

An invasive urban forest pest invades natural environments – Asian longhorned beetle in northeastern US hardwood forests

Kevin J. Dodds and David A. Orwig

Abstract: An infestation of Asian longhorned beetle (ALB) (*Anoplophora glabripennis* (Motschulsky)) was detected in Worcester, Massachusetts, in 2008. The discovery of this pest, previously only seen in urban environments of North America, led to the unprecedented establishment of a 243 km² quarantine zone that included urban parks, neighborhoods, and natural forests. Because ALB behavior in forested stands is virtually unknown, two closed-canopied forested stands (Bovenzi and Delaval) infested with ALB within this zone were sampled during 2008–2010 to document stand conditions, assess ALB host selection, and determine ALB impact on tree growth. Thirty-two percent of the *Acer* sampled in Bovenzi were infested with ALB compared with 63% in Delaval. In Delaval where three maple host species were available, ALB was found more often in *Acer rubrum* L. than in *Acer saccharum* Marsh. or *Acer platanoides* L. Radial growth patterns did not differ between ALB-infested and uninfested *Acer* trees in Bovenzi. In contrast, ALB-infested trees in Delaval were significantly older and larger than uninfested trees and exhibited slower radial growth and ring width index patterns compared with uninfested trees. Results suggest that if left uncontrolled, ALB can readily disperse into natural forest landscapes and alter the makeup of North America's hardwood forest region.

Résumé : Une infestation du capricorne asiatique (CA) (*Anoplophora glabripennis* (Motschulsky)) a été détectée en 2008 à Worcester, au Massachusetts. La découverte de ce ravageur, observé jusqu'à maintenant seulement en milieu urbain en Amérique du Nord, a entraîné l'établissement d'une zone de quarantaine sans précédent de 243 km² qui incluait des parcs urbains, des quartiers et des forêts naturelles. Parce que le comportement du CA dans les peuplements forestiers est pratiquement inconnu, deux peuplements forestiers avec un couvert fermé (Bovenzi et Delaval), situés à l'intérieur de la zone de quarantaine et infestés par le CA, ont été échantillonnés au cours de 2008 à 2010 pour documenter l'état du peuplement, évaluer le choix d'hôte du CA et déterminer son impact sur la croissance des arbres. Trente-deux pour cent des érables (*Acer*) échantillonnés dans la forêt de Bovenzi étaient infestés par le CA comparativement à 63 % dans la forêt de Delaval. Dans la forêt de Delaval où trois espèces d'érable étaient disponibles, le CA a été retrouvé plus souvent sur *Acer rubrum* L. que sur *Acer saccharum* Marsh. ou *Acer platanoides* L. Les patrons de croissance radiale des érables non infestés et ceux des érables infestés par le CA n'étaient pas différents dans la forêt de Bovenzi. Dans la forêt de Delaval par contre, les arbres infestés par le CA étaient significativement plus vieux et plus gros que les arbres non infestés et avaient des patrons de croissance radiale et d'indice de largeur des cernes annuels plus lents comparativement aux arbres non infestés. Les résultats indiquent que si aucune mesure n'est prise, le CA peut facilement se propager dans les paysages de forêt naturelle et modifier la composition de la forêt feuillue en Amérique du Nord.

[Traduit par la Rédaction]

Introduction

Forests of the northeastern United States have undergone a series of invasions by organisms that have changed the composition and structure of impacted stands (Orwig and Foster 1998; Bohlen et al. 2004; Orwig et al. 2008). The first significant introduction was in the late 1860s when gypsy moth (*Lymantria dispar* (L.)) was accidentally released into Massachusetts' forests. Subsequently, this species spread throughout much of the eastern United States where at times it has caused mortality to *Quercus* spp. and other tree species (Davidson et al. 1999). Two pathogens that arrived during the

20th century had a more species-specific impact than gypsy moth but nonetheless changed the structure and function of northeastern forests. The fungi associated with Dutch elm disease (*Ophiostoma novo-ulmi* (Brasier) and *Ophiostoma ulmi* (Buisman) Melin & Nannf.) and with chestnut blight (*Cryphonectria parasitica* (Murrill) M.E. Barr) altered the composition of forests and functionally removed *Ulmus americana* L. and *Castanea dentata* (Marsh.) Borkh., respectively, from forest communities. In addition, the loss of *Ulmus* spp. was dramatic in many cities and towns where they had been extensively planted and were a dominant fixture along main streets (Campanella 2003).

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Invasive forest pests have wide-ranging impacts on forested ecosystems. Obvious impacts include effects on tree growth or increased tree mortality, resulting in changes in forest stand composition, structure, and nutrient cycling (Orwig and Foster 1998; DiGregorio et al. 1999; Orwig et al. 2008; Dodds et al. 2010). Nontree impacts, including effects on wildlife populations and (or) watersheds, can also occur (Tingley et al. 2002; Gandhi and Herms 2010). However, the impact that invasive species are having on native communities is often difficult to estimate accurately (Parker et al. 1999). Factors such as tree resistance, time since establishment, ecosystem resiliency, and competition with native species must all be considered. Unfortunately, large information gaps often exist when assessing impacts of invasive species. In cases where tree death is imminent and damage is obvious, estimating impacts and drawing conclusions based on insect activity is generally straightforward. However, in cases where impacts are less obvious or tree mortality is not rapid, it is difficult to assess the true level of threat that an insect poses to an ecosystem type.

The health of northeastern forests is currently threatened by several species (e.g., beech bark disease, hemlock woolly adelgid (*Adelges tsugae* Annand), emerald ash borer (*Agrilus planipennis* Fairmaire), European winter moth (*Operophtera brumata* L.), and Asian longhorned beetle (ALB) (*Anoplophora glabripennis* (Motschulsky))). ALB, considered one of the world's 100 worst invasive species (Simberloff and Rejmánek 2011), is of great concern to the region because of the ecological and economic importance of *Acer* spp., one of its primary host genera. *Acer* spp. are commonly planted along streets, are a prominent component of the northern hardwood forests that range from southeastern Canada to central New England west to the Great Lakes region, and are economically important in the region for their colorful fall foliage and maple syrup products.

