Species characterization and responses of subcortical insects to trap-logs and ethanol in a hardwood biomass plantation

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- **Abstract** 1 We characterized subcortical insect assemblages in economically important eastern cottonwood (*Populus deltoides* Bartr.), sycamore (*Platanus occidentalis* L.) and sweet-gum (*Liquidambar styraciflua* L.) plantations in the southeastern U.S.A. Furthermore, we compared insect responses between freshly-cut plant material by placing traps directly over cut hardwood logs (trap-logs), traps baited with ethanol lures and unbaited (control) traps.
 - 2 We captured a total of 15 506 insects representing 127 species in four families in 2011 and 2013. Approximately 9% and 62% of total species and individuals, respectively, and 23% and 79% of total Scolytinae species and individuals, respectively, were non-native to North America.
 - 3 We captured more Scolytinae using cottonwood trap-logs compared with control traps in both years, although this was the case with sycamore and sweetgum only in 2013. More woodborers were captured using cottonwood and sweetgum trap-logs compared with control traps in both years, although only with sycamore in 2013.
 - 4 Ethanol was an effective lure for capturing non-native Scolytinae; however, not all non-native species were captured using ethanol lures. *Ambrosiophilus atratus* (Eichhoff) and *Hypothenemus crudiae* (Panzer) were captured with both trap-logs and control traps, whereas *Coccotrypes distinctus* (Motschulsky) and *Xyleborus glabratus* Eichhoff were only captured on trap-logs.
 - 5 Indicator species analysis revealed that certain scolytines [e.g. *Cnestus mutilatus* (Blandford) and *Xylosandrus crassiusculus* (Motschulsky)] showed significant associations with trap-logs or ethanol baits in poplar or sweetgum trap-logs. In general, the species composition of subcortical insects, especially woodboring insects, was distinct among the three tree species and between those associated with trap-logs and control traps.

Keywords Buprestidae, Cerambycidae, Curculionidae, non-natives, Scolytinae, Siricidae.

Introduction

The southeastern U.S.A. is one of the largest timber producing regions in North America (Howard, 2007), and has over 77 billion ha of natural and plantation-grown forestland (USDA Forest Service, 2011). Recent research has shown that hardwood trees such as eastern cottonwood (*Populus deltoides* Bartr.), American sycamore (*Platanus occidentalis* L.) and sweetgum (*Liquidambar styraciflua* L.) may attain economically profitable productivity levels in the southeastern region (Wright

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& Cunningham, 2008; Merkle & Cunningham, 2011; Coyle *et al.*, 2013). In addition to forests, an additional 2 million ha of farmland can be potentially developed for biomass production (Munsell & Fox, 2010). If poplar, sycamore, sweetgum and other hardwood species are to be potential candidates for intensive forestry operations for wood and/or biofuels production (Kline & Coleman, 2010), then a comprehensive examination of the ecological ramifications of hardwood monocultures may be necessary for long-term sustainable fibre production.

Subcortical insects [i.e. bark, ambrosia, and woodboring beetles (Coleoptera: Buprestidae, Cerambycidae, and Curculionidae) and woodwasps (Hymenoptera: Siricidae)] are critical components of forest ecosystems and, via tree colonization, they contribute to tree dieback and mortality, as well as the breakdown of coarse-woody debris. Communities of ecologically and economically important native and non-native subcortical insects colonizing southern pine species are well known (Miller, 2006; Miller & Rabaglia, 2009; Miller et al., 2011). By contrast, little is known about the communities of subcortical insects that utilize hardwood trees (Oliver & Mannion, 2001; Coyle et al., 2005; Gandhi & Herms, 2010). Subcortical insects in several genera (e.g. Agrilus, Corthylus, Platypus and Xylosandrus) are known to attack living and stressed hardwood trees (Kühnholz et al., 2001), sometimes contributing to tree mortality and economic damage (Fierke et al., 2005; Chong et al., 2009; Kovacs et al., 2010; Coleman et al., 2012). Similarly, piles of recently cut timber are not immune to insect damage (Allen & Rudinsky, 1959; Wilson, 1960, 1962; Mathew, 1987). Any increase in poplar, sycamore or sweetgum production for wood products, biomass and/or bioenergy would result in large quantities of logged material/wood, either at the processing plant or in the field, which may further lead to increased subcortical insect populations. Hence, a thorough understanding of the insect communities associated with these tree species may be necessary if hardwood biomass plantations are to be economically and ecologically viable over the long-term.

Monitoring populations and communities of non-native and native pestiferous subcortical insects requires effective trapping methods. Traditionally, these trapping methods have included various trap-types (e.g. funnel and intercept panel traps) and attached chemical attractants (e.g. monoterpenes and ethanol) (Borden, 1989; Flechtmann et al., 2000; Allison et al., 2004; Gandhi et al., 2010) and/or bringing back logs infested with beetles from the field to capture emerging adults (Ferro et al., 2009; Lu et al., 2012). Freshly cut logs are known to attract subcortical insects that use hardwood and conifer hosts (Flechtmann et al., 1999; Maier, 2008; Domingue et al., 2011; Lee et al., 2011). Using direct host material to attract subcortical insects may be considered optimal compared with using refined baits that may be missing minor but important host attractants (Barnes et al., 2014). However, few studies have used cut hardwood trees as baits to monitor subcortical insects (Švihra & Koehler, 1981; Mayfield & Hanula, 2012). To our knowledge, no similar studies have been conducted in poplar, sycamore or sweetgum plantations, and none have assessed whether subcortical insects would be better sampled using host material, ethanol baits or unbaited traps placed in the stand.

