



Vertical and horizontal distribution of bark and woodboring beetles by feeding guild: is there an optimal trap location for detection?

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Abstract

Bark and woodboring beetles include some of the most economically important forest pests. Understanding how these species are distributed in forests is critical for optimizing detection strategies. We placed traps at three heights above ground level at the edge and in the interior of two forests and focused on two groups: phloem/wood-feeding beetles (Coleoptera: Buprestidae, Cerambycidae, and some Curculionidae: Scolytinae) and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae). We recorded temperature, humidity, and canopy cover for each trap. Species richness increased with height for phloem-/wood-feeding beetles and decreased with height for ambrosia beetles, even when microclimatic variables were included in the models. Community composition differed greatly among heights but little between horizontal placements. Indicator species analysis found eight species (seven of which were phloem/wood feeders) to be significantly associated with traps at 15 m and eight species (six of which were ambrosia beetles) associated with traps at 0 m. Only one species was significantly associated with the forest edge and one species associated with the interior, but a total of thirteen species were associated with particular combinations of horizontal placement and height. While distance from the forest edge was an important factor for some species, trap height more strongly influenced the species of phloem-/wood-feeding and ambrosia beetles captured and is a more important consideration with respect to optimizing trapping programs.

Keywords Bark and ambrosia beetles · Saprophytic · Microclimate · Non-native species · Invasive

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Key message

- Few studies have simultaneously explored the influence of trap height and position relative to the forest edge on capture rates of insects.
- The role microclimatic variables play in driving these patterns remains mostly unknown.
- Ambrosia and phloem-/wood-feeding beetles were more strongly associated with the lower and higher traps, respectively, even after taking microclimatic variables into account.
- Community composition varied greatly among heights but relatively little between the forest edge and interior.

Introduction

Invasive species are considered one of the most serious threats facing biodiversity, perhaps second only to habitat loss (Wilcove et al. 1998; Bellard et al. 2016). The

introduction of new species can negatively affect ecosystems in many ways such as through competition, predation, habitat structure alteration, niche displacement, and trophic cascades (Mooney and Cleland 2001; Walsh et al. 2016). Invasive species cause significant economic damage as well, with an estimated cost to the USA alone of almost \$120 billion per year (Pimentel et al. 2005).

Some of the most economically important forest insect pests include beetles that bore into trees. These can be separated into two general feeding guilds: fungal feeders (“ambrosia beetles”) and phloem/wood feeders. Fungal feeders consist of members in the curculionid subfamilies Scolytinae and Platypodinae, as well as the small family of ship-timber beetles (Coleoptera: Lymexylidae). These ambrosia beetles create galleries inside trees in which they cultivate a symbiotic fungus for food. This relationship between beetle and fungus has evolved independently numerous times between multiple clades of both beetles and fungi (Hulcr and Stelinski 2017). Ambrosia beetles feed on the fungal symbiont, not the tree directly; however, beetles can kill trees by inoculating them with associated fungi. One of the most damaging invasive ambrosia beetles in North America is the redbay ambrosia beetle (*Xyleborus glabratus* Eichoff, 1877), which carries a symbiotic fungus (*Raffaelea* sp.) that causes laurel wilt disease. This disease has already eliminated over 90% of redbay trees (*Persea borbonia* (L.) Spreng.) on the southeastern US coast and also poses a threat to the avocado industry (Fraedrich et al. 2008; Spiegel and Leege 2013). Several other species of ambrosia beetle have successfully invaded North America and are among the most abundant species of bark beetles in surveys, e.g., *Cnestus mutilatus* (Blandford, 1894) (Gandhi et al. 2009; Leavengood 2013; Barringer 2016), *Xylosandrus crassiusculus* (Motschulsky, 1866) (Werle et al. 2011), and *Xylosandrus compactus* (Eichoff, 1875) (Werle et al. 2011).

The phloem-/wood-feeding guild consists of long-horned beetles (Coleoptera: Cerambycidae), jewel beetles (Coleoptera: Buprestidae), and bark beetles (non-ambrosia scolytines). These beetles bore into trees and create galleries, where they feed on the phloem and/or wood directly. While adult Scolytinae primarily feed only on the host tree (Anderson 2002) or fungal symbiont, adults of Cerambycidae and Buprestidae exhibit diverse feeding patterns such as eating pollen and flowers, foliage, bark, or nothing at all during the adult stage (Bellamy and Nelson 2002; Turnbow and Thomas 2002). Most of these species bore into dead or dying trees, but some species can attack healthy trees (Hanks et al. 1999). The buprestid *Agrilus planipennis* Fairmare, 1888 (emerald ash borer) continues to spread throughout North America where it was introduced from China and has already killed hundreds of millions of healthy ash trees and caused billions of dollars’ worth of damages (Herms and McCullough 2014). Similarly, Nowak et al. (2001) estimated

the cerambycid *Anoplophora glabripennis* (Motchulsky, 1853) (Asian long-horned beetle) could cause maximum potential damage of \$669 billion in the USA.

Detecting new arrivals quickly so that efforts can be made to eradicate them before they spread widely is an important line of defense. This is especially imperative near ports or other common entry points. The Animal and Plant Health Inspection Service (APHIS) launched the Cooperative Agricultural Pest Survey to detect exotic plant pests, disease, and weeds. The US Forest Service established a similar program, the Early Detection and Rapid Response Program (EDRR) in 2001, which found five new, non-native species of bark and ambrosia beetles in its first 5 years (Rabaglia et al. 2008). Other examples of international programs include those ongoing in New Zealand (Brockerhoff et al. 2006), Australia (Wylie et al. 2008), and China (Wan and Yang 2016).

To make these programs as effective as possible, there is interest in information that optimizes trapping techniques. Examples of variables already tested include trap type (Francese et al. 2008; Dodds et al. 2010, 2015; Allison and Redak 2017), lure type (Miller et al. 2015), lure placement (Dodds et al. 2010; Miller et al. 2013), and trap color (Francese et al. 2008; Allison and Redak 2017). It is well established that forest insect communities exhibit a high degree of vertical stratification in both tropical (Basset et al. 2003; Grimbacher and Stork 2007; Davis et al. 2011; Sebek et al. 2016; Stork et al. 2016) and temperate (Ulyshen 2011; Stireman et al. 2012; Maguire et al. 2014; Holdsworth et al. 2016; Weiss et al. 2016) forests, although these patterns are sometimes inconsistent among taxa. A notable amount of research supports differences in distribution relative to canopy height for members of Cerambycidae, Buprestidae, and Scolytinae, as well as between the two feeding guilds, although often with conflicting results.

Particularly conflicting patterns have been reported for Cerambycidae, with some studies showing higher abundance and/or species richness at the ground level (Vance et al. 2003; Wermelinger et al. 2007; Dodds 2014) and other studies showing higher abundance and/or species richness in the canopy (Ulyshen and Hanula 2007; Maguire et al. 2014; Rassati et al. 2018). Even when a group exhibits no significant differences in species richness or abundance, community composition can still differ. For example, numerous studies have found several species to be associated only with particular heights (Vance et al. 2003; Graham et al. 2012; Schmeelk et al. 2016). Webster et al. (2016) recorded several cerambycid species new to Nova Scotia—six exclusively from traps in the canopy and five exclusively from traps near the forest floor. Buprestids generally exhibit higher abundance and species richness in the canopy compared to ground level (Rassati et al. 2018), as well as at the forest edge compared to interior (Wermelinger et al. 2007; Francese et al. 2008). Ulyshen and Hanula (2007) found no

significant differences among heights for buprestid abundance or species richness, however.