ALB is native to China and Korea (Lingafelter and Hoebeke 2002) and has successfully invaded many parts of the world (Hu et al. 2009; Haack et al. 2010). ALB has been found in several Western Hemisphere countries including Austria, France, Germany, and Italy (Hérard et al. 2006, 2009). Based on climate, much of eastern North America is considered at risk to this species (Peterson and Scachetti-Perreira 2004). Several infestations have been found in North America since the mid-1990s, including New York, New York (1996), Chicago, Illinois (1998), Jersey City, New Jersey (2002), Toronto, Ontario (2003), Carteret, New Jersey (2004), Worcester, Massachusetts (2008) (Haack et al. 2010), and most recently Boston, Massachusetts (2010) (North American Plant Protection Organization Phytosanitary Alert System 2010). To date, the Worcester infestation is the only outbreak of ALB where they escaped from urban settings and infested closed-canopied forests. In addition, the scale of the Worcester infestation is the largest in terms of infested trees found (>18 800), trees searched (>860 000), trees removed (>20 000), and size of quarantine area (243 km²) in North America (Jones 2011).

ALB is a polyphagous sapwood borer found in many hardwood species of *Acer*, *Aesculus*, *Salix*, *Platanus*, *Ulmus*, *Betula*, *Populus*, and occasionally other genera (Hu et al. 2009). Females locate host trees and chew oval oviposition pits through the bark and into the phloem tissue where they lay

an egg. The egg hatches and the larva feeds in the phloem–cambium area. After feeding in the phloem, ALB larvae begin mining into the sapwood where pupation occurs. Adults emerge at least a year later but may take longer to complete development (Turgeon et al. 2007). ALB larval development can structurally compromise trees and reduce the movement of photosynthates, leading to physiologically weakened trees as well.

Most North American infestations have been urban-focused and isolated from natural forests. In contrast, the ALB introductions into Massachusetts are adjacent to large tracts of forests containing several species of *Acer* and other host species. The proximity of this infestation to these forests provides a pathway to even larger areas of northern hardwoods dominated by *Acer saccharum* Marsh. and other economically important tree species. An unprecedented effort is underway to eradicate ALB from Worcester, and it is unknown at this time if these efforts will be successful. Because much of the data collected on ALB behavior and damage come from urban settings (Haack et al. 2006), its native range (Williams et al. 2004; Bancroft and Smith 2005; Yan et al. 2008), or laboratory studies (Bancroft et al. 2002; Keena 2002; Morewood et al. 2003, 2004b), it is uncertain how this insect will behave in more intact North American forest ecosystems if it becomes naturalized. Various factors could influence ALB populations in forested settings, including availability of susceptible trees, natural predation and (or) parasitism, and host tree defenses (Smith 1999; Solter et al. 2001; Williams et al. 2004). Understanding the potential impact of ALB in forests is important for considering future management options if this species becomes established.

In the current study, we used a retrospective approach to assess the impacts that ALB had in two forested stands in Worcester, Massachusetts, USA. We were interested in (i) documenting stand conditions prior to tree removal, (ii) assessing ALB host preference, and (iii) determining ALB impact on tree growth.

Materials and methods

Site descriptions

Bovenzi Conservation Area

The approximately 40 ha Bovenzi Conservation Area (hereafter Bovenzi) (42.32043°N, -71.80662°W) contained several forest types situated on gently sloping terrain with elevations ranging from approximately 190 to 245 m. The area was not actively managed for forest resources but contained some recreational trails. At the base of the area, a small creek ran through an *Acer rubrum* L. swamp. Forest composition changed with increasing elevation towards a mix of *Quercus* and *Carya* species. As of 2010, ALB had been found in all neighborhoods and streets surrounding Bovenzi.

In the fall of 2008, a volunteer-led survey of Bovenzi located signs of ALB presence on *Acer* trees throughout the area. Initial finds by the volunteer group were confirmed by USDA Animal and Plant Health Inspection Service (APHIS) personnel and tree climbers were brought in to survey the eastern half of Bovenzi. Tree climbers thoroughly examined all potential host tree canopies and boles looking for oviposition sites or exit holes and marked every host tree as ALB infested or uninfested. Infested trees were originally thought

to be concentrated in the eastern half of Bovenzi, the location of our survey efforts, but were later found throughout the entirety of Bovenzi.

Delaval Tract

In 2009, ALB was also confirmed in a stand approximately 0.7 km south of Bovenzi (hereafter Delaval) (42.31209°N, -71.80894°W). This approximately 6 ha forest parcel served as a forest buffer between a residential community and an interstate highway. Delaval was on an east-facing slope that ranged from approximately 180 to 200 m and was comprised of various hardwoods with some *Pinus* spp. intermixed. The northern end of the stand contained an *A. rubrum* swamp. As in Bovenzi, surveys of all host trees were conducted by tree climbers, with infested and uninfested trees marked differently. Infested trees were found throughout the entire 6 ha area.

Vegetation plots

To thoroughly document stand composition prior to eradication efforts, forest stand surveys were conducted in Bovenzi and Delaval using the same methodology. Several fixed-radius circular plots (452 m²) were established in each site. In each plot, tree species, diameter at breast height (DBH), crown class, living–dead, and ALB presence–absence was recorded for every tree ≥ 7.5 cm DBH. ALB presence was based on results from tree climbing surveys where tree boles and crowns were closely surveyed by trained surveyors. Crown classes were differentiated based on exposure to light, including overtopped, intermediate, codominant, and dominant (cf. Smith 1986).

In Bovenzi, 20 plots were placed along transects oriented in a north–south direction parallel to the primary slope of the study area to estimate tree and stand parameters and ALB activity. Each plot was separated by at least 30 m. Four plots were established along a transect running parallel to the midslope of Delaval following the same methods. Forest stand surveys and increment coring occurred in December 2008 within a 10 ha section of Bovenzi and during September 2009 in Delaval. All ALB host trees were removed during winter 2009 in Bovenzi and during winter 2010 in Delaval. To estimate forest composition changes resulting from host tree removal, we assumed that all host trees classified as preferred and occasional (Sawyer 2011) with the exception of *Populus grandidentata* Michx. were removed during the control phase of the eradication program efforts.