The present study aimed to: (i) determine the differences in subcortical insect assemblages among poplar, sycamore, and sweetgum plantations and (ii) test the suitability of trap-logs and ethanol as monitoring tools for the detection of native and non-native subcortical insect species.

Materials and methods

Study location and experimental design

The present study took place at the Savannah River Site, a National Environmental Research Park, located near Aiken, South Carolina, U.S.A. (33°23'N, 81°40'E). This area is part of the Carolina Sandhills Ecoregion, and is characterized by

warm, humid summers and mild winters, with highly variable precipitation.

The study was conducted in an experimental forest (planted in spring 2000) containing eastern cottonwood clones ST66 and S7C15, sycamore, sweetgum and loblolly pine (*Pinus taeda* L.) (Coleman *et al.*, 2004). Within each of three replicated blocks, four plots per tree genotype were arranged in a randomized complete block design. Trees were planted in 0.22-ha plots at a spacing of $2.5 \times 3.0 \text{ m}^2$. During 2000–2008, the four plots in each block received one of four treatments: fertilization, irrigation, fertilization + irrigation, or no treatment (control). Treatments were applied equally each week from 1 April to 30 September annually.

We conducted experiments in 2011 and 2013 in eastern cottonwood S7C15, sycamore and sweetgum plots that received the fertilization + irrigation treatment. We chose the fertilization + irrigation treatment because these trees were approximately 33% larger than the other treatments (Coyle & Coleman, 2005; Coyle *et al.*, 2008) and we assumed that they would be more attractive to insects as a result of increased amounts of volatiles being emitted from wood and foliage.

We established four traps in each plot, arranged in a square. For the first experiment, we monitored beetle captures over cut trees or an untreated control. Three trees were felled in each of the fertilization + irrigation plots (n = 9 trees per species) on 19 April 2011. Apparently healthy trees with no dieback were chosen based on similar size [mean \pm SE diameter to breast height (DBH): cottonwood, 16.9 ± 1.0 cm; sycamore, 16.1 ± 0.6 cm; sweetgum, 18.2 ± 0.7 cm; tree DBH was not significantly different from each other: P = 0.19, PROC ANOVA in SAS; SAS Inc., version 9.2, Cary, North Carolina]. Trees were separated by ≥ 25 m and logs were cut into approximately 2-m sections. Branches and leaves were left on the stem sections to add to the volatile plume from the trap-logs. Unbaited 12-unit Lindgren funnel traps were installed next to each tree's stump, with the cut bolts and foliage stacked in a log cabin formation under the trap and surrounding the stump, thereby using the volatiles produced by logs as insect attractants. One Lindgren funnel control trap, devoid of any cut plant material, was installed in each plot (n = 3traps per tree species), approximately 25 m away from trap-logs.

We conducted the second experiment in the same plots, monitoring beetle captures over cut trees, ethanol lures or an untreated control over bare ground. We chose trees in the same manner (mean \pm SE DBH: cottonwood, 21.4 \pm 0.3 cm; sycamore, 20.7 \pm 0.4 cm; sweetgum, 19.6 \pm 0.8 cm; tree DBH was not significantly different from each other: *P* = 0.08, PROC ANOVA in SAS, version 9.2] and felled two trees per plot on 25 April 2013. Each plot also contained a funnel trap baited with one UHR ethanol lure (changed every 4 weeks in accordance with the manufacturer instructions; Contech Enterprises, Inc., Canada) and a control trap away from any cut plant material.

Insect trapping

Trap collection cups were filled with a 50:50 blend of propylene glycol (Prestone Products Corp., Danbury, Connecticut) and water, and checked every 2 weeks. In 2011, traps were open from 19 April to 23 August (nine trapping periods) and, in 2013, traps were open from 25 April to 12 September (10 trapping periods).

Coleoptera (Buprestidae, Cerambycidae and Curculionidae: Scolytinae) and Hymenoptera (Siricidae) were identified using published keys (Franklin & Lund, 1956; Wood, 1982; Lingafelter, 2007; Schiff *et al.*, 2012). We used the 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 have been deposited in the Georgia Museum of Natural History, University of Georgia, Athens, Georgia.

Statistical analysis

Traditional data transformations failed to achieve normality required for a classic analysis of variance. Hence, nonparametric analyses (PROC NPARIWAY in SAS, version 9.2) were used to test for the main effect of tree species (Kruskal–Wallis test) or trap-type (trap-log versus control in 2011, trap-log versus ethanol, trap-log versus control or ethanol versus control in 2013) within tree species (Wilcoxon rank-sum test). We tested all species of Scolytinae together as a single group (referred to as total Scolytinae) and all woodboring insects (Coleoptera: Buprestidae, Cerambycidae, and Hymenoptera: Siricidae) together (referred to as total woodborers), as well as the most common individual species (i.e. those that comprised $\geq 4\%$ of total catches in a given year). Tests were conducted separately for each sampling year and $\alpha = 0.05$ was considered statistically significant.