Members of Scolytinae generally show higher abundance at the ground level compared to the canopy (Ulyshen and Hanula 2007; Dodds 2014) but some studies also show no significant differences for abundance when pooled across species (Leksono et al. 2005; Wermelinger et al. 2007; Maguire et al. 2014). Inconsistencies for this group may be partly explained by the fact that scolytines include two feeding guilds, suggesting that vertical stratification patterns should be analyzed separately for the different guilds. Indeed, two recent studies found phloem-/wood-feeding beetle abundance and species richness to increase with height and ambrosia beetle abundance and species richness to decrease with height (Ulyshen and Sheehan 2017; Procházka et al. 2018), although Procházka et al. (2018) found patterns for ambrosia beetles to vary between montane and lowland forests.

Many possible factors could explain these differences in distribution aside from the trap height itself. According to Basset et al. (2003), factors that vary with height include forest physiognomy and tree architecture (e.g., leaf area index, tree trunk size, height of the canopy), resource availability (quantity and quality of food source, etc.), arthropod behavior (e.g., sexual selection, competition, and predator avoidance), and abiotic factors. We predict that microclimatic factors—specifically temperature, humidity, and canopy cover—may strongly influence observed vertical distribution patterns as many are highly correlated with height. This hypothesis—although poorly studied for these specific groups—has a reasonable amount of support. For example, temperature and humidity can affect insect activity, dispersal, development, flight patterns, adhesion to substrate, etc. (Hanks et al. 1999; Zhang et al. 2008; Jaworski and Hilszczański 2013; Drury et al. 2016; Heepe et al. 2016). Sunlight and canopy cover also influence insect distribution (Jonsell et al. 1998; Gossner 2009) as well as plant diversity (Aavik et al. 2008). In particular, many species of Buprestidae and Cerambycidae exhibit preferences for either sun or shade, especially considering the wood substrates in which the larvae grow (Lindhe et al. 2005; Buse et al. 2007; Vodka et al. 2009; Vodka and Cizek 2013). Recent support for the idea that vertical stratification patterns can be driven by microclimate comes from Berkov (2018) who found some cerambycids to be more abundant near the ground during the dry season but more abundant in the canopy during the rainy season in French Guiana.

Vertical stratification of microclimatic variables becomes less pronounced at the edge of forests compared to the interior of forests (Didham and Ewers 2014). One may expect the edge of a forest to be more vertically uniform in terms of microclimatic factors due to increased sun exposure compared to the forest interior. Vodka and Cizek (2013) found

differences in species richness and community composition to be more significant along horizontal gradients than vertical gradients.

Although many have studied the vertical distribution of woodboring beetles, few have examined what role microclimatic variables may play in driving these patterns. For this study, we looked at beetles that belong to two different feeding guilds at three different heights above ground at both the edge and interior of the forest, while recording three key microclimatic variables: temperature, humidity, and canopy cover for each trap. Although this study targeted beetle species native to or already established in North America, we expect the distribution patterns observed for phloem/wood feeders and ambrosia beetles to be representative of those guilds and can thus be used to anticipate how future arrivals are likely to be distributed in invaded forests.

Materials and methods

Study sites

Beetles were sampled in two separate mixed hardwood forests in Athens, Clarke County, Georgia: Whitehall Forest—a ~340 ha experimental forest managed by the University of Georgia's Warnell School of Forestry and Natural Resources—and Tallassee Forest—a ~125 ha tract of undeveloped land managed by the Athens-Clarke County government. They are separated by approximately 15 km, but the Middle Oconee River runs through both. Whitehall Forest mainly consists of secondary mixed ~60–70-year-old southern hardwood and pine forest (Nowakowski and Maerz 2009; King et al. 2013). Dominant overstory tree species for Whitehall Forest include white oak (*Quercus alba* L.), tulip poplar (*Liriodendron tulipifera* L.), southern red oak (*Q. falcata* Michaux), American sweetgum (*Liquidambar styraciflua* L.), and to a lesser extent loblolly pine (*Pinus taeda* L.) and shortleaf pine (*P. echinata* L.). It is an experimental forest and has numerous research facilities located on site. It is closed to the public, but sees relatively heavy use for research, instruction, and land management.

In contrast, Tallassee Forest is a relatively intact and undisturbed tract of land. While the exact age of Tallassee Forest is not known, it is clear from a 1938 aerial photograph that our study area has been covered in mature forest for well over 80 years (Porter 2014). Dominant overstory tree species for Tallassee Forest include white oak (*Q. alba*), southern red oak (*Q. falcata*), mockernut hickory (*Carya tomentosa* Sargent), and tulip poplar (*L. tulipifera*). Tallassee contains the largest American holly (*Ilex opaca* Aiton) forest in Georgia, which dominates much of the subcanopy and understory; it also contains a remarkably small amount

of the invasive Chinese privet (*Ligustrum sinense* Loureiro) (Porter 2014).

Because we were interested in looking at edge effects, the forests we worked in at both sites were adjacent to regularly mowed utility lines. At Tallassee Forest (33°58'43.0"N 83°29'21.0"W), the utility line was about 30 m wide and had an east–west orientation, whereas at Whitehall (33°53'23.5"N 83°21'53.0"W), the utility line was about 20 m wide and had a northwest–southeast orientation.

Experimental design

Beetles were sampled at each site using flight intercept traps (described below), separated by at least 50 m, placed at five points along the edge between the forest and cleared utility line. Beetles were also sampled in the forest interior, approximately 50 m into the forest from the edge traps. At each edge and interior point, traps were installed at three heights above the ground: 0, 5, and 15 m. We treat each group of six traps associated with each pair of edge and interior sampling points as a block in the analysis. The design thus consisted of two factors: horizontal placement (edge vs. interior) and height (0, 5, and 15 m). Each combination of factors had ten replicates (blocks) for a total of 60 traps.

Trap design and installation

We constructed flight intercept traps using two intersecting sheets of Plexiglas 30.5 cm × 20.3 cm placed above a single Lindgren funnel, attached with metal wire. To increase the likelihood of catching large specimens, we cut and removed a portion of the bottom part of the funnel. This enlarged the opening to the wet collection cup to about 8 cm diameter (see Miller et al. 2013). Several studies have found that wet collection cups far outperform dry cups (Morewood et al. 2002; de Groot and Nott 2003; Miller and Duerr 2008; Allison and Redak 2017). We applied sprayable dry lube with Teflon (Blaster Corporation, Valley View, Ohio, USA) to the funnel prior to the collecting season, which has been shown to increase trap yield of Cerambycidae (Graham et al. 2010; Allison et al. 2011, 2014; Allison and Redak 2017).

