



Plant-Insect Interactions

Distribution of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) damage in tree canopies: implications for survey efficacy

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Anoplophora glabripennis Motschulsky is an invasive woodboring beetle in North America and Europe that threatens a broad range of tree genera. Eradication is a costly and time-consuming process that requires visual surveys to detect beetle damage on host trees. Knowing the distribution of beetle damage within trees could directly benefit survey efforts by focusing surveys on high-risk areas and indirectly by identifying habitat factors that structure beetle populations. In the *A. glabripennis* infestation in South Carolina, we identified an isolated and actively growing subpopulation on an island that had not fully occupied the available host trees. With host resources still abundant for the beetle, the distribution of oviposition pits and exit holes is expected to be the result of habitat preference and (in the case of exit holes) larval performance. We examined the distribution of eggs and emerging adults by cataloging the >14,000 oviposition sites and >1,400 exit holes distributed among the 33 infested and uninfested host trees on the island, documenting the stem height, diameter, surface area, and bark thickness for all damage. Oviposition pits and exit holes were neither randomly nor evenly distributed within tree canopies; however, the distribution of available habitat (ie stem space within the canopy) seemed to drive most of the distribution, and the presence of damage was biased toward larger/taller trees. These results suggest some preference in egg placement with regard to canopy height, stem diameter, and bark thickness within canopies, but the responses are subtle and may have limited utility in guiding visual surveys.

Keywords: *Acer*, Asian longhorned beetle, forest health, invasive species, monitoring

Introduction

Eradicating an invasive species requires managers to detect and delimit the extent of an infestation (Panetta and Lawes 2005), and the methods used to find and delimit infestations depend on available tools based on the biology and behavior of the target species. Traps, for example, can take advantage of pheromones, kairomones, or visual cues to attract a target species (Sharov et al. 2002). For some high-impact invasive species such as the spongy moth (*Lymantria dispar* L., Lepidoptera: Erebiidae) and brown-tail moth (*Euproctis chrysorrhoea* L., Lepidoptera: Noctuidae), baited traps have been an efficient, cost-effective method for conducting surveys at landscape scales. Regardless of the survey method used, however, increasing the sensitivity and accuracy of surveys is paramount to detecting the target

species with maximum efficiency and cost-effectiveness (Berec et al. 2015).

Native to China and the Korean peninsula, *Anoplophora glabripennis* Motschulsky (Coleoptera: Cerambycidae; colloquially known as the Asian longhorned beetle) is an invasive woodboring beetle that has established breeding populations in both North America and Europe (Haack et al. 2010). Left unchecked, the spread of *A. glabripennis* into urban and rural wooded landscapes could lead to significant ecological and structural changes to forests, resulting in substantial economic impacts (Nowak et al. 2001, MacLeod et al. 2002, Pedlar et al. 2020). In response to this threat, the United States, Canada, and members of the European and Mediterranean Plant Protection Organization (EPPO) have adopted policies of eradication, and

populations of *A. glabripennis* have been successfully eliminated in several areas in both North America (Turgeon et al. 2022a, Supplementary Fig. S1) and Europe (Eyre and Barbrook 2021, Marchioro and Faccoli 2021, EPPO Global Database 2025). In the United States, 13 active infestations have been found since 1996, of which 9 have been eradicated (Supplementary Fig. S1).

Efficient survey and detection methods (eg traps) are not available for *A. glabripennis*, and eradication programs depend on simple but labor-intensive visual surveys by field staff to identify infested host material (Turgeon et al. 2007, 2010, Haack et al. 2010). To delimit infestations and identify infested trees for removal and destruction, visual surveyors are tasked with searching the entire surface of branches and trunks from the ground using binoculars and spotting scopes, as well as by tree climbers within the canopies of host trees, to find the pits chewed into the bark by ovipositing females and the ~1 cm diameter exit holes left by emerging adults (Fig. 1). Signs of *A.*

glabripennis can also include evidence of cambial damage and fresh wood shavings ejected from larval galleries (Haack et al. 2010, Turgeon et al. 2010, Meng et al. 2015, Coyle et al. 2021), though these indications of damage are not considered diagnostic in the absence of oviposition pits and exit holes. With a broad host range that includes maples (*Acer*), poplars (*Populus*), and willows (*Salix*), and with infested landscapes potentially covering hundreds of square kilometers, eradication programs face the challenge of surveying complex landscapes with millions of individual host trees. In the context of limited resources while sometimes facing challenges in accessing properties, conducting a complete survey of a large landscape can require multiple years, and multiple surveys of a landscape may be required to achieve an acceptable level of confidence in eradication (eg Eyre and Barbrook 2021, Turgeon et al. 2022a).

Detailed information describing the distribution of *A. glabripennis* damage within tree canopies could serve two related