Indicator species analyses (PC-ORD, version 5.1; MjM Software Design, Gleneden Beach, Oregon) were used to determine whether particular subcortical insect species ($\geq 4\%$ of total captures in a given year) were associated with any tree species or trapping method (Dufrêne & Legendre, 1997; McCune & Mefford, 1999; McCune & Grace, 2002). Analyses were conducted separately for scolytine beetles and woodborers. Monte Carlo tests using 1000 runs were used to generate randomized indicator values for each species. These randomized indicator values were then compared with the observed indicator values to assess statistical significance of the strength of species affinity for combinations of tree species and trap-types.

We used non-metric multidimensional scaling (NMS) (PC-ORD, version 5.1, MjM Software Design) to determine differences in Scolytinae and woodborer assemblages attracted to trap logs, ethanol baits and control traps for each tree species. Bray–Curtis dissimilarities were used on square root +1 (in 2011) or log +1 (in 2013) transformed data. We based NMS on 50 runs with real data with a 0.0001 stability criterion, 15 runs to evaluate stability, 250 maximum iterations, with a step-down in dimensionality and an initial step length of 0.20 (McCune & Grace, 2002). After checking the scree plot for optimal dimensions and model stability, the final NMS was run using three dimensions with a 0.00001 stability criterion, and one run without a step-down in dimensionality. Two-dimensional ordination graphs with mean \pm SE distance were created using the two axes (x, y or z) that explained the most variation (r^2) in each of the data sets.

Results

We caught a total of 15 506 subcortical insects represented by 115 native and 12 non-native species (see Supporting

Table 1	Native and non-native woodborer and scolytine captures during
summer	2011 and 2013 at the Savannah River Site near Aiken, South
Carolina,	, U.S.A.

Group	Family	Origin	Number of species	Total captures
Woodborers	Buprestidae	Native	8	120
		Non-native	0	0
	Cerambycidae	Native	41	936
	2	Non-native	0	0
	Siricidae	Native	1	30
		Non-native	0	0
	Total		50	1086
Scolytinae	Scolytinae	Native	40	2582
-	-	Non-native	12	9646
	Total		52	12228
Weevils*	Various	Native	25	2192
		Non-native	0	0
	Total		25	2192

For a complete species list and abundance, see Supporting information, Table S1.

*excluding Scolytinae.

information, Table S1). Overall, 12 non-native species of Scolytinae comprised > 72% of all woodborers and scolytines caught in traps (Table 1). The non-native species Cnestus mutilatus (Blandford), Dryoxylon onoharaensis (Murayama), Xyleborinus saxesenii (Ratzeburg) and Xylosandrus crassiusculus (Motschulsky) dominated our catches, and accounted for > 61%of all subcortical insects. Other non-native species included Ambrosiodmus rubricollis (Eichhoff), Ambrosiophilus atratus (Eichhoff), Coccotrypes distinctus (Motschulsky), Cyclorhipidion bodoanum (Reitter), Euwallacea interjectus (Blandford), Hypothenemus californicus Hopkins, Hypothenemus crudiae (Panzer) and Xyleborus glabratus Eichhoff. A native weevil species, Dryophthorus americanus Bedel, comprised over half of our total insect catches in 2011. Catches of all nonscolytine weevils were low in 2013, as were woodborer catches in both years.

Tree species had a significant effect on insect catches for several insect groups (Table 2). Catches of total Scolytinae were almost equal on poplar and sweetgum, which were > 80% and > 64% greater than sycamore, respectively, in both years. *Xyleborinus saxesenii* catches in poplar were 60% greater than sweetgum and 84% greater than sycamore in 2011, and > 69% greater than either sweetgum or sycamore in 2013. *Xylosandrus crassiusculus* was caught most often on sweetgum in 2011, and relatively equally among tree species in 2013. *Pityophthorus liquidambarus* Blackman, as its name suggests, was caught almost exclusively in sweetgum plots each year. *Cnestus mutilatus* was caught over four times as often in sweetgum than poplar or sycamore in 2013. Catches of total woodboring insects did not differ among tree species (Table 2).

There were generally greater insect catches in traps placed over trap-logs compared with control traps in 2011, although captures were dependent upon tree species and insect taxa (Fig. 1 and Table 3). In 2013, the most insects were caught on either trap-logs or ethanol lures (Fig. 2 and Table 4). Total Scolytinae catches in 2011 were greater with poplar trap-logs than control traps but not in sycamore or sweetgum plots.