We used propylene glycol—with a drop of soap to break surface tension—as both the killing and preserving agent, changed once every 2 weeks. We attached one low release ethanol lure from Synergy Semiochemicals Corp., Burnaby, British Columbia, Canada (Item #3344) to each trap directly above the Plexiglas and replaced it once every 8 weeks, as recommended by the manufacturer. These lures have a release rate of ~10 mg/day at 20 °C. We did not attempt to replicate traps and lures used in existing exotic species detection surveys such as CAPS and EDRR and recognize that the importance of trap height and position may vary among lures and trap types for some taxa. On June 7, we attached

a colored card to each Plexiglas frame to attract bees for a separate study; there were four different colors: blue, yellow, white, and neon yellow (see Supplementary Figure 1). The ropes for suspending the highest traps were installed using a combination of a Big Shot throw-line launcher (Sherrill-Tree Inc., Greensboro, NC, USA)—a slingshot mounted on a 2.4-m fiberglass pole—and a Big Launcher rope gun (Sherrill-Tree Inc., Greensboro, NC, USA) to launch rope to the appropriate height. We selected sturdy branches that were clear enough underneath for ease of raising and lowering of traps, indiscriminate of tree species. Selecting all the same species of tree would have been ideal, but was not possible due to the limited number of satisfactory branches at the forest edge.

Data collection

Each trap had an iButton Hygrochron Temperature/Humidity Logger (Maxim Integrated, San Jose, CA, USA) to record temperature and humidity once every 2 h for the duration of the sampling period. To record canopy cover, we took a hemispherical photograph of the canopy for each trap location. For the trap locations at 5 m and 15 m, we used an improvised cage to pull the camera up to the proper height and used ropes to stabilize the camera from the ground prior to capturing the images. We took pictures of Whitehall Forest on June 6, 2016, and Tallassee Forest on August 4, 2016, both overcast days after leaf expansion. These images were analyzed using WinSCANOPY software (Regent Instruments Inc., Quebec, Canada) which calculates a percentage of pixels designated as open sky (as opposed to canopy cover), termed gap fraction.

Specimens were collected approximately once every 2 weeks from March 15 to September 28, 2016. All specimens were identified to species, with five exceptions that were identified to genus: *Hypothenemus*, *Pityophthorus*, *Pseudopityophthorus*, *Thysanoes*, and *Trischidias*, all in the subfamily Scolytinae. Members of Scolytinae were identified to genus or species using Wood (1982), Rabaglia et al. (2006), and Cognato et al. (2015). Members of Cerambycidae were identified to species using Lingafelter (2007). Members of Buprestidae were identified to species using Harpootlian and Bellamy (2014). Fourteen specimens were too damaged to identify and were not included in any analysis. Voucher specimens were deposited in the UGA Collection of Arthropods of the Georgia Museum of Natural History. Members of Scolytinae were placed in either guild using Wood (1982) and Kirkendall et al. (2015). Two species of *Hypothenemus* feed on fungus: *Hypothenemus concolor* (Hagedorn, 1909) and *Hypothenemus curtipennis* (Schedl, 1950) (Beaver 1986; Hulcr and Stelinski 2017). Although *Hypothenemus* specimens were only identified to genus, both of these species are fairly distinctive (Vega et al. 2015)

and neither have been reported in the USA; thus, we placed *Hypothenemus* spp. in the phloem-/wood-feeding guild, as reported in Wood (1982) and Atkinson et al. (1988).

For each trap, we calculated the average temperature and humidity over the entire period of trap operation. In addition, beetle species richness was calculated by summing the total number of species collected per trap. As described below, nonmetric multidimensional scaling was used to obtain the community metrics used in the analyses.

Data analysis

Prior to analysis, we limited the dataset to trapping periods (May 10–August 2) and trap locations for which we had complete data. This was made necessary by broken traps, broken tree limbs, and iButton failures. Data from 52 of the 60 traps were used in the final analysis, with traps at the following locations having fewer than 10 traps: edge 15 m ($n=8$), interior 15 m ($n=8$), edge 5 m ($n=9$), interior 5 m ($n=8$), and edge 0 m ($n=9$). The final dataset used in all analyses described below (although further reduced for community analysis) consisted of 87 species and 3334 specimens (Table 1).

We performed ANOVAs using the mixed procedure of SAS[®] software (SAS Institute 1999) to examine how abiotic variables (temperature, relative humidity, and gap fraction) and beetle data (species richness of ambrosia and phloem/wood feeders and community composition) differed with height above the ground (0, 5, and 15 m) and with horizontal placement (edge vs. interior). We treated height and horizontal placement as fixed effects and treated block (each group of six traps at the edge and interior) as a random effect. Because we were interested in looking at the effects of trap location on the number of beetles collected after taking abiotic variables into account, we wanted to include one or more of these covariates in the model. Temperature and relative humidity were highly negatively correlated ($r=-0.87$, $p<0.0001$) so we included them one at a time in the model. Because these variables were never significant in models that also contained gap fraction, we used gap fraction as the only covariate in all final models after confirming there were no significant interactions between gap fraction and any of the independent variables.

For all response variables, the normality assumption was tested by examining frequency histograms and Q–Q plots for residuals. All variables met this assumption, although several required transformation. Phloem-/wood-feeding beetle species richness and ambrosia beetle species richness were square-root transformed, while the values for axes two and three in the nonmetric multidimensional scaling (see below) were square-root($x+2$) transformed. Untransformed data are presented in all tables and figures. In addition, plots of residuals versus predicted values were examined to verify that the

homoscedasticity assumption was not violated for any of the response variables. Abundance and species richness data for common (>20 individuals) families (Buprestidae, Cerambycidae and Curculionidae) and subfamilies (Cerambycinae, Lamiinae, Lepturinae, and Scolytinae) are provided in Supplementary Table 1. When an effect was found to be significant, we compared means using LS means (Tukey–Kramer adjusted t statistic). When there were significant two-way interactions between factors, mean separation tests were done separately for each level of the interacting factor.

We performed sample-based rarefaction in EstimateS using the Mao Tau estimator, Equation 17 in Colwell et al. (2012). We used the classic formula for Chao1 and Chao2, as recommended by the program, instead of the bias-corrected formula. All other settings remained default. We plotted separate rarefaction curves for each guild and horizontal placement, with the number of traps on the x -axis to demonstrate expected number of species for similar trapping efforts. We also plotted rarefaction with individual abundance on the x -axis due to large differences in abundance among different heights, as recommended by Gotelli and Colwell (2001).

We used PC-ORD (McCune and Mefford 2011) to perform nonmetric multidimensional scaling, using the Bray–Curtis distance measure, to assess differences in beetle composition among the various factors of interest in this study. We limited the dataset to species present in at least three of the trapping locations, resulting in a matrix with 46 species. Data were then relativized by species maximum. The values for the three resulting axes were used as community response variables in the ANOVA model described above. We also used PC-ORD to perform indicator species analysis on the same reduced dataset. This analysis follows the approach of Dufrêne and Legendre (1997) to assess species-level associations with particular sites, horizontal placements, or heights. We also tested whether any species were significantly associated with particular horizontal placement \times height combinations.