Data analyses

Fisher's exact tests were used to test for differences in the frequency of attacks on trees in different crown classes, the distribution of trees in crown classes by *Acer* spp., and the frequency of attacks on the three *Acer* species found in Delaval. For crown class analysis, codominant and dominant trees were grouped together to reduce the number of tests needed and because there were low numbers of dominant trees. An adjusted significance level was calculated using the Bonferroni correction for the frequency of attacks and crown class analyses because three separate Fisher exact tests were used for each set of analyses. The adjusted level was $P < 0.017$. *t* tests were used to compare DBH estimates of infested and uninfested trees at each site. Data transformation

was not necessary, as data were normally distributed and variances were not heteroscedastic.

Dendroecological analysis of infested and noninfested trees

In Bovenzi, 25 infested *A. rubrum*, one infested *A. saccharum*, and 27 uninfested *A. rubrum* were cored for age determinations and radial growth analyses. Within Delaval, a total of 23 uninfested trees and 23 infested trees were cored from *A. rubrum*, *A. saccharum*, and *Acer platanoides* L. trees. One increment core from each tree was taken at breast height (approximately 1.4 m). Whenever possible, cores were taken from trees within the vegetation plots. All increment cores were air dried, sanded, and aged with a dissecting microscope. Annual rings were measured to the nearest 0.01 mm using a Velmex measuring system (Velmex, East Bloomfield, New York). Samples were visually cross-dated by identifying pointer years common to most trees in each population (Yamaguchi 1991). Two years were particularly useful in these stands: 1981, which was narrow and light colored resulting from severe gypsy moth defoliation that even impacted *Acer* spp. (cf. Pederson 2005), and 1953, which corresponded to the 9 June tornado that dramatically impacted the greater Worcester area (Chittick 2003) and led to growth reductions in most surviving trees. The program COFECHA (Holmes 1983) was used to test potential dating or measurement errors. All cores were reexamined and corrected or omitted. This process eliminated four infested trees and seven uninfested trees within the Bovenzi stand. Tree age was considered as the number of rings measured at breast height, with no additional estimation for cores that missed the pith.

To remove age-related growth trends, raw ring width data for each tree were detrended by fitting either a modified negative exponential curve or a horizontal line using the dplR computer package (Bunn 2008) within the R statistical programming environment (R Development Core Team 2009). Dimensionless ring width index (RWI) values were created by dividing the observed raw values by expected values from the fitted curves. Mean RWI chronologies were created for infested and uninfested trees at each location by averaging each tree's annual RWI values. Current and past radial growth and RWI patterns were examined in all cores to assess the impact of ALB on tree growth and to determine whether tree growth influenced ALB host selection. Average tree age, RWI values, and growth rates determined from increment cores of ALB-infested and uninfested trees were tested for differences using *t* tests.

Results

Bovenzi Conservation Area

Vegetation present before eradication

In the sampled area of Bovenzi, there were 500 stems/ha and 27.1 m²/ha of basal area distributed among 14 tree species (Table 1). *Acer rubrum* represented 26% of the stand basal area and had the highest relative importance value (31.8) followed by *Quercus velutina* Lam. (20.2), *Quercus rubra* L. (14.0), and *Carya glabra* (Mill.) (11.8). *Acer rubrum* or *Quercus* spp. dominated every size class (Fig. 1A). *Quercus* spp., *A. rubrum*, *Carya* spp., and *Fraxinus ameri-*

Table 1. Average diameter, basal area, density, and importance values for Asian longhorned beetle (*Anoplophora glabripennis*) host trees and nonhost trees in Bovenzi.

Species	Average \pm SE DBH (cm)	Basal area (m ² /ha)	Stems/ha	Relative basal area (%)	Relative density (%)	Importance value
Host trees^a						
<i>Acer rubrum</i>	19.1 \pm 0.8	6.4	169	26.1	37.6	31.8
<i>Fraxinus americana</i> ^b	22.5 \pm 1.5	1.4	30	5.6	6.7	6.1
<i>Betula lenta</i>	17.5 \pm 2.0	0.6	19	2.3	4.2	3.3
<i>Ulmus</i> sp.	22.6 \pm 4.7	0.2	5	0.9	1.1	1.0
<i>Acer saccharum</i>	26.4 \pm 0.0	0.05	1	0.2	0.2	0.2
Total		8.6	224			
Total/ha		9.5	249			
Nonhost trees^c						
<i>Quercus velutina</i>	37.0 \pm 2.1	6.9	55	28.3	12.2	20.2
<i>Quercus rubra</i>	28.6 \pm 2.0	4.1	51	16.7	11.3	14.0
<i>Carya glabra</i>	20.7 \pm 1.5	2.6	59	10.5	13.1	11.8
<i>Quercus alba</i>	21.0 \pm 1.5	1.5	36	6.0	8.0	7.0
<i>Carya ovata</i>	23.6 \pm 3.4	0.6	11	2.4	2.4	2.4
<i>Ostrya virginiana</i>	11.7 \pm 1.5	0.1	9	0.4	2.0	1.2
<i>Populus grandidentata</i> ^d	31.8 \pm 0.0	0.08	1	0.3	0.2	0.3
<i>Pinus strobus</i>	26.5 \pm 0.0	0.06	1	0.2	0.2	0.2
<i>Hamamelis virginiana</i>	8.4 \pm 1.4	0.02	3	0.1	0.7	0.4
Total		15.9	226			
Total/ha		17.6	251			
Stand total		27.1	500			