Table 2 Mean \pm SE insects per trap captured and Kruskal–Wallis analyses for subcortical insect groups and individual species comprising > 4% of total captures during the 2011 and 2013 study periods

Таха	Year	Poplar	Sycamore	Sweetgum	χ ²	Р
Total Scolytinae	2011	2.94 ± 0.32	1.56 ± 0.18	2.56 ± 0.33	14.05	0.001
-	2013	39.16 ± 2.42	21.43 ± 1.34	35.39 ± 2.70	36.95	< 0.001
Non-native Scolytinae	2011	1.88 ± 0.27	0.49 ± 0.08	1.25 ± 0.21	11.18	< 0.001
-	2013	37.22 ± 2.39	17.60 ± 1.10	22.35 ± 1.74	54.62	< 0.001
Total Woodborers	2011	1.27 ± 0.24	1.06 ± 0.13	1.25 ± 0.15	1.54	0.463
	2013	1.83 ± 0.29	1.64 ± 0.17	1.48 ± 0.16	1.05	0.591
Cnestus mutilatus	2011	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	na	na
	2013	1.28 ± 0.24	1.23 ± 0.24	5.85 ± 1.23	42.92	< 0.001
Dryoxylon onoharaensis	2011	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	na	na
	2013	6.33 ± 0.68	1.73 ± 0.24	1.91 ± 0.22	41.59	< 0.001
Elaphidion mucronatum	2011	0.23 ± 0.05	0.70 ± 0.12	0.45 ± 0.08	9.24	0.010
	2013	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	na	na
Euderces pini	2011	0.55 ± 0.20	0.03 ± 0.02	0.13 ± 0.07	20.43	< 0.001
	2013	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	na	na
Hypothenemus rotundicollis	2011	0.39 ± 0.08	0.15 ± 0.04	0.05 ± 0.02	20.59	< 0.001
	2013	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	na	na
Hypothenemus seriatus	2011	0.17 ± 0.04	0.23 ± 0.05	0.19 ± 0.06	2.25	0.324
	2013	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	na	na
Monarthrum mali	2011	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	na	na
	2013	0.33 ± 0.09	0.87 ± 0.22	3.45 ± 0.57	53.52	< 0.001
Pityophthorus liquidambarus	2011	0.01 ± 0.01	0.04 ± 0.02	0.48 ± 0.12	35.93	< 0.001
	2013	0.03 ± 0.01	0.10 ± 0.03	7.10 ± 1.20	180.69	< 0.001
Xyleborinus saxesenii	2011	1.60 ± 0.25	0.26 ± 0.05	0.65 ± 0.15	40.81	< 0.001
-	2013	20.88 ± 2.15	6.37 ± 0.64	5.94 ± 0.54	60.01	< 0.001
Xylosandrus crassiusculus	2011	0.08 ± 0.03	0.12 ± 0.04	0.33 ± 0.08	8.42	0.015
-	2013	8.52 ± 1.13	7.95 ± 0.82	8.14 ± 1.00	1.31	0.520

Insects were captured in intensively-managed stands of three tree species in South Carolina, U.S.A. In 2011, each tree species plot contained three traps baited with cut trees and a control trap; in 2013, each plot contained two cut tree-baited traps, a trap baited with an ethanol lure and a control trap.

Significant *P*-values are indicated with boldface type. na not applicable.

In 2013, the highest numbers of Scolytinae were caught in trap-logs for sycamore and sweetgum, and ethanol lures for poplar. Catches of non-native Scolytinae mirrored those of total Scolytinae. Total woodboring insect catches were greater on trap-logs of each tree species compared with control traps in 2011, although they did not differ in sycamore traps in 2013. Xyleborinus saxesenii and Euderces pini (Olivier) were the only individual species that responded to poplar trap-logs, whereas both Elaphidion mucronotum (Say) and Hypothenemus rotundicollis (Eichhoff) responded to sycamore trap-logs. Cnestus mutilatus and D. onoharaensis were caught in the greatest numbers in ethanol-baited traps, whereas E. mucronotum, Monarthrum mali (Fitch) and P. liquidambarus showed a clear preference for sweetgum trap-logs. With the exception of poplar in 2013, X. crassiusculus catches tended to be greater over trap-logs, although they were not statistically different from controls.

Indicator species analysis revealed that four species of scolytine beetles caught only with poplar and sweetgum trap-logs in 2011 had significant indicator values (Table 5). *Hypothenemus rotundicollis* and *X. saxesenii* were primarily associated with poplar trap-logs, whereas *P. liquidambarus* and *X. crassiusculus* were associated with sweetgum trap-logs. Among woodborers, only *E. mucronotum* was associated with unbaited funnel traps placed in sweetgum stands (Table 5). In 2013, *M. mali* and *P. liquidambarus* were associated with sweetgum trap-logs, whereas *C. mutilatus* was associated with ethanol lures in both poplar and sweetgum plots (Table 5).

The NMS ordination diagram in two dimensions for total Scolytinae in 2011 (final stress = 16.14, final instability = 0.00001) indicated that beetle assemblages in the three stand types were distinct along at least one of the hypothetical gradients (Fig. 3A). Total woodboring insect community assemblages (final stress = 12.93, final instability = 0.00007) captured over trap-logs were distinct among the three host types, although assemblages captured in control traps were quite similar (Fig. 3B). Assemblages of total Scolytinae were somewhat distinct on all three tree species in 2013 (final stress = 13.61, final instability = 0.00047) (Fig. 4A), whereas total woodboring insect community assemblages were less distinct (final stress = 14.77, final instability = 0.0045) (Fig. 4B). Insect community assemblages captured with the ethanol lure tended to have the characteristics of assemblages captured on both trap-logs and control traps.