Results

As mentioned above, the reduced dataset used in the analyses consisted of 87 species and 3334 specimens. Of these, 65 species and 466 specimens belong to the phloem-/wood-feeding guild in the families Cerambycidae, Buprestidae, and Curculionidae (Scolytinae) and 22 species and 2868 specimens belong to the ambrosia-feeding guild in the family Curculionidae (Scolytinae and Platypodinae) (Table 1). Although we collected 10 lymexyloid specimens in our traps, none were included in the reduced dataset used in the analyses. Non-native beetles represented 11 of 22 (50%) species and 2737 of 2868 (95%) specimens in the ambrosia-feeding

Table 1 List of species included in the main analysis (from the limited dataset for trap locations with complete data) with number of specimens for each height and horizontal placement combination

Family/subfamily	Species	Guild	Edge 0 (m)	Edge 5 (m)	Edge 15 (m)	Int 0 (m)	Int 5 (m)	Int 15 (m)	Total
Buprestidae	<i>Agrilus bilineatus</i> (Weber)	p/w	0	0	1	0	0	0	1
Agrilinae	<i>Agrilus carpini</i> Knull	p/w	0	0	0	0	1	0	1
	<i>Agrilus subrobustus</i> Saunders [†]	p/w	0	0	0	1	0	0	1
	<i>Brachys ovatus</i> (Weber)	p/w	0	0	1	0	0	2	3
Buprestinae	<i>Actenodes acornis</i> (Say)	p/w	0	0	1	0	0	0	1
	<i>Anthaxia dichroa</i> Bílý	p/w	0	2	1	0	0	0	3
	<i>Chrysobothris rugosiceps</i> Melsheimer	p/w	1	0	4	0	1	0	6
	<i>Chrysobothris sexsignata</i> Say	p/w	0	1	0	0	0	0	1
Chrysochroinae	<i>Dicerca lurida</i> (Fabricius)	p/w	0	0	0	0	0	1	1
Polycestinae	<i>Acmaeodera tubulus</i> (Fabricius)	p/w	0	1	2	0	0	1	4
Cerambycidae	<i>Anelaphus moestus</i> (LeConte)	p/w	0	0	1	0	0	0	1
Cerambycinae	<i>Anelaphus parallelus</i> (Newman)	p/w	0	1	3	0	1	0	5
	<i>Anelaphus villosus</i> (Fabricius)	p/w	2	15	18	3	11	16	65
	<i>Clytus marginicollis</i> Laporte & Gory	p/w	1	1	1	5	1	0	9
	<i>Cyrtophorus verrucosus</i> (Olivier)	p/w	0	0	0	0	1	1	2
	<i>Eburia quadrigeminata</i> (Say)	p/w	0	1	7	0	0	7	15
	<i>Elaphidion mucronatum</i> (Say)	p/w	1	8	4	6	5	1	25
	<i>Enaphalodes atomarius</i> (Drury)	p/w	0	0	1	0	0	0	1
	<i>Euderces picipes</i> (Fabricius)	p/w	2	3	5	1	1	3	15
	<i>Euderces pini</i> (Olivier)	p/w	0	1	0	0	0	0	1
	<i>Euderces reichi reichi</i> LeConte	p/w	0	0	1	0	0	0	1
	<i>Heterachthes quadrimaculatus</i> Newman	p/w	0	0	0	0	1	1	2
	<i>Molorchus bimaculatus</i> Say	p/w	0	0	1	0	0	0	1
	<i>Neoclytus acuminatus</i> (Fabricius)	p/w	2	1	0	1	2	0	6
	<i>Neoclytus mucronatus</i> (Fabricius)	p/w	0	0	0	0	1	0	1
	<i>Neoclytus scutellaris</i> (Olivier)	p/w	0	5	8	1	0	15	29
	<i>Obrium maculatum</i> (Olivier)	p/w	3	3	2	0	0	2	10
	<i>Parelaphidion aspersum</i> (Haldeman)	p/w	0	0	1	0	0	2	3
	<i>Parelaphidion incertum</i> (Newman)	p/w	0	0	5	0	0	6	11
	<i>Psyrassa pertenuis</i> (Casey)	p/w	0	1	3	0	0	0	4
	<i>Xylotrechus colonus</i> (Fabricius)	p/w	0	0	0	3	0	0	3
Disteniinae	<i>Distenia undata</i> (Fabricius)	p/w	1	2	4	0	2	3	12
Lamiinae	<i>Aegomorphus modestus</i> (Gyllenhal)	p/w	0	2	0	0	0	3	5
	<i>Doraschema cinereum</i> (Olivier)	p/w	0	1	0	0	0	0	1
	<i>Ecyrus dasycerus</i> (Say)	p/w	0	1	0	2	1	1	5
	<i>Eupogonius pauper</i> LeConte	p/w	0	0	1	0	0	0	1
	<i>Goes debilis</i> LeConte	p/w	0	0	1	0	0	0	1
	<i>Goes tigrinus</i> (DeGeer)	p/w	1	0	0	0	0	0	1
	<i>Hyperplatys aspersa</i> (Say)	p/w	0	0	0	0	0	1	1
	<i>Hyperplatys maculata</i> Haldeman	p/w	1	0	0	0	1	0	2
	<i>Lepturges confluens</i> (Haldeman)	p/w	0	0	2	0	0	2	4
	<i>Saperda discoidea</i> Fabricius	p/w	0	0	0	0	0	2	2
	<i>Saperda lateralis</i> Fabricius	p/w	0	5	0	0	2	0	7
	<i>Urgleptes facetus</i> (Say)	p/w	0	0	0	0	1	0	1
	<i>Urographis fasciatus</i> (DeGeer)	p/w	0	0	0	3	0	0	3
Lepturinae	<i>Analeptura lineola</i> (Say)	p/w	0	0	0	0	1	2	3
	<i>Bellamira scalaris</i> (Say)	p/w	0	0	0	0	1	0	1
	<i>Brachyleptura vagans</i> (Olivier)	p/w	0	0	1	0	0	0	1
	<i>Metacmaeops vittata</i> (Swederus)	p/w	0	3	0	1	0	0	4
	<i>Stenocorus cylindricollis</i> (Say)	p/w	0	0	4	0	0	1	5
	<i>Strangalia luteicornis</i> (Fabricius)	p/w	8	3	2	4	8	5	30
	<i>Strangalia bicolor</i> (Swederus)	p/w	0	2	0	0	0	0	2

Table 1 (continued)

