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ORIGINAL PAPER

Trap height considerations for detecting two economically important forest beetle guilds in southeastern US forests

Michael D. Ulyshen[1] · **Thomas N. Sheehan**[2]

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Abstract Wood-infesting beetles continue to be introduced into new areas at high rates through global trade. Once established, these species can be difficult or impossible to eradicate and can be extremely damaging to both ecosystems and economies. Efforts to detect newly arrived species before they become widespread represent an important early line of defense against these threats. There is considerable interest in optimizing trapping methods to best detect taxa of greatest concern. The purpose of this paper is to explore the role of trap height in influencing detection rates for two economically important guilds of forest Coleoptera [phloem/wood feeders (Buprestidae, Cerambycidae and some scolytine Curculionidae) and ambrosia beetles (scolytine Curculionidae)]. We examine this question using three datasets from southeastern US forests. In general, we found phloem/wood feeders and ambrosia beetles to exhibit contrasting vertical distribution patterns. Whereas phloem/wood feeders generally became more species-rich and abundant with increasing trap height, the opposite pattern was found for ambrosia beetles. Moreover, all species found to be significantly associated with the highest traps were phloem/wood feeders, whereas all but one of the species significantly associated with the lowest traps were ambrosia beetles. It is clear from these findings that detection efforts targeting both guilds will be most effective when traps are deployed at multiple heights in southeastern US forests.

Keywords Bark beetles · Invasive · Saproxylic · Vertical stratification · Woodborers · Xylophagous

Key message

- Decisions about trap height can greatly influence how effective these devices are at detecting target insect taxa, including forest pest species. Guidelines for general detection efforts remain poorly developed due to inconsistent findings among studies, however.
- We found two economically important forest beetle guilds to exhibit contrasting vertical distribution patterns, suggesting that detection efforts targeting both groups will be most successful when traps are deployed at multiple heights.

Introduction

Invasive species are an increasingly serious threat to ecosystems around the world, including forests. Human activities, such as global trade and travel, have allowed novel species to reach new locations where they can have negative economic and ecological effects. Aukema et al. (2010) report that over 450 non-indigenous insects have

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✉ Michael D. Ulyshen
mulyshen@fs.fed.us

[1] USDA Forest Service, 320 Green Street, Athens, GA 30602, USA

[2] Department of Entomology, University of Georgia, Athens, GA 30602, USA

colonized forest and urban trees in the continental US since European settlement. Of these, detection rates for non-indigenous phloem and wood-boring insects have increased dramatically in recent decades, representing 56% of new detections between 1980 and 2006 (Aukema et al. 2010). This is probably due to the widespread use of solid-wood packing materials such as crates and pallets during this time period. Indeed, some of the most destructive wood-boring beetle pests to reach the USA in recent years [e.g., emerald ash borer (*Agrilus planipennis* Fairmaire), Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky) and redbay ambrosia beetle (*Xyleborus glabratus* Eichhoff)] are presumed to have arrived through this route (Haack 2006). In 2001, the USDA Forest Service initiated the Early Detection and Rapid Response (EDRR) program to detect non-indigenous phloem and wood-boring insect species near ports, airports and other points of entry (Rabaglia et al. 2008). The EDRR program and others like it (Brockerhoff et al. 2006; Rassati et al. 2015; Wylie et al. 2008) are designed to detect and respond to newly introduced species before they become established across large areas. There is great interest in optimizing trapping methods to best detect targeted taxa, and many papers have been published on the efficacy of different trap designs, chemical attractants and trap positions (Allison and Redak 2017; Chénier and Philogéne 1989; Flechtmann et al. 2000; Graham et al. 2010; Hanks et al. 2012; Kendra et al. 2016; McIntosh et al. 2001; Miller and Rabaglia 2009; Morewood et al. 2002; Rassati et al. 2015).

Two guilds of phloem and wood-boring beetles are commonly targeted in these detection efforts. The first includes phloem/wood-feeding species of Cerambycidae, Buprestidae and certain curculionid scolytines (bark beetles). Most of these species bore through the bark of dying or dead trees and feed within the phloem and/or underlying wood and include some extremely damaging invasive species like emerald ash borer and Asian longhorned beetle. The other guild consists of ambrosia beetles (certain scolytines and platypodines as well as lymexylids) which create tunnels in wood within which symbiotic fungi are cultivated for food. Although most non-native ambrosia beetles and their fungal associates cause little damage within their introduced range, there are some notable exceptions such as the redbay ambrosia beetle (Fraedrich et al. 2008). Studying how readily resident (including native and established non-native species) phloem/wood-feeding and ambrosia beetle assemblages are captured using various trapping methods should help optimize trapping strategies for detecting newly introduced members of these guilds.

Decisions about trap placement are known to affect capture rates of both phloem/wood feeders and ambrosia beetles. A growing body of the literature indicates that both guilds are sensitive to trap height, for example, with some species being captured most readily in the crowns of trees, whereas others are largely concentrated near the ground (Dodds 2014; Graham et al. 2012; Hardersen et al. 2014; Schmeelk et al. 2016; Ulyshen and Hanula 2007; Wong and Hanks 2016). Although most studies targeting ambrosia beetles indicate these insects are more active overall near the ground (Hanula et al. 2011; Hardersen et al. 2014; Reding et al. 2011), this is not the case for all species (Dodds 2014; Roling and Kearby 1975) and some studies have shown no differences in scolytine abundance among strata (Maguire et al. 2014). Findings for phloem/wood feeders are even less consistent, with some studies reporting more species and/or individuals overall near the ground (Dodds 2014; Hardersen et al. 2014), others finding no differences among trap heights (Graham et al. 2012; Vance et al. 2003) and a few reporting significantly more species and individuals in the forest canopy (Maguire et al. 2014; Ulyshen and Hanula 2007). Such discrepancies make it difficult to determine the optimal trap height for detection efforts targeting both guilds. Few studies have considered the impact of trap height on capture rates of phloem/wood feeders and ambrosia beetles simultaneously (Dodds 2014; Ulyshen and Hanula 2007). In this paper, we combine three datasets to provide better clarity on the vertical distribution patterns of phloem/wood feeders and ambrosia beetles in forests of the southeastern USA.

