

Colonization Dynamics of Subcortical Insects on Forest Sites With Relatively Stressed and Unstressed Loblolly Pine Trees

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Abstract

Loblolly pine (*Pinus taeda* L.) is the most important commercial tree species in the southeastern United States. Since the 1950s, there have been reports of loblolly pines showing reduced growth and increased mortality, particularly in central Alabama and western Georgia, United States; the phenomenon is termed as southern pine decline (SPD). Recently, the role of rhizophagous (root-feeding) insects in loblolly pine health within the context of SPD has come under greater scrutiny. We investigated the impacts of subcortical insects, particularly rhizophagous weevils (Coleoptera: Curculionidae), on loblolly pine health in northeastern Georgia. We created plots—representing a gradient of increased relative tree stress—from ungirdled trees, ungirdled trees baited with ethanol and turpentine (ungirdled-baited), and girdled trees. In total, 10,795 subcortical insects from four families (Buprestidae, Cerambycidae, Curculionidae, and Siricidae) and >82 species were trapped in two years. Almost half of the insects trapped (46% of individuals and 11% of species) were nonnative to North America. Insect captures in plots with girdled trees were 61 and 187% greater than those with ungirdled-baited and ungirdled trees, respectively. Tree treatment impacted captures of native, but not nonnative insects. Relative feeding area by the rhizophagous weevils *Hylobius pales* (Herbst) and *Pachylobius picivorus* (Germar) on pine twigs placed in pitfall traps was 1, 17, and 82% in plots with ungirdled, ungirdled-baited, and girdled trees, respectively. Hence, there was a strong association of native subcortical insects, especially rhizophagous weevils, with relatively highly stressed trees, confirming that they are secondary instead of primary pine colonizers.

Abstract

Die Weihrauch-Kiefer (*Pinus taeda* L.) ist die wirtschaftlich wichtigste Baumart im Südosten der USA. Bereits seit den 1950er Jahren zeigen sich jedoch in den Beständen vermehrt Zuwachseinbußen sowie eine zunehmende Mortalität der Bäume. Um zu untersuchen, welche Rolle holz- und rindenbrütende Insekten, insbesondere rhizophage Rüsselkäferarten (Coleoptera: Curculionidae), dabei spielen, wurden in undurchforsteten Jungbeständen im Norden des Bundesstaats Georgia Freilandversuche in Versuchsblöcken mit ungeschädigten Kontrollbäumen, mit Ethanol und Terpentin beköderten Bäumen sowie mit geringelten Bäumen durchgeführt. Die Versuchsvarianten repräsentieren dabei eine Zunahme des Stressgradienten der Bäume. In zwei Jahren wurden 10.795 holz- und rindenbrütende Insekten aus vier Familien (Buprestidae, Cerambycidae, Curculionidae, Siricidae) und mindestens 82 Arten gefangen. Fast die Hälfte der gefangenen Insekten und 11 % der Arten zählen nicht zur einheimischen Fauna Nordamerikas. Insgesamt wurden in Blöcken mit geringelten Bäumen 61 % mehr Insekten als in Blöcken mit beköderten Bäumen und 187 % mehr Insekten als in Blöcken mit ungeschädigten Kontrollbäumen gefangen. Der Gesundheitszustand der Bäume hatte signifikante Auswirkungen auf die Fangergebnisse einheimischer Arten, jedoch keine Auswirkungen auf nichteinheimische Arten. Von dem durch die rhizophagen Arten *Hylobius pales* (Herbst) und *Pachylobius picivorus* (Germar) verursachten Rindenfraß an Kiefernästen in Bodenfallen wurden 1 % in Blöcken mit ungeschädigten Kontrollbäumen, 17 % in Blöcken mit beköderten Bäumen und 82 % in Blöcken mit geringelten Bäumen aufgenommen. Es kann geschlossen werden, dass in Nordamerika heimische holz- und

rindenbrütende Insekten, insbesondere rhizophage Rüsselkäferarten, stark an hochgradig gestresste Bäume gebunden sind und als sekundäre und nicht als primäre Schadorganismen an Kiefern auftreten.

Key words: Curculionidae, pine decline, *Pinus taeda*, rhizophagous beetle, Scolytinae

Known as the “wood basket of the world,” forests in the southern United States annually generate ~60% of the Nation’s and 16% of the world’s timber resources (Wear and Greis 2002, Smith et al. 2009). Although this region represents only 2% of the global forest cover, it produces more timber than any other country in the world (Wear and Greis 2002, Hanson et al. 2010). As such, forestry is a major economic factor in the southern United States, and in 2011 alone contributed >1 million jobs and US\$53 billion of labor income to the region’s economy (Brandeis and Hodges 2015).

Pines (*Pinus* spp.) are among the most common as well as economically and ecologically important tree species in the southern United States, occupying 34% of the forested area (Wear and Greis 2012). More than half of the pine forests are composed of planted stands. In 2010, planted pine comprised 19%, or ~16 million ha, of southern forests (Huggett et al. 2013). It is estimated that by year 2060, planted pine will comprise about 24–36% of the total forest area in this region (Huggett et al. 2013). Among the major southern pine species, loblolly pine (*Pinus taeda* L.) is the most economically important, accounting for half the volume of southern pine growing stock (Schultz 1997). Although originally confined to moist fringes of the Coastal Plain and Piedmont physiographic regions, the ability of loblolly pine to regenerate and grow rapidly on diverse sites along with its versatile uses has made it the most important commercial tree species in southern forests (Schultz 1997). There are an estimated 13.6 million ha of loblolly pines (Dickens et al. 2003), which has largely replaced longleaf pine (*Pinus palustris* Mill.) in planted areas (U.S. Department of Agriculture [USDA] 2012).

Southern pine forests harbor many insect species of aboveground herbivores feeding on needles (foliophagous), bark (cambiofagous), and wood (xylophagous), as well as belowground herbivores feeding on structural roots and stem collars (rhizophagous). The most important aboveground herbivores in southern pine forests are bark and woodboring insects, including jewel beetles (Buprestidae), longhorn beetles (Cerambycidae), woodwasps (Siricidae), and bark and ambrosia beetles (Curculionidae: Scolytinae). In particular, bark beetle outbreaks can lead to severe damage in forest stands and extensive economic losses, and are therefore considered the most serious forest insect pests worldwide (Wood 1982, Kurz et al. 2008, Pye et al. 2011). However, amongst thousands of subcortical insect species, only a few (e.g., mountain pine beetle, *Dendroctonus ponderosae* Hopkins, or southern pine beetle, *Dendroctonus frontalis* Zimmermann) can cause major tree damage on a landscape scale.