Family/subfamily	Species	Guild	Edge 0 (m)	Edge 5 (m)	Edge 15 (m)	Int 0 (m)	Int 5 (m)	Int 15 (m)	Total
	<i>Strangalia famelica famelica</i> Newman	p/w	0	1	0	0	0	1	2
	<i>Strangalia famelica solitaria</i> Haldeman	p/w	0	0	1	0	0	0	1
	<i>Typocerus velutinus</i> (Olivier)	p/w	0	2	1	0	0	0	3
	<i>Typocerus zebra</i> (Olivier)	p/w	0	2	0	0	0	0	2
Prioninae	<i>Orthosoma brunneum</i> (Forster)	p/w	3	0	0	1	1	0	5
	<i>Prionus imbricornis</i> (L.)	p/w	2	0	0	4	0	0	6
	<i>Sphenostethus taslei</i> (Buquet)	p/w	0	0	1	0	0	1	2
Curculionidae	<i>Euplatypus compositus</i> (Say)	a	1	3	1	0	0	0	5
Platypodinae	<i>Oxoplatypus quadridentatus</i> (Olivier)	a	0	1	0	0	0	0	1
Scolytinae	<i>Ambrosiodmus obliquus</i> (LeConte)	a	4	1	1	25	16	7	54
	<i>Ambrosiodmus rubricollis</i> (Eichhoff) [†]	a	4	0	0	2	1	1	8
	<i>Ambrosiophilus atratus</i> (Eichhoff) [†]	a	3	0	0	0	0	0	3
	<i>Cnesinus strigicollis</i> LeConte	p/w	4	3	0	1	1	0	9
	<i>Cnestus mutilatus</i> (Blandford) [†]	a	32	376	324	9	60	176	977
	<i>Corthylus punctatissimus</i> (Zimmerman)	a	0	0	0	2	0	0	2
	<i>Cyclorhipidion bodoanum</i> (Reitter) [†]	a	2	5	4	16	2	7	36
	<i>Dryoxylon onoharaense</i> (Murayama) [†]	a	21	3	5	51	14	4	98
	<i>Euwallacea interjectus</i> (Blandford) [†]	a	3	1	0	9	5	0	18
	<i>Gnathotrichus materiarius</i> (Fitch)	a	0	0	0	0	0	1	1
	<i>Hylocurus rudis</i> (LeConte)	p/w	0	2	2	0	3	0	7
	<i>Hypothenemus</i> spp. Westwood	p/w	29	12	3	37	5	7	93
	<i>Ips avulsus</i> (Eichhoff)	p/w	0	0	1	0	0	0	1
	<i>Micracisella nanula</i> (LeConte)	p/w	0	2	0	1	0	0	3
	<i>Monarthrum mali</i> (Fitch)	a	3	4	3	3	4	2	19
	<i>Pseudopityophthorus</i> sp. Swaine	p/w	1	0	1	0	0	0	2
	<i>Scolytus multistriatus</i> (Marsham) [†]	p/w	1	5	0	0	0	0	6
	<i>Xyleborinus gracilis</i> (Eichhoff)	a	0	1	1	0	0	0	2
	<i>Xyleborinus saxeseni</i> (Ratzeburg) [†]	a	46	21	6	92	21	8	194
	<i>Xyleborus affinis</i> Eichhoff	a	1	0	0	1	0	0	2
	<i>Xyleborus bispinatus</i> Eichhoff ^a	a	51	0	1	38	1	0	91
	<i>Xyleborus celsus</i> Eichhoff	a	0	3	2	0	0	1	6
	<i>Xyleborus impressus</i> Eichhoff	a	40	5	0	44	0	0	89
	<i>Xyleborus viduus</i> Eichhoff	a	0	0	0	0	1	0	1
	<i>Xyleborus xylographus</i> (Say)	a	2	0	0	1	0	0	3
	<i>Xylosandrus crassiusculus</i> (Motschulsky) [†]	a	396	116	11	438	120	33	1114
	<i>Xylosandrus germanus</i> (Blandford) [†]	a	61	0	0	79	3	1	144
	Grand Total (Abundance)		733	632	455	885	311	328	3334
	Grand Total (Number of species)		48	58	61	48	48	52	

Int Interior; Guild refers to phloem/wood feeders (p/w) or ambrosia feeders (a)

[†]Non-native species

guild and 2 of 65 (3%) species and 7 of 466 (1.5%) specimens in the phloem-/wood-feeding guild.

Abiotic factors

We found significant positive correlations between height and temperature ($r=0.4706$, $p=0.0004$), height and gap fraction ($r=0.5726$, $p<0.0001$), as well as temperature and gap fraction ($r=0.5592$, $p<0.0001$). We found significant negative correlations between relative humidity and height

($r=-0.6444$, $p<0.0001$), relative humidity and gap fraction ($r=-0.5617$, $p<0.0001$), as well as relative humidity and temperature ($r=-0.8671$, $p<0.0001$).

Temperature differed significantly between horizontal placements ($F_{1,37}=9.92$, $p=0.0032$), being higher at the edge than in the interior (results not shown); temperature also significantly increased with height ($F_{1,37}=8.04$, $p=0.0013$) (Table 2; Fig. 1). Relative humidity differed significantly between horizontal placements ($F_{1,37}=6.67$, $p=0.0139$), being higher in the interior (results not

shown), and also varied significantly among trap heights ($F_{2,37}=26.04$, $p < 0.0001$), decreasing with increasing height (Table 2; Fig. 1). For gap fraction, there was a significant interaction between horizontal placement and height ($F_{2,37}=7.49$, $p=0.0019$) (Table 2). Gap fraction was significantly higher at 15 m than at 0 m ($t_{14}=-5.70$, $p < 0.0001$; $t_{14}=-3.21$, $p=0.0063$) and 5 m ($t_{14}=-6.13$, $p < 0.0001$; $t_{14}=-2.26$, $p < 0.0001$) at both the edge and interior, respectively (Fig. 1). Furthermore, gap fraction was significantly higher at the edge than in the interior at 0 m ($t_8=4.38$,

$p=0.0024$) and 15 m ($t_8=4.86$, $p=0.0028$), but not at 5 m ($t_8=1.93$, $p=0.0948$).

Species richness

Species richness significantly decreased with height for the ambrosia-feeding guild ($F_{2,36}=22.78$, $p < 0.0001$), and increased with height for the phloem-/wood-feeding guild ($F_{2,36}=3.72$, $p=0.0340$) (Table 3; Fig. 2). Phloem-/wood-feeding species richness also significantly increased with gap fraction ($F_{1,36}=9.98$, $p=0.0032$).

Many of the rarefaction curves did not reach an asymptote, implying that sampling is incomplete for particular trap locations (Fig. 3). Still, it is clear that lower traps collected more species of ambrosia beetles and higher traps collected more species of phloem-/wood-feeding beetles, although there is a fair amount of overlap with the error bars.

Table 2 ANOVA results evaluating the impact of horizontal placement, height, and the interaction between horizontal placement and height on temperature, relative humidity, and gap fraction

	Num DF/ denom DF	Temp. <i>F</i> value	RH <i>F</i> value	Gap fraction <i>F</i> value
Horiz Plcmt	1/37	9.92**	6.67*	36.55***
Height	2/37	8.04**	26.04***	27.22***
Horiz Plcmt × Height	2/37	0.52	0.06	7.49**