Discussion

Non-native Scolytinae clearly dominated trap catches in these biomass plantations. Although only a small proportion of scolytine species were non-native, most individuals caught were non-native to North America (Table 1). The probable reason why non-native species comprised such a large proportion of

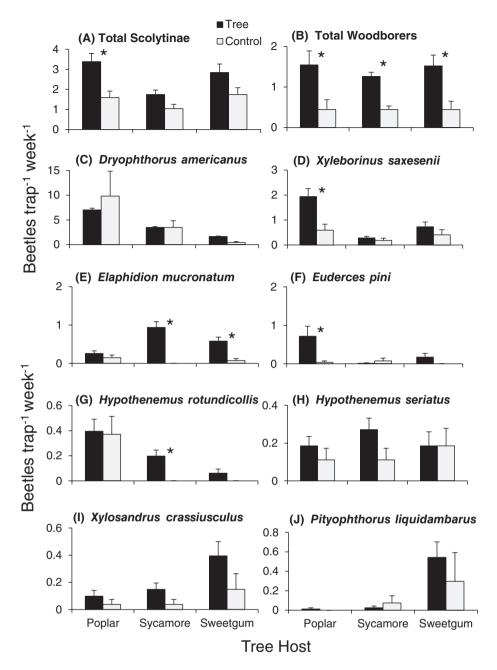


Figure 1 Effect of trap trees on captures (mean \pm SE) of (A) total Scolytinae, (B) total woodborers, (C) *Dryophthorus americanus*, (D) *Xyleborinus saxesenii*, (E) *Elaphidion mucronatum*, (F) *Euderces pini*, (G) *Hypothenemus rotundicollis*, (H) *Hypothenemus seriatus*, (I) *Xylebandrus crassiusculus* and (J) *Pityophthorus liquidambarus* during summer 2011 in an intensively-managed hardwood plantation in South Carolina, U.S.A. Within an insect group x tree host, an asterisk indicates significant differences between traps over cut trees and controls (Wilcoxon rank sum test, $\alpha = 0.05$).

total captures is because these species posess characteristics (e.g. life-history traits, behavioural plasticity) common to invasive species that enhance their ability to colonize and establish in new environments (Sakai *et al.*, 2001). Several species, such as *X. saxesenii*, *X. crassiusculus*, *C. mutilatus* and *D. onoharaensis*, have established breeding populations, as indicated by the high numbers of individuals captured in this and other studies (Coyle *et al.*, 2005; Ulyshen & Hanula, 2009). *Cnestus mutilatus* appears to be in the process of a rapid range expansion

across the southeastern U.S.A. It was first collected in South Carolina in 2010 (Chong *et al.*, 2012) and the escalation of our capture rates from 2011 to 2013 from few individuals to hundreds of beetles (see Supporting information, Table S1) further supports this notion. Although these three species are among some of the most common ambrosia beetles in the southeastern U.S.A. (Turnbow & Franklin, 1980; Atkinson *et al.*, 1988; Miller & Rabaglia, 2009), several less-common non-native scolytines such as *A. atratus* and *H. crudiae* were also captured in very low

Table 3 Wilcoxon rank-sum test of the effect of trap-trees on captures of the most common subcortical insects in intensively-managed stands of three
hardwood tree species during 2011 in South Carolina, U.S.A.

	Poplar		Sycamore		Sweetgum	
Таха	χ^2	P	χ^2	Р	χ^2	Р
Total Scolytinae	7.42	0.007	1.86	0.173	0.40	0.525
Non-native Scolytinae	10.47	0.001	1.76	0.185	1.60	0.207
Total Woodborers	6.00	0.014	9.53	0.002	11.51	0.001
Dryophthorus americanus	0.11	0.743	0.02	0.893	3.02	0.082
Xyleborinus saxesenii	11.64	0.001	0.39	0.530	0.04	0.850
Elaphidion mucronatum	0.29	0.588	16.99	< 0.001	8.77	0.003
Euderces pini	4.89	0.027	0.70	0.403	1.73	0.188
Hypothenemus rotundicollis	0.01	0.922	5.75	0.017	1.37	0.242
Hypothenemus seriatus	0.43	0.512	1.73	0.189	0.25	0.615
Xylosandrus crassiusculus	0.48	0.490	1.67	0.194	2.78	0.096
Pityophthorus liquidambarus	0.33	0.564	1.37	0.242	0.02	0.891

See also Fig. 1 for a graphical comparison of these data.

Significant P-values are indicated with boldface type.

numbers. It remains to be determined whether these species will increase in numbers with time or continue to persist at low levels.