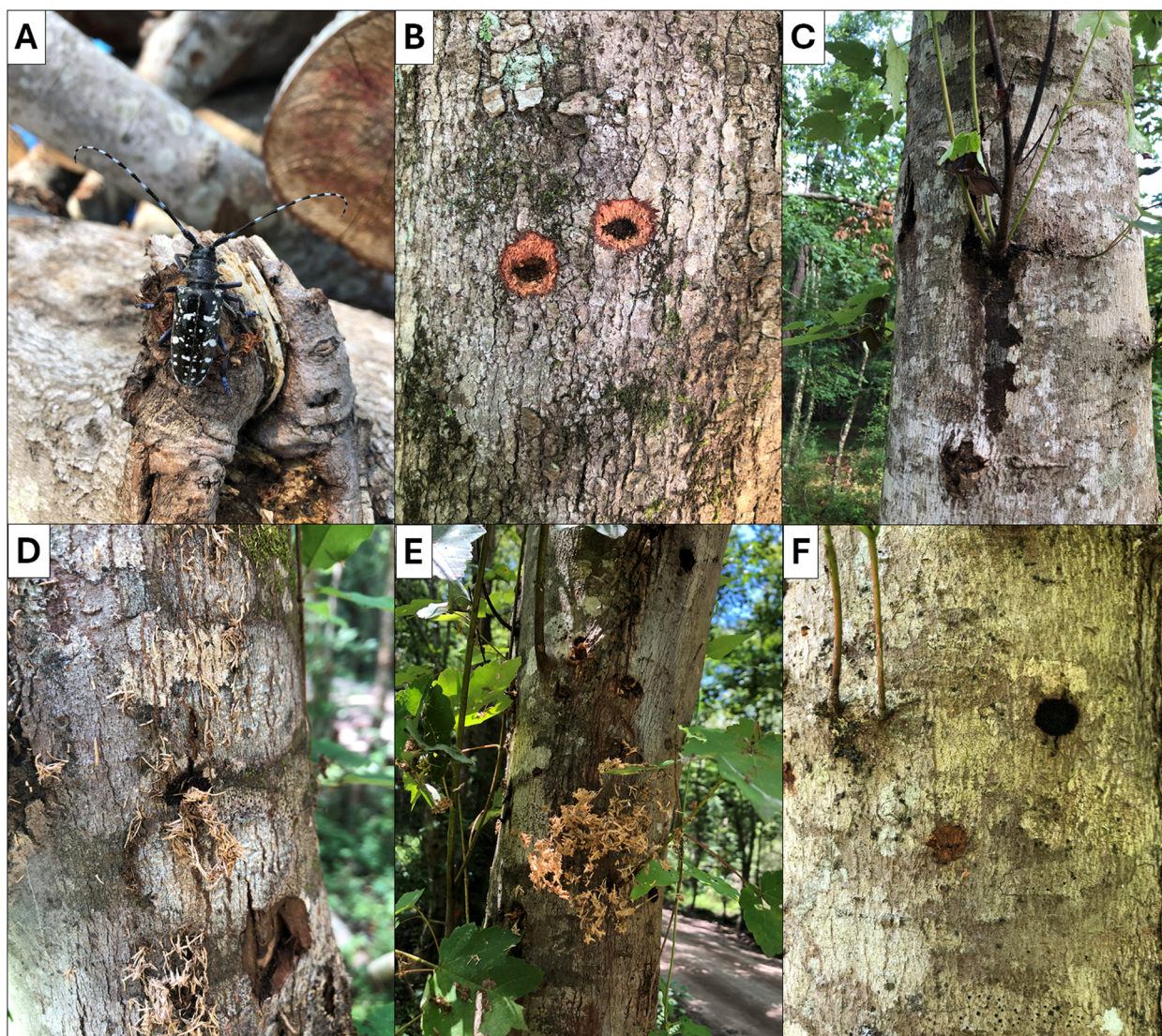


Fig. 1. *Anoplophora glabripennis* adult (A) and damage. After mating, adult females chew oviposition pits (B) into the bark, into which they may insert an egg. Larvae first feed in the phloem, which causes disfigured bark, discoloration, and epicormic shoots (C). Older larvae feed in the heartwood, and their feeding may push out frass and wood shavings (D), which may fall onto surrounding vegetation (E). Adults chew a round exit hole (F) to leave the tree and start the cycle again. Photos by D.R. Coyle and M.S. Bean, all taken on *Acer rubrum* host trees.

purposes. First, information that can focus visual survey efforts in tree canopies has the potential to accelerate surveys and/or improve survey efficacy. Second, knowledge of oviposition and exit hole distribution may provide insight into the biological and behavioral factors that structure the growth and spread of local infestations. This, in turn, could identify potential links between the locations where eggs are deposited by females (preference) and where adults emerge (performance). Therefore, information describing the distribution of damage both within and among trees has the potential to both benefit survey efforts and provide insight into the biological and behavioral factors that govern the spread of *A. glabripennis* within and among host trees.

Two key studies on the distribution of *A. glabripennis* within tree canopies have been conducted (Haack et al. 2006, Turgeon et al. 2022b) and provide much of what is known about the selection of hosts and the distribution of damage within host trees. Using infested trees that were cut during eradication activities in Chicago, Illinois, United States, and wind-break trees planted in China, Haack et al. (2006) found that *A. glabripennis* exit holes and oviposition pits were generally centered on the portion of the trunk near the base of the canopy. In Canada, Turgeon et al. (2022b) used records collected during two periods of eradication in the Toronto area. These data included more than 150,000 stems, >90,000 of which were suitable for infestation by *A. glabripennis*. Data from more than 650 infested trees revealed *A. glabripennis* oviposition pits and exit holes occurred most frequently on host trees with a 10 to 20 cm diameter at breast height (1.37 m), with *A. glabripennis* showing a bias toward infesting *Acer*, particularly *A. platanoides* L. The infested trees included >47,000 oviposition sites and >1,800 exit holes and, based on records of the locations of the highest and lowest points of damage from 608 trees, Turgeon et al. (2022b) found that the lowest damage (oviposition pit or exit hole) was in the lower half of the tree on approximately 90% of the studied trees, and that the lowest damage was within 3 m of the ground in 65% of the trees, and within 5 m on 85% of the trees. The height of the highest damage was closely correlated with the height of the tree.

While these data provided much needed information on the distribution of *A. glabripennis* damage within trees, there are limitations; specifically, the Chicago data were limited by the availability of infested trees and the method of tree selection (ie trees were taken from those made available by removal crews during eradication, rather than being systematically sampled), and the data from China represented a native *A. glabripennis* population grown in artificially planted windbreaks along the edges of agricultural fields (Haack et al. 2006). Data collected from the infestations in the Toronto area included large sample sizes and information on host selection, but data on the distribution of damage within trees were limited to the height of the highest and lowest points of damage (Turgeon et al. 2022b).

We expand on this work by quantifying the distribution of oviposition pits and exit holes within the canopies of host trees in a small, actively growing, and relatively isolated *A. glabripennis* population. In May of 2020, a new *A. glabripennis* infestation was found in South Carolina, United States (Coyle et al. 2021), and in December of 2020, delimiting surveys found infested trees on a small island. Using this island as a naturally occurring discrete population, we documented the locations of all detectable oviposition pits and exit holes on

each of the host trees present to determine if (i) *A. glabripennis* damage (oviposition pits and exit holes) was randomly distributed within host trees with respect to available space within the tree, (ii) there were differences in the distribution of oviposition pits and exit hole heights, suggesting either shifts in oviposition or differences between where eggs are laid and where larvae are successful, and (iii) the distribution of oviposition pits and exit holes related to canopy factors, including host material diameter and bark thickness.

Materials and Methods

Site Description and History

The *A. glabripennis* infestation in South Carolina remains under active eradication management by the Cooperative Asian Longhorned Beetle Eradication Program (<https://www.aphis.usda.gov/plant-pests-diseases/alb>) and includes portions of Charleston and Dorchester counties in USDA Plant Hardiness Zone 9a, a climate that is substantially warmer than that of any former or current infestation previously found in North America. The site used for this study comprised the entire forested system on a 3.4 ha island in the Stono River southwest of Charleston, SC, with the island making up a portion of the Stono River County Park (32° 47' 09.0" N, 80° 06' 44.0" W) within the Charleston County Parks and Recreation Commission system (Fig. 2). The Stono River County Park was first opened to the public in early 2020 when a 330 m long elevated boardwalk causeway was built connecting the island to the mainland. This boardwalk provides the only direct access to the island, which is surrounded by the river and sections of tidal marsh. This small artificial island was created in the early part of the 19th century when the site was used as a dumping location for material dredged from the Stono River to support marine navigation, and from material collected as drainage ditches were excavated from tidal marshes. Prior to the removal of infested trees, the island's forest canopy was dominated by invasive *Triadica sebifera* (L.) Small, and native species, including *Juniperus virginiana* L., *Celtis laevigata* (Willd.), *A. rubrum*, *Quercus laurifolia* (Michx.), and *Morus rubra* L., and scattered, mature *Pinus taeda* L., *Liquidambar styraciflua* L., and *Ulmus americana* L. (Bean 2022).

Tree Surveys and Removals

In December 2020, USDA Asian Longhorned Beetle Cooperative Eradication Program survey personnel carried out a complete ground survey of the island using standard eradication survey protocols (Rose 2014) and found a total of 33 *A. rubrum* trees (Fig. 2). Ground survey crews documented signs of infestation (oviposition pits and exit holes) on 23 of these trees, suggesting *A. glabripennis* had spread within and among the host trees but had not yet fully utilized the available host resource on the island. The preliminary level of infestation for each of the trees was documented by survey personnel using the 4-level infestation category system (A, B, C, and D) used by the Asian Longhorned Beetle Eradication Program. A-level trees are those with oviposition pits, but no adult exit holes. B-, C-, and D-level trees are those with 1 to 10, 11 to 100, and >100 exit holes, respectively. All host trees were marked and numbered in preparation for removal.