Materials and methods

Studies

We consider data from three studies conducted in Georgia or South Carolina, USA, in 2005 and 2006. In each study, as described below, the same trap design (see below for description) was used to sample insects near the forest floor (0.5–1 m) and in the forest canopy (≥11 m). For two of the studies, traps were also placed at an intermediate height (5–6 m). Although results for the overall beetle community have already been published for two of the studies (Ulyshen and Hanula 2007; Ulyshen et al. 2010), those papers did not specifically explore differences in the vertical distribution patterns of ambrosia and phloem/wood-feeding beetles, the two feeding guilds considered here. Phloem/-wood feeders include species that feed either on the phloem layer beneath the bark or on wood. Many of these species begin feeding on phloem but become woodborers later in development. Phloem/wood feeders include the families Cerambycidae and Buprestidae as well as members of the curculionid subfamily Scolytinae. Ambrosia beetles include members of the subfamily Scolytinae. All scolytines collected in this study were assigned to one of these two guilds using information summarized by Kirkendall et al. (2015).

Study 1

A total of 24 flight intercept traps were operated for 2-week periods over a span of 24 weeks (April–October 2005) at a single hardwood-dominated location in Oglethorpe Co., Georgia. Beetles were sampled by suspending a pair of flight intercept traps at either 0.5 m or $\geq$15 m above the ground from twelve trees, evenly divided among four species: *Quercus phellos* L., *Liquidambar styraciflua* L., *Platanus occidentalis* L. and *Pinus taeda* L. The traps consisted of clear plastic panels (20 cm × 30 cm) attached to a white plastic bucket (diameter 16 cm, depth 15 cm). The traps were unbaited, and propylene glycol was used as the solution for preserving any captured insects. Distance between trap sets ranged from 11 to 915 m, with an average distance of 290 m. For more information about this study, see Ulyshen and Hanula (2007).

Study 2

A total of 48 flight intercept traps were operated for 1 week per month in March–August 2006 in Clarke, Oglethorpe and Greene counties, Georgia. The traps were equally divided among four forested locations dominated by bottomland hardwood forests. There were two ~2 ha plots at each location from which Chinese privet (*Ligustrum sinense* Lour.), an invasive shrub, had been eradicated using one of two methods. In one plot, privet had been removed by a machine that chopped the material into a mulch, whereas, in the other plot, the privet was felled by hand and the debris was left in piles <1 m high on the forest floor. The reference treatment in that study, where privet was left undisturbed, is not included in the current analysis to avoid the potentially confounding effects of privet invasion on how insects are vertically distributed. A set of traps identical to those described for study 1 was suspended from two trees in each plot (i.e., four trees per location), with a distance of ~50–100 m between the two trap sets in each plot. There were three unbaited traps per set, suspended at 0.5, 5 and 15 m above the ground. For more information about this study, see Ulyshen et al. (2010).

Study 3

A total of 36 flight intercept traps were operated for 2-week periods in June, August and October of 2006 and also in March 2007 on the Savannah River Site, South Carolina. Half of these were placed at an upland location [a forest dominated by Loblolly pine (*P. taeda* L.)], whereas the others were placed at a bottomland location (a hardwood-dominated forest) about 25 km from the upland forest. Sets of three unbaited traps were suspended from ropes thrown over branches of three living and three dead standing trees within each forest type, with trap sets within each location being separated by at least 100 m. The dead trees were killed for this purpose on June 5–6, 2006, by girdling them and spraying the wounds with glyphosate. Trees treated in this way appeared dead when beetle sampling began about two weeks later. The tree species used were *P. taeda* L., *Quercus nigra* L. and *L. styraciflua* L., and we had one living and one dead tree of each species in both upland and bottomland forests. Traps identical to those described for study 1 were suspended at 1, 6 and 11 m above the ground.

Statistical analysis

Counts were pooled across sampling periods for each study. Major response variables were the number of individuals (abundance) and the number of species (richness) per guild per trap. To merge the three datasets and to conduct analyses on the combined data from the three studies (to better identify general patterns), we defined the following class variables: study, location, treatment, trap set, height and guild. As described above, and summarized in Supplemental Table 1, there was just one location for study 1, four for study 2 and two (i.e., upland vs. bottomland) for study 3. Treatment refers to tree species for study 1 (oak, pine, sweetgum and sycamore), privet-removal method for study 2 (mulching machine or by hand) and tree condition for study 3 (living or dead). Trap set refers to each pair of traps in study 1 or triplet of traps in studies 2 and 3. Height was assigned to two or three levels depending on the study: lower (0.5–1 m), middle (5–6 m) and upper (>11 m). The two guilds were phloem/wood-feeding beetles and ambrosia beetles. Locations within study, trap sets within location and traps within trap sets were considered to represent different levels of replication and viewed as random, whereas height and guild were the effects of interest and considered fixed factors. Study was also viewed as fixed because of the inherent differences, including the length of sampling periods and the absence of one guild in study 3 (i.e., ambrosia beetles were not sampled in that study).

For our analyses of abundance patterns, we used abundance per week (log-transformed to improve normality and reduce variance heteroscedasticity) to account for differences in sampling periods among studies. To get a sense of how abundance per week was affected by the main effects (i.e., study, height and guild) and their interactions, we used SAS (SAS Institute 1999) to conduct an initial mixed model ANOVA that treated the combined data from the three studies as from an unbalanced split–split–split plot design (see above about different levels of replication). As described above, study, height, guild and all interaction terms were treated as fixed effects and we included three random effects representing variation among locations within studies, among trap sets within locations and among traps within trap sets. Effects involving guild were tested against residuals which represents within-trap error.

A second mixed model was carried out to specifically facilitate comparison of regressions of abundance and richness on height for the two guilds. The height effect was first partitioned into a linear component and a second component representing higher-order terms (i.e., lack-of-fit to linear) in order to check the importance of the linear term and to justify fitting straight line regressions. After confirming significant linear relationships, lack-of-fit to linear was pooled with error in the final models for both abundance and richness. The final model included intercepts and slopes for each guild in each study as the only fixed effects to specifically focus on the interaction between guild and trap height for each study separately. Random effects were the same as those used in the preliminary model. Significance of the slopes for the regression on height for each response variable (abundance per week (log-transformed) and species richness) was assessed for each combination of guild and study separately. We also compared the slopes for phloem/wood feeders and ambrosia beetles both averaged over studies 1 and 2 and separately (study 3 did not include ambrosia beetles).

We also performed sample-based rarefaction in EstimateS (Colwell 2013), using the Mao Tau expected richness function, to compare the expected number of species collected at different trap heights for each guild × study combination. The rarefaction curves were first plotted with the number of samples on the *x*-axis to reflect the number of species likely to be captured with the same trapping effort. Because there were large differences in abundance among trap heights, however, we replotted the curves against an *x*-axis of individual abundance, as recommended by Gotelli and Colwell (2001).

