and Forrest, 2003; Ulyshen and Hanula, 2009; Greenberg et al., 2010; Guénard and Dunn, 2010; Iglay et al., 2012; Rodriquez-Cabal et al., 2012; Grodsky et al., 2018, and others). Pitfall traps were 0.47-L plastic containers with a diameter of ~8.5 cm filled with equal amounts of propylene glycol and water and a drop of liquid dish soap to reduce surface tension (Spence and Niemelä, 1994). 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 (hereafter "array"). To control for edge effects, we situated all arrays ≥100 m from treatment and block edges.

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

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

At the conclusion of each sampling period, we strained ants from each pitfall trap and stored specimens in 60-ml Nalgene® bottles filled with 70% ethanol and labeled with trap locality data. We identified all specimens to genus or species using taxonomic keys (e.g., Fischer and Cover, 2007; MacGown, 2013) and confirmation for type specimens representative of each ant genus or species. We submitted voucher specimens of identified ant genera and species to the North Carolina State University Insect Museum.

We plotted relative abundances for all non-native and native ant genera and species per state and binned all ant groups into one of the following three abundance levels: (1) superabundant; (2) abundant; and (3) rare (*see* Grodsky et al., 2018). We set the cutoff for inclusion of individual genera and species in the microsite analyses at the break between abundant and rare ant groups, thereby excluding all rare ant groups with relatively low relative abundances. For example, the cutoff between abundant and rare invertebrate groups for microsites in NC was 84 because counts of invertebrate captures dropped from 84 to 20 at that point on the plot. Following the same procedure, we also binned counts of all ants into three groups [e.g., RIFA, other non-native ants (i.e., all non-native, non-RIFA ants), and native ants] for stand-scale analyses. Within our system, we defined invasive ants as non-native ants with known noxious ecological effects and non-invasive ants as non-native ants with minimal, known detrimental ecological effects (*see* Table SI.1 for designations).

2.3. Quantifying stand-scale and microsite habitat characteristics

We measured scattered and piled coarse woody debris in each treatment at the NC and GA blocks using the line-intersect sampling technique (Van Wagner, 1968) and a visual encounter method (Fritts et al., 2014). For the visual encounter method in NC, we located each pile of coarse woody debris 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 width and height and visually estimated packing ratio every 50 m along each windrow and at each spot-pile. Because windrows often ran the entire length of treatments, we measured length of each windrow in ArcGIS using post-harvest aerial imagery (Google Maps, Mountain View, California). For both states, we summed volume of piled coarse woody debris estimated from the visual encounter method and volume of scattered coarse woody debris estimated using the line-intersect sampling method to generate total volume of coarse woody debris (m^3 ha^{-1}) for each treatment plot. Volume and spatial distribution of coarse woody debris in treatment plots in NC was shown to accurately match that of our original experimental design. Fritts et al., (2014) calculated the following volumes of harvest residues in each treatment in NC: INTREM = 20.65 ± 1.45; 15DISP = 40.80 ± 13.11; 15CLUS = 37.76 ± 9.42; 30DISP = 55.75 ± 12.49; 30CLUS = 55.17 ± 12.49; NOREM = 108.20 ± 20.05. Efficacy of treatment implementation in GA was less clear because windrowing altered spatial arrangement of coarse woody debris from that in the original experimental design.

We visually estimated decay class of hardwood piles, pine piles, and windrows following Forest Inventory and Analysis protocols (USDA, 2007). Hardwood and pine piles and windrows ranked as Decay Class 2 in 2012 and Decay Class 3 in 2013 [*see* Forest Inventory and Analysis protocol for definitions; USDA (2007)], indicating increased decay through time. In NC and GA, July 2012 and 2013, we quantified microsite groundcover 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 estimated percent groundcover (total = 100%) for the following categories: (1) bare ground, (2) fine woody debris, and (3) vegetation (included all living grasses, forbs, and woody shrubs and vines).