The first reports on health issues in southern pine stands originated from the Piedmont region of Alabama and date back to the 1950s, with symptoms being described as yellowing and shortening of needles, thinning crowns, and increased tree mortality (Brown and McDowell 1968, Roth and Peacher 1971). These issues continue to be reported and have garnered more concern during the past few decades (Eckhardt et al. 2007, 2010; Menard et al. 2010). Collectively, these symptoms have been known as “southern pine decline” (SPD) (Zeng et al. 2014). There is still considerable debate on the suitability of these terms, as well as on the causal agents (see Coyle et al. 2015a). However, in general, it is agreed that the interactions of several biotic and abiotic factors, such as climate, land-use history, and current management, are having at least localized

effects on pine health (Eckhardt et al. 2007, 2010; Eckhardt and Menard 2008; Coyle et al. 2015a).

Rhizophagous beetles and the fungi that they carry have been suggested to be associated with SPD (Eckhardt et al. 2007, Zanzot et al. 2010). Several rhizophagous beetle species occur in the pine ecosystems of the southern United States: native species such as *Dendroctonus terebrans* (Olivier), *Hylastes porculus* Erichson, *Hylastes salebrosus* Eichhoff, *Hylastes tenuis* Eichhoff, *Hylobius pales* (Herbst), *Pachylobius picivorus* (Germar), and *Pissodes nemorensis* Germar, as well as the nonnative species, *Hylastes opacus* Erichson. While mass attacks by *D. terebrans* can occasionally kill healthy mature trees (Drooz 1985, Staeben et al. 2010), *Hylastes*, *Hylobius*, and *Pachylobius* species primarily attack the lower bole or roots of weakened, stressed, dying, or dead trees (Matusick et al. 2013), and mostly breed in stumps or logs (Warner 1966, Wood 1982, Drooz 1985, Nord et al. 1997). Hence, most of these species are considered secondary colonizers of trees (Hunt and Raffa 1989, Phillips 1990, Hoffmann et al. 1997, Sullivan et al. 2003, Matusick et al. 2013).

Pine-infesting rhizophagous beetles transmit ophiostomatoid fungi (e.g., *Leptographium* and *Grossmannia* spp.), commonly referred to as blue stain fungi (Nevill and Alexander 1992, Zanzot et al. 2010, Jankowiak 2013), which are associated with several tree disease complexes (Klepzig et al. 1991, Erbilgin and Raffa 2002, Eckhardt et al. 2007, Ploetz et al. 2013). One example is in the Great Lakes Region, where red pine (*Pinus resinosa* Aiton) is experiencing a syndrome known as “red pine pocket decline” that is initiated by native rhizophagous weevils and their fungal symbionts (Klepzig et al. 1991, Erbilgin and Raffa 2003, Aukema et al. 2010). The stress resulting from the infection with this insect–fungal complex does not typically kill mature red pine trees but impairs their defenses against lethal stem-colonizing bark beetle–fungal complexes (Klepzig et al. 1996, Zhu et al. 2008). Little is known about similar roles of rhizophagous weevils in the southern United States; this issue merits investigation especially under the umbrella of SPD.

To gain a better understanding of the ecological role of rhizophagous weevils, as well as other subcortical insects in the context of relative loblolly pine health, we tested the attractiveness of loblolly pine in different health stages to bark and woodboring insect communities. We hypothesized that native and nonnative subcortical insects would be most attracted to dying trees, somewhat attracted to trees baited with common chemical lures, and least attracted to healthy trees.

Materials and Methods

Study Sites

Three trials were conducted during 2012–2013 in unthinned loblolly pine sites in Jackson County, GA. Sites were located in the Southern Outer Piedmont in the Piedmont ecoregion (Griffith et al. 2001), with typical weather consisting of long, hot summers and short, mild winters. Soils consist of deep saprolite and mostly red, clayey subsoils (Georgia Department of Natural Resources [GDNR] 2001). Loblolly pine is the dominant conifer species in this region. The

Table 1. Selected forest attributes in three 18- to 21-yr-old loblolly pine-dominated sites in 2012–2013 in northeastern Georgia, United States.

Trial	Tree type	Stems ha ⁻¹	Basal area (m ² ha ⁻¹)	Mean ± SE DBH (cm)
(I) Fall 2012	Pine	1,061.0 ± 104.5	41.2 ± 2.1	21.5 ± 0.8
	Dead pine	275.9 ± 94.3	1.0 ± 0.6	6.4 ± 1.1
	Hardwood	201.6 ± 69.6	0.9 ± 0.2	6.4 ± 1.1
	Dead hardwood	137.9 ± 74.3	0.5 ± 0.4	5.6 ± 1.6
(II) Spring 2013	Pine	1,931.1 ± 403.6	39.3 ± 4.6	15.4 ± 0.8
	Dead pine	180.4 ± 59.1	0.7 ± 0.4	6.6 ± 0.4
	Hardwood	753.3 ± 104.5	3.1 ± 0.5	6.1 ± 0.4
	Dead hardwood	21.2 ± 21.2	0.1 ± 0.1	6.4 ± 1.4
(III) Fall 2013	Pine	817.0 ± 42.4	35.6 ± 2.6	22.9 ± 0.4
	Dead pine	519.9 ± 130.4	3.7 ± 1.9	16.5 ± 1.0
	Hardwood	53.1 ± 10.6	1.4 ± 1.0	7.9 ± 0.9
	Dead hardwood	95.5 ± 66.3	1.6 ± 1.2	13.5 ± 1.2

study sites in 2012 and 2013 were 21 and 18 yr old, respectively, and had not been thinned. All trees were planted at 2- by 3-m spacing, which is standard for this region. We visually divided each stand into three sections, each approximately equal in area. We established a 10-m-radius circular plot at the approximate center of each stand section. We recorded DBH (diameter at breast height; 1.37 m) of all trees >2.5 cm in diameter, as well as whether they were hardwood, pine, dead hardwood, or dead pine. Stand-level metrics were calculated from these measurements. Live pine basal area ranged from 35.6 m²ha⁻¹ (155.0 ft²ac⁻¹) to 41.2 m²ha⁻¹ (179.3 ft²ac⁻¹; Table 1). These sites are considered to be at high risk for insect outbreaks, especially southern pine beetle due to high basal density (Nowak et al. 2008, 2015). Understories consist mainly of hardwoods such as sweetgum (*Liquidambar styraciflua* L.), tulip poplar (*Liriodendron tulipifera* L.), black cherry (*Prunus serotina* Ehrhart), and various oak (*Quercus*) species.