Much greater numbers of Scolytinae were caught with trap-logs than unbaited traps. Similarly, in Norway, traps baited with either Scots pine (Pinus sylvestris L.) or downy birch (Betula pubescens Ehrh.) caught up to 420-fold more Scolytinae than unbaited controls (Brattli et al., 1998). Konara oak (Ouercus serrata Murray) trap logs were successfully used to describe a guild of Scolytinae and Platypodidae in Japan (Sanguansub et al., 2012) and loblolly pine and sweetgum trap-logs were used to describe saproxylic beetle assemblages in South Carolina, U.S.A. (Ulyshen & Hanula, 2009). The responses of insects varied among tree species, as reported in other studies (Maier, 2008; Ulyshen & Hanula, 2009). Trap catches of total Scolytinae, X. saxesenii, E. pini, D. onoharaensis and H. rotundicollis were greater on poplar, whereas those of C. mutilatus, M. mali and P. liquidambarus were greater on sweetgum. Catches of X. crassiusculus were greatest on sweetgum in 2011, although they were even among the three host types in 2013. Xyleborinus saxesenii is attracted to and utilizes many hosts, including chestnut (Castanea spp.), plum (Prunus spp.) and pear (Pvrus spp.) trees (Deyrup & Atkinson, 1987; Batt, 2000; Oliver & Mannion, 2001). The lack of response to sweetgum trap-trees in 2011 was particularly unexpected, considering the high levels of adult emergence recorded by Ulyshen and Hanula (2009) from sweetgum in the same area. This difference could be the result of inter-annual variation, or possibly climatic factors. By contrast, catches of *H. rotundicollis* were greater in sycamore trap-logs, and this species is also known to utilize several hardwood hosts, such as hickory (Carya spp.), oak (Quercus spp.) and beech (Fagus spp.) trees (Salsbury, 2004). Catches of total woodboring insects appeared to be particularly responsive to trap-logs of every tree species in 2011 but not 2013, and catches of E. pini and E. mucronatum appeared to vary based on tree species (poplar, as well as sycamore and sweetgum, respectively). Both of these cerambycids are polyphagous, utilizing several hardwood species (and a conifer species in the case of E. mucronotum) as hosts (Turnbow & Hovore, 1979; Linsley & Chemsak, 1997; Morris, 2002).

Similarly, indicator species analysis revealed that X. saxesenii and H. rotundicollis were associated primarily with poplar trap-logs, and M. mali, X. crassiusculus and P. liquidambarus were associated with sweetgum trap-logs. These trends are likely the result of a different volatile profile emitted by phloem and xylem layers, as well as the leaves of the three host species, because all aboveground host material was used in the present study (Geron et al., 2001). Although certain insect species were caught in these hardwood stands, and showed an association with particular tree species, they may or may not be using these trees as viable hosts. For example, Ips avulsus (Eichhoff), Ips calligraphus (Germar) and Ips grandicollis (Eichhoff) were caught in relatively low numbers (35 individuals) in our traps. Ips species are known only to infest conifers (Wood, 1982), and it is likely that they were either flying in the general area to find a host or were attracted to decaying coarse-woody debris. Furthermore, the native weevil D. americanus was the most commonly caught subcortical beetle in 2011 and this species has previously been associated with pine trees (Downie & Arnett, 1996; Aukema & Raffa, 2005; Ulyshen & Hanula, 2010). Future studies should be conducted aiming to determine log colonization rates, which would indicate actual host usage in addition to attraction.

Ethanol is a widely used attractant for various species of Scolytinae, and is considered the standard lure type (Montgomery & Wargo, 1983; Miller & Rabaglia, 2009; Ranger et al., 2011; Reding et al., 2011; Kelsey et al., 2013). Nationwide exotic pest detection efforts regularly use ethanol to detect non-native bark and ambrosia beetles (Rabaglia et al., 2008). Ethanol is also emitted from cut logs as part of the decomposition process (Kelsey, 1994), which supports our use of cut logs as baits for subcortical insects. The inclusion of ethanol-baited traps led to increases in the overall numbers of insects caught in traps, especially of C. mutilatus and D. onoharaensis. Although no Scolytinae species were caught solely in traps baited with ethanol, certain Cerambycidae [e.g. Methia necydalia (F.), Monochamus notatus (Drury) and Xylotrechus saggitatus Germar] were caught only with ethanol-baited traps (Table 1). In addition, we identified six new state records (Table 1) in traps baited with trap-logs or ethanol

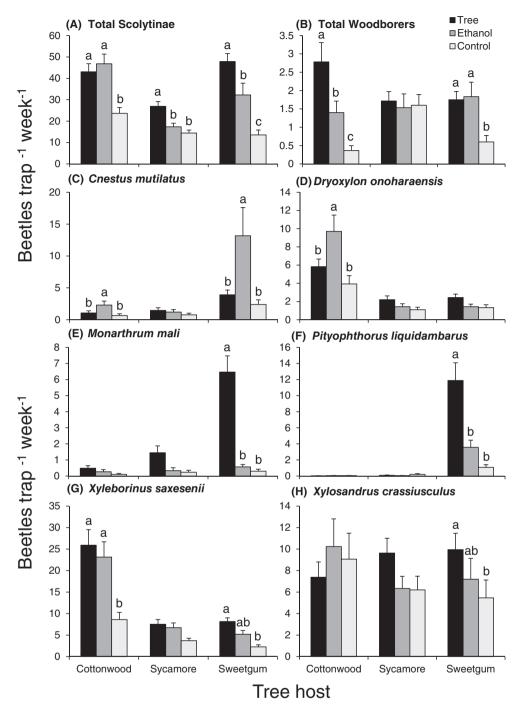


Figure 2 Effect of trap trees and ethanol lures on captures (mean \pm SE) of (A) total Scolytinae, (B) total woodborers, (C) *Cnestus mutilatus*, (D) *Dryoxylon onoharaensis*, (E) *Monarthrum mali*, (F) *Pityophthorus liquidambarus*, (G) *Xyleborinus saxesenii* and (H) *Xylosandrus crassiusculus* during summer 2013 in an intensively-managed hardwood plantation in South Carolina, U.S.A. Within an insect group x tree host, letters indicate significant differences in captures among traps over cut trees, ethanol lures, and controls (Wilcoxon rank sum test, $\alpha = 0.05$).

lures, as well as the northernmost capture of *C. distinctus* in North America.