2.4. Statistical framework and analysis

We conducted Poisson generalized linear models (GLMs) with counts of individual ant genera or species as dependent variables to test response of the ant community to coarse woody debris manipulations in young plantations at the stand-scale and at microstes in NC and GA (*see* Grodsky et al., 2018). 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 quasi-poisson GLMs when we detected overdispersion. To account for variation in trapping effort within each state, we also included average number of active traps per treatment plot and average number of active traps per array as an additive effect (*sensu* relative abundance) in all stand-scale and microsite models, respectively, for NC and GA. For categorical covariates in all stand-scale and microsite models, we performed *post hoc* Tukey's pairwise comparisons of means using general linear hypothesis testing (glht function; single-step method) in the R package "multcomp" (Hothorn et al., 2013). We set $\alpha = 0.05$.

2.4.1. Stand-scale models

We used treatment plot as the experimental unit and number of captures of RIFA, other non-native ants, and native ants pooled over all arrays at each treatment plot in each state as dependent variables. In NC, the "Other non-native ants" category was comprised of Argentine ant (*Linepithema humile*), Asian needle ant, and pavement ant (*Tetramorium* cf. *caespitum*). In GA, the "Other non-native ants" category was only comprised of Argentine ant and Asian needle ant. We first included a treatment × year interaction term, treatment, year, block, and effort 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, block, and effort as explanatory variables. Otherwise, we included treatment, year, block, and effort as explanatory variables. For other non-native ant and native ant models, we also included count of RIFAs as a continuous, fixed effect to determine effects of RIFA abundance on these ant groups in young plantations. For GA sites, we replaced the categorical, fixed effect for treatment with volume (m^3 ha^{-1}) of harvest residues in windrows in each treatment (*see* Quantifying large- and local-scale habitat characteristics) and first tested for harvest residue volume × year interactions following the same procedure outlined for NC.

2.4.2. Microsite models

We used each array as the experimental unit in NC (n = 68) and GA (n = 48) and number of captures of each ant genus or species in each state as dependent variables. We first included percent groundcover of fine woody debris and vegetation and effort as continuous explanatory variables, and year, location, and a location × year interaction term as explanatory variables in each model. If we detected a significant location × year interaction, we consequently developed a model for each year separately and included location, groundcover of fine woody debris and vegetation, and effort as explanatory variables. Otherwise, we included location, groundcover of fine woody debris and vegetation, year, and effort as explanatory variables. For both NC and GA, bare ground was inversely correlated with vegetation groundcover and consequently was excluded as a covariate in all microsite models.

3. Results

We captured 22,241 individual ants of 27 genera (Table SI.1). We identified three invasive ant species (Argentine ant, Asian needle ant, RIFA) and two non-invasive, non-native ants to species [pavement ant; rimose fungus ant (*Cyphomyrmex rimosus*)]. Although non-native ants only represented 19% (5 species) of ant taxa richness, the group comprised 94% (21,180) of the 22,241 total ant captures. In order of decreasing abundance, total non-native ant captures were comprised of RIFA (18,721; 88%), Asian needle ant (1541, 7%), Argentine ant (637; 3%), rimose fungus ant (182, < 1%), and pavement ant (99, < 1%). We identified six native ants to species and the remaining 16 native ants to genus (Table SI.1).

3.1. Stand-scale models

In NC, relative abundance of RIFA did not differ among treatments. Relative abundance of other non-native ants was greater in NOREM and 30DISP than INTREM, and relative abundance of native ants was greater in NOREM and 30CLUS than INTREM (Fig. 3; Table SI.2). Relative abundance of other non-native ants decreased with increasing relative abundance of RIFA, and relative abundance of all ant groups increased from 2012 to 2013 (Fig. 3; Table SI.3). In GA, each ant group was unaffected by volume of coarse woody debris in clearcuts, and other non-native ant and native ant relative abundance increased with increasing relative abundance of fire ants (Table SI.3).

3.2. Microsite models

In NC, relative abundance of Asian needle ant was greater in hardwood pile and pine pile locations than no pile locations, whereas RIFA relative abundance was unaffected by locations (Fig. 4a and b, respectively). Relative abundances of pavement ant and the native ant genus *Nylanderia* were greater in hardwood pile locations than no pile locations in 2012 and 2013, respectively (Table 1). Relative abundance of Asian needle ant decreased with increasing vegetation groundcover. In 2012, relative abundance of pavement ant increased with increasing vegetation groundcover. In 2013, relative abundance of the native ant genus *Nylanderia* decreased with increasing fine woody debris groundcover.