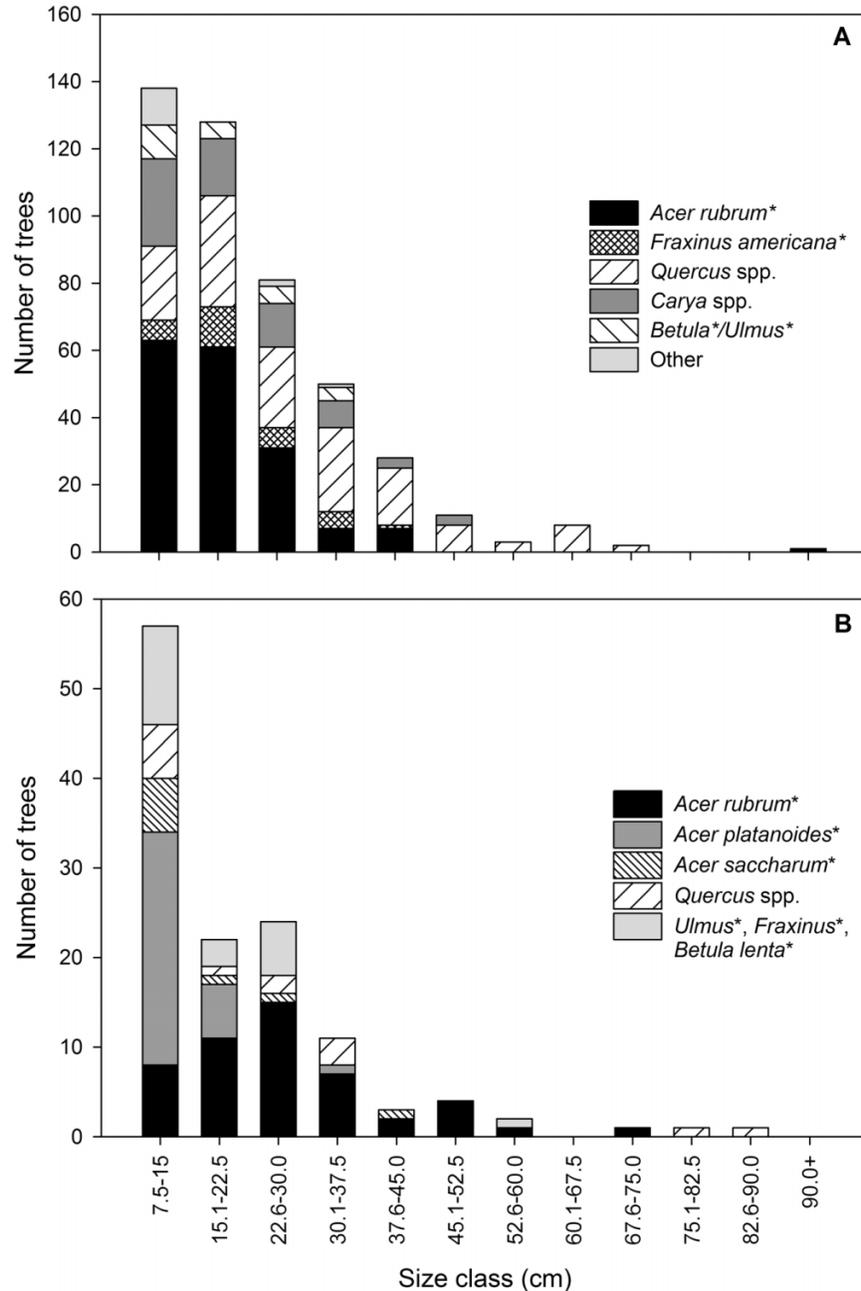
^aPreferred and occasional hosts according to Sawyer (2011).

^bListed as occasional host by Sawyer (2011) but colonized in Worcester, Massachusetts.

^cQuestionable hosts (Sawyer 2011) or no host records.

^dMembers of genus confirmed hosts but no information on *Populus grandidentata*.

Fig. 1. Distribution of trees with DBH ≥ 7.5 cm among arbitrary classes of DBH in (A) Bovenzi and (B) Delaval. Species with an asterisk are preferred or occasional Asian longhorned beetle (*Anoplophora glabripennis*) hosts. Trees in the “other” category included *Populus grandidentata*, *Ostrya virginiana*, *Hamamelis virginiana*, and *Pinus strobus*. One 43.7 cm DBH *Prunus serotina* was omitted from the Delaval graph to reduce the number of categories on the figure. Data on this tree can be found in Table 3.



cana L. were the only trees found in the larger size classes (DBH > 40 cm), and these species along with *Ulmus* sp., *Betula lenta* L., and *Ostrya virginiana* (Mill.) K. Koch were also found in smaller size classes (DBH < 20 cm) (Fig. 1A).

ALB host trees

Five known host species, which included two *Acer* spp., were found in Bovenzi (Table 1). *Fraxinus americana* is the only species considered to be an occasional host (Sawyer 2011). Host trees comprised 249 stems/ha and 9.5 m²/ha of basal area in Bovenzi (Table 1). The most abundant host species and tree in the stand was *A. rubrum*, which contributed