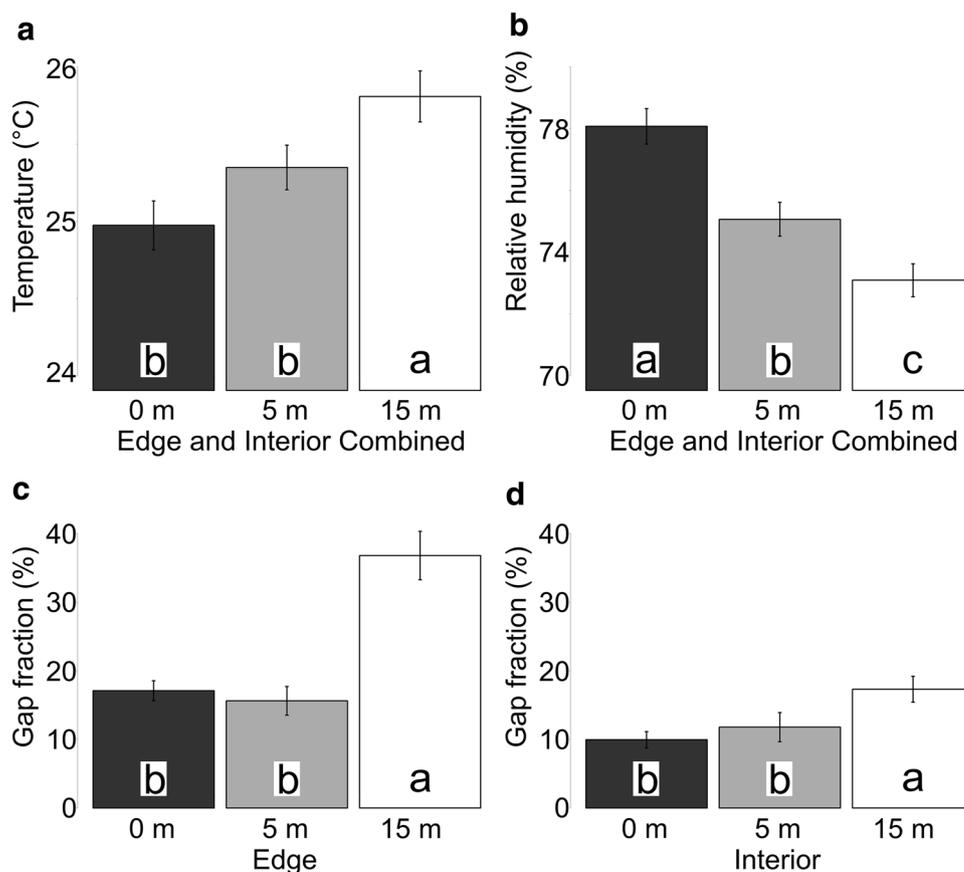
Num DF numerator degrees of freedom, *Denom DF* denominator degrees of freedom, *Horiz Plcmt* horizontal placement (edge vs. interior), *Temp.* temperature, *RH* relative humidity

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$

Indicator species

Eight species were significantly associated with the 0 m traps and eight species were significantly associated with the 15 m traps—no species were significantly associated with the 5 m traps (Table 4). All but two of the species associated with the 0 m traps were in the ambrosia-feeding guild, while

Fig. 1 Mean \pm SE values of abiotic variables at different trap heights: **a** temperature with both edge and interior combined; **b** humidity with both edge and interior combined; **c** gap fraction near forest edge; and **d** gap fraction in forest interior. Within each graph, means with different letters differ significantly ($p < 0.05$)



all but one of the species associated with the 15 m traps were in the phloem-/wood-feeding guild.

One species, *C. mutilatus*, was significantly associated with the forest edge, and one species, *Ambrosiodmus obliquus* (LeConte, 1878), was significantly associated with the forest interior. Thirteen species were significantly associated with certain height and horizontal placement combinations: three ambrosia beetle species for edge 0 m, one ambrosia beetle species for edge 5 m, three phloem-/wood-feeding species for edge 15 m, three ambrosia beetle species and one phloem-/wood-feeding species for interior 0 m, and two phloem-/wood-feeding species for interior 15 m (Table 4). No species were significantly associated with interior 5 m traps (Table 4).

Community composition

Nonmetric multidimensional scaling recommended a three-dimensional solution with a final stress of 18.29. The R^2 values were 0.411, 0.141, and 0.147 for the three axes, respectively. As can be seen by the two-dimensional depiction using axes 1 and 3, the traps at 0 m above ground are different in composition to the traps at 15 m, with traps at 5 m being intermediate between the other heights (Fig. 4). The ordination also shows that, at each trap height, there is significant overlap between traps placed at the forest edge and in the interior (Fig. 4). Gap fraction ($r = -0.58$), temperature ($r = -0.53$), and phloem-/wood-feeding species richness ($r = -0.68$) were negatively correlated with axis 1, whereas relative humidity ($r = 0.69$) and ambrosia beetle species richness ($r = 0.77$) were positively correlated with that axis.

When the axes values were used as response variables in our ANOVA model, axis 1 values varied significantly with height ($F_{2,36} = 77.62$, $p < 0.0001$) and gap fraction ($F_{1,36} = 8.14$, $p = 0.0071$). There was also a significant

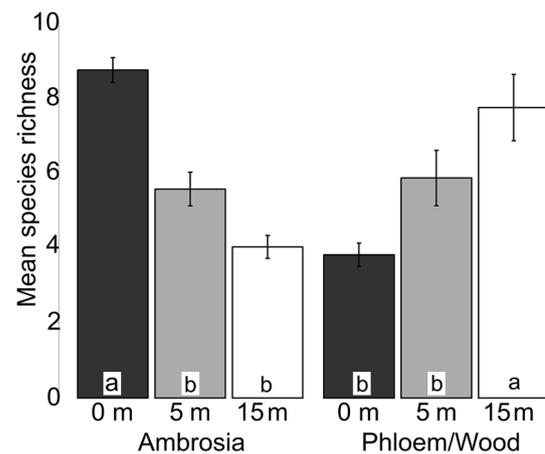


Fig. 2 Mean \pm SE species richness by height, separated by guild. Within guild, means with different letters were significantly different ($p < 0.05$). Means of untransformed data are presented here

interaction between height and horizontal placement ($F_{2,36} = 6.60$, $p = 0.0036$). At the forest edge, axis 1 values differed between traps at 0 m and those at 5 m ($t_{13} = 11.75$, $p < 0.0001$) as well as traps at 0 m and those at 15 m ($t_{13} = 7.85$, $p < 0.0001$) but there was no significant difference between 5 and 15 m. In the forest interior, by contrast, all three heights had significantly different axis 1 values: 0 and 5 m ($t_{13} = 3.60$, $p = 0.0032$), 0 and 15 m ($t_{13} = 7.85$, $p < 0.0001$), and 5 and 15 m ($t_{13} = 7.85$, $p < 0.0001$). Axis 1 values were significantly different between edge and interior at 5 m ($t_6 = -2.52$, $p = 0.0451$) and 15 m ($t_6 = 2.58$, $p = 0.0494$) but not at 0 m (results not shown). Axis 3 values varied significantly only with height ($F_{2,36} = 3.91$, $p = 0.0290$), with a significant difference between traps at 0 and 15 m ($t_{36} = -2.64$, $p = 0.0122$). No factors were significant sources of variation for axis 2 values.

Discussion

In this study, we measured the spatial distribution of two separate feeding guilds of beetles (phloem-/wood-feeding and ambrosia-feeding) captured in traps placed at varying heights and either along a forest edge or 50 m inside the forest. We included the key microclimatic variables of temperature, relative humidity, and gap fraction in our model to better isolate the effects of trap height and horizontal placement.