Finally, we performed indicator species analysis using PC-ORD (McCune and Mefford 2011) to determine which species were significantly associated with a particular trap height for studies 1 and 2 separately. Species present in fewer than three samples were excluded in these analyses, and abundance data were relativized by maxima. For study 2, the same dataset was used to perform non-metric multidimensional scaling to visualize differences in the composition of beetle assemblages at the three heights. The autopilot mode of PC-ORD was used to conduct this analysis using the Bray Curtis distance measure. This was followed by PERMANOVA to make pair-wise comparisons of community composition among the three heights.

Results

For the three studies combined, a total of 120 species and 2991 specimens of phloem/wood-feeding and ambrosia beetles were collected (Table 1). There were 103 species and 1533 specimens of phloem/wood feeders and 17 species and 1458 specimens of scolytine ambrosia beetles. Among phloem/wood feeders, there were 18 species and 273 specimens of Buprestidae, 67 species and 1060 specimens of Cerambycidae and 18 species and 200 specimens of bark beetles (i.e., non-ambrosia scolytine Curculionidae). Means and standard errors for these groups, by study and trap height, are provided in Supplemental Table 2. Based simply on the total numbers of species and individuals collected in each study, it is clear that high traps yield a more complete representation of the local phloem/wood-feeding beetle assemblage than traps near the forest floor. The highest traps yielded 17 (49%), 12 (63%) and 12 (100%) more phloem/wood-feeding species than the lowest traps in studies 1, 2 and 3, respectively (Table 2). Traps placed near the forest floor, by contrast, were much more efficient at sampling ambrosia beetles. The lowest traps yielded 2 (25%) and 5 (100%) more ambrosia beetle species than the highest traps in studies 1 and 2, respectively. These patterns are clearly depicted in Fig. 1 which shows the rarefaction results separately for the five guild × study combinations. It is also clear from Table 2 and Fig. 1 that traps placed at an intermediate height are about equally effective as the highest traps at sampling phloem/wood feeders and are also about as effective as the lowest traps at sampling ambrosia beetles. Re-scaling the *x*-axes to reflect differences in abundance among trap heights shows that although traps placed near the ground can accumulate more species of phloem/wood feeders per given number of specimens than those suspended in the canopy, many more trapping locations would be needed near the ground than in the canopy to achieve the same overall number of species (Fig. 2).

Abundance

All fixed effects in our initial mixed model ANOVA, including all interaction terms, were significant, with the strongest effect being the interaction between guild and height (Supplemental Table 3). Our second model, specifically focused on the interaction between guild and trap height for each study separately, indicated that phloem/wood-feeding beetle abundance significantly increased with increasing trap height in studies 1 ($t(68) = 3.05$, $p < 0.01$) and 2 ($t(68) = 2.89$, $p < 0.01$). A positive but statistically nonsignificant relationship was

Table 1 Complete list of species collected at different trap heights for studies 1, 2 and 3 (see text). Species were assigned to one of two guilds: phloem/wood feeders and ambrosia beetles

Family	Species	Guild	Study 1		Study 2			Study 3			Total
			>15 m	0.5 m	15 m	5 m	0.5 m	11 m	6 m	1 m	
Buprestidae	*Acmaeodera ornata* (Fabricius)	Phloem/wood	1	0	0	0	2	0	1	0	4
	Acmaeodera tubulus (Fabricius)	Phloem/wood	86	50	5	10	47	2	11	24	235
	Actenodes acornis (Say)	Phloem/wood	0	0	0	0	0	0	1	0	1
	Agrilus lecontei Saunders	Phloem/wood	0	0	3	5	0	0	0	0	8
	Agrilus defectus LeConte	Phloem/wood	1	0	0	0	0	0	0	0	1
	Anthaxia quercata (Fabricius)	Phloem/wood	0	0	0	0	1	0	0	0	1
	Anthaxia viridifrons Gory	Phloem/wood	0	0	1	0	0	0	0	0	1
	Buprestis lineata Fabricius	Phloem/wood	0	0	0	0	0	1	1	2	4
	Buprestis rufipes Olivier	Phloem/wood	0	0	0	0	0	1	0	0	1
	Chalcophora virginiensis (Drury)	Phloem/wood	0	0	0	0	1	0	1	0	2
	Chrysobothris chrysoela (Illiger)	Phloem/wood	0	1	0	1	0	0	0	0	2
	Chrysobothris femorata (Olivier)	Phloem/wood	0	0	1	0	2	0	0	0	3
	Chrysobothris sexsignata Say	Phloem/wood	0	0	1	0	0	0	0	0	1
	Chrysobothris viridiceps Melsheimer	Phloem/wood	3	0	0	0	0	0	0	0	3
	Dicerca asperata (Laporte & Gory)	Phloem/wood	0	0	0	0	0	1	1	0	2
	Dicerca punctulata (Schonherr)	Phloem/wood	0	0	0	0	0	0	1	0	1
	Mastogenius crenulatus Knull	Phloem/wood	3	0	0	0	0	0	0	0	3
	Unidentified	Phloem/wood	0	0	0	1	0	0	0	0	1
Cerambycidae	*Acanthocinus obsoletus* (Olivier)	Phloem/wood	0	0	0	0	0	3	0	1	4
	Aegomorphus modestus (Gyllenhal)	Phloem/wood	2	3	0	0	0	2	0	0	7
	Analeptura lineola (Say)	Phloem/wood	5	5	22	4	2	0	0	0	38
	Anelaphus parallelus (Newman)	Phloem/wood	10	1	1	0	0	0	0	0	12
	Anelaphus pumilus (Newman)	Phloem/wood	2	0	1	3	0	2	4	0	12
	Anelaphus villosus (Fabricius)	Phloem/wood	0	0	0	0	0	3	2	0	5
	Astylopsis macula (Say)	Phloem/wood	0	2	0	0	0	0	0	0	2
	Bellamira scalaris (Say)	Phloem/wood	0	0	0	1	0	0	0	0	1
	Brachyleptura circumdata (Olivier)	Phloem/wood	2	0	4	0	0	0	0	0	6
	Brachyleptura vagans (Olivier)	Phloem/wood	1	0	0	0	0	0	0	0	1
	Callimoxys sanguinicollis (Olivier)	Phloem/wood	1	0	3	2	0	0	0	0	6
	Clytoleptus albofasciatus (LaPorte & Gory)	Phloem/wood	0	0	1	1	0	0	0	0	2
	Clytus marginicollis Laporte & Gory	Phloem/wood	1	2	0	0	0	0	0	0	3
	Clytus ruricola (Olivier)	Phloem/wood	22	7	0	0	1	0	0	0	30
	Curius dentatus Newman	Phloem/wood	0	3	0	0	0	0	0	0	3
	Cyrtinus pygmaeus (Haldeman)	Phloem/wood	0	1	0	0	0	0	0	0	1
	Cyrtophorus verrucosus (Olivier)	Phloem/wood	20	0	2	0	0	0	0	0	22
	Eburia quadrigeminata (Say)	Phloem/wood	0	0	0	0	0	2	2	0	4
	Ecyrus dasycerus (Say)	Phloem/wood	2	0	0	0	0	1	1	0	4
	Elaphidion mucronatum (Say)	phloem/wood	0	0	1	0	0	2	0	1	4
	Enaphalodes atomarius (Drury)	Phloem/wood	0	0	0	0	0	1	0	0	1
	Enaphalodes rufulus (Haldeman)	Phloem/wood	1	0	0	0	0	0	0	0	1
	Euderces picipes (Fabricius)	Phloem/wood	12	0	1	1	0	0	0	0	14
	Euderces pini (Olivier)	Phloem/wood	0	0	6	4	0	3	7	1	21
	Euderces reichei LeConte	Phloem/wood	1	2	0	0	0	0	0	0	3
	Gaurotes cyanipennis (Say)	Phloem/wood	0	1	0	1	0	0	0	0	2
	Grammoptera exigua (Newman)	Phloem/wood	0	0	1	0	0	0	0	0	1
	Grammoptera haematites (Newman)	Phloem/wood	165	6	47	3	1	0	0	0	222