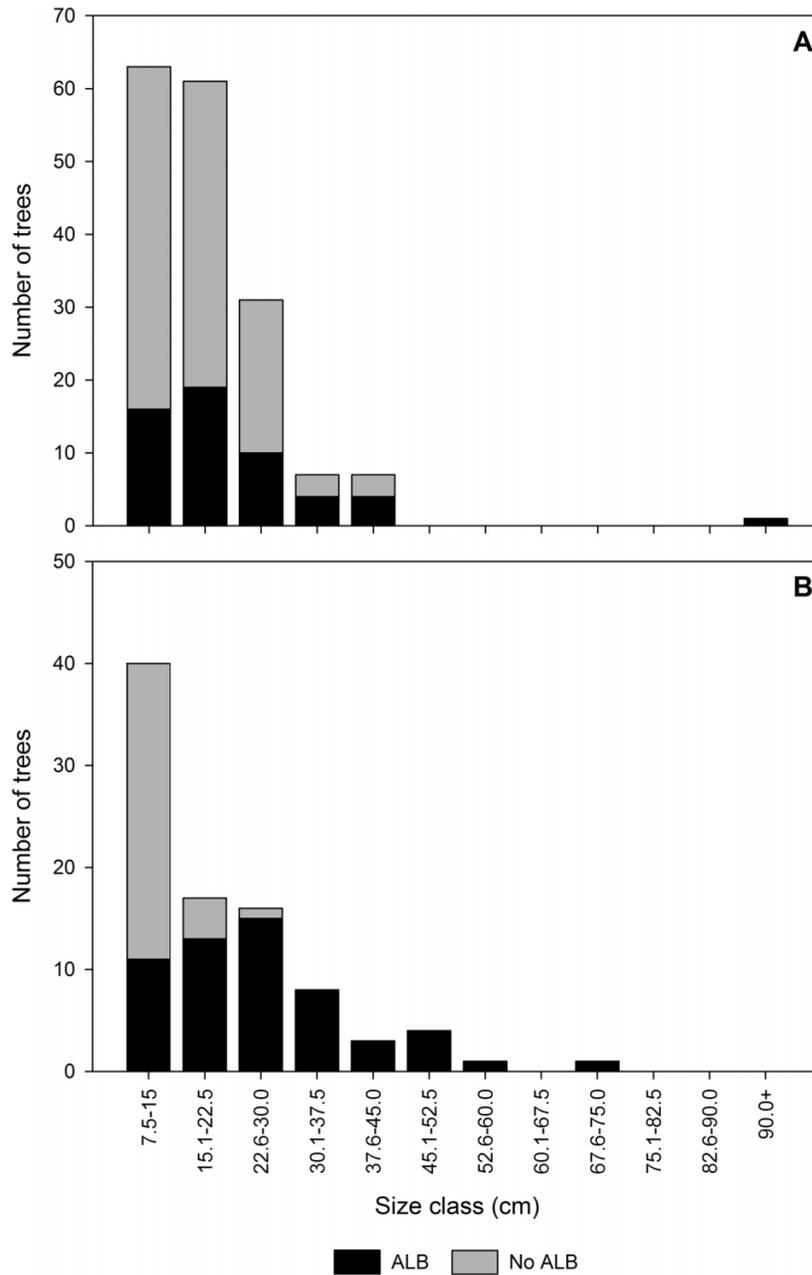
the most basal area (6.4 m²/ha) and number of stems (169/ha). *Fraxinus americana*, *B. lenta*, and *Ulmus* sp. had low importance values in the stands, with values of 6.1, 3.3, and 1.0, respectively. In all, ALB host species comprised 34% of the basal area present in the stand.

ALB-infested trees

Despite the presence of several trees considered preferred or occasional ALB hosts in Bovenzi, oviposition scars or exit holes were found only on *Acer*. Of the *Acer* present in the Bovenzi plots, 32% had signs of ALB attacks and these were distributed throughout a range of size classes (Fig. 2A).

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Fig. 2. Distribution of Asian longhorned beetle (*Anoplophora glabripennis*) infested and uninfested *Acer* spp. among arbitrary classes of DBH in (A) Bovenzi and (B) Delaval.

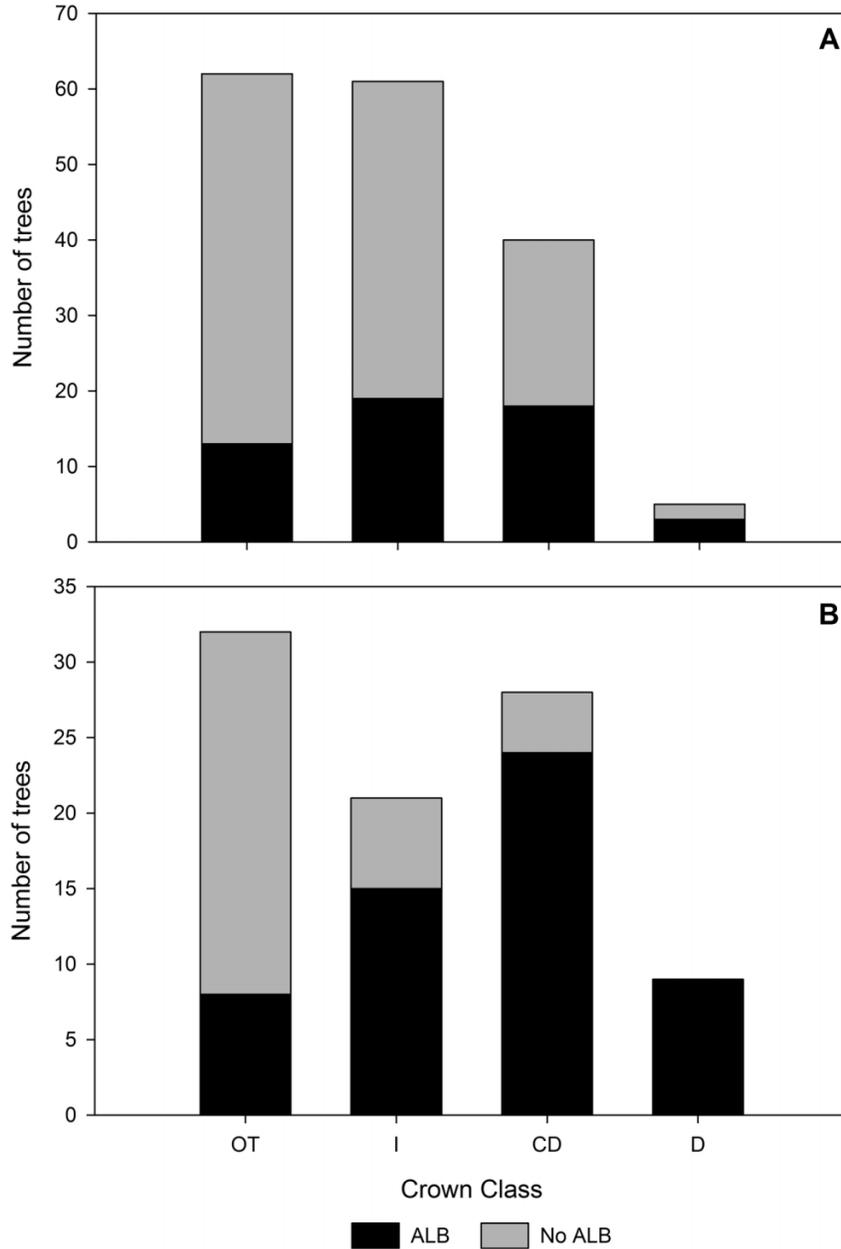


Only one host tree over 50 cm was sampled in Bovenzi, a 108 cm *A. rubrum* with ALB present. There were significant differences in the number of ALB-infested trees among crown classes (Fig. 3A), as there was a higher proportion of codominant–dominant trees infested by ALB than overtopped trees ($P = 0.006$). There were no differences between intermediate and codominant–dominant trees ($P = 0.11$) or intermediate and overtopped trees ($P = 0.22$). Average diameter of infested *Acer* trees (21.0 ± 0.7 cm) was larger than that of uninfested trees (17.5 ± 0.7 cm) ($t = 2.4$, $df = 167$, $P = 0.02$).