By creating a 'hot-spot' of downed woody debris, we were able to determine whether certain subcortical insect species may cue to the debris instead of flying randomly throughout a forest searching for hosts; unbaited traps in the present study were used to assess the flying activity of subcortical insects in these hardwood plantations and/or the effect of visual attraction to a bole-shaped structure by tree-infesting insects. For example, indicator species analyses found that at least five scolytine beetle species (*H. rotundicollis, M. mali, X. saxesenii, P. liquidambarus* and *X. crassiusculus*) were associated primarily with trap-logs

Table 4 Wilcoxon rank-sum test of the effect of trap-trees and ethanol lures on captures of the most common subcortical insects in intensively-managed stands of three hardwood tree species during 2013 in South Carolina, U.S.A.

	Poplar		Sycamore		Sweetgum	
Таха	χ^2	Р	χ^2	Р	χ^2	Р
Total Scolytinae	19.06	< 0.001	15.98	< 0.001	44.15	< 0.001
Non-native Scolytinae	19.53	< 0.001	12.12	0.002	24.71	< 0.001
Total woodborers	19.37	< 0.001	1.29	0.525	11.95	0.003
Cnestus mutilatus	10.16	0.006	0.90	0.637	14.46	< 0.001
Dryoxylon onoharaensis	6.78	0.034	2.17	0.338	3.12	0.210
Monarthrum mali	4.22	0.121	5.49	0.064	50.53	< 0.001
Pityophthorus liquidambarus	0.34	0.844	2.38	0.304	27.49	< 0.001
Xyleborinus saxesenii	16.63	< 0.001	3.95	0.138	26.39	< 0.001
Xylosandrus crassiusculus	2.05	0.359	2.43	0.296	7.82	0.020

See also Fig. 2 for a graphical comparison of these data.

Significant P-values are indicated with boldface type.

Table 5 Significant indicator values for subcortical insect species that comprised > 4% of total captures in a given year on three tree species and two (2011) or three (2013) trap-types in an intensively-managed hardwood plantation in South Carolina, U.S.A.

Year	Tree species	Trap-type	Insect species	Observed indicator value (IV)	IV from randomized groups ^a Mean \pm SD	P-value ^b
2011	Poplar	Trap-log	Hypothenemus rotundicollis	38.6	24.0 ± 6.65	0.027
			Xyleborinus saxesenii	46.9	27.9 ± 5.28	0.002
	Sweetgum	Trap-log	Pityophthorus liquidambarus	57.1	24.5 ± 9.29	0.004
			Xylosandrus crassiusculus	40.6	25.9 ± 6.52	0.028
		Unbaited trap	Elaphidion mucronatum	35.8	24.7 ± 4.40	0.015
2013	Poplar	Ethanol	Dryoxylon onoharaensis	33.0	20.3 ± 3.26	0.001
	Sweetgum	Trap-log	Monarthrum mali	63.4	30.1 ± 8.04	< 0.001
	-		Pityophthorus liquidambarus	70.2	27.1 ± 9.26	< 0.001
		Ethanol	Cnestus mutilatus	48.9	27.6 ± 5.33	< 0.001

^aA Monte Carlo test at 1000 runs was used to generate randomized indicator values.

^bPairwise comparisons were performed between the observed and randomized indicator values for each species.

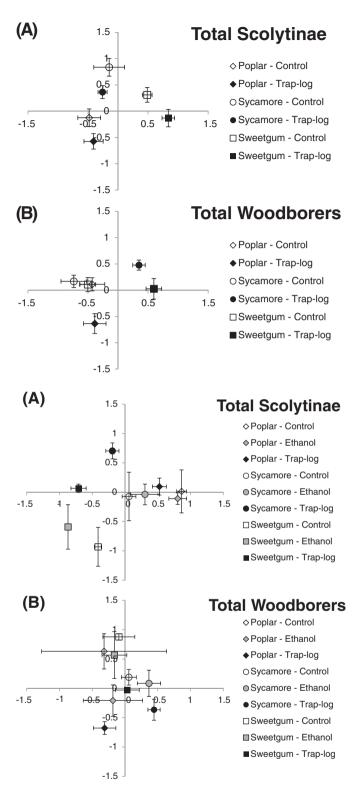
Significant *P*-values are indicated with boldface type.

of poplar and sweetgum, and not with the unbaited traps placed in stands. Three non-native species ($H.\ crudiae,\ H.\ californicus$ and $X.\ glabratus$) were also captured primarily with trap-logs suggesting the importance of cut plant material. More than three times as many woodborer or scolytine species were captured with trap-logs compared with ethanol-baited or unbaited control traps, including two non-native species (Table 6), highlighting the importance of using trap-logs or other natural baits for monitoring insect communities.