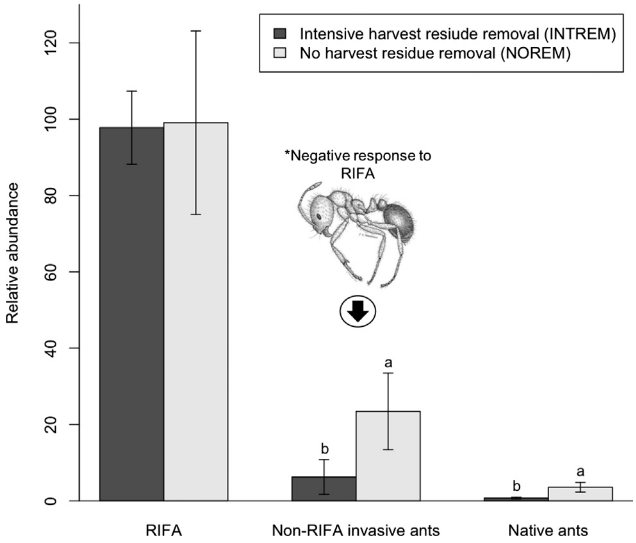

Fig. 3. Response of red imported fire ant ("RIFA"), non-RIFA invasive ants, and native ants to intensive harvest residue removal (INTREM) and no harvest residue removal (NOREM) treatments in young plantations, North Carolina (2012 and 2013 combined). Relative abundance represents count/average number of active traps per treatment unit. Different letters indicate significantly different, pair-wise comparisons of treatment means. We set α = 0.05. Error bars = SE. Fire ant drawing by Joe MacGown (used with permission). See SI.Table 1 for ant taxa group assignments.

During the month of August in GA, relative abundance of Asian needle ant was unaffected by location, whereas RIFA relative abundance was greater in the no windrow location than the windrow location in 2012 and was unaffected by location in 2013 (Table 2; Fig. 4c and d, respectively). Relative abundance of rimose fungus ant was greater in windrow locations than no windrow locations. In 2013, relative abundance of the native ant genus *Dorymyrmex* was greater in windrow locations than no windrow locations and decreased with increasing vegetation groundcover (Table 2).

4. Discussion

Non-native and native ants demonstrated variable stand-scale and microsite relationships with harvest residues in young plantations, which may indicate that coarse woody debris availability worked in conjunction with forest disturbance to shape ant distribution and community structure in regenerating forests following forest bioenergy harvests. RIFA – a notorious invasive species around the world – dominated the ant community following clearcuts, supporting the notion that the species frequently colonizes young, disturbed plantations (Callcott and Collins, 1996; Zettler et al., 2004). Yet, RIFA also negatively responded to harvest residue retention in GA, where the dichotomy between coarse woody debris and other habitat conditions (e.g., bare ground) was most apparent, and at least showed an indifference to coarse woody debris in NC. Contrary to the more abundant RIFA, other non-native ants and native ants as groups exhibited positive relationships with coarse woody debris in young plantations. Most studies of Asian needle ant have focused on its invasion of mature, deciduous forests (e.g., Guénard and Dunn, 2010; Warren et al., 2015) or disturbed, urban environments (e.g., Rice and Silverman, 2013). We documented that Asian needle ant also invades recently harvested pine forests, especially in areas with retained coarse woody debris. Dual invasions of RIFA and Asian needle ant in young plantations of the