Differences in species composition observed among heights in this study were largely driven by the contrasting vertical distribution patterns exhibited by ambrosia beetles and phloem/wood feeders. Similar to Ulyshen and Sheehan (2017), our results indicate that species richness increases with height for the phloem-/wood-feeding guild,

Table 3 ANOVA results evaluating the impact of horizontal placement, height, the interaction between horizontal placement and height, and gap fraction on species richness for both feeding guilds

	Num DF/ denom DF	Ambrosia richness <i>F</i> value	Phloem/ wood rich- ness <i>F</i> value
Horiz Plcmt	1/36	0.13	1.22
Height	2/36	22.78***	3.72*
Horiz Plcmt \times Height	2/36	0.32	1.15
Gap Fraction	1/36	1.45	9.98**

Num DF numerator degrees of freedom, *Denom DF* denominator degrees of freedom, *Horiz Plcmt* Horizontal Placement (edge vs. interior)

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$

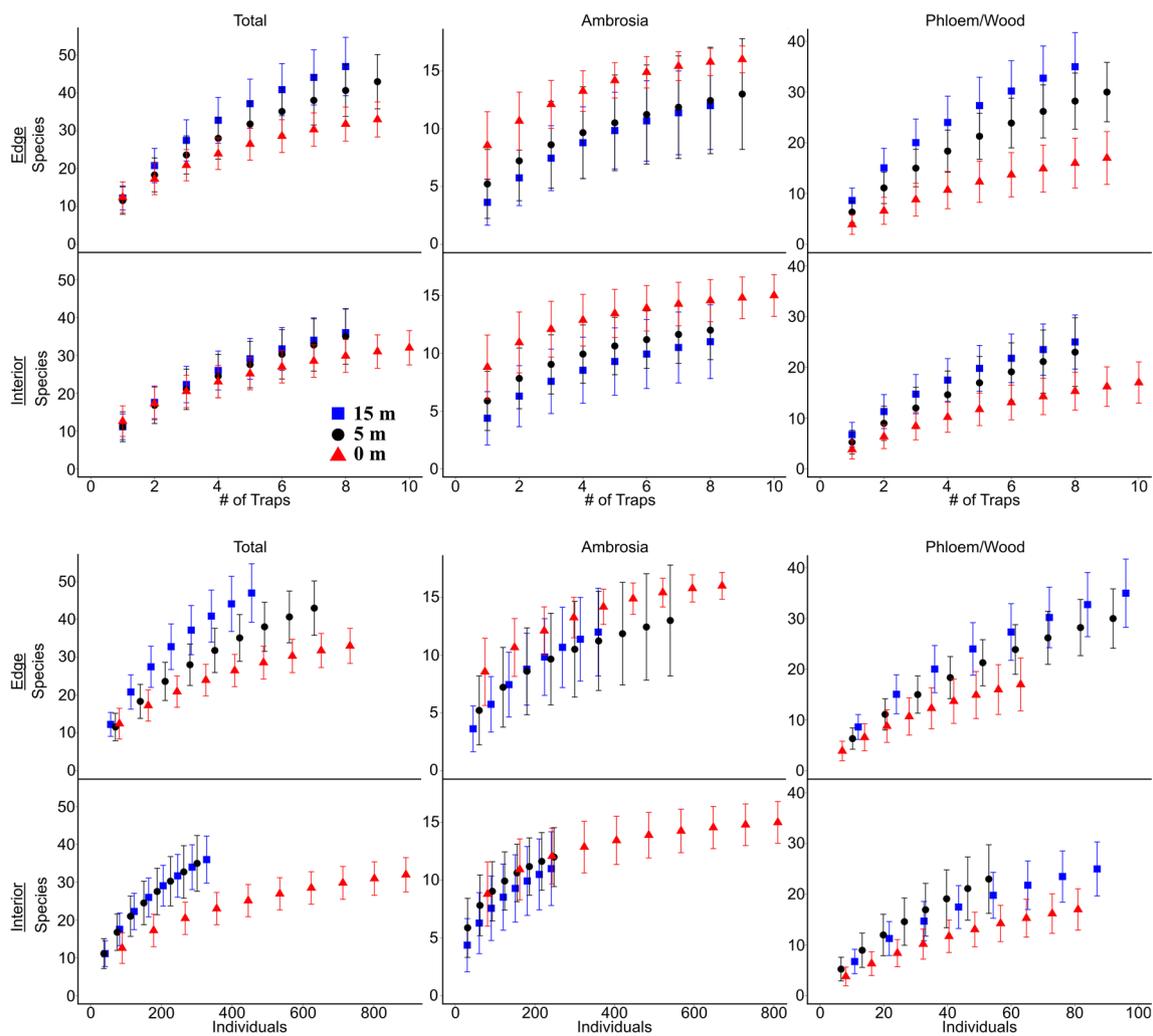


Fig. 3 Sample-based rarefaction using estimated number of species (S_{est}) with 95% confidence intervals for both guilds together and separately. Triangles, circles, and squares represent traps placed at 0, 5, and 15 m, respectively. Scaled on the x-axis by both number of traps and individuals

but decreases with height for the ambrosia-feeding guild. The concentrations of ambrosia and phloem-/wood-feeding beetles near the ground and in the canopy, respectively, may be explained by differences in life history between these two guilds. One possible explanation for the concentration of ambrosia beetles near the forest floor, for instance, is that their symbiotic fungi grow better under more humid conditions. By contrast, phloem/wood feeders may have greater reproductive success higher above ground where conditions are less favorable to fungal diseases, such as high temperatures, lower humidity, and more sunlight (Hajek and Leger 1994). Studies addressing these possibilities would be of interest.

This study differs from Ulyshen and Sheehan (2017) in our aim to determine how distance from the forest edge affects vertical distribution patterns. We found beetle communities to be highly and similarly vertically stratified

at both the edge and interior. Compositional differences between traps placed at 5 and 15 m were significant only in the forest interior. In addition, we found significant differences in beetle composition between the edge and interior at 5 and 15 m but not at 0 m, suggesting that distance from edge may be less important for species active near the forest floor. Vodka and Cizek (2013) found horizontal stratification to be a more important determinant of beetle diversity than height but that study included many other families of saproxylic beetles. Our findings show that detection efforts targeting ambrosia and phloem/wood feeders specifically will benefit most from trapping at multiple heights with lesser benefits from sampling at both the forest edge and interior.

Indicator species analysis provides further support for these general conclusions. Eight species each were significantly associated with the lowest and highest traps in this study, with ambrosia beetles and phloem/wood feeders

Table 4 Significant indicator species for particular trap heights, horizontal placement (edge vs. interior), and combinations of height and horizontal placement

Family	Species	Guild	Height (m)	IV	Horiz Plcmt	IV	Horiz Plcmt × Height (m)	IV
Buprestidae	<i>Brachys ovatus</i> (Weber)	p/w	15	18.8*	–	–	–	–
	<i>Chrysobothris rugosiceps</i> Melsheimer	p/w	–	–	–	–	Edge 15	34.0*
Cerambycidae	<i>Anelaphus villosus</i> (LeConte)	p/w	15	40.7*	–	–	–	–
	<i>Eburia quadrigeminata</i> (Say)	p/w	15	52.7**	–	–	Int 15	29.4*
	<i>Lepturges confluens</i> (Haldeman)	p/w	15	25.0**	–	–	–	–
	<i>Neoclytus scutellaris</i> (Olivier)	p/w	15	45.3**	–	–	Int 15	33.2**
	<i>Parelaphidion incertum</i> (Newman)	p/w	15	37.5**	–	–	–	–
	<i>Prionus imbricornis</i> (L.)	p/w	0	26.3**	–	–	–	–
	<i>Psyrassa pertenuis</i> (Casey)	p/w	–	–	–	–	Edge 15	28.9*
	<i>Stenocorus cylindricollis</i> (Say)	p/w	15	25.0**	–	–	Edge 15	30.0*
Curculionidae	<i>Ambrosiodmus obliquus</i> (LeConte) [†]	a	–	–	Int	54.7**	–	–
	<i>Cnestus mutilatus</i> (Blandford) [†]	a	15	52.9**	Edge	72.0**	Edge 5	35.9*
	<i>Dryoxylon onoharaense</i> (Murayama) [†]	a	0	67.1**	–	–	Int 0	47.9**
	<i>Hypothenemus</i> spp. (Westwood)	p/w	0	61.0**	–	–	Int 0	32.9**
	<i>Xyleborinus saxeseni</i> (Ratzeburg) [†]	a	0	68.5**	–	–	Int 0	43.8**
	<i>Xyleborus bispinatus</i> Eichoff [†]	a	0	82.1**	–	–	Edge 0	45.4**
	<i>Xyleborus impressus</i> Eichoff	a	0	88.8**	–	–	Edge 0	47.3**
	<i>Xylosandrus crassiusculus</i> (Motschulsky) [†]	a	0	72.5**	–	–	Edge 0	36.3**
	<i>Xylosandrus germanus</i> (Blandford) [†]	a	0	91.8**	–	–	Int 0	46.8**