Table 1 continued

Family	Species	Guild	Study 1		Study 2			Study 3			Total
			>15 m	0.5 m	15 m	5 m	0.5 m	11 m	6 m	1 m	
	Hippopsis lemniscata (Fabricius)	Phloem/wood	0	0	0	0	1	0	0	0	1
	Judolia cordifera (Olivier)	Phloem/wood	0	0	0	0	2	0	0	0	2
	Knulliana cincta cincta (Drury)	Phloem/wood	0	0	0	0	0	0	1	0	1
	Leptostylus asperatus (Haldeman)	Phloem/wood	2	3	0	1	0	1	2	0	9
	Lepturges confluens (Haldeman)	Phloem/wood	2	0	0	0	0	0	0	0	2
	Liopinus alpha (Say)	Phloem/wood	0	0	0	0	0	1	1	0	2
	Lycochoriolaus lateralis (Olivier)	Phloem/wood	2	0	0	0	0	0	0	0	2
	Metacmaeops vittata (Swederus)	Phloem/wood	3	0	1	0	0	0	0	0	4
	Molorchus bimaculatus Say	Phloem/wood	78	3	77	65	5	7	8	0	243
	Monochamus titillator (Fabricius)	Phloem/wood	2	0	0	0	0	14	2	0	18
	Neoclytus acuminatus (Fabricius)	Phloem/wood	0	2	0	2	4	0	0	0	8
	Neoclytus scutellaris (Olivier)	Phloem/wood	0	0	0	0	0	6	2	0	8
	Oberea sp.	Phloem/wood	0	0	0	0	0	0	1	0	1
	Obrium maculatum (Olivier)	Phloem/wood	0	0	0	1	0	1	0	0	2
	Obrium rufulum Gahan	Phloem/wood	0	0	1	0	0	0	0	0	1
	Orthosoma brunneum (Forster)	Phloem/wood	0	13	0	0	0	0	0	2	15
	Parelaphidion incertum (Newman)	Phloem/wood	0	0	0	0	0	1	1	1	3
	Phymatodes amoenus (Say)	Phloem/wood	0	0	1	0	0	0	0	0	1
	Prionus pocularis Dalman	Phloem/wood	0	0	0	0	0	0	0	2	2
	Psyrassa pertenuis (Casey)	Phloem/wood	0	0	1	0	0	0	0	0	1
	Rhagium inquisitor (Linnaeus)	Phloem/wood	1	0	0	0	0	0	0	0	1
	Saperda lateralis Fabricius	Phloem/wood	0	1	0	0	0	0	0	0	1
	Scaphinus muticus (Fabricius)	Phloem/wood	0	0	0	0	0	0	1	2	3
	Stenocorus cinnamopterus (Randall)	Phloem/wood	1	0	1	0	0	0	0	0	2
	Stenocorus cylindricollis (Say)	Phloem/wood	2	0	0	0	0	0	0	0	2
	Stenosphenus notatus (Olivier)	Phloem/wood	1	0	0	0	0	0	0	0	1
	Strangalia acuminata (Olivier)	Phloem/wood	1	0	0	0	0	0	0	0	1
	Strangalia famelica Newman	Phloem/wood	3	0	0	0	0	0	0	0	3
	Strangalia luteicornis (Fabricius)	Phloem/wood	44	8	7	6	5	0	0	0	70
	Styloleptus biustus (LeConte)	Phloem/wood	4	3	0	0	0	0	0	0	7
	Tilloclytus geminatus (Haldeman)	Phloem/wood	12	1	0	0	0	1	2	0	16
	Trachysida mutabilis (Newman)	Phloem/wood	8	0	0	0	1	0	0	0	9
	Trigonarthris minnesotana (Casey)	Phloem/wood	1	0	0	2	1	0	0	0	4
	Typocerus acuticauda Casey	Phloem/wood	34	4	2	0	0	0	0	0	40
	Typoceras zebra (Olivier)	Phloem/wood	17	5	3	11	54	0	1	0	91
	Urgleptes facetus (Say)	Phloem/wood	0	0	0	1	0	0	0	0	1
	Urogrpahis fasciatus (DeGeer)	Phloem/wood	4	0	0	0	0	5	1	5	15
	Xylotrechus colonus (Fabricius)	Phloem/wood	2	1	0	0	0	9	0	1	13
	Xylotrechus sagittatus (Germar)	Phloem/wood	0	0	0	0	0	10	5	6	21
Curculionidae	*Ambrosiodmus obliquus* (LeConte)	Ambrosia	2	59	4	2	1	na	na	na	68
	Ambrosiodmus tachygraphus (Zimmerman)	Ambrosia	0	0	0	2	0	na	na	na	2
	Ambrosiophilus atratus (Eichhoff)	Ambrosia	0	0	1	0	2	na	na	na	3
	Chramesus chapuisi LeConte	Phloem/wood	1	0	0	0	0	na	na	na	1
	Cnesinus strigicollis LeConte	Phloem/wood	0	0	1	1	0	na	na	na	2
	Corthylus columbianus Hopkins	Ambrosia	0	0	0	0	1	na	na	na	1
	Crypturgus alutaceus Schwarz	Phloem/wood	1	1	0	0	0	na	na	na	2