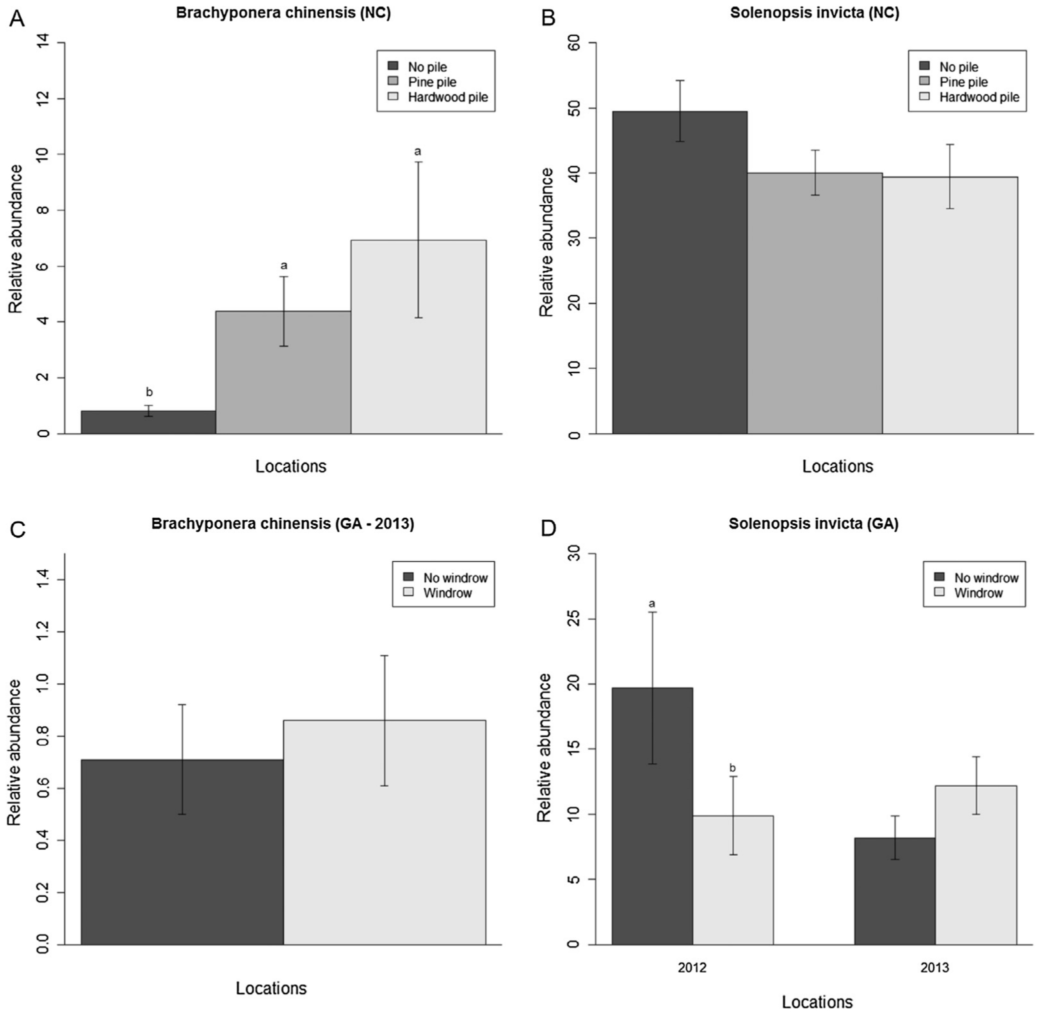

Fig. 4. Response of Asian needle ant (*Brachyponera chinensis*) and red imported fire ant (*Solenopsis invicta*) to coarse woody debris availability in young plantations in North Carolina (NC) and Georgia (GA) – (2012 and 2013 combined unless otherwise noted). We tested species' response to no pile, pine pile, and hardwood pile locations in NC (A and B, respectively) and response to no windrow and windrow locations in GA (C and D, respectively). Relative abundance represents count/average number of active traps per array. Different letters indicate significantly different, pair-wise comparisons of treatment means. Error bars = SE. We set α = 0.05.

Table 1

Mean (SE) relative abundance (count/average number of active traps per array) and response to groundcover of ant taxa captured at 68 pitfall trap arrays situated amongst no pile, pine pile, and hardwood pile locations following woody biomass harvesting in young forests ($n = 4$), North Carolina, pooled among 2012 and 2013. Only taxa meeting cutoff requirements were included in analyses. ϒ indicates significant increase in relative abundance from 2012 to 2013. Different letters indicate significantly different, pair-wise comparisons of location means. + or − indicates positive or negative response, respectively. Ø indicates no response. We set α = 0.05.