Horiz Plcmt horizontal placement (edge vs. interior), Int interior, Guild refers to phloem/wood feeders (p/w) or ambrosia feeders (a), IV indicator value

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.0001$

[†]Non-native species

dominating the former and latter, respectively. Of the eight indicator species for height belonging to the phloem-/wood-feeding guild, all but the native cerambycid *Prionus*

imbricornis (L., 1767) and bark beetles belonging to the genus *Hypothenemus* were significantly associated with 15 m traps (Table 4). Similarly, of the eight indicator species for height belonging to the ambrosia-feeding guild, all but the non-native scolytine, *C. mutilatus*, were significantly associated with 0 m traps (Table 4). These exceptions can possibly be explained by the natural history of these species. *Prionus imbricornis* was significantly associated with 0 m traps most likely because it is a root borer, often targeting the roots of grapevine, pear, and herbaceous plants (Beutenmuller 1896). It is also large in size, with adults reaching approximately 25 mm in length (Lingafelter 2007). Another prionine cerambycid, *Orthosoma brunneum* (Forster, 1771), was the only phloem-/wood-feeding species found to be significantly associated with traps near the forest floor in a previous study (Ulyshen and Sheehan 2017), suggesting members of this subfamily may focus their activities near the ground. In contrast, the association of *C. mutilatus* with 15 m may be explained because it targets stems with relatively small diameters (Kajimura and Hijii 1992; Schiefer and Bright 2004). In a study of host plants, Stone et al. (2007) found no successful attacks under 0.5 m above ground by *C. mutilatus*. Although they found a mean height

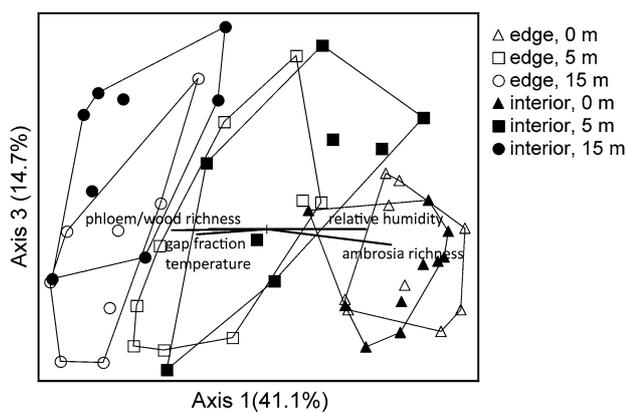


Fig. 4 Nonmetric multidimensional scaling ordination with convex hulls surrounding the six combinations of height and horizontal placement. Triangles, squares, and circles represent traps placed at 0, 5, and 15 m, respectively. White and black symbols represent traps placed at the edge and in the interior, respectively. Vectors show correlations between those variables and the axes

of attack of about 2 m, they only used saplings that presumably did not reach 15 m in height (Stone et al. 2007). Perhaps there is a different explanation however, as there should still be twigs in the understory.

While our findings hint at some general patterns, exceptions to these trends, such as the preference of *C. mutilatus* for the forest canopy, suggest that both guilds exhibit a high degree of variability at the species level. *Cnestus mutilatus* is a particularly interesting example because this species was first detected in North America in 1999 (Schiefer and Bright 2004). It is clear from our results that traps placed in the canopy, especially on the forest edge, would have been more effective at detecting this species. Exceptions to general patterns are common in the literature. Wermelinger et al. (2007) found members of Cerambycidae to generally prefer open land, but also found some species to contradict this pattern and prefer the forest interior. Similarly, Bouget et al. (2011) found conflicting results for abundance and species richness of saproxylic beetles by height, mainly due to differences in forest composition. Numerous other studies found species-specific exceptions to general patterns (Vance et al. 2003; Dodds 2014; Schmeelk et al. 2016). The associations with particular height and horizontal placement combinations detected in our study further indicate that height and horizontal placement are both important factors influencing the distribution of both guilds.

We accounted for the important microclimatic variables temperature, relative humidity, and gap fraction, but there are still numerous others that could influence distribution. Some abiotic factors that could further influence distribution are wind speed, wind direction, rainfall, barometric pressure, orientation of gap exposure, etc. For example, both temperature and wind speed affected flight activity of *Orthotomicus erosus* (Wollaston 1857) and *Pityogenes calcaratus* (Eichhoff, 1878) in a pine plantation in Israel (Mendel et al. 1991). The interactions of all these variables further complicate the issue (Pawson et al. 2017). Chen and Seybold (2014) found temperature, light intensity, wind speed, and barometric pressure to affect flight activity of the wood–phloem-feeding scolytine *Pityophthorus juglandis* (Blackman, 1928) both individually as well as in combination. In addition to affecting flight activity, other abiotic factors may affect distribution in other ways, such as through altering pheromone plumes. Östrand and Anderbrant (2003) found recapture rates of male pine sawflies *Neodiprion sertifer* (Geoffroy, 1785) to increase with wind speed when using pheromone-baited traps.

To conclude, it is clear from our results that sampling from multiple heights is necessary to collect a representative sample of the phloem-/wood-feeding and ambrosia beetles present in an area. Though less important, sampling at both the edge and interior of a forest will also

increase the probability of detecting certain species. Ulyshen and Sheehan (2017) found no difference in the composition of ambrosia and phloem-/wood-feeding beetles sampled in traps placed at 15 and 5 m in a previous study. Based on those results, they suggested that 5 m may be an adequate height for efforts aimed at detecting high-flying members of these taxa. These results are only partly supported by the current study; we found no difference in beetle composition between traps at 15 and 5 m at the forest edge, but beetles captured at these trap heights did differ significantly in the forest interior. Taken together, these findings indicate that traps placed at 5 m will yield a good representation of beetles more active in the canopy but may miss taxa active at greater heights.

Authors contribution statement

MDU designed the study. TNS, SH, and MDU performed the fieldwork. TNS and ERH identified the specimens. TNS and MDU wrote the paper. All authors read and approved of the manuscript.

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Compliance with ethical standards

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

Human and animal rights This article does not contain any studies with human participants or animals performed by any of the authors. The use of product names does not imply endorsement by the United States Department of Agriculture, the University of Georgia, or the Joseph W. Jones Ecological Research Center.

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