In February 2021, sawyers (Davey Resource Group, Kent, Ohio, United States) felled all 33 *A. rubrum* trees. Once felled,

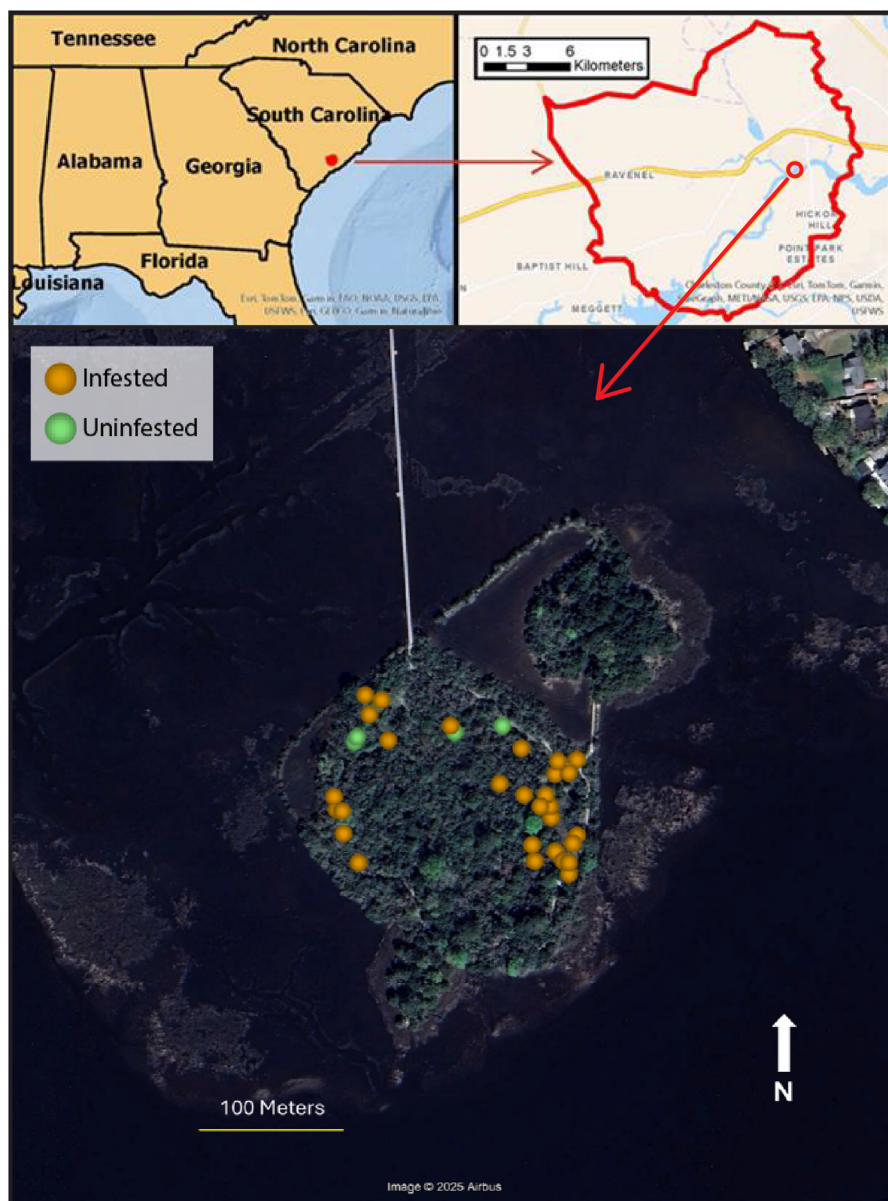


Fig. 2. Map showing the relative position of the *Anoplophora glabripennis* federal quarantine area in Charleston Co., South Carolina, United States, along with the location of the island within the quarantine zone from which all study trees used were collected. Orange dots represent host trees infested with *A. glabripennis*, and green dots represent uninfested trees.

the canopy of each tree was intensively re-inspected for *A. glabripennis* damage and during this process an additional 5 *A. rubrum* trees (of the original 33) were found to be infested. Canopy material smaller than 3.8 cm in diameter and verified as uninfested was chipped on-site in compliance with USDA APHIS-PPQ Asian Longhorned Beetle Eradication Program requirements (Rose 2014). The remaining portions of the infested trees with diameters greater than 3.8 cm and/or with evidence of infestation were cut on-site into sections that varied in length between 0.05 and 3.5 m. At each cut, the ends of the adjoining sections were labeled with corresponding identification codes denoting the tree and cut to facilitate the reassembly of trees and data collection off-site. Tree sections were removed from the island by hand and by UTV and transported to the field station at the College of Charleston Stono Preserve (32° 44' 39.4" N, 80° 10' 55.1" W) for processing.

Sample Processing

Tree sections were processed from March through June 2021. Processing consisted of arranging sections of each of the 33 trees on the ground with the relative position of each section determined by the matching cut identification values, allowing the architecture of each tree to be reconstructed (Fig. 3). The length of each tree section was documented, and the height (as measured along the stem) of the lower cut of each section was tabulated as the sum of the lengths of each section between ground level and the cut.

To quantify the location of each oviposition pit, each section was subdivided into 3.05 cm (1/10 ft) long increments. For simplicity, we refer to these increments as “slices” though we note these slices represent sampling units for analysis; tree sections were often not physically cut into individual slices. We also note that these slice heights represent lengths along the stem of



Fig. 3. Cut portions of sample *Acer rubrum* trees collected from an island in Charleston Co., South Carolina, United States, were transported to the field laboratory at the Stono facility and each tree—from the branches (A) to the main stem (B) to the stump (C)—was reconstructed. The vertical location and host diameter were then recorded for all *Anoplophora glabripennis* oviposition pit and exit hole locations. Photos by M.S. Bean.

the tree, rather than true vertical heights. While true vertical height would be valuable, collecting this data would have required in situ measurements of each oviposition pit and exit hole using climbers and plumb bobs prior to tree felling. Given the number of oviposition pits and exit holes, the total length of tree stems evaluated (>1,600 m or >53,000 slices), the risks associated with tree climbers accessing small limbs in damaged trees, and the time limits in place for the closure of the park and the removal of trees, this approach was not feasible. Taken collectively, the slices within and among the trees provide a representation of the total amount of habitat within the tree that is available to the beetles and the phrases “distribution of slices” and “distribution of available tree habitat” may be used interchangeably. The bark thickness and diameter for each cut section within the tree was measured at the lower cut, and these values were applied to each of the slices within the section. For each slice, the number of oviposition pits was documented and the height recorded as the height of the lower edge of the slice. The locations of exit holes were documented in a similar fashion, but the locations of exit holes were measured individually rather than being placed within height bins defined by slices.

Statistical Analyses of Height, Diameter, Surface Area, and Bark Thickness

To maintain consistency with infestation categories used by the USDA APHIS Asian Longhorned Beetle Cooperative Eradication Program and in prior studies (eg Trotter and Hull-Sanders 2015, Hull-Sanders et al. 2017, Trotter et al. 2023), the distribution of damage within trees was analyzed on tree categories comprising Uninfested trees and A-, B-, C-, and D-level trees, as well as a pooled group containing all infested trees. Categories of infestation in these analyses are derived from the total type and quantity of damage found on trees after complete canopy surveys, rather than initial categories assigned by ground survey crews.

All statistics were completed using R (version 4.4.1 “Race for your Life”) in RStudio (Build 764) (R Core Team 2024);

packages and functions used in the following analyses are indicated in parentheses. Because damage represents a binary variable distributed along a continuous height variable, rank heights of oviposition pits and exit holes were compared with the rank heights of available tree habitat (ie all slices within a tree) using a Wilcox test (EnvStats, wilcox.test). The distribution of oviposition pits, exit holes, and overall available canopy heights was compared using a 2-sided Kolmogorov-Smirnov test (EnvStats, ks.test).