Experimental Design

We established seven replicate plots for each of three treatments in each trial ($N=21$ per trial). Treatments were randomly assigned to each plot and included: 1) un-girdled unbaited trees (un-girdled), 2) un-girdled trees baited with ethanol and turpentine (un-girdled-baited), and 3) girdled unbaited trees (girdled). Each plot consisted of four loblolly pine trees arranged in a rectangle. Plots were >25 m from each other, and >10 m from the edge of the site. We chose apparently healthy loblolly pines with no visible damage by abiotic or biotic factors. For baited plots in 2012, two six-dram screw cap vials (BioQuip Products, Rancho Dominguez, CA)—one containing ethanol (95% pure, Decon Labs, Inc., King of Prussia, PA) and the other containing turpentine (100% pure, W.M. Barr & Co., Inc., Memphis, TN) were attached to insect traps within the plot. Ethanol and turpentine are plant volatile organic compounds naturally emitted by pine trees, and are important olfactory cues for host location of many pine-infesting insects (Fatzinger 1985, Hunt and Raffa 1989, Byers 1992). As emission levels of ethanol rise with increasing plant stress (Kimmerer and Kozlowski 1982), the baited treatment served to mimic a stressed tree. A hole was drilled into the vial cap, and an 8-cm-long piece of chenille stem was inserted to act as a wick to facilitate fluid emission. Semipermeable plastic vials (20 ml, Contech Inc., Victoria, British Columbia, Canada) were used in 2013 trials. The vials were replaced about every two weeks. For girdled tree plots, pines were girdled by cutting twice around the outside of the trunk at approximately DBH using a chainsaw. Glyphosate (Foresters, 53.8% AI, Nufarm Americas Inc., Burr

Table 2. Timing of experiments in 18- to 21-yr-old loblolly pine-dominated sites in 2012–2013 in northeastern Georgia, United States

Trial	Trees baited or girdled	Insect sampling
I	9 July 2012	20 July–1 Nov. 2012
II	24 April 2013	6 May–23 July 2013
III	13 Aug. 2013	23 Aug.–5 Nov. 2013

Ridge, IL) was then applied to the wound via hand sprayer to accelerate tree death.

Three types of insect traps were used to monitor aboveground and belowground subcortical insects in each plot. A 12-unit Lindgren funnel trap (main stem trap) was hung in the center of the plot. Bread pan traps (lower stem trap), which consisted of an aluminum loaf pan (21.6 by 11.4 by 6.4 cm³) with a piece of clear plexiglass pane (25.4 by 38.1 cm²) and roof (15.3 by 30.5 cm²) attached to one side, were attached to the trunk base about 40 cm above the soil line of two of four trees per plot. Propylene glycol (Prestone Products Corp., Danbury, CT) was used as trapping liquid in main stem and lower stem traps. At the base of each of the four loblolly pines, a pitfall trap (root-zone trap) was installed in the soil to capture rhizophagous beetles (Rieske and Raffa 1990, Zanzot et al. 2010). Two fresh loblolly pine bait sticks (~12 cm long by 1 cm diameter) were placed into each trap and replaced after each sampling period.

Adult insect sampling took place approximately every two weeks in 2012 and 2013 (Table 2). About two weeks prior to the start of the sampling, baits were installed on trees for the un-girdled-baited treatment, and trees were girdled for the girdled treatment (Table 2). The number of pine sticks with feeding from the root-zone traps was recorded, and the feeding area was independently estimated by two observers using a transparent grid.

Coleoptera (Buprestidae, Cerambycidae, and Curculionidae: Scolytinae) and Hymenoptera (Siricidae) were identified using published keys (Franklin and Lund 1956, Wood 1982, Lingafelter 2007, Schiff et al. 2012). The curculionid subfamilies Cryptorhynchinae, Entiminae, Mesoptiliinae, and Molytinae were identified using reference collections and expert assistance. We used nomenclature from Wood (1982) and Wood and Bright (1992), with updates from Alonso-Zarazaga and Lyal (2009) and Bright (2014), for all Scolytinae identifications. Voucher specimens were deposited in the Georgia Museum of Natural History, University of Georgia, Athens, GA.

Table 3. Subcortical insect species collected during 2012–2013 using main stem, lower stem, and root-zone traps in three 18- to 21-yr-old unthinned loblolly pine sites in northeastern Georgia, United States

Family	Subfamily	Species	Fall 2012 ^a	Spring 2013	Fall 2013	Total numbers
Buprestidae	Buprestinae	<i>Buprestis lineata</i> F.	1	0	0	1
		<i>Buprestis maculipennis</i> Gory	0	1	0	1
		<i>Chrysobothris rotundicollis</i> Gory & Laporte	0	3	0	3
Cerambycidae	Chrysochroinae	<i>Chalcophora virginiensis</i> (Drury)	1	0	0	1
	Cerambycinae	<i>Anelaphus villosus</i> (F.)	0	1	0	1
		<i>Clytus ruricola</i> (Olivier)	0	7	0	7
		<i>Curius dentatus</i> Newman	0	9	12	21
		<i>Cyrtophorus verrucosus</i> (Olivier)	0	4	0	4
		<i>Elaphidion mucronatum</i> (Say)	0	4	0	4
		<i>Euderces pini</i> (Olivier)	0	1	0	1
		<i>Molorchus bimaculatus bimaculatus</i> Say	0	4	0	4
		<i>Molorchus bimaculatus semiustus</i> (Newman)	0	16	0	16
		<i>Neoclytus acuminatus</i> (F.)	5	11	0	16
		<i>Phymatodes amoenus</i> (Say)	0	1	0	1
		<i>Xylotrechus colonus</i> (F.)	1	12	0	13
		<i>Xylotrechus sagittatus</i> (Germar)	38	88	21	147
		Lamiinae	<i>Acanthocinus nodosus</i> (F.)	3	13	1
<i>Acanthocinus obsoletus</i> (Olivier)	1		42	0	43	
<i>Aegomorphus modestus</i> Gyllenhal	0		1	0	1	
<i>Astylopsis arcuata</i> (LeConte)	0		9	3	12	
<i>Astylopsis sexguttata</i> (Say)	0		1	0	1	
<i>Eupogonius pauper</i> LeConte	0		1	0	1	
<i>Monochamus complex</i> ^b	1		25	4	30	
<i>Psenocerus supernotatus</i> (Say)	0		3	0	3	
<i>Sternidius variegatus</i> (Haldeman)	0		1	0	1	
Lepturinae	<i>Judolia cordifera</i> (Olivier)		0	3	0	3
	<i>Rhagium inquisitor</i> (L.)		0	4	0	4
	<i>Strangalia luteicornis</i> (F.)		0	1	0	1
	<i>Typocerus zebra</i> (Olivier)		0	3	0	3
Spondylidinae	<i>Arhopalus rusticus</i> (L.)	0	1	1	2	
	<i>Asemum striatum</i> (L.)	0	30	0	30	
Prioninae	<i>Orthosoma brunneum</i> (Forster)	0	2	0	2	
	<i>Prionus pocularis</i> Dalman	7	0	0	7	
Curculionidae	Cryptorhynchinae	<i>Cryptorhynchus tristis</i> LeConte	0	0	1	1
	Entiminae	<i>Panscopus impressus</i> Pierce	0	1	1	2
	Mesoptiliinae	<i>Magdalis perforata</i> Horn	0	0	1	1
		<i>Hylobius pales</i> (Herbst)	0	248	46	294
	Molytinae	<i>Pachylobius picivorus</i> (Germar)	0	25	0	25
		<i>Pissodes nemorensis</i> Germar	0	12	22	34
	Scolytinae	<i>Ambrosiodmus rubricollis</i> (Eichhoff) ^c	5	9	2	16
		<i>Carphoborus</i> spp. Eichhoff	0	2	0	2
		<i>Cnestus mutilatus</i> (Blandford) ^c	3	612	0	615
		<i>Corthylus columbianus</i> Hopkins	0	0	1	1
		<i>Crypturgus alutaceus</i> Schwarz	0	95	7	102
		<i>Cyclorhipidion bodoanum</i> (Reitter) ^c	0	15	0	15
		<i>Dendroctonus frontalis</i> Zimmermann	8	18	9	35
<i>Dendroctonus terebrans</i> (Olivier)		42	60	25	127	
<i>Dryoxylon onoharaensis</i> (Murayama) ^c		18	120	1	139	
<i>Euwallacea interjectus</i> (Blandford) ^c		0	20	0	20	
<i>Euwallacea validus</i> (Eichhoff) ^c		28	0	0	28	
<i>Gnathotrichus materiarus</i> (Fitch)		79	271	201	551	
<i>Hylastes porculus</i> Erichson		92	104	55	251	
<i>Hylastes salebrosus</i> Eichhoff		11	69	4	84	
<i>Hylastes tenuis</i> Eichhoff		176	214	33	423	
<i>Hypothenemus</i> spp. ^d		0	2	4	6	
<i>Hypothenemus eruditus</i> Westwood		0	58	4	62	
<i>Hypothenemus pubescens</i> Hopkins	0	65	28	93		
<i>Hypothenemus rotundicollis</i> (Eichhoff)	0	5	0	5		
<i>Hypothenemus seriatus</i> (Eichhoff)	0	31	2	33		
<i>Ips avulsus</i> (Eichhoff)	106	47	3	156		
<i>Ips calligraphus</i> (Germar)	60	120	22	202		
<i>Ips grandicollis</i> (Eichhoff)	15	197	2	214		