Dendroecology

Acer trees examined for radial growth patterns did not differ in age (63–68 years) or size (22–23 cm DBH) among ALB-infested and uninfested trees within Bovenzi (Table 2). Average radial growth was not significantly different between infested and uninfested trees. Radial growth and RWI values during the last 10 years, presumably the estimated duration of the infestation period in Worcester, were also not significantly different among trees with and without ALB (Fig. 4A).

Fig. 3. Distribution of Asian longhorned beetle (*Anoplophora glabripennis*) infested and uninfested *Acer* spp. among four crown classes in (A) Bovenzi and (B) Delaval. For statistical analysis, codominant and dominant trees were combined into one category but depicted separately here. Crown classes: OT, overtopped; I, intermediate; CD, codominant; D, dominant.



Estimated remaining forest

Assuming total removal of all ALB host trees listed in Table 1, Bovenzi is now dominated by *Quercus* spp. and *Carya* spp. Thirty-five percent of the basal area and 50% of the stems per hectare were removed during the eradication effort. *Quercus velutina*, *Q. rubra*, and *C. glabra* are now the most important species on the site and together comprise 85% of the remaining live basal area.

Delaval Tract

Vegetation present

In the sampled area of Delaval, overstory density and basal area were both higher than in Bovenzi, with 708 stems/ha

and 37.2 m²/ha distributed among 11 tree species (Table 3). *Acer* spp. represented 63% of the stand basal area and dominated relative importance values, as *A. rubrum* (45.1) and *A. platanoides* (16.5) had the highest values followed by *Q. rubra* (13.6). *Acer* also dominated every size class except for those >75 cm DBH where *Quercus* was present (Fig. 1B). *Ulmus* sp., *B. lenta*, *F. americana*, and *Quercus* spp. were also common in the smaller size classes.

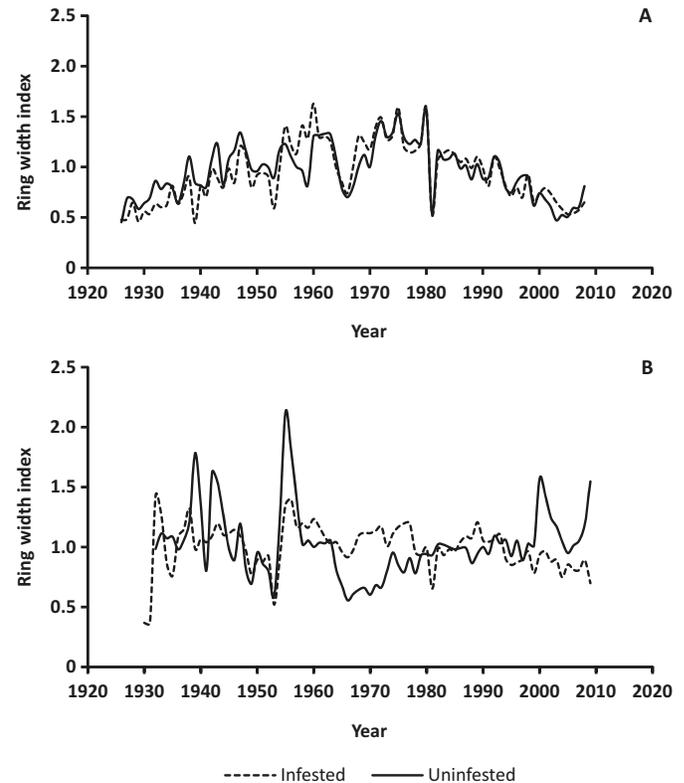
ALB host trees

Six ALB host species, including three *Acer* spp., were found in Delaval (Table 3). As in Bovenzi, *F. americana* was the only species considered an occasional ALB host. Host trees comprised 108 stems/ha and 4.9 m²/ha of basal

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Table 2. Average growth parameters, age, and size of cored trees with and without Asian longhorned beetle (*Anoplophora glabripennis*) within Bovenzi and Delaval.

Tree parameter	Bovenzi (red maple)		Delaval (pooled maple species)		P
	ALB (n = 21)	No ALB (n = 20)	ALB (n = 23)	No ALB (n = 23)	
Average radial growth (mm/year)	1.50±0.14	1.45±0.09	1.59±0.10	1.96±0.12	0.02
Last 10 years' growth	0.81±0.12	0.64±0.11	1.23±0.09	1.79±0.20	0.03
Last 10 years' ring width index	0.61±0.06	0.65±0.06	0.85±0.07	1.22±0.09	0.003
Tree age (years)	63±3	68±2	61±3	45±3	0.0002
Tree DBH (cm)	22.4±2.1	23.2±1.0	30.1±2.3	17.8±2.0	0.002

Fig. 4. Mean ring-width index values of Asian longhorned beetle (*Anoplophora glabripennis*) infested and uninfested *Acer* trees in (A) Bovenzi and (B) Delaval. There were 21 infested and 20 uninfested trees in Bovenzi and 23 infested and 23 uninfested trees in Delaval.

area in Delaval (Table 3). *Acer rubrum* had the highest density of stems and basal area of host trees. While *A. platanoides* had a relatively high importance value (16.5), other host species including *A. saccharum* (5.5), *Ulmus* sp. (2.7), *F. americana* (4.9), and *B. lenta* (4.0) had low values. There was only one potential host tree over 60 cm DBH in the stand (Fig. 1B). In all, ALB host species comprised 73% of the basal area present in the stand.