Predictive relationships between the presence of oviposition pits and exit holes and canopy height, branch diameter, and bark thickness were evaluated using a Multinomial Logistic Regression (tidyverse, multinom_reg); goodness of fit was evaluated using deviance as a representation of goodness of fit. Overall performance was evaluated by comparing predicted and observed outcomes for the 4 groups of slices (Uninfested, Oviposition Pit, Exit Hole, and Slices with both Oviposition Pits and Exit Holes, referred to hereafter as Both) to produce a simple confusion matrix.

Results

Stand Damage

Nearly 85% (28 of 33) of the host trees on the island were found to be infested by *A. glabripennis*, with the number of trees distributed among Uninfested, A-, B-, C-, and D levels following a roughly bimodal distribution (Fig. 4). Overall, infested trees contained 57,504 slices that included 14,615 oviposition pits (Table 1) distributed across 7,083 slices, demonstrating the distribution of oviposition pits was clustered within the canopy. Slices that included oviposition pits frequently included multiple pits, with damaged slices including a mean of 2.1 pits. A total of 1,451 exit holes were found on the 28 infested trees (Table 1) with a distribution very similar to that of the oviposition pits. The quantity of tree habitat in each group, represented by the total number of slices, was skewed with the bulk being found in C-level trees and the

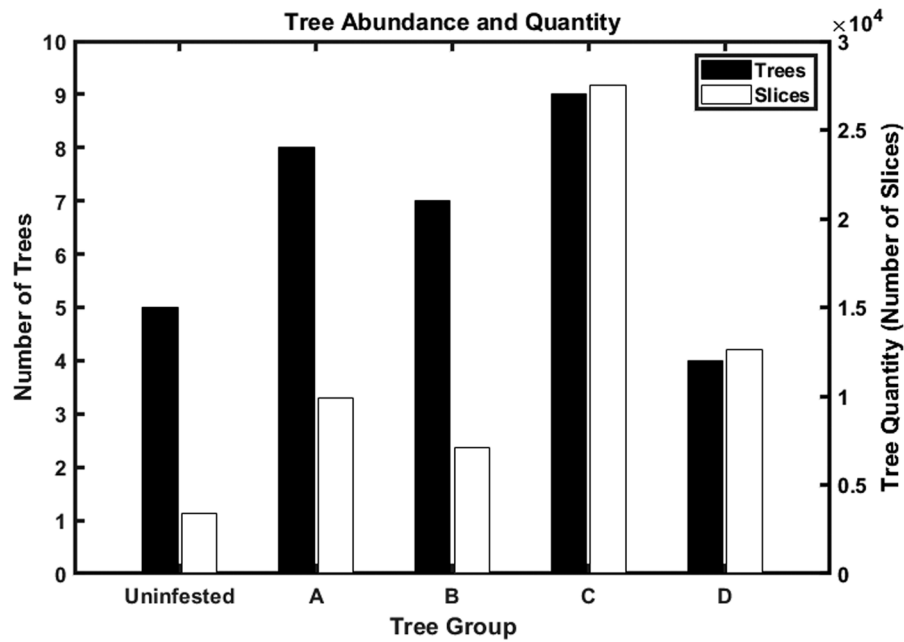


Fig. 4. Number of *Acer rubrum* trees and quantity of slices in each *Anoplophora glabripennis* infestation level category collected from trees on an island in Charleston Co., South Carolina, United States.

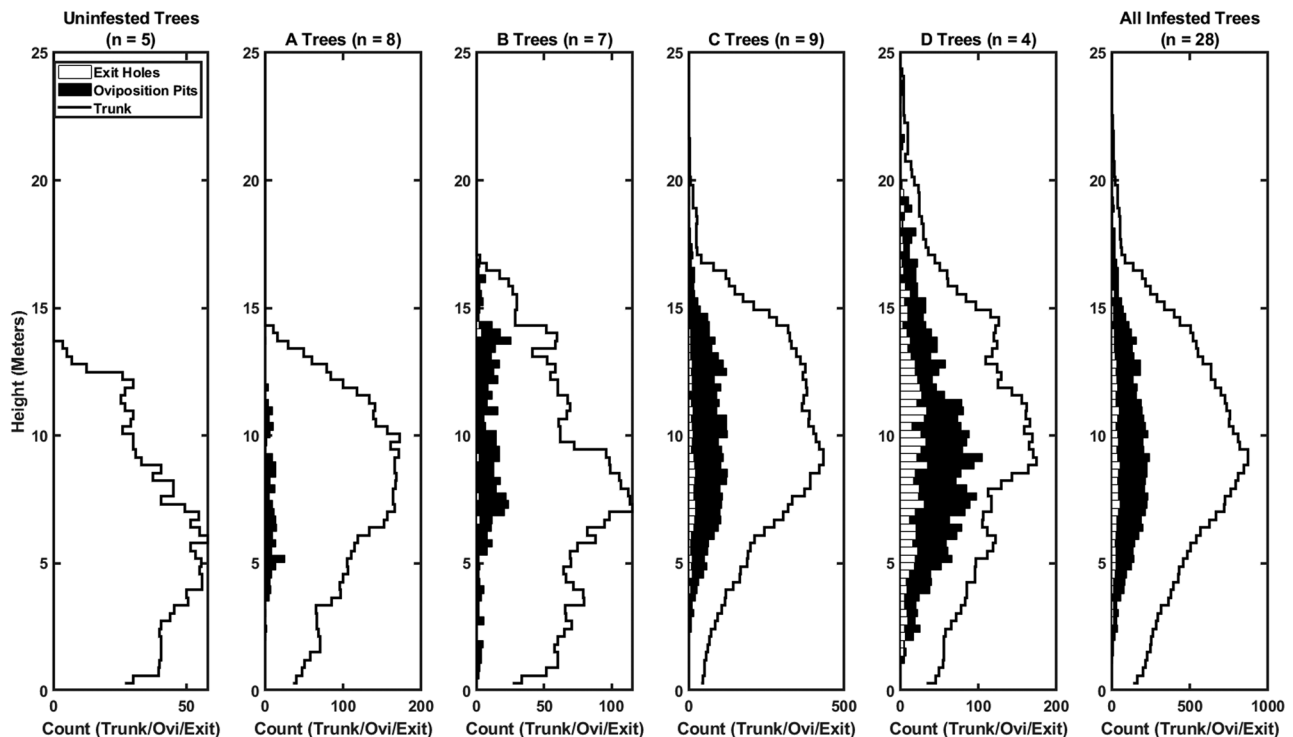


Fig. 5. Relative position of *Anoplophora glabripennis* adult exit holes and oviposition pits on *Acer rubrum* trees collected from an island in Charleston Co., South Carolina, United States in spring 2021. When the damage across all infested trees is pooled, the distribution of both oviposition pits and exit holes deviates from the overall distribution of available habitat ("Trunk") within the site, however the deviations are very small.

lowest quantities in the Uninfested and D-level trees (Fig. 4). The 4 uninfested trees present on the island were generally shorter with a lower overall distribution of canopy space than which were infested, and infested trees in the A-, B-, C-, and D-level infestation categories suggest a trend in increasing median canopy habitat height (Fig. 5).

Distribution of *Anoplophora glabripennis* Oviposition Pits Within Tree Canopies

Within A-level infested trees (ie trees with no exit holes), the median height of the oviposition pits was about 1 m lower than the median distribution of available trunk habitat (Table 1), though the overall distribution was very similar (Fig. 5).