(continued)

Table 3. continued

Family	Subfamily	Species	Fall 2012 ^a	Spring 2013	Fall 2013	Total numbers
		<i>Monarthrum fasciatum</i> (Say)	0	4	0	4
		<i>Monarthrum mali</i> (Fitch)	0	23	0	23
		<i>Orthotomicus caelatus</i> (Eichhoff)	30	18	1	49
		<i>Pityophthorus</i> spp. ^d	0	5	1	6
		<i>Pityophthorus confusus bellus</i> Blackman	0	404	19	423
		<i>Pityogenes hopkinsi</i> Swaine	0	1	0	1
		<i>Pityophthorus annectens</i> LeConte	0	59	19	78
		<i>Pityophthorus crinalis</i> Blackman	0	49	3	52
		<i>Pityophthorus lautus</i> Eichhoff	0	24	8	32
		<i>Pityophthorus liquidambarus</i> Blackman	0	25	0	25
		<i>Pityophthorus pulicarius</i> (Zimmermann)	0	46	5	51
		<i>Xyleborinus saxesenii</i> (Ratzeburg) ^c	12	625	34	671
		<i>Xyleborus affinis</i> Eichhoff	13	132	70	215
		<i>Xyleborus ferrugineus</i> (F.)	52	98	108	258
		<i>Xyleborus pubescens</i> Zimmermann	35	876	152	1063
		<i>Xyleborus xylographus</i> (Say)	5	363	32	400
		<i>Xylosandrus crassiusculus</i> (Motschulsky) ^c	222	2825	379	3426
		<i>Xylosandrus germanus</i> (Blandford) ^c	4	36	5	45
Siricidae	Siricinae	<i>Sirex nigricornis</i> F.	21	0	11	32
		<i>Urocerus cressoni</i> Norton	2	0	1	3
	Tremecinae	<i>Xeris tarsalis</i> (Cresson)	2	0	0	2

^a No root-zone trap data available for this trial.

^b Contains *Monochamus carolinensis* (Olivier) and *Monochamus titillator* (F.), as these species are only reliably identified via dissection.

^c Species not native to North America.

^d Species not identifiable due to poor condition or damage.

Statistical Analyses

Data were analyzed using the SPSS Version 15.0 statistical software program (SPSS Inc., Chicago, IL). To account for defective traps and differences in sample periods, feeding area and catch numbers were calculated as $\text{mm}^2 \text{day}^{-1}$ and insects $\text{trap}^{-1} \text{day}^{-1}$, respectively. Unit of replication was individual plot ($n = 7$). Kolmogorov–Smirnov test was used to analyze data for normal distribution and resulted in a rejection of the null hypothesis; log transformed data yielded similar results. To determine the treatment effects, data were then evaluated using the nonparametric Kruskal–Wallis one-way analysis of variance, with Mann–Whitney U test serving as post hoc test. For all tests, statistical significance was set at $P = 0.05$.

For analyzing insect captures, we grouped the insects according to their guilds into aboveground Curculionidae (Cryptorhynchinae, Entiminae, Mesoptiliinae, and Scolytinae except for *D. terebrans* and *Hylastes* spp.), belowground Curculionidae (Molytinae and Scolytinae: *D. terebrans* and *Hylastes* spp.), and woodborers (Buprestidae, Cerambycidae, and Siricidae). The effects of treatment on insect groups were analyzed separately for trials (I–III) and trap types (lower and main stem traps). The use of root-zone traps in 2013 was aimed at monitoring rhizophagous weevils by analyzing their feeding on pine stick baits. Root zone captures were included in presented total captures, but no statistical analyses were performed on these data, as insects were allowed to escape from these traps after feeding. Insect captures were analyzed with and without distinguishing between native and nonnative insect species.

Results

We caught 10,795 forest insects including 10,357 Curculionidae, 395 Cerambycidae, 37 Siricidae, and 6 Buprestidae (Table 3). We most commonly captured aboveground Curculionidae (85%) followed by belowground Curculionidae (11%) and woodborers (4%). The three

most abundant species were aboveground Curculionidae including *Xylosandrus crassiusculus* (Motschulsky), *Xyleborus pubescens* Zimmermann, and *Xyleborinus saxesenii* (Ratzeburg) (all nonnative Scolytinae). Among belowground Curculionidae, the scolytines *H. tenuis* and *H. salebrosus*, and the molytine weevil *H. pales*, were caught in highest numbers. The most commonly caught woodborers were *Xylotrechus sagittatus* (Germar), *Acanthocinus obsoletus* (Olivier), and *Asemum striatum* (L.) (Table 3).

Overall, aboveground Curculionidae catches were 62 and 143% greater, respectively, in plots with ungirdled-baited and girdled trees than with ungirdled trees (Fig. 1; Table 4). There were no differences in aboveground Curculionidae catches in plots with ungirdled-baited and girdled trees except in trial III with 211% greater catches in stem traps in the latter treatment. The two most common species of aboveground Curculionidae, the nonnative *X. crassiusculus* and the native *X. pubescens*, accounted for 38 and 12% of the total capture of this insect guild, respectively.