		Location [mean (SE)]			Percent groundcover	
Ant genera/species	# of captures	No pile	Pine pile	Hardwood pile	Fine woody debris	Vegetation
Non-native ants						
B. chinensis ϒ	1431	0.80^{b} (0.20)	4.38^{a} (1.24)	6.94^{a} (2.79)	Ø	−
L. humile (2013)	612	2.64 (1.02)	4.52 (1.94)	2.89 (1.12)	Ø	Ø
S. invicta ϒ	16,172	49.52 (4.70)	40.04 (3.49)	39.45 (4.92)	Ø	Ø
T. caespitum (2012)	97	0.63^{b} (0.26)	1.71^{ab} (0.53)	2.05^{a} (0.68)	Ø	+
Native ants						
Aphaenogaster (2013)	36	0.21 (0.15)	0.25 (0.09)	0.09 (0.05)	Ø	Ø
H. opacior (2013)	101	0.60^{ab} (0.10)	0.30^{b} (0.09)	0.78^{a} (0.17)	Ø	Ø
Nylanderia (2013)	83	0.44^{b} (0.15)	0.31^{ab} (0.11)	0.58^{a} (0.21)	−	Ø

eastern United States may commonly occur because the two species may not compete for resources on the forest floor.

Coarse woody debris retention may indirectly diminish deleterious effects of RIFA on biodiversity in young plantations. We determined that RIFA avoided high concentrations of coarse woody debris in young plantations of the southeastern United States. Todd et al. (2008) also implemented large-scale manipulations of coarse woody debris in clearcuts in South Carolina, USA and determined that RIFA was more abundant in stands with coarse woody debris removed than in those with coarse woody debris retained. Many imperiled, early-successional vertebrates that exhibit demonstrable behavioral and spatial associations with coarse woody debris are negatively affected by RIFA

Table 2
Mean (SE) relative abundance (count/average number of active traps per array) and response to groundcover of ant taxa captured at 48 pitfall trap arrays situated amongst no windrow and windrow locations following woody biomass harvesting in young forests ($n = 4$), Georgia, pooled among 2012 and 2013. Only taxa meeting cutoff requirements were included in analyses. ζ indicates significant year X treatment interaction, in which case years were analyzed separately. Different letters indicate significantly different, pair-wise comparisons of location means. + or − indicates positive or negative response, respectively. Ø indicates no response. We set $\alpha = 0.05$.

			Location [mean (SE)]		Percent groundcover	
Ants genera/species		# of captures	No windrow	Windrow	Fine woody debris	Vegetation
Invasive ants						
B. chinensis (2013)		110	0.71 (0.21)	0.86 (0.25)	Ø	Ø
S. invicta ζ						
	2012	1117	19.69^{a} (5.84)	9.88^{b} (3.00)	Ø	Ø
	2013	1432	8.19 (1.67)	12.20 (2.19)	Ø	Ø
Native ants						
Cyphomyrmex		182	0.49^{b} (0.14)	1.02^{a} (0.19)	Ø	+
Dorymyrmex ζ						
	2012	52	0.94 (0.67)	0.37 (0.25)	Ø	Ø
	2013	134	0.18^{b} (0.06)	1.75^{a} (1.01)	−	Ø
Nylanderia (2013)		236	1.49 (0.42)	1.87 (0.34)	+	Ø
Pheidole (2013)		149	0.96 (0.22)	1.16 (0.21)	Ø	Ø

(Litvaitus, 1993; Lanham and Guynn, 1996; Wojcik et al., 2001; Allen et al., 2004). Reduced presence of RIFA in areas supporting high volumes of coarse woody debris could benefit early-successional vertebrates, including amphibians, reptiles, and ground-nesting birds, and invertebrates (e.g., other ant species) co-occurring in those same areas and competing for food, cover, and nesting sites (Allen et al., 1995; Fritts et al., 2015; Fritts et al., 2016; Grodsky et al., 2015; Grodsky, 2016). Although increased harvest residue retention may inhibit RIFA colonization, it may facilitate Asian needle ant invasions; Asian needle ant may outcompete some downed-wood associated taxa for resources, especially other invertebrates.

The Asian needle ant may outcompete native ants for dead-wood nesting sites and prey, potentially leading to displacement of some species (e.g., *Aphaenogaster rudis* – Warren et al., 2015). We documented co-occurrence of Asian needle ant and several native ants that also nest in dead wood, including *Hypoponera opacior* and ants in the genus *Aphaenogaster*. Therefore, native ants were not fully displaced by Asian needle ant at microsites around coarse woody debris during the timespan of our study. However, Asian needle ant may have indirectly affected population densities of downed-wood associated native ants in the young plantations we studied. The positive association between Asian needle ant and coarse woody debris piles and negative response of the species to microsite vegetation cover likely were driven, in part, by availability of nesting sites and termite prey exclusively provided by coarse woody debris in young plantations. Asian needle ant is a voracious predator of termites (Bednar et al., 2011; Bednar et al., 2013); termites are downed-wood obligates, important ecosystem engineers, and prey for many vertebrates (Jones et al., 1994). Additionally, Asian needle ant may disrupt ant-seed dispersal mutualisms in forests because it is a less efficient seed disperser than the native, seed-dispersing ants it displaces (Rodriquez-Cabal et al., 2012; Warren et al., 2015).