Table 1. Statistical values for Wilcoxon and Kolmogorov–Smirnov tests to evaluate the relative position of *Anoplophora glabripennis* adult exit holes and oviposition pits on whole *Acer rubrum* trees and tree slices of different *A. glabripennis* infestation levels from an island in Charleston Co., South Carolina, United States

		Damage location ~ Available trunk					
		<i>n</i>	Med. Height (m)	Wilcoxon <i>W</i>	<i>P</i>	Kolmogorov–Smirnov <i>D</i>	<i>P</i>
All infested	Oviposition pits	14,615	9.24	19,70,19,272	<0.00001	0.07419	<0.00001
	Trunk (slices)	57,504	9.17				
	Exit holes	1,451	9.02	4,15,10,974	0.7511	0.06613	<0.00001
A Trees	Oviposition pits	326	6.68	15,92,512	0.00147	0.15856	<0.00001
	Trunk (slices)	10,342	7.64				
	Exit holes	0	NA				
B Trees	Oviposition pits	696	9.3	13,24,491	<0.00001	0.2149	<0.00001
	Trunk (slices)	7,107	7.57				
	Exit holes	25	8.6	68,143	0.04404	0.26582	0.05917
C Trees	Oviposition pits	6,338	9.65	5,05,19,211	<0.00001	0.5923	<0.00001
	Trunk (slices)	27,477	9.97				
	Exit holes	467	8.44	76,47,428	<0.00001	0.18363	<0.00001
D Trees	Oviposition pits	7,255	9.02	1,85,55,262	<0.00001	0.090055	<0.00001
	Trunk (slices)	12,578	9.81				
	Exit holes	959	9.45	62,50,326	0.05047	0.08878	<0.00001

Oviposition pits on B-level infested trees (ie those with 10 or fewer exit holes) demonstrated the opposite pattern, with a median oviposition pit height more than 1.7 m higher than the median distribution of available canopy (Table 1). C- and D-level infested trees had median oviposition pit heights slightly lower than the median height of available canopy (Table 1). When pooled across all infested trees, the deviation in median oviposition height from median available canopy was statistically significant, but with a median difference of roughly 7 cm, the deviation is small.

Although median heights are informative, the shape of the distribution of variation between damage height and available canopy height provides additional information (Fig. 6). When all infested trees are combined, the distribution of oviposition pits shows a maximum deviation of 6% fewer accumulated at a height of 5 m (Fig. 6A), and while significant, the deviation in the proportion of the population of oviposition pits remains small. For each of the individual infestation levels (A, B, C, and D; Figs. 6B, 6C, 6D, and 6E, respectively), there is a tendency for fewer than expected oviposition pits to occur at heights lower than 5 m. Among A-level trees in particular, this pattern reverses with increasing height as 15% more oviposition pits occurred at heights near 9 m, suggesting a clustering of damage within the height range of 6 to 12 m.

Distribution of *Anoplophora glabripennis* Exit Holes Within Tree Canopies

The median exit hole height in B-level trees was less than 1 m higher than the median height of available canopy, and the overall distribution of exit holes was not significantly different from the available canopy (Fig. 5, Table 1). The median height of exit holes in C-level trees was approximately 1.5 m lower than the available canopy (Fig. 5, Table 1), with exit holes generally occurring more often than expected at central heights (Fig. 6). D-level trees were generally similar, though the

difference in median heights was smaller (<0.5 m). The deviation from the expected distribution of exit holes (Fig. 6) suggests a tendency for exit holes to be clustered near the median (~10 m) height of the available canopy.

Deviations in the Distribution of Oviposition Pits and Exit Holes Within Tree Canopies

Within the A-, B-, C-, and D-level infestation groups, there were few statistically significant deviations between the distribution of oviposition pits and exit holes (Table 2, Figs 5 and 6), and trends among groups were not consistent. Within B- and C-level infested trees, holes had a slightly lower median height than oviposition pits, and in D-level trees the height was slightly higher, though only the C-level trees exhibited a significant difference in median rank heights between oviposition pits and exit holes. In C-level trees, median height of oviposition pits was 1.2 m above that of the exit holes. The difference in the distribution of oviposition pits and exit holes was also different among C-level infested trees, as exit holes occurred more often between 7 and 15 m than would be expected based on the distribution of oviposition pits. However, when pooled across all infested trees, neither the shape ($D = 0.03$, $P = 0.017$) nor the center of the distribution of oviposition pits and exit holes ($W = 5292973$, $P = 0.071$) were different (Table 2).

The Utility of Height, Diameter, and Bark Thickness in Predicting the Distribution of Damage

Pooled across all infested trees, the parameters for height, stem diameter, and bark thickness are significantly different in slices that include oviposition pits, exit holes, or both types of damage from slices that have no damage (Table 3). For example, an increase in height of 1 m increases the odds that the slice is infested by both an oviposition pit and an exit hole by 19%. An increase in bark thickness of 1 mm increases the odds that the slice will include an oviposition pit by 72%.