Five scolytine species each comprised >5% of the total main and lower stem trap captures (Table 5). Two are native species [*X. pubescens*: 10.1%, *Gnathotrichus materiarius* (Fitch): 5.3%] and three are nonnative species [*X. crassiusculus*: 32.7%, *X. saxesenii*: 6.4%, *Cnestus mutilatus* (Blandford): 5.9%]. Catches of *X. pubescens* were greatest in plots with ungirdled-baited trees: 516% greater than in plots with ungirdled trees and 25% greater than in plots with girdled trees. The majority of *G. materiarius* individuals were caught in plots with girdled trees (93%), whereas only 6 and 1% were caught in plots with ungirdled-baited and ungirdled trees, respectively. In contrast, catches of nonnative species that comprised >5% of the total main and lower stem trap captures did not differ among treatments with one exception: catches of *X. crassiusculus* in trial III in plots with girdled trees were 200% greater than catches in plots with ungirdled trees.

Similarly, belowground Curculionidae catches were 515 and 1,456% greater in plots with ungirdled-baited and girdled trees than

with ungirdled trees (Fig. 2; Table 4). In plots with ungirdled-baited trees, belowground Curculionidae catches were 61% lower than in plots with girdled trees. Seven species of this guild were caught in main and lower stem traps: *H. tenuis* (total=410), *H. porculus* (231), *D. terebrans* (122), *H. salebrosus* (79), *H. pales* (43), *P. nemorensis* (30), and *P. picivorus* (16). Averaging 69%, the majority of all species were caught in plots with girdled trees ranging from 55% for *H. tenuis* to 97% for *P. nemorensis*.

In comparison with aboveground (9,133 individuals) and belowground Curculionidae (931 individuals), the number of woodborers caught in main and lower stem traps was low (435) (Fig. 3;

Table 4). Total woodborer catches in plots with girdled trees were 345% greater than those with ungirdled trees. The most common woodborers, *X. sagittatus* and *A. obsoletus*, accounted for 34 and 9%, respectively. Whereas 97% of *X. sagittatus* individuals were caught in plots with ungirdled-baited and girdled trees, all 41 individuals of *A. obsoletus* were caught in plots with girdled trees.

Almost half of the insects caught (46%) are not native to North America, and were mostly captured in the spring 2013 trial. In total, we caught nine nonnative species, all of which were scolytines belonging to the guild of aboveground Curculionidae (Table 4). Numerically dominant nonnative species in the study were

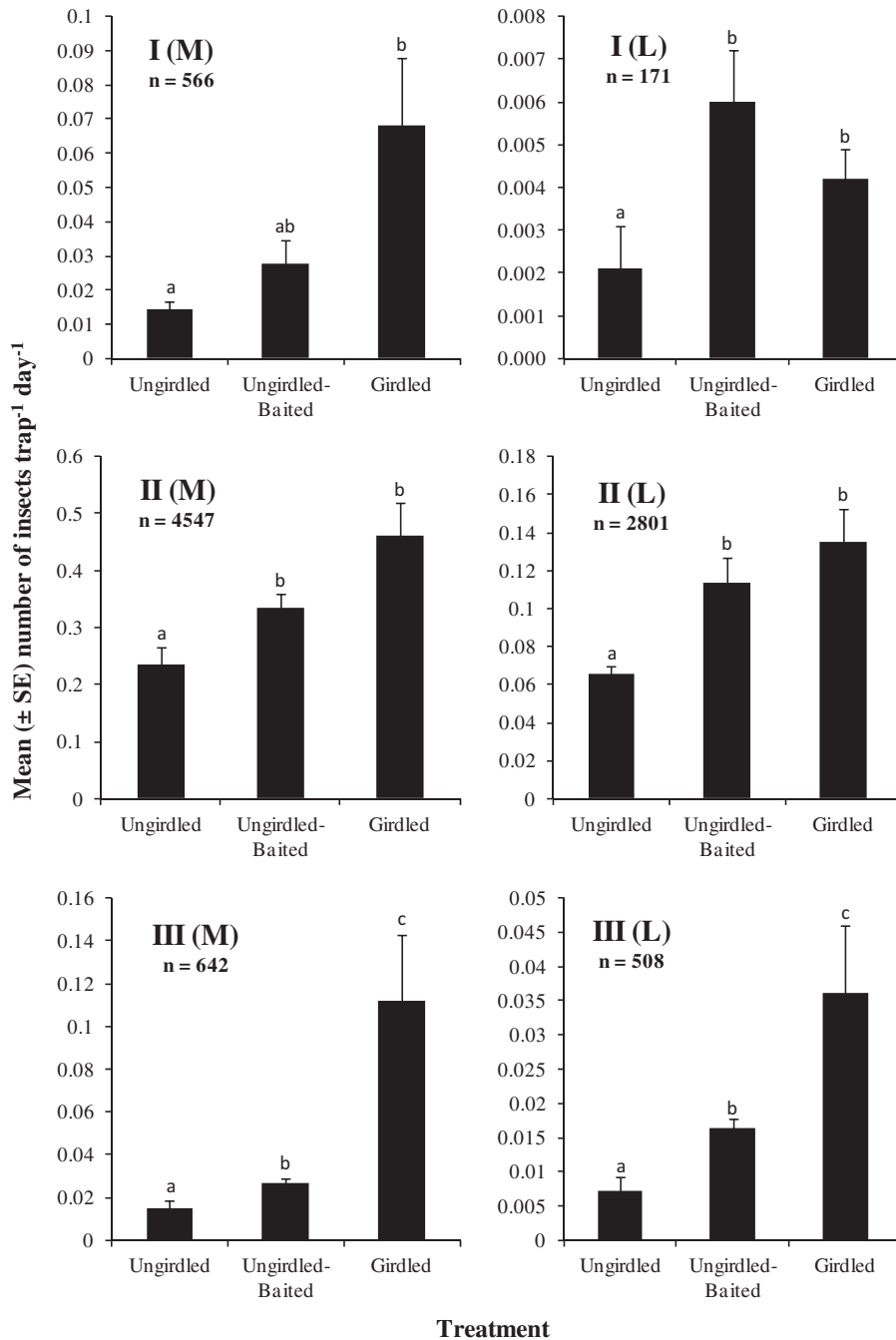


Fig. 1. Mean number (\pm SE) of insects trap⁻¹ day⁻¹ of aboveground Curculionidae collected in three trials (I–III) during 2012–2013 using main stem traps (M) and lower stem traps (L) in three 18- to 21-yr-old thinned loblolly pine sites in northeastern Georgia, United States. Different letters indicate significant differences among treatments ($P=0.05$, Mann–Whitney U Test).

X. crassiusculus (69%), *X. saxesenii* (13%), and *C. mutilatus* (12%). Tree treatment affected total catches of native but not nonnative insects (Table 6). Total captures of native insects were lowest in plots with ungirdled trees. On average, 8, 27, and 65% of native insects were caught in plots with ungirdled, ungirdled-baited, and girdled trees, respectively. In contrast, nonnative insects showed a relatively equal distribution among treatments with 29, 37, and 34% in plots with ungirdled, ungirdled-baited trees, and girdled trees, respectively.