Table 1 continued

Family	Species	Guild	Study 1		Study 2			Study 3			Total
			>15 m	0.5 m	15 m	5 m	0.5 m	11 m	6 m	1 m	
	Dryoxylon onoharaensis (Murayama)	Ambrosia	7	3	4	1	3	na	na	na	18
	Euwallacea interjectus (Blandford)	Ambrosia	0	0	0	3	4	na	na	na	7
	Euwallacea validus (Eichhoff)	Ambrosia	2	29	0	0	0	na	na	na	31
	Gnathotrichus materiarus (Fitch)	Ambrosia	0	2	0	0	0	na	na	na	2
	Hylastes tenuis Eichhoff	Phloem/wood	0	18	1	0	0	na	na	na	19
	Hylesinus aculeatus Say	Phloem/wood	0	2	1	0	0	na	na	na	3
	Hylocurus flaglerensis Blackman	Phloem/wood	1	2	0	0	0	na	na	na	3
	Hylocurus rudis (LeConte)	Phloem/wood	0	0	0	1	0	na	na	na	1
	Hypothenemus spp.	Phloem/wood	28	21	1	10	6	na	na	na	66
	Ips grandicollis (Eichhoff)	Phloem/wood	0	0	0	1	0	na	na	na	1
	Monarthrum fasciatum (Say)	Ambrosia	2	0	0	1	0	na	na	na	3
	Monarthrum mali (Fitch)	Ambrosia	2	1	0	0	1	na	na	na	4
	Orthotomicus caelatus (Eichhoff)	Phloem/wood	1	1	0	0	0	na	na	na	2
	Phloeotribus sp.	Phloem/wood	1	0	0	0	0	na	na	na	1
	Phloeotribus frontalis (Olivier)	Phloem/wood	0	0	0	2	1	na	na	na	3
	Pityogenes meridians Blackman	Phloem/wood	0	1	0	0	0	na	na	na	1
	Pityophthorus spp.	Phloem/wood	23	6	0	1	0	na	na	na	30
	Pseudopityophthorus spp.	Phloem/wood	1	0	0	0	0	na	na	na	1
	Pseudothysanoes spp.	Phloem/wood	1	1	0	0	0	na	na	na	2
	Scolytus multistriatus (Marsham)	Phloem/wood	2	1	0	0	0	na	na	na	3
	Scolytus muticus Say	Phloem/wood	6	2	26	18	7	na	na	na	59
	Xyleborinus saxesenii (Ratzeburg)	Ambrosia	2	18	2	5	64	na	na	na	91
	Xyleborus atratus Eichhoff	Ambrosia	0	1	0	0	0	na	na	na	1
	Xyleborus bispinatus Eichhoff	Ambrosia	0	0	0	3	31	na	na	na	34
	Xyleborus ferrugineus Fabricius	Ambrosia	0	16	0	0	0	na	na	na	16
	Xyleborus xylographus (Say)	Ambrosia	4	60	0	0	0	na	na	na	64
	Xylosandrus crassiusculus (Motschulsky)	Ambrosia	9	99	9	68	866	na	na	na	1051
	Xylosandrus germanus (Blandford)	Ambrosia	0	0	0	4	58	na	na	na	62
		Total	661	472	245	249	1175	80	61	48	2991

Table 2 Summary of phloem/wood-feeding and ambrosia beetle abundance and richness by study and trap height

Study	Height	*n*	Phloem/wood feeders				Ambrosia beetles			
			Abundance		Richness		Abundance		Richness	
			Total	Mean ± SE	Total	Mean ± SE	Total	Mean ± SE	Total	Mean ± SE
1	>15 m	12	631	52.58 ± 6.32	52	14.33 ± 0.76	30	2.50 ± 0.58	8	1.92 ± 0.40
	0.5 m	12	184	15.33 ± 3.46	35	7.00 ± 1.02	288	24.00 ± 4.20	10	5.75 ± 0.30
2	15	16	225	14.06 ± 2.30	31	4.44 ± 0.47	20	1.25 ± 0.32	5	0.88 ± 0.22
	5	16	160	10.00 ± 1.26	28	4.50 ± 0.48	89	5.56 ± 1.33	9	1.94 ± 0.23
	0.5	16	144	9.00 ± 4.69	19	2.38 ± 0.47	1031	64.44 ± 14.29	10	3.88 ± 0.30
3	11	12	80	6.67 ± 1.66	24	3.08 ± 0.57	na	na	na	na
	6	12	61	5.08 ± 1.10	25	3.50 ± 0.66	na	na	na	na
	1	12	48	4.00 ± 1.45	12	1.83 ± 0.32	na	na	na	na