NMS ordination revealed that Scolytinae assemblages were largely influenced by tree species rather than trap-type (Figs 3 and 4). The subcortical insect assemblage associated with poplar trees was distinct from those of sweetgum or sycamore trees. In evidence, a total of 94 species were associated with poplar trees with 26 unique species such as *Xyleborus celsus* Eichhoff, *Trischidias atomas* Hopkins and *Hyperplatys maculata* Haldeman (Table S1). A total of 83 species were captured in sycamore and 79 in sweetgum-dominated stands, with only 16 and 14 unique species, respectively. Hence, poplar-dominated stands may have a more species-rich and unique subcortical beetle assemblage compared with sweetgum and sycamore in the study sites. These data suggest that, even with our relatively small plots (0.22 ha), these highly mobile insects are greatly influenced by plot composition.

Differences in species composition of subcortical insects among trapping methods were particularly evident for total woodboring insects. In 2011, the woodboring insect assemblage around trap-logs differed markedly among the three hosts; however, all control traps caught almost identical woodboring insects (Fig. 3). This trend suggests that the ambient or background woodboring insect assemblage was ubiquitous among the three tree species tested, although different species were attracted to trap-logs. In 2013, although the patterns were less distinct, woodboring insect assemblages were still more influenced by tree species than by the trapping method (Fig. 4). Hence, the use of trap-logs is a better method than unbaited traps for monitoring woodboring beetle assemblages in these plantation stands, although annual variation in community composition must be considered. Our woodborer capture rates (approximately 15 individuals per trap per year) were similar to other studies examining woodborers in the eastern U.S.A. (capture rates ranged from <1 to ~55 individuals per trap per year; Miller & Duerr, 2008; Dodds, 2011; Miller et al., 2011). Although trap-logs are effective for monitoring populations of bark and woodboring insects, ethanol-baited traps appear to be more effective than trap-logs or unbaited control traps for monitoring non-native Scolytinae, although care must be taken to account for species-specific attraction to different trapping methodologies.

In conclusion, both trap-logs and ethanol lures hold value as attractants compared with unbaited traps for subcortical insects, especially for non-native species detection and monitoring.



Although some non-native scolytinae will attack and injure live trees, few native Scolytinae species will do so (Kühnholz *et al.*, 2001; Coyle *et al.*, 2005). At present, it is unclear whether the non-native species captured in the present study are causing any economic or ecological damage or whether they are just utilizing

Figure 3 Total Scolytinae (A) and total woodborer (B) assemblages during summer 2011 in an intensively-managed hardwood plantation in South Carolina, U.S.A. The beetle assemblage captured in traps baited with cut poplar, sycamore, and sweetgum trap trees and control traps is compared for each group. The two graphed axes represented 58.9% of the variation for Scolytinae and 67.4% of the variation for woodborers.

Figure 4 Total Scolytinae (A) and total woodborer (B) assemblages during summer 2013 in an intensively-managed hardwood plantation in South Carolina, U.S.A. The beetle assemblage captured around traps baited with cut poplar, sycamore, and sweetgum trap trees, ethanol lures, and control traps is compared for each group. The two graphed axes represented 57.4% of the variation for Scolytinae and 60.1% of the variation for woodborers.

empty niches in these ecosystems (Stone *et al.*, 2007; Ranger *et al.*, 2010). Subcortical insect assemblages and populations differed based on the tree species and trapping methods. Additional key relevant questions for sustainable forest management include whether certain subcortical insect species may become

Table 6 Woodborers and Scolytinae captured only with a single trap type

Trap type Control	Ethanol	Trap-log
Dicerca obscura (F.) ^a Bellamira scalaris Say ^b Stenelytrana emarginata (F.) ^b Hylastes porculus Erichson ^c Hylocurus langstoni Blackman ^c Ips calligraphus (Germar) ^c	Methia necydalia (F.) ^b Xylotrechus saggitatus (Germar) ^b Cyrtinus pygmaeus (Haldeman) ^b Monochamus notatus (Drury) ^b	Buprestis apricans Herbst ^a Buprestis rufipes Olivier ^a Chalcophora virginiensis (Drury) ^a Anelaphus pumilis (Newman) ^b Knuliana cincta spinifera (F,) ^b Neoclytus mucronotus (F,) ^b Acanthocinus pusillus Kirby ^b Lepturges angulatus (LeConte) ^b Sterniclius variegatus (Haldeman) ^b Prionus imbricornis (L.) ^b Arhopalus rusticus (LeConte) ^b Coccotrypes distinctus (Motschulsky) ^c , ^d Xyleborus glabratus Eichhoff ^c , ^d Crypturgus alutaceus Schwart ^c Phleotribus frontalis (Oliver) ^c Pseudopityophthorus minutissimus (Zimmermann) ^c Pseudopityophthorus pruinosus (Eichhoff) ^c Trischidias atomus (Hopkins) ^c Xyleborus celsus Eichhoff ^c

^aBuprestidae.

^bCerambycidae.

^cScolytinae.

^dNon-native species.

either rare or abundant under different management scenarios; would the proportion of native versus non-native species change; and would certain insect species become pestilent in a monocultural environment.

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Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12101

Table S1. Total subcortical insect captures during summer 2011 and 2013 at the Savannah River Site near Aiken, South Carolina, U.S.A.

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