ALB-infested trees

As in Bovenzi, despite several potential host species being present, ALB was found only on *Acer* spp. including *A. rubrum*, *A. saccharum*, and *A. platanoides*. Sixty-three percent of the *Acer* in Delaval plots had ALB signs, including all trees >30 cm DBH (Fig. 2B). There were significant differences among trees in overtopped, intermediate, and codominant–dominant crown classes in terms of ALB presence (Fig. 3B). More intermediate ($P = 0.0016$) and codominant–dominant ($P < 0.0001$) trees were infested by ALB than overtopped trees. There were no significant differences between the number of intermediate and codominant–dominant ALB infested trees ($P = 0.15$). Average diameter of infested *Acer* trees (26.6 ± 1.5 cm) was larger than that of uninfested trees (11.3 ± 1.9 cm) ($t = -6.4$, $df = 88$, $P < 0.0001$). Comparisons among crown class distributions suggested no significant differences between *A. saccharum* and *A. platanoides* ($P = 0.6$) or *A. rubrum* ($P = 0.026$), although *A. rubrum* crown class distribution was different from that of *A. platanoides* ($P < 0.0001$).

Table 3. Average diameter, basal area, density, and importance values for Asian longhorned beetle (*Anoplophora glabripennis*) host trees and nonhost trees in Delaval.

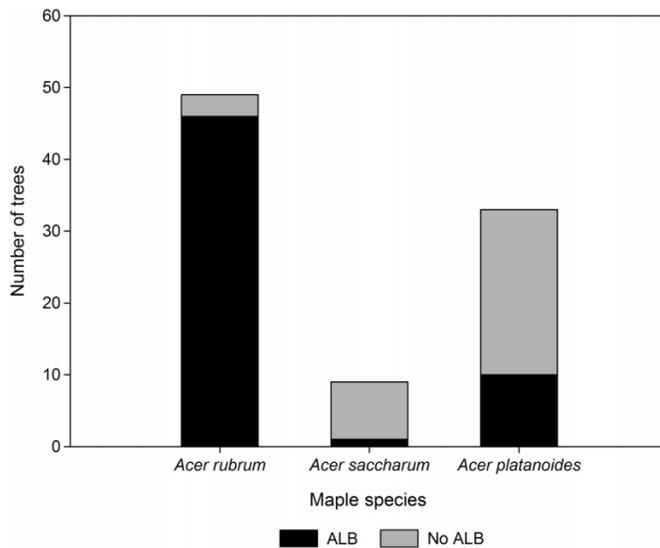
Species	Average \pm SE DBH (cm)	Basal area (m ² /ha)	Stems/ha	Relative basal area (%)	Relative density (%)	Importance value
Host trees^a						
<i>Acer rubrum</i>	27.2 \pm 1.9	3.5	49	51.9	38.3	45.1
<i>Acer platanoides</i>	12.6 \pm 0.9	0.48	33	7.1	25.8	16.5
<i>Acer saccharum</i>	16.1 \pm 4.0	0.27	9	4.0	7.0	5.5
<i>Fraxinus americana^b</i>	27.9 \pm 7.2	0.39	5	5.8	3.9	4.9
<i>Betula lenta</i>	20.8 \pm 2.9	0.22	6	3.3	4.7	4.0
<i>Ulmus</i> sp.	10.2 \pm 0.9	0.05	6	0.7	4.7	2.7
Total		4.9	108			
Total/ha		27.2	597			
Nonhost trees^c						
<i>Quercus rubra</i>	30.7 \pm 8.9	1.3	10	19.3	7.8	13.6
<i>Quercus velutina</i>	20.5 \pm 6.4	0.17	4	2.5	3.1	2.8
<i>Tilia</i> sp.	15.9 \pm 2.0	0.08	4	1.2	3.1	2.2
<i>Prunus serotina</i>	43.7 \pm 0.0	0.15	1	2.2	0.8	1.5
<i>Carya ovata</i>	40.7 \pm 0.0	0.13	1	1.9	0.8	1.4
Total		1.8	20			
Total/ha		10.0	111			
Stand total		37.2	708			

^aPreferred and occasional hosts according to Sawyer (2011).

^bListed as occasional host by Sawyer (2011) but colonized in Worcester, Massachusetts.

^cQuestionable hosts (Sawyer 2011) or no host records.

Fig. 5. Frequency of Asian longhorned beetle (*Anoplophora glabripennis*) in *Acer rubrum*, *Acer saccharum*, and *Acer platanoides* in Delaval.



The frequency of ALB-infested trees varied among three *Acer* spp. (Fig. 5). The proportion of *A. rubrum* infested by ALB was greater than that of *A. platanoides* ($P < 0.0001$) or *A. saccharum* ($P < 0.0001$). However, there were no differences in ALB presence between *A. platanoides* and *A. saccharum* ($P = 0.4$). Of the available host trees, 94% of *A. rubrum*, 30% of *A. platanoides*, and 11% of *A. saccharum* were infested. Average diameter of infested *Acer* trees (26.6 ± 1.8 cm) was larger than that of uninfested trees (11.3 ± 0.8 cm) ($t = 6.4$, $df = 88$, $P < 0.0001$).

Dendroecology

Aged *Acer* trees displayed similar patterns with the overall population of *Acer* within the site, as infested trees were significantly larger than uninfested trees (30.1 versus 18.8 cm DBH) and significantly older (61 versus 45 years) (Table 2). ALB-infested trees had significantly lower overall average growth as well as growth and RWI values during the last 10 years. Average RWI for infested and uninfested trees in Delaval showed different growth patterns over time and it is difficult to determine the duration of infestation from these patterns (Fig. 4B). RWI values for infested trees have experienced a downward trend during the last 20 years, while values for uninfested trees were higher and diverged from those of infested trees over the last 10 years.

Estimated remaining forest

Following removal of all ALB host trees listed in Table 3, Delaval is now dominated by *Quercus* spp. Seventy-three percent of the basal area was removed and 84% of the stems were lost. *Quercus rubra* and *Q. velutina* are the most important species on the site and together comprise 80% of the living remaining basal area.

Discussion

While previous ALB infestations occurred in urban environments, the scope of the recent outbreak in Worcester, Massachusetts (~19 000 infested trees, ~860 000 trees

searched within a 243 km² quarantine zone), make it unprecedented in North America. Thousands of *Acer* trees have been removed along streets in the area, leaving entire blocks and neighborhoods devoid of trees. In addition, for the first time, ALB dispersed into closed-canopied forests with connectivity to even larger tracts of natural forests containing an abundance of potential host species, making this infestation a significant threat to mixed-hardwood forests of the region.