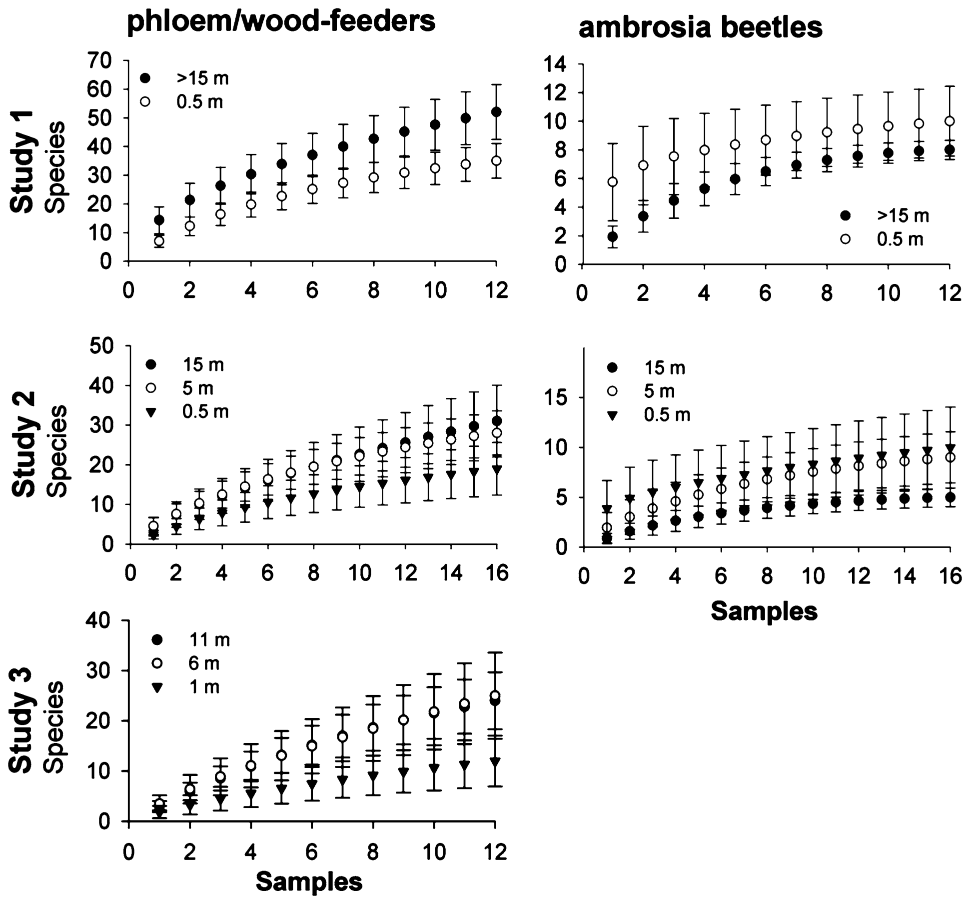

Fig. 1 Sample-based rarefaction for studies 1, 2 and 3, showing estimated numbers of species (S_{est}) with 95% confidence intervals

observed for this guild in study 3 ($t(68) = 0.96$, $p = 0.34$). Our second model also indicated that ambrosia beetle abundance significantly decreased with increasing trap height in studies 1 ($t(68) = -2.73$, $p < 0.01$) and 2 ($t(68) = -10.88$, $p < 0.001$). Our tests for equality of slopes found significant differences between phloem/wood feeders and ambrosia beetles both averaging over studies 1 and 2 ($t(68) = 9.96$, $p < 0.001$) and also separately in studies 1 ($t(68) = 4.09$, $p < 0.001$) and 2 ($t(68) = 9.74$, $p < 0.001$). These patterns can be visualized in Fig. 3.

Richness

Similar to the patterns for abundance, we found phloem/-wood-feeding beetle richness significantly increased with increasing trap height in studies 1 ($t(68) = 9.06$, $p < 0.001$) and 2 ($t(68) = 2.63$, $p = 0.01$). A positive but statistically nonsignificant relationship was observed for the species richness of this guild in study 3 ($t(68) = 1.63$, $p = 0.11$). Our second model also indicated that ambrosia beetle richness significantly decreased with increasing trap height in studies 1 ($t(68) = -4.66$, $p < 0.001$) and 2 ($t(68) = -4.26$, $p < 0.001$). Our tests for equality of slopes found significant differences between phloem/wood feeders and ambrosia beetles both averaging over studies 1 and 2 ($t(68) = 10.15$, $p < 0.001$) and also separately in studies 1 ($t(68) = 9.73$, $p < 0.0001$) and 2 ($t(68) = 4.88$, $p < 0.001$).

Indicator species

For study 1, eight and seven beetle species were significantly associated with traps placed in the canopy and near the ground, respectively (Table 3). All the species associated with the canopy were phloem/wood-feeding cerambycids, whereas all but one of those associated with ground traps were ambrosia beetles. A single phloem/wood-feeding species, the prionine cerambycid *Orthosoma brunneum* (Forster), was significantly associated with traps near the forest floor. For study 2, three and four species were significantly associated with traps placed in the canopy and near the ground, respectively (Table 4). Again, all the species associated with the canopy traps were phloem/-wood-feeding cerambycids, while all those associated with the lowest traps were ambrosia beetles. Two cerambycid species were associated with highest traps in both studies (*Grammoptera haematites* (Newman) and *Molorchus bimaculatus* Say), and two species of ambrosia beetles

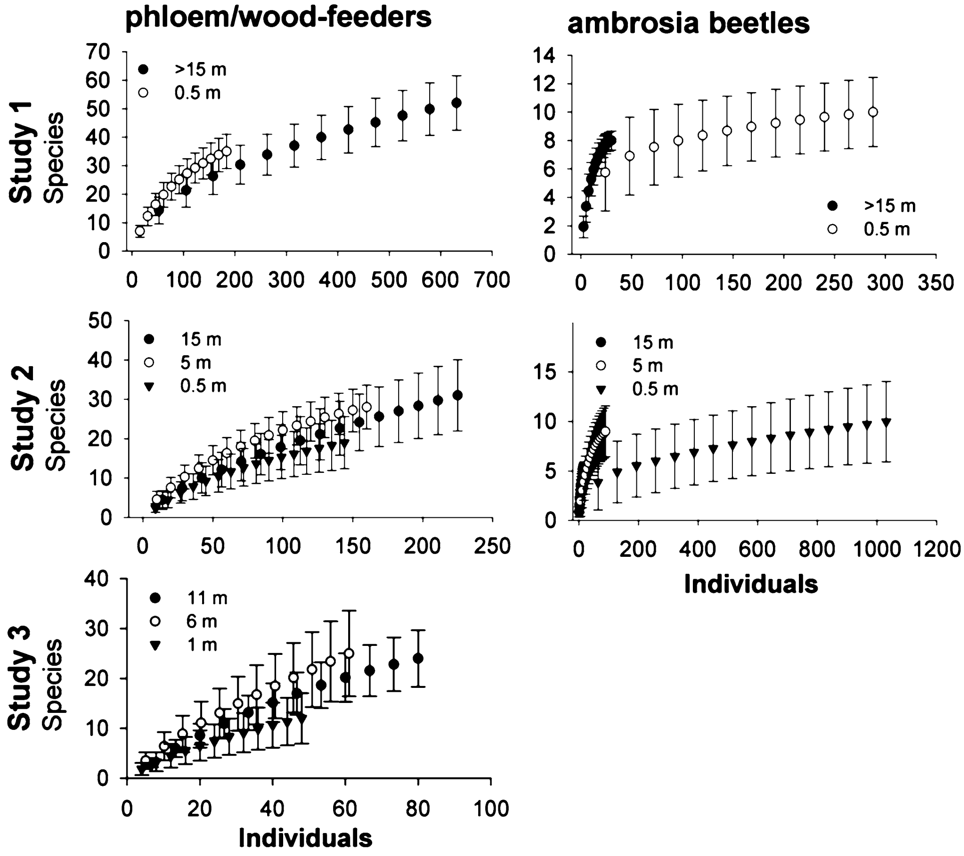

Fig. 2 Sample-based rarefaction, re-scaled by estimated number of individuals, for studies 1, 2 and 3. Estimated numbers of species (S_{est}) with 95% confidence intervals are shown