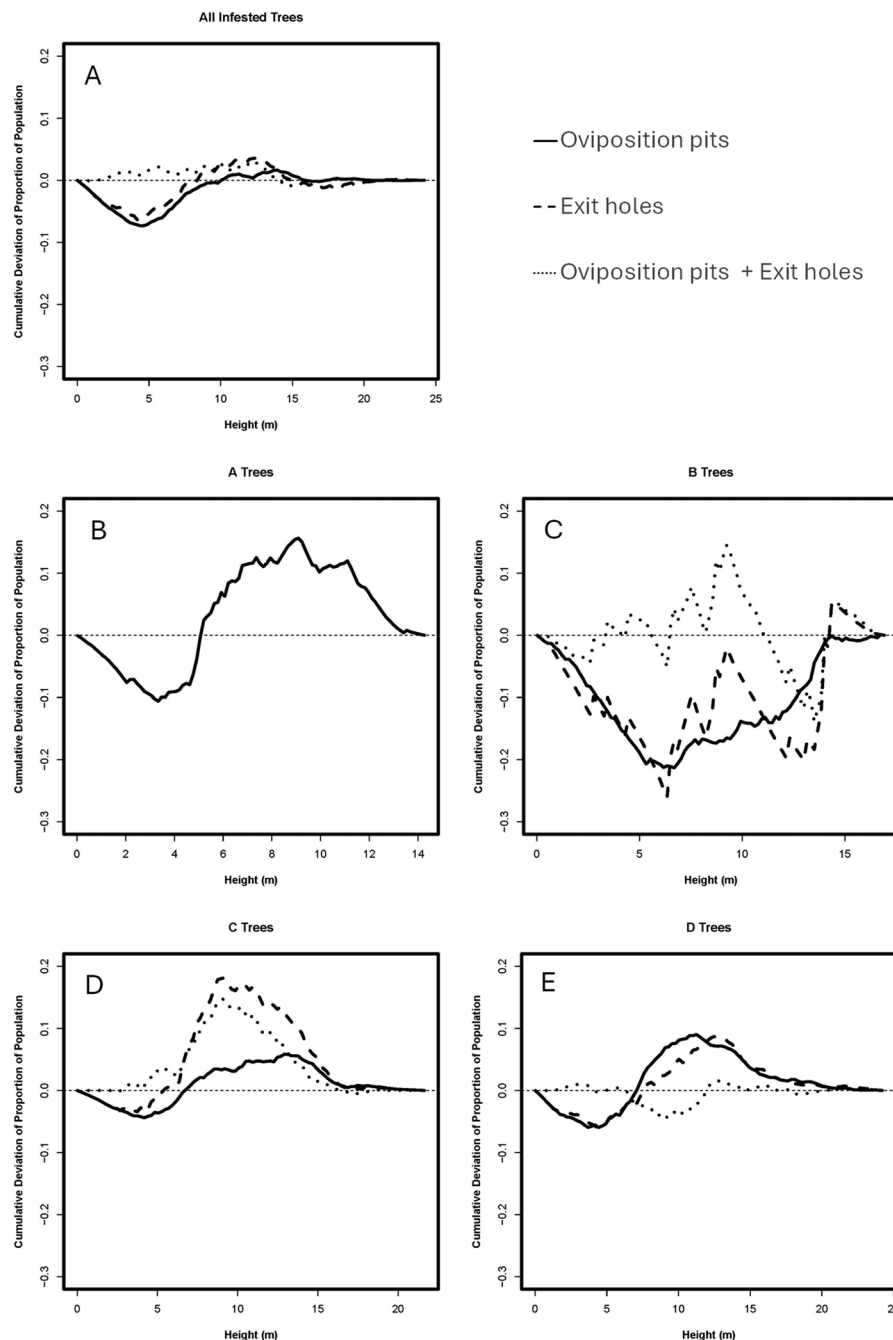


Fig. 6. Deviations in the distribution of *Anoplophora glabripennis* damage from the expected distributions based on available tree habitat, and deviations in the expected height of oviposition pits based on the distribution of exit holes. Data represent summary of 28 infested *Acer rubrum* trees collected on an island in Charleston Co., South Carolina, United States in spring 2021. Figure shows all trees combined (A), A-level damage trees (B), B-level damage trees (C), C-level damage trees (D), and D-level damage trees (E). Values above the zero base line indicate distributions higher than expected, values below represent lower than expected distributions.

Discussion

Knowing where to look for invasive species—while a simple and somewhat obvious notion—can drastically influence survey efficacy in finding the target species, especially invasive woodborers. Past studies have shown that the within-canopy distribution of woodboring species can be variable and that this variation can affect survey efficacy. Timms et al. (2006) found that visual surveys of *Fraxinus* for damage by the emerald ash borer, *Agrilus planipennis* F. (Coleoptera: Buprestidae),

may be improved by focusing on stems with a diameter of ≥ 7 cm. Most eucalyptus longhorned borer (*Phoracantha semipunctata* F., Coleoptera: Cerambycidae) emergence occurred on the tree stem between 2 and 4 m from the ground (Seaton et al. 2020), and the greatest density of goldspotted oak borer (*Agrilus auroguttatus* Schaefer, Coleoptera: Buprestidae) emergence holes was found in trees with a diameter at breast height of >76.2 cm (Coleman et al. 2014). The distribution of *A. glabripennis* oviposition pits and exit holes in our study mirrored the distribution of available habitat (ie stem space) within the

canopies of individual trees (Supplementary Fig. S2) and trees grouped by level of damage (Fig. 5). The distribution of both types of damage did exhibit statistically significant deviations from the overall distribution of habitat (Fig. 6, Tables 1 and 2); however, these deviations were typically on the scale of 1.5 m or less.

Previous work by Haack et al. (2006) described the distribution of oviposition pits in host trees as “throughout the trunk and major branches of host trees but often starts along the upper trunk and lower portions of major branches” (p 13) and the distribution of exit holes centered on the “mid-crown trunk section” (p 5). Our results generally agree with these past findings and provide some additional spatial resolution pertaining to the preferred habitat of *A. glabripennis*. Haack et al. (2006) note that the distribution of damage was driven by the distribution of available habitat, and the description of damage centered on the “upper trunk and lower major branches.” Haack et al. (2006) also discuss the potential for the “mid-crown trunk” exit holes to represent the earliest part of the population growth in the infested trees and that under these conditions it appeared that this was the first part of the tree to receive oviposition pits with the infestation spreading with time. The data described here from an intact population also

shows that exit holes appear centered in the middle heights (at least within C-level trees) at a canopy position that likely reflects the lower crown sections as described by Haack et al. (2006).

The deviation between the locations of oviposition pits and exit holes may be driven by multiple and non-exclusive factors. First, the differences may be driven by a slight bias in survival, with eggs oviposited at different heights having either a slightly increased or reduced probability of developing to maturity. This variation may be a function of intrinsic factors such as host condition and quality or by extrinsic factors such as predation. Ongoing studies in South Carolina have found evidence that *A. glabripennis* eggs placed in the cambium are subject to predation by ants, specifically, the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae) (Lindsey Stone, pers. obs), which is common in this area. The distribution of *S. invicta* nests would drive a patchy expression in this predation on the landscape, and because the ants are ground-nesting, eggs placed lower on the canopy may be more exposed to detection by foraging scouts. Host quality likely also plays a role in structuring the establishment and expansion of an *A. glabripennis* infestation in a host tree, and these data may indicate links between oviposition sites and adult emergence holes. The link between maternal preference and offspring performance has been observed in multiple insect systems and described by Price (1991) as a preference–performance link. *Anoplophora glabripennis* attacks trees with a wide range of sizes, including those with larger trunk diameters (Straw et al. 2015, Hull-Sanders et al. 2017, Turgeon et al. 2022b, 2025). In some cases, trees with slower radial growth rates are attacked first and become the most heavily infested (Dodds and Orwig 2011). Previous studies have investigated host colonization by examining the density of adult emergence holes, typically by calculating the density of exit holes per tree (Haack et al. 2010, Turgeon et al. 2022b) or per cm diameter at breast height (Yan 1985, Peng and Liu 1992, Dodds and Orwig 2011). Our data suggest the potential for an interaction between the level of infestation within a tree and the distribution of both oviposition pits and adult exit holes. Among A-, C-, and D-level infested trees, oviposition pits were placed approximately 1 m lower on the trunk than would be suggested by the distribution of habitat within the tree. Whether this

Table 2. Relationship of the abundance of *Anoplophora glabripennis* oviposition pits to adult exit holes from *Acer rubrum* trees of differing levels of infestation on an island in Charleston Co., South Carolina, United States

Oviposition pits ~ Exit holes				
	Wilcoxon W	P	Kolmog- orov– Smirnov D	P
All infested trees	52,92,937	0.07	0.031944	0.17
A Trees	NA	NA	NA	NA
B Trees	6,378	0.90	0.16087	0.57
C Trees	9,48,404	<0.00001	0.1494	<0.00001
D Trees	13,03,505	0.23	0.046218	0.09

Table 3. Influence of tree height, host diameter, and bark thickness on the presence of *Anoplophora glabripennis* exit holes and oviposition pits from a small infestation in Charleston Co., South Carolina, United States

Term		Odds Est.	P	Lower 95% CI	Upper 95% CI
Exit hole and oviposition pit	(Intercept)	0.0000819	2.33e ⁻²⁵	0.0000139	0.000482
	Height (m)	1.19	5.08e ⁻³	1.05	1.35
	Bark thickness (mm)	2.29	5.10e ⁻⁴	1.44	3.65
	Stem diameter (cm)	0.931	3.92e ⁻¹	0.79	1.1
Exit hole	(Intercept)	0.0013	8.74e ⁻²⁴	0.000355	0.00474
	Height (m)	1.09	8.16e ⁻²	0.989	1.21
	Bark thickness (mm)	1.16	5.31e ⁻¹	0.726	1.86
	Stem diameter (cm)	0.977	7.74e ⁻¹	0.835	1.14
Oviposition pit	(Intercept)	0.017	2.17e ⁻¹³⁹	0.0124	0.0234
	Height (m)	1.08	1.45e ⁻⁹	1.05	1.11
	Bark thickness (mm)	1.72	3.62e ⁻²¹	1.54	1.93
	Stem diameter (cm)	0.879	6.01e ⁻⁹	0.842	0.918

deviation represents idiosyncratic responses by ovipositing females or is suggestive of a response to perceived variation in host quality is unknown. Similarly, the vertically higher occurrence of emergence holes relative to the distribution of oviposition pits suggests there may be a slight difference in larval performance dictated by heights, or alternatively, that oviposition site height may shift as an infestation progresses such that early oviposition pits placed higher in the canopy may emerge prior to later oviposition pits placed lower on the canopy as higher and smaller stems become limiting as an infestation progresses.