Table 4. Subcortical insect captures (AC—aboveground Curculionidae, BC—belowground Curculionidae, W—woodborers) during 2012–2013 using main stem traps and lower stem traps in three 18- to 21-yr-old unthinned loblolly pine sites in northeastern Georgia, United States

Trial	Trap types	Insect guild	P values		
			U:B	U:G	B:G
I	Main stem traps	AC	0.142	0.013	0.142
		BC	0.008	0.003	0.224
		W	0.102	0.008	0.482
	Lower stem traps	AC	0.025	0.046	0.274
		BC	0.014	0.002	0.009
		W	1.000	0.073	0.073
II	Main stem traps	AC	0.035	0.009	0.110
		BC	0.010	0.002	0.003
		W	0.018	0.002	0.006
	Lower stem traps	AC	0.018	0.002	0.482
		BC	0.001	0.001	0.009
		W	0.656	0.001	0.001
III	Main stem traps	AC	0.028	0.002	0.002
		BC	0.227	0.001	0.003
		W	0.422	0.109	0.386
	Lower stem traps	AC	0.010	0.003	0.015
		BC	0.002	0.001	0.002
		W	1.000	0.027	0.027

Plots contained ungirdled trees (U), ungirdled-baited trees (B), and girdled trees (G). Bold numbers indicate significant differences across tree treatments at $P \leq 0.05$.

Table 5. Mean number (\pm SE) of species that make up >5% of the total capture in trap⁻¹ day⁻¹ collected in 2012–2013 using main stem and lower stem traps in three 18- to 21-yr-old unthinned loblolly pine sites in northeastern Georgia, United States

Species	Treatment	Trial I			Trial II			Trial III		
		χ^2	P	Mean \pm SE	χ^2	P	Mean \pm SE	χ^2	P	Mean \pm SE
<i>X. crassiusculus</i> (32.7%)	U	3.12	0.211	0.009 \pm 0.002a	2.18	0.337	0.150 \pm 0.026a	7.21	0.027	0.014 \pm 0.004a
	B			0.015 \pm 0.002a			0.208 \pm 0.025a			0.019 \pm 0.002ab
	G			0.014 \pm 0.005a			0.162 \pm 0.014a			0.038 \pm 0.009b
<i>X. pubescens</i> (10.1%)	U	8.62	0.013	0.000 \pm 0.000a	15.64	0.000	0.014 \pm 0.003a	14.82	0.001	0.001 \pm 0.000a
	B			0.003 \pm 0.001b			0.078 \pm 0.010b			0.008 \pm 0.002b
	G			0.002 \pm 0.001ab			0.052 \pm 0.005c			0.016 \pm 0.003b
<i>X. saxesenii</i> (6.4%)	U	1.82	0.402	0.000 \pm 0.000a	0.52	0.773	0.040 \pm 0.007a	2.02	0.364	0.001 \pm 0.000a
	B			0.000 \pm 0.000a			0.041 \pm 0.006a			0.002 \pm 0.000a
	G			0.002 \pm 0.001a			0.033 \pm 0.005a			0.003 \pm 0.002a
<i>C. mutilatus</i> (5.9%)	U	2.11	0.348	0.000 \pm 0.000a	0.05	0.974	0.052 \pm 0.013a	0.00	1.000	0a
	B			0.000 \pm 0.000a			0.040 \pm 0.006a			0a
	G			0a			0.039 \pm 0.006a			0a
<i>G. materiarius</i> (5.3%)	U	10.81	0.005	0a	14.31	0.001	0.001 \pm 0.000a	14.95	0.001	0.001 \pm 0.000a
	B			0.004 \pm 0.002b			0.000 \pm 0.000a			0.004 \pm 0.001b
	G			0.013 \pm 0.006b			0.057 \pm 0.017b			0.044 \pm 0.019c

Plots contained ungirdled trees (U), ungirdled-baited trees (B), and girdled trees (G). Different letters indicate significant differences between treatments ($P < 0.05$).

Feeding area by *H. pales* and *P. picivorus* on pine sticks in root-zone traps was greatest in girdled plots (Fig. 4). In plots with ungirdled, ungirdled-baited, and girdled trees, 1, 16, and 83% of the total feeding area were recorded on average in spring and fall 2013, respectively. The differences in feeding area between treatments were even more pronounced in the fall trial, with almost 90% of feeding occurring in plots with girdled trees (Fig. 4).

Discussion

Our two-year study on subcortical insects associated with varying levels of pine tree health indicated that most insect species were associated with trees with compromised health. Similarly, rhizophagous weevils showed the strongest attraction to girdled trees, even over ungirdled trees baited with ethanol and turpentine. This attraction was also reflected in the damage by *H. pales* and *P. picivorus* on pine sticks in pitfall traps. Stressed, wounded, dying, or dead trees and stumps are generally attacked by a particular guild of insects, which includes coleopteran families Buprestidae, Cerambycidae, Curculionidae, and Hymenoptera: Siricidae (Savely 1939, Wallace 1953, Lindhe and Lindelöw 2004, DiGirolomo et al. 2013, Thorn et al. 2014, Ranger et al. 2015). Larvae of several *Hylobius* species (e.g., *Hylobius radialis* Buchanan, *Hylobius assimilis* Boheman, and *H. pales*) develop in roots of cut stumps (York 1933, Warner 1966), recently felled trees (Peirson 1921, Savely 1939), bolts (Hertel 1970), dying pines (Beal and McClintick 1943), girdled trees (Hines and Heikkinen 1977), and trees previously wounded by insects (Hill and Fox 1972) or otherwise stressed (Ebel and Merkel 1967). *Hylastes* species (including *H. salebrosus* and *H. tenuis*) infest dying or dead conifers (Blackman 1941, Matusick et al. 2013), and “may well be erroneously considered the cause of the tree’s death” (p. 1, Blackman 1941). *Pissodes* species (including *P. nemorensis*) attack weakened or dying trees (Hopkins 1911, Dietrich 1931) and only rarely act as primary mortality agents (e.g., Ollieu 1971, Overgaard and Nachod 1971) though even these reports indicate some initial stress (e.g., drought, overstocking) on most attacked trees. Egan (1978) examined healthy, girdled, and severed loblolly pine over a 3-yr period in Virginia, United States where an average of 0.2, 9.6,