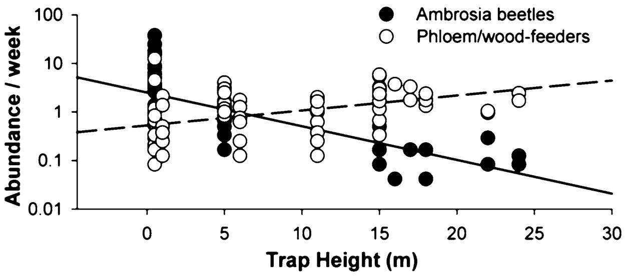

Fig. 3 Relationships between abundance per week (note the log-scale) and trap height, pooled across all three studies, for ambrosia beetles (*black dots*, *solid line*) and phloem/wood-feeding beetles (*white dots*, *dashed line*)

were associated with the lowest traps in both studies [*Xyleborinus saxesenii* (Ratzeburg) and *Xylosandrus crassiusculus* (Motschulsky)].

Community composition

Non-metric multidimensional scaling yielded a three-dimensional solution with a final stress of 17.46. The R^2 values were 0.27, 0.19 and 0.16 for the three axes. It is clear from the two-dimensional depiction of these results (using axes 1 and 2 which had the highest R^2 values) that the beetle assemblage sampled at 0.5 m was compositionally distinct from that sampled at 5 or 15 m (Fig. 4). There was considerable overlap in assemblages at 5 and 15 m, however. The PERMANOVA results support these conclusions, indicating that the beetle assemblage sampled at 0.5 m was compositionally distinct from that at 5 m ($t = 2.8$, $p < 0.001$) or 15 m ($t = 3.4$, $p < 0.001$). There was no significant difference in assemblage composition between traps placed at 5 and 15 m ($t = 1.3$, $p = 0.08$), however.

Discussion

Our results show that phloem/wood-feeding beetles and ambrosia beetles exhibit contrasting vertical distribution patterns in hardwood-dominated forests of the southeastern USA. We can generally conclude (1) a positive relationship between both abundance and richness and trap height for phloem/wood-feeding beetles and (2) a negative relationship between both abundance and richness and trap height for ambrosia beetles. Moreover, all indicator taxa found to be significantly associated with the highest traps were phloem/wood feeders and all but one of the species associated with the lowest traps were ambrosia beetles. It is clear from these findings that detection efforts targeting

Table 3 Significant trap height associations for study 1 based on indicator species analysis. Guild refers to phloem/wood feeders (p/w) or ambrosia beetles (a)

Height association	Species	Guild	IV	*p*
≥15 m	*Anelaphus parallelus* (Newman)	p/w	60.6	0.007
	Clytus ruricola (Olivier)	p/w	63.2	0.011
	Cyrtophorus verrucosus (Olivier)	p/w	66.7	0.0012
	Grammoptera haematites (Newman)	p/w	96.5	0.0002
	Molorchus bimaculatus Say	p/w	96.3	0.0002
	Strangalia luteicornis (Fabricius)	p/w	70.5	0.0084
	Trachysida mutabilis (Newman)	p/w	41.7	0.038
	Typocerus acuticauda Casey	p/w	52.2	0.053
0.5 m	*Ambrosiodmus obliquus* (LeConte)	a	96.7	0.0002
	Euwallacea validus (Eichhoff)	a	78	0.0014
	Orthosoma brunneum (Forster)	p/w	50	0.0134
	Xyleborinus saxesenii (Ratzeburg)	a	60	0.0182
	Xyleborus ferrugineus (Fabricius)	a	66.7	0.0026
	Xyleborus xylographus (Say)	a	93.7	0.0002
	Xylosandrus crassiusculus (Motschulsky)	a	91.7	0.0002

Table 4 Significant trap height associations for study 2. Guild refers to phloem/wood feeders (p/w) or ambrosia beetles (a)

Height association	Species	Guild	IV	*p*
15 m	*Euderces pini* (Olivier)	p/w	22.5	0.0356
	Grammoptera haematites (Newman)	p/w	51.8	0.001
	Molorchus bimaculatus Say	p/w	49.1	0.0064
0.5 m	*Xyleborinus saxesenii* (Ratzeburg)	a	78.9	0.0002
	Xyleborus bispinatus Eichhoff	a	51.3	0.0004
	Xylosandrus crassiusculus (Motschulsky)	a	91.8	0.0002
	Xylosandrus germanus (Blandford)	a	81.9	0.0002

both guilds will be most effective when traps are deployed at multiple heights, at least in southeastern US forests. Because traps placed at 5 and 15 m in study 2 yielded similar total numbers of phloem/wood-boring beetle species and the composition of the entire beetle assemblage (i.e., both guilds combined) did not differ significantly between these two heights, traps placed just 5 m above the ground may provide nearly the same benefit to detection efforts as those placed much higher. This is consistent with Weiss et al. (2016) who found beetle assemblages to overlap greatly among traps placed at 7, 14 and 21 m above the ground in both lowland and upland forests in the Czech Republic. By contrast, the assemblages collected at 0.4 and 1.2 m in that study were distinct from one another as well as from all the higher traps. These findings suggest that it may not be necessary to deploy detection traps at great heights to obtain a good representation of the local beetle fauna. It is important to note that some species are known to be more readily captured in the higher traps

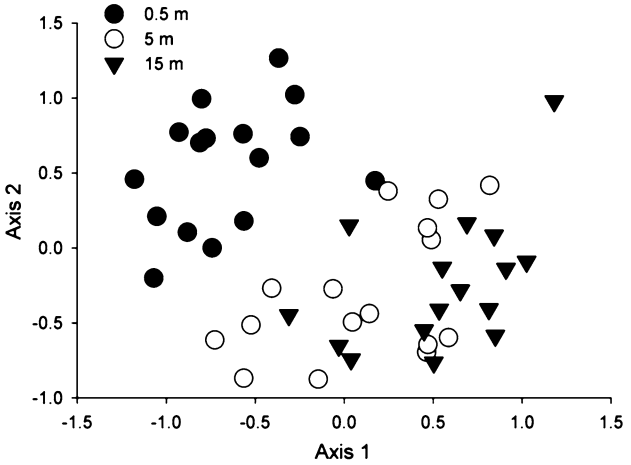

Fig. 4 Non-metric multidimensional scaling ordination for study 2. Phloem/wood-feeding and ambrosia beetles were combined for this analysis, and the three trap heights are represented by different symbols

(Table 4), however, and these could be missed if trapping is limited to within just a few meters above the ground.