Managed forests often support lower native ant diversity than unmanaged forests, thus differences in abundances between native and non-native ants may be related to factors other than competition for resources, including colonization and recruitment (King and Tschinkel, 2006). Zettler et al. (2004) determined that RIFA abundance in harvested forests of the southeastern United States increased following clearcutting; whereas, native ant abundances significantly decreased following clearcutting. Some studies suggest that RIFA does not competitively suppress co-occurring native ants in disturbed areas (Morrison, 2002; King and Tschinkel, 2006). Therefore, greater abundance of RIFA relative to abundances of all other ants in our study may be attributable to RIFA's ability to rapidly colonize clearcuts, rather than outcompete other ants for resources in young plantations. On the other hand, other non-native ant abundance decreased with increasing RIFA abundance in NC, suggesting that the RIFA may have suppressed other non-native ant populations in these young plantations.

In addition to biological factors affecting ant colonization of young plantations, non-native ant invasions may also be linked to site preparation practices used in intensively managed forests. Despite reduced sampling effort in GA relative to NC, we documented some clear differences in ant response to shearing (NC) versus windrowing (GA). RIFA strongly avoided coarse woody debris condensed into large windrows and instead colonized expanses of bare ground between windrows in GA. Meanwhile, RIFA was unaffected by coarse woody debris availability after shearing in NC. Both coarse and fine woody debris were widely distributed in the NC stands, thus bare ground nesting sites for RIFA were patchily distributed throughout young plantations rather than centralized in swaths between windrows as in GA. On the other hand, Asian needle ant positively responded to coarse woody debris retention after shearing in NC, but was unaffected by coarse woody debris availability in windrows. Asian needle ant was far more abundant in NC than GA, potentially indicating that windrowing deterred colonization of young plantations by this invasive species. However, differences in Asian needle ant abundance between states may also have been a function of the regional abundance and distribution of the species, which is not well-known.

Increased market viability of harvest residues as a forest bioenergy feedstock may intensify coarse woody debris removal, particularly in intensively managed forests (Riffell et al., 2011). Concerns regarding potential ecological effects of woody biomass harvesting have led to development of non-regulatory biomass harvesting guidelines for wood-basket regions, including the southeastern United States; these guidelines identified target coarse woody debris retention percentages in young plantations that would potentially promote biodiversity (Perschel et al., 2012). Our results indicate that downed-wood associated ants largely were unaffected by stand-scale, coarse woody debris manipulations that emulated percent (i.e., 15 vs. 30%) and distribution (i.e., clustered vs. dispersed) prescriptions of preexisting biomass harvesting guidelines. Further, ants did not preferentially use harvest residues comprised of hardwood more than pine or vice versa. Therefore, deciphering between hardwood or coniferous bioenergy feedstock during woody biomass harvests in young plantations may be unnecessary in relation to ant conservation in regenerating stands. However, we demonstrated that downed-wood associated ants negatively responded to intensive coarse woody debris removal at stand-scales and microsites. As such, intensified woody biomass harvesting likely will negatively affect non-RIFA ant species and potentially promote RIFA colonization.

5. Conclusion

Coarse woody debris retention favored non-RIFA ants, including the invasive Asian needle ant and several native ants. Although RIFA may negatively respond to coarse woody debris retention, this invasive species is likely to remain the dominant ant species following clearcuts regardless of harvest residue availability because of its capacity to exploit disturbance in forests. Studies spanning further along the timeline of pine tree maturation and changing plantation forest structure following timber harvests could shed new light on the interplay between coarse woody debris availability and interactions between non-native and native ants. However, our study directly addressed ant response to coarse woody debris removal during the time period that harvest residues are most often gleaned for forest bioenergy, and ant community composition is likely to shift as dead wood rapidly decays and pine trees mature, ultimately leading to canopy-closure (e.g., Punttila et al., 1991).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.02.010.

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