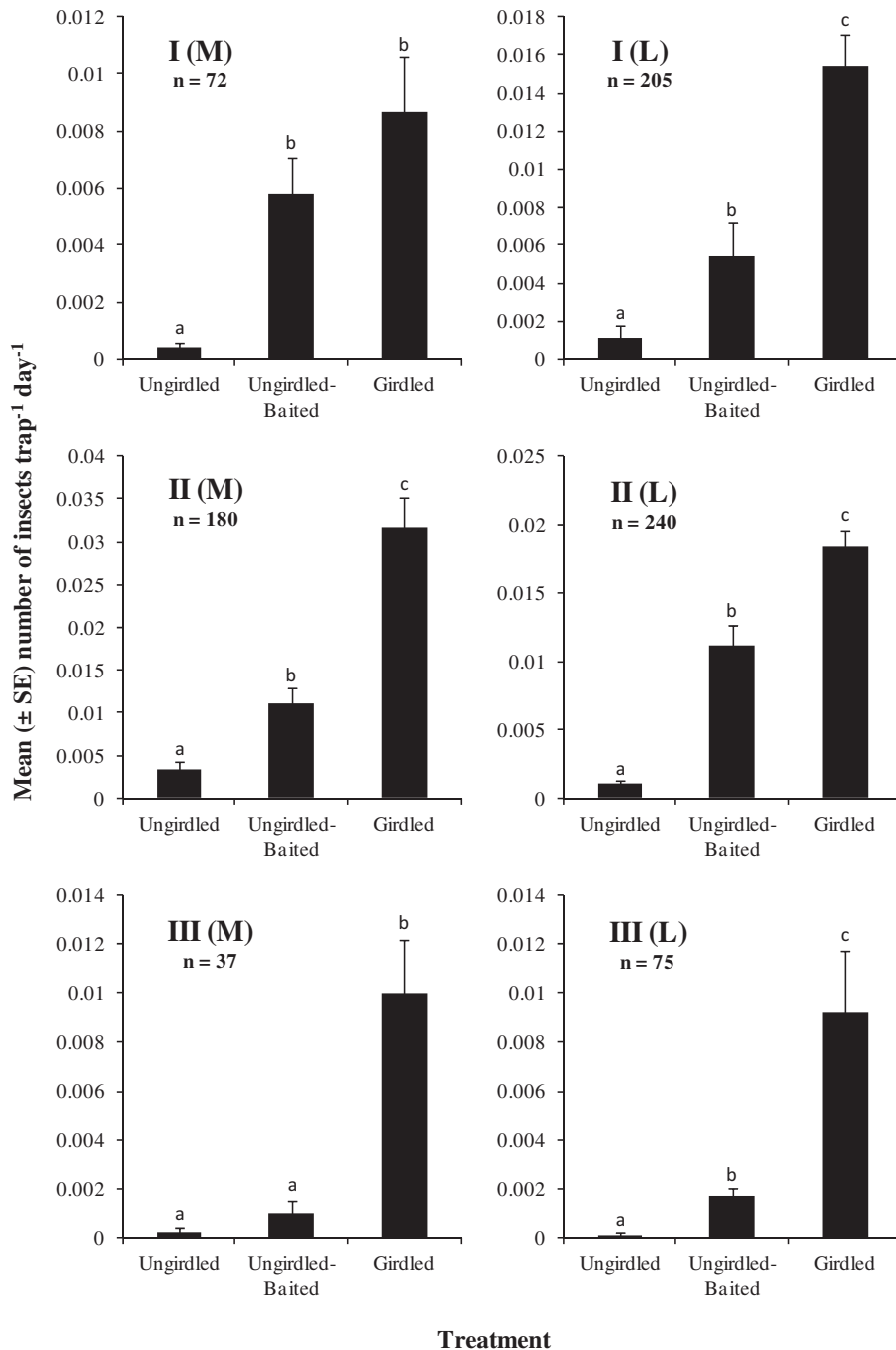


Fig. 2. Mean number (\pm SE) of insects trap⁻¹ day⁻¹ of belowground Curculionidae collected in three trials (I–III) during 2012–2013 using main stem traps (M) and lower stem traps (L) in three 18- to 21-yr-old unthinned loblolly pine sites in northeastern Georgia, United States. Different letters indicate significant differences among treatments ($P=0.05$, Mann–Whitney U Test).

and 77.4 *Hylastes* spp. beetles were captured per healthy, girdled, and severed tree, respectively. This study (and several others) reinforces the ecological role of this group of insects as secondary organisms that assist in the breakdown of dying and dead woody material.

Several belowground curculionids (especially *Hylastes* spp.) act as vectors for *Leptographium* and *Grosmannia* spp. fungi, which can contribute to southern pine health issues and have been associated with SPD (Eckhardt et al. 2007, 2010). The role of these insects and their associated fungi in relation to SPD has been questioned, particularly whether or not they are causal agents of mortality or

merely secondary colonizers of weakened or stressed trees (Coyle et al. 2015a). The southeastern pine system appears to be similar to that in the North American Great Lakes region, where red pine can be weakened by rhizophagous beetles after initial stress by abiotic factors (Klepzig et al. 1991, Aukema et al. 2010).

Nonnative subcortical insects especially *C. mutilatus*, *X. crassiusculus*, and *X. saxesenii* comprised a significant portion of our total trap captures (Table 3). Nonnative scolytines are commonly captured in many forest types in the southeastern United States (Atkinson et al. 1988, Oliver and Mannion 2001, Miller and Rabaglia 2009, Reed and Muzika 2010, Coyle et al. 2015b); hence,