The findings from this and previous studies addressing the vertical distribution patterns of phloem/wood-feeding and/or ambrosia beetles are somewhat inconsistent. Although it has commonly been shown that fungus feeders are generally more concentrated near the ground and phloem/wood feeders are frequently more numerous in the canopy (Weiss et al. 2016), some studies have reported the opposite patterns and there are many exceptions at the species level. For both guilds, the activities of many species are largely restricted to a particular height and so the patterns at the family or guild level are to some extent determined by the combination of species present. Inconsistent findings among studies are probably also attributable to differences in selected trap heights among studies. The importance of trap height was demonstrated very clearly by Weiss et al. (2016), for example, who found major compositional changes in beetle communities captured at 0.4, 1.2 and ≥ 7 m but only weak differences in composition among traps placed at 7, 14 and 21 m. Another factor potentially responsible for inconsistent results among studies concerns differences in plant diversity among study areas. Arthropod assemblages are expected to be more concentrated near the ground in forests with low plant diversity (Ulyshen 2011), for instance, and this may be the case for cerambycid communities. This may help explain why, for example, Dodds (2014) found cerambycids to be more species-rich overall near the ground in pine forests in Maine, whereas they were shown in the current study to exhibit the opposite pattern in southeastern US forests with comparatively high plant diversity.

Climatic gradients likely play an especially important role in determining how insects are vertically distributed in forests. For example, temperature and humidity are known to vary greatly from the forest floor to the tree tops with stronger gradients occurring in mature closed-canopy forests compared to more open stands (Ulyshen 2011). These patterns are largely driven by changes in sun exposure, and sun-loving insects, including many cerambycids, can be expected to be attracted to the relatively bright and warm conditions of the canopy in closed forests. In French Guiana, Lee et al. (2014) found some cerambycids make a seasonal shift in stratum preference. During the dry season, these species appear to more readily colonize wood provided near the forest floor but preferentially colonize wood in the canopy during the wet season. According to the researchers, this shift may be due to excessively high substrate moisture content near the forest floor during the wet season. High moisture content has been shown to negatively affect the reproductive success of other cerambycid species (Hanks et al. 1999), possibly by reducing oxygen availability. Another possible explanation is that there is a reduced risk of fungal disease as well as parasitism in the relatively dry conditions of the canopy compared to the forest floor as Fernandes and Price (1992) found for gall-forming insects. By contrast, ambrosia beetles may be less sensitive to high moisture content because they live in tunnels open to the external environment and their fungal symbionts may grow better in more humid environments.

The extent to which the concentration of phloem/wood-feeding beetles in the forest canopy is due to resource availability versus preferences for microclimatic conditions remains unclear. If these patterns are driven primarily by differences in temperature and humidity, communities can be expected to exhibit less vertical stratification in open environments with less extreme climatic gradients. The forest edge is one such environment where canopy conditions (e.g., sun exposure, higher temperature and lower humidity) are thought to extend to the ground and weaker stratification patterns have been reported at these locations compared to the forest interior. In Switzerland, Wermelinger et al. (2007) found Buprestidae to be less limited to the canopy on the forest edge than in the forest interior, for example. Also in Europe, Vodka and Cizek (2013) found saproxylic beetle diversity to be at least 50% higher at the forest edge than in the interior regardless of trap height. They also found beetles to exhibit stronger vertical stratification in the forest interior than at the edge, with a greater proportion of species in the forest interior being more abundant in canopy traps compared to at the forest edge. The researchers concluded that the vertical stratification of saproxylic beetle communities is highly context-dependent and determined in large part by sun exposure. Such findings suggest that detection efforts may be more effective and trap height less important at the forest edge than in the interior. Studies specifically addressing this question are needed.

The findings from this study indicate that the optimal trap height for detection depends on which group—phloem/wood-feeding beetles or ambrosia beetles—is being targeted. If targeting the former, traps placed high above the ground may yield the greatest variety of taxa. Traps placed near the forest floor may be more effective for ambrosia beetles, however. While our indicator species analyses support these general recommendations, it should be noted that many previous studies have reported exceptions to these patterns at the species level (Dodds 2014; Graham et al. 2012; Schmeelk et al. 2016; Wong and Hanks 2016) and one species of phloem/wood feeder captured in study 1 presented here was significantly associated with traps near the ground. Consistent with Weiss et al. (2016), our findings also suggest that traps placed at an intermediate height (5 m) perform almost as well at capturing phloem/wood feeders and ambrosia beetles as those placed higher in the canopy and just above the forest floor, respectively. This may therefore be a good placement when it is not possible or practical to sample at multiple heights.

Finally, it should be noted that the traps constructed specifically for use in these studies differ in several important ways from those typically used in many detection efforts. Multiple funnel traps, large panel traps, and Malaise traps, for example, are commercially available options used in many studies (Dodds et al. 2015). In addition, it is commonplace for one or several chemical attractants (e.g., pheromones or host volatiles) to be attached to traps as these are known to greatly increase captures of many phloem/wood feeders and ambrosia beetles (Hanks et al. 2012; Miller and Rabaglia 2009). More research is needed to determine how the performance of different trap types and traps baited with various chemical attractants may differ across a range of trap heights. Depending on the attraction radius of various chemical lures, and the willingness of insects to move vertically, baited traps have the potential to somewhat reduce the importance of trap height in detection efforts. There is a shortage of information on the ranges of attraction for various compounds, but the anti-aggregation pheromone verbenone has been shown to have an effective range of <4 m for *Dendroctonus* (Fettig et al. 2009; Miller 2002). If other compounds act across similarly short distances, adding baits to traps may have only modest effects on observed vertical distribution patterns. Studies addressing this question would be of interest.

Author contributions

MDU conducted experiments and analyzed the data. MDU and TNS wrote the paper.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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