Alternatively, it is possible that the deviation in positions of oviposition pits and exit holes may be indicative of a directional trend in oviposition placement through time. Beetles require ~1 yr to complete development in South Carolina (Schmitt et al. 2025); consequently, the distribution of exit holes is based on the distribution of eggs oviposited in prior years. If there is a directional trend in oviposition pits within trees (eg females selecting progressively higher positions in the tree with each generation within a tree), the time lag between oviposition and emergence could drive a deviation between the distribution of oviposition pits and exit holes. A more detailed analysis, including the dates of each point of damage, would be necessary to determine whether this is the case. Finally, the variation in distribution may be related to the response of ovipositing beetles to variations in bark thickness and trunk diameter. Our data show that these variables are predictive of oviposition and adult emergence; however, more detailed information on the interactions of these factors with the architecture of the tree may be needed to apply these findings.

In a study of more than 600 infested trees in the Toronto area (Turgeon et al. 2022b), the position of the lowest damage was often within 3 m of the ground. In our data set, which is limited to only 28 trees, exit holes were found as low as 92 cm above ground level, and oviposition pits were found as low as 64 cm above ground level. Whether the apparent differences in the lowest heights observed within this wooded island are the result of differences in host type, quality, climate, and habitat, or differences in infestation intensity is not known. However, the presence of damage low on the trunk bodes well for the detection of infestations. In addition to the presence of some damage low on the tree, the distribution of oviposition pits within these trees is shifted toward the lower range of available canopy habitat, bringing the damage closer to the ground where it may be more visible to survey personnel. An assessment of survey efficacy by Turgeon et al. (2010) found that detections were made more consistently and quickly when damage was located below 2.5 m, with oviposition pits having a higher detectability than exit holes. In conditions such as those described with the distribution of damage, including points low on the trunk, detection rates by ground survey crews may range from 60% to 70%, supporting the observation that ground surveys offer an effective method to detect and delimit infestations by *A. glabripennis*.

The successful management of an invasive woodboring pest relies on the rapid and reliable detection of target pest populations. While newer technologies may show promise in terms of improving current detection methods (eg remote sensing [Valicharla et al. 2023, Zhou et al. 2025] or eDNA [Kyle et al. 2024] for *A. planipennis*; detector dogs for *Ips typographus* L. [Coleoptera: Curculionidae: Scolytinae], Johansson et al. 2019), the cryptic nature of woodboring pests often necessitates a reliance on visual ground surveys and hands-on detection tactics (eg Coleman et al. 2014, Ryall 2015, Jiang

et al. 2022). Prior to this study, most data describing the vertical distribution of *A. glabripennis* in host trees were dependent on qualitative descriptions and information limited to the highest and lowest points of damage. For example, Meng et al. (2015) described how oviposition (and subsequent adult emergence) often begins on a tree's "upper branches or main trunk" prior to shifting downward after heavily infesting the crown. Haack et al. (2006) outlined the differences between initial attack patterns noticed in China compared to Chicago as "along the main trunk near the first crown branches" to "upper trunk and major crown branches," respectively. Research in Italy specifically excluded trunks based on the statement "Asian longhorned beetle mainly infests the upper part of the trees and the main branches in the canopy" (Faccoli et al. 2015).

In the context of these observations, the efficacy of ground surveys is highly dependent on the proportion of the canopy that is visible from the ground and the distance of the surveyor from the tree surface. It would be logical to expect the efficacy of the survey to decrease as tree height and canopy density increase (ie total available beetle habitat). If *A. glabripennis* distributions were biased toward difficult-to-survey portions of the canopy, survey efficacy would be expected to decline. However, our data show that the distribution of *A. glabripennis* damage within the canopy very closely approximates the distribution of the available space in the canopy. As described by Turgeon et al. (2010) and by others elsewhere, experienced surveyors can consistently find *A. glabripennis*-infested trees, especially those that are heavily infested or infested closer to the ground. The data described here suggest that while the distribution of damage is not randomly distributed, the biases in distribution are very limited but may contribute in some way to increasing the detectability of infestations.

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Supplementary material

Supplementary material is available at *Environmental Entomology* online.

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Conflicts of interest

None declared.