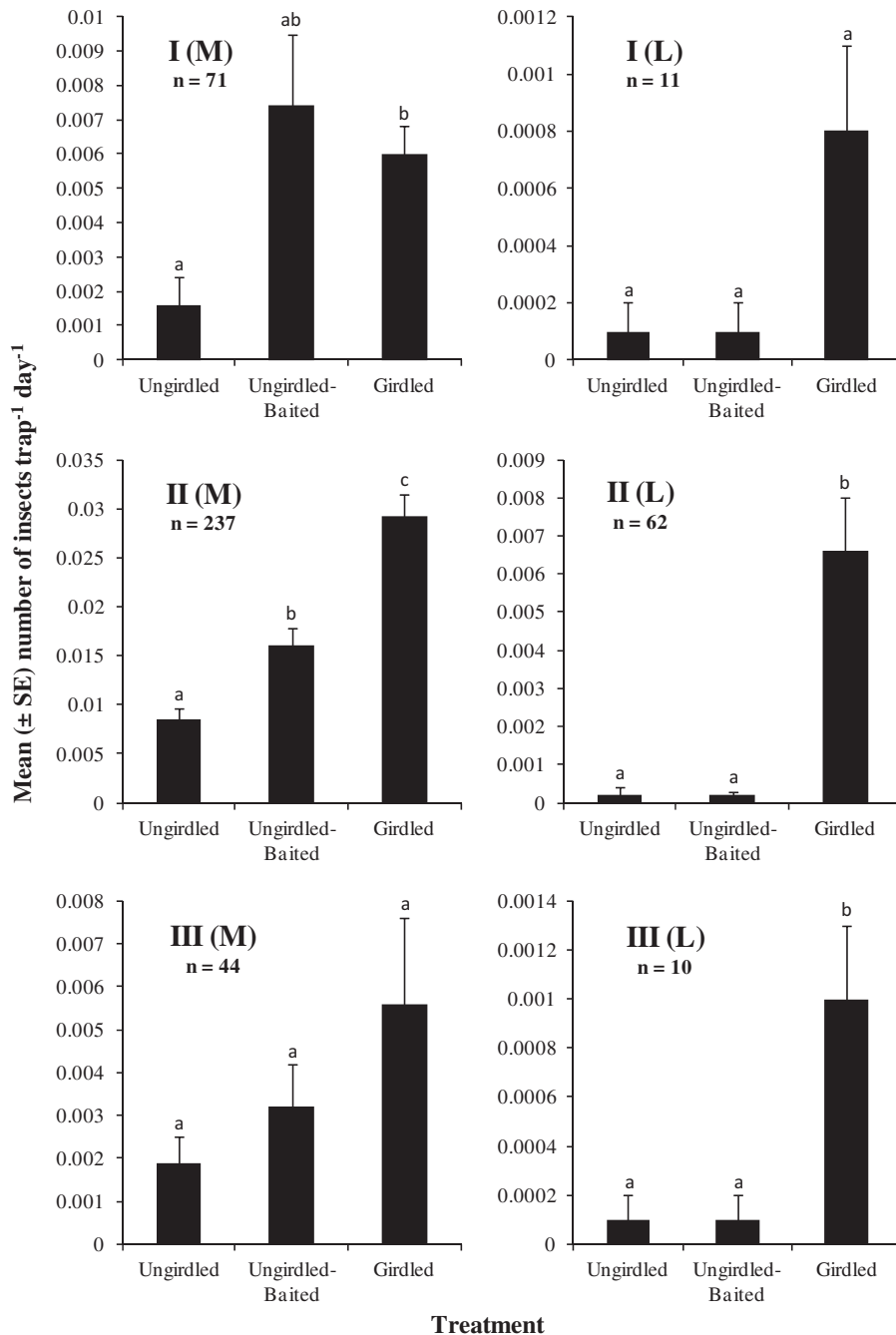


Fig. 3. Mean number (\pm SE) of insects trap⁻¹ day⁻¹ of woodborers collected in three trials (I–III) during 2012–2013 using main stem traps (M) and lower stem traps (L) in three 18- to 21-yr-old unthinned loblolly pine sites in northeastern Georgia, United States. Different letters indicate significant differences among treatments ($P=0.05$, Mann–Whitney U Test).

their presence is not surprising. However, catches of nonnative subcortical insects did not show a similar response to the different tree treatments as did native insects. Nonnative subcortical insects were equally caught in all three treatments (ungirdled, ungirdled-baited, and girdled trees). Miller and Rabaglia (2009) captured most nonnative species, including many that were also collected in our study, in funnel traps baited with ethanol alone or with α -pinene in mature pine stands in the southeastern United States. Only a small percent of individuals were caught in unbaited traps or those baited with α -pinene alone. Reding et al. (2011) caught much higher numbers of

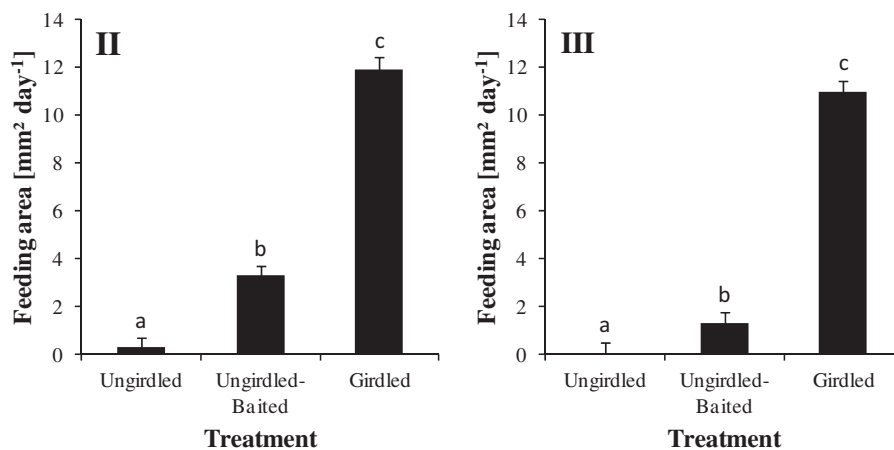
X. crassiusculus and *X. saxesenii* in ethanol-baited bottle traps than in unbaited traps in nurseries in Ohio and Virginia. Catches of *C. mutilatus*, *X. crassiusculus*, and *X. saxesenii* differed among cut tree or ethanol-baited and control funnel traps only when surrounded by certain tree monocultures (Coyle et al. 2015b). This indicates that results for nonnative subcortical insects and host attractants may vary by trapping designs and the surrounding environmental matrix.

Forests in the southern United States are a vital component to the ecology and economy of the region, and most receive intensive

Table 6. Mean number (\pm SE) of native and nonnative subcortical insects trap⁻¹ day⁻¹ collected during 2012–2013 using main stem and lower stem traps in three 18- to 21-yr-old unthinned loblolly pine sites in northeastern Georgia, United States

Trial	Treatment	Native insects			Nonnative insects		
		χ^2	<i>P</i>	Mean \pm SE	χ^2	<i>P</i>	Mean \pm SE
I	U	14.09	0.001	0.006 \pm 0.002a	1.21	0.546	0.013 \pm 0.002a
	B			0.033 \pm 0.006b			0.019 \pm 0.003a
	G			0.085 \pm 0.020c			0.019 \pm 0.006a
II	U	17.12	0.000	0.059 \pm 0.005a	2.23	0.327	0.255 \pm 0.036a
	B			0.188 \pm 0.015b			0.300 \pm 0.029a
	G			0.434 \pm 0.059c			0.249 \pm 0.008a
III	U	16.76	0.000	0.010 \pm 0.002a	6.59	0.037	0.015 \pm 0.004a
	B			0.028 \pm 0.004b			0.021 \pm 0.002ab
	G			0.132 \pm 0.038c			0.042 \pm 0.010b

Plots contained ungirdled trees (U), ungirdled-baited trees (B), and girdled trees (G). Different letters indicate significant differences between treatments ($P < 0.05$).

**Fig. 4.** Mean feeding area (\pm SE) in mm² day⁻¹ by *H. pales* and *P. picivorus* on pine sticks in root-zone traps in two trials (II and III) in two 18-yr-old unthinned loblolly pine sites in northeastern Georgia, United States. Different letters indicate significant differences between treatments ($P = 0.05$, Mann–Whitney *U* Test).

management. According to Sinclair (1966), trees are subjected to predisposing, inciting, and contributing factors that affect their health. Current recommendations for management of pines putatively suffering from SPD focus on contributing factors (rhizophagous beetles). Our data suggest that altering management practices due to the presence of rhizophagous beetles in stands is premature. For example, even though greater numbers of rhizophagous beetles were trapped in thinned stands, there is little evidence these otherwise healthy trees are being attacked by this guild (Zeng et al. 2014). It may be more appropriate and effective to manage to reduce tree stress, maintain and promote stand health, and minimize risk of insect infestation. In contrast, stressed, damaged, or dying trees will generally attract a wide range of subcortical insects, which may further contribute to tree dieback and breakdown of woody tissue by attacking, feeding, and transmitting fungi.

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