References

- Bean MS. 2022. If you give a beetle a maple: population dynamics of the Asian longhorned beetle on an island in South Carolina [Master's thesis]. Clemson University. https://open.clemson.edu/all_theses/3943.
- Berec L, Kean JM, Epanchin-Neill R, et al. 2015. Designing efficient surveys: spatial arrangement of sample points for detection of invasive species. *Biol. Invasions* 17:445–459. <https://doi.org/10.1007/s10530-014-0742-x>.
- Coleman TW, Chen Y, Graves AD, et al. 2014. Developing monitoring techniques for the invasive goldspotted oak borer (Coleoptera: Buprestidae) in California. *Environ. Entomol.* 43:729–743. <https://doi.org/10.1603/EN13162>.
- Coyle DR, Trotter RS, Bean III. MS, et al. 2021. First recorded Asian longhorned beetle (Coleoptera: Cerambycidae) infestation in the southern U.S. *J. Integr. Pest Manage* 12:10. <https://doi.org/10.1093/jipm/pmab007>.
- Dodds KJ, Orwig DA. 2011. An invasive urban forest pest invades natural environments—Asian longhorned beetle in northeastern US hardwood forests. *Can. J. For. Res.* 41:1729–1742. <https://doi.org/10.1139/x11-097>.
- EPPO Global Database. 2025. *Anoplophora glabripennis*. Last accessed on 19 January 2025. <https://gd.eppo.int/taxon/ANOLGL/distribution>.
- Eyre D, Barbrook J. 2021. The eradication of Asian longhorned beetle at Paddock Wood, UK. *CABI Agric. Biosci* 2:12. <https://doi.org/10.1186/s43170-021-00034-x>.
- Faccoli M, Favaro R, Smith MT, et al. 2015. Life history of the Asian longhorn beetle *Anoplophora glabripennis* (Coleoptera Cerambycidae) in southern Europe. *Agr. Forest Entomol.* 17:188–196. <https://doi.org/10.1111/afe.12096>.
- Haack RA, Bauer LS, Gao RT, et al. 2006. *Anoplophora glabripennis* within-tree distribution, seasonal development, and host suitability in China and Chicago. *Great Lakes Entomol.* 39:69–183. <https://doi.org/10.22543/0090-0222.2163>.
- Haack RA, Hérard F, Sun J, et al. 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. *Annu. Rev. Entomol.* 55:521–546. <https://doi.org/10.1146/annurev-ento-112408-085427>.
- Hull-Sanders H, Pepper E, Davis K, et al. 2017. Description of an establishment event by the invasive Asian longhorned beetle (*Anoplophora glabripennis*) in a suburban landscape in the northeastern United States. *PLoS One*. 12:e0181655. <https://doi.org/10.1371/journal.pone.0181655>.
- Jiang Q, Liu Y, Ren L, et al. 2022. Acoustic detection of the wood borer, *Semanotus bifasciatus*, as an early monitoring technology. *Pest Manag. Sci.* 78:4689–4699. <https://doi.org/10.1002/ps.7089>.
- Johansson A, Birgersson G, Schlyter F. 2019. Using synthetic semiochemicals to train canines to detect bark beetle-infested trees. *Ann. For. Sci.* 76:58. <https://doi.org/10.1007/s13595-019-0841-z>.
- Kyle KE, Allen MC, Siegert NW, et al. 2024. Design of eDNA sampling method for detection of an endophagous forest pest. *NB.* 95:149–164. <https://doi.org/10.3897/neobiota.95.118267>.
- MacLeod A, Evans HF, Baker RHA. 2002. An analysis of pest risk from an Asian longhorned beetle (*Anoplophora glabripennis*) to hardwood trees in the European community. *Crop Protection* 21:635–645. [https://doi.org/10.1016/S0261-2194\(02\)00016-9](https://doi.org/10.1016/S0261-2194(02)00016-9).
- Marchioro M, Faccoli M. 2021. Successful eradication of the Asian longhorn beetle, *Anoplophora glabripennis*, from North-Eastern Italy: protocol, techniques and results. *Insects* 12:877. <https://doi.org/10.3390/insects12100877>.
- Meng PS, Hoover K, Keena MA. 2015. Asian longhorned beetle (Coleoptera: Cerambycidae), an introduced pest of maple and other hardwood trees in North America and Europe. *J. Integr. Pest Manage* 6:4. <https://doi.org/10.1093/jipm/pmv003>.
- Nowak DJ, Pasek JE, Sequeira RA, et al. 2001. Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. *J. Econ. Entomol.* 94:116–122. <https://doi.org/10.1603/0022-0493-94.1.116>.
- Panetta FD, Lawes D. 2005. Evaluation of weed eradication programs: the delineation of extent. *Divers. Distrib.* 11:435–442. <https://doi.org/10.1111/j.1366-9516.2005.00179.x>.
- Pedlar JH, McKenney DW, Yemshanov D, et al. 2020. Potential economic impacts of the Asian longhorned beetle (Coleoptera: Cerambycidae) in Eastern Canada. *J. Econ. Entomol.* 113:839–850. <https://doi.org/10.1093/jee/toz317>.
- Peng J, Liu Y. 1992. Iconography of forest insects in Hunan China. *Hunan Forestry Department/Institute of Zoology, Academia Sinica*. 1473 p.
- Price PW. 1991. The plant vigor hypothesis and herbivore attack. *Oikos* 62:244–251. <https://doi.org/10.2307/3545270>.
- R Core Team. 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Rose R. 2014. Asian longhorned beetle response guidelines. USDA APHIS PPQ Technical Document. Available at <https://www.aphis.usda.gov/sites/default/files/response-guidelines.pdf>
- Ryall K. 2015. Detection and sampling of emerald ash borer (Coleoptera: Buprestidae) infestations. *Can. Entomol.* 147:290–299. <https://doi.org/10.4039/tce.2015.7>.
- Seaton S, Matusick G, Hardy G. 2020. Within-tree distribution and survival of the *Eucalyptus* longhorned borer *Phoracantha semipunctata* (Coleoptera: Cerambycidae) in a Mediterranean-type ecosystem. *Insects* 11:225. <https://doi.org/10.3390/insects11040225>.
- Sharov AA, Leonard D, Liebhold AM, et al. 2002. “Slow the Spread”: a national program to contain the gypsy moth. *jof.* 100:30–36. <https://doi.org/10.1093/jof/100.5.30>.
- Schmitt LR, Trotter RT, Bishop III. CJ, et al. 2025. Phenology and voltinism of the Asian longhorned beetle, *Anoplophora glabripennis* (Coleoptera: Cerambycidae), in South Carolina. *Environ. Entomol.* 54:367–377. <https://doi.org/10.1093/ee/nvae128>.
- Straw NA, Tilbury C, Fielding NJ, et al. 2015. Timing and duration of the life cycle of Asian longhorn beetle *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in southern England. *Agric. For. Entomol* 17:400–411. <https://doi.org/10.1111/afe.12120>.
- Timms LL, Smith SM, de Groot P. 2006. Patterns in the within-tree distribution of the emerald ash borer *Agrilus planipennis* (Fairmaire) in young, green-ash plantations of south-western Ontario, Canada. *Agric. For. Entomol.* 8:313–321. <https://doi.org/10.1111/j.1461-9563.2006.00311.x>.
- Trotter III., RT, Hull-Sanders HM. 2015. Quantifying dispersal of the Asian longhorned beetle (*Anoplophora glabripennis*, Coleoptera) with incomplete data and behavioral knowledge. *Biol. Invasions* 17:3359–3369. <https://doi.org/10.1007/s10530-015-0961-9>.
- Trotter III. RT, Ryan JK, Chandler JL, et al. 2023. Tracking the push towards extinction: combining dispersal and management data to

- monitor Asian longhorned beetle eradication in the U.S. *Front. Insect Sci.* 3:1286935. <https://doi.org/10.3389/finsc.2023.1286935>.
- Turgeon JJ, Ric J, de Groot P, et al. 2007. Détection des signes et des symptômes d'attaque par le longicorne étoilé: guide de formation. Service canadien des forêts, Ressources naturelles Canada, Ottawa, Ontario. 131 p.
- Turgeon JJ, Pedlar J, de Groot P, et al. 2010. Density and location of simulated signs of injury affect efficacy of ground surveys for Asian longhorned beetle. *Can. Entomol.* 142:80–96. <https://doi.org/10.4039/n09-049>.
- Turgeon JJ, Gasman B, Smith MT, et al. 2022a. Canada's response to invasion by Asian longhorned beetle (Coleoptera: Cerambycidae) in Ontario. *Can. Entomol.* 154:e1. <https://doi.org/10.4039/tce.2021.60>.
- Turgeon JJ, Smith MT, Pedlar JH, et al. 2022b. Tree selection and use by the polyphagous xylophage *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in Canada. *Can. J. For. Res.* 52:622–643. <https://doi.org/10.1139/cjfr-2021-0244>.
- Turgeon JJ, Pedlar JH, Fournier RE, et al. 2025. Characteristics of logs with signs of oviposition by the polyphagous xylophage Asian longhorned beetle (Coleoptera: Cerambycidae). *Environ. Entomol.* 54:699–709. <https://doi.org/10.1093/ee/nvae041>.
- Valicharla SK, Li X, Greenleaf J, et al. 2023. Precision detection and assessment of ash death and decline caused by the emerald ash borer using drones and deep learning. *Plants* 12:798. <https://doi.org/10.3390/plants12040798>.
- Yan JJ. 1985. Research on distribution of basicosta whitespotted longicorn (*Anoplophora glabripennis*) in east China. *Journal of North-Eastern Forestry College, China* 13:62–69. in Chinese).
- Zhou Q, Zhang X, Lu L, et al. 2025. Determining the optimal time window to detect emerald ash borer damage for effective management. *Pest Manag. Sci.* 81:1333–1344. <https://doi.org/10.1002/ps.8533>.