Understanding ALB behavior in forested settings is critical to developing long-term management plans for this insect if it becomes more widely established and to more accurately estimate the risk that this species poses to natural and managed forests. In natural forests of Korea, ALB is relegated to forest margins and riparian habitat (Williams et al. 2004). In North America, predictions of ALB behavior in forests are speculative at this point, although there are observations from urban forests (Haack et al. 2006). The current study provides a unique opportunity to examine ALB behavior and impacts resulting from several years of infestation prior to rapid eradication efforts by regulatory agencies. Both Worcester study sites are located adjacent to the area where ALB was first detected and subsequently found to be heavily infested.

Our two study locations are in close proximity to each other but differ in terms of stand history and condition. Bovenzi was a large forested conservation area and was a more “natural” forest than the Delaval strip forest. The edge environment of Bovenzi was disturbed by vegetation management activities that occurred adjacent to an interstate highway, but the interior forest was intact and much less disturbed. Delaval was a forested buffer (~70 m) between an interstate highway and a residential neighborhood that had been highly disturbed in recent years by wind, ice storms, and human activities. Bovenzi represents an example of mixed-hardwood forests found throughout the region and Delaval represents some of the smaller forested stands encountered within city limits and in the peri-urban environment.

Forest stands

Overall stand structure was similar in Bovenzi and Delaval. The majority of trees were found in smaller size classes (<30 cm DBH), with few large trees present in either stand that were >50 cm. *Acer rubrum* dominated Bovenzi in terms of the number of stems and importance value, whereas *Quercus* spp. had the next highest basal area totals and importance values. Small size classes were dominated by *A. rubrum*, *Quercus* spp., *F. americana*, and *Carya* spp. in Bovenzi. Delaval was also dominated by *A. rubrum*, with this species having a much higher importance value than any other tree species. This site also contained *A. platanoides*, which likely escaped from trees in nearby back yards and along streets. *Acer platanoides* and *Q. rubra* were the next two most important species in the stand. Small size classes were dominated by *Acer* spp., with *Quercus* spp. as a much smaller component.

Pattern of ALB infestation

Host trees at both sites were surveyed by trained tree climbers looking for signs of ALB presence (oviposition sites and exit holes). Detection of ALB signs of attack can be affected by density and location of signs (Turgeon et al. 2010).

Surveys conducted by tree climbers are more reliable than ground-based surveys (Turgeon et al. 2007), but even this technique can result in false negatives (i.e., trees considered uninfested that are actually infested). Consequently, it could be possible that ALB was present in more host trees in these stands but went undetected. Host trees in all size classes were available and colonized by ALB at both sites. Only trees ≥ 7.5 cm DBH were sampled during our stand surveys and no trees smaller than this diameter were found infested in the stand. In non-*Acer* hosts, ALB has been found in trees as small as 8 cm DBH (Haack et al. 2006) and all trees with a stem diameter ≥ 2.5 cm are generally inspected during surveys (Turgeon et al. 2007). Despite several potential host species in both areas, ALB only infested *Acer* spp., the apparent species of choice in North America and in its native range (Smith et al. 2009). Of the available *Acer* in Bovenzi, 32% had signs of ALB presence, including all size classes. In comparison, 63% of maples in Delaval had evidence of ALB, including all trees >30 cm DBH, and several had visible exit holes. Only 28% of the *Acer* under 15 cm DBH had signs of ALB presence in Delaval. In general, the codominant–dominant crown classes were infested at higher rates than smaller trees.

In Delaval where three *Acer* host species were present, ALB was found more frequently in *A. rubrum* compared with *A. platanoides* and *A. saccharum*. This is in contrast with laboratory studies where ALB preferred either potted *A. saccharum* (Morewood et al. 2003) or *A. platanoides* log bolts (Smith et al. 2002) over comparable *A. rubrum*. However, in our forested study, *A. rubrum* was more abundant in the codominant and dominant size classes than the other *Acer* spp. Tree selection by ALB within the range of acceptable hosts may be more a factor of tree and crown size than tree species type. This could be the result of these trees having larger silhouette size and shape or color patterns (Moericke et al. 1975; Prokopy and Owens 1983; Goyer et al. 2004) to dispersing beetles or the intermingling crowns providing pathways for movement in tree crowns from one tree to another. Additional factors not examined in this study including bark thickness (McCann and Harman 1990; Timms et al. 2006), host volatiles (Nehme et al. 2009), individual tree defensive compounds (Morewood et al. 2004a), or other factors may also have played a role in ALB host selection among *Acer* spp.

ALB attack density on individual trees was not measured in Bovenzi, but few trees in either stand had obvious large numbers of oviposition sites or exit holes apparent from the ground. In Delaval, where trees were cut for further sampling, some trees had high numbers of oviposition sites but comparatively few exit holes (K.J. Dodds, unpublished data). Repeated ALB attacks and subsequent larval development on the same tree can weaken trees and may eventually lead to mortality. However, we observed no evidence of tree mortality in either stand that could be directly attributed to ALB. Several cerambycids select host trees that have reduced growth compared with other available trees (Newton and Allen 1982; Galford 1984; Haavik et al. 2010), and we found that infested trees within Delaval were growing at a significantly slower overall average rate than uninfested trees. In addition, over the period of time when ALB is believed to have inhabited the region (at least 10 years; Hammel 2008), in-

festated trees in Delaval also had significantly lower average radial growth and RWI values compared with uninfested trees. In contrast, Bovenzi *Acer* trees did not differ significantly prior to ALB infestation or after. If number of trees infested in an area is an index of duration and (or) intensity, the greater number of infested trees in Delaval also suggests that this forest suffered greater ALB impacts and for likely longer periods of time. Additional work examining duration and intensity is necessary to resolve this uncertainty.

Previous work has suggested that ALB is essentially an edge specialist, evolving in riparian habitats (Williams et al. 2004). While ALB was widely distributed throughout the narrow Delaval site with abundant edge habitat, it was also fully capable of dispersing readily throughout the larger Bovenzi forest. The age of the infestation is unknown in Bovenzi and Delaval, but ALB is thought to have been present in the Worcester area for at least 10 years. While infestations may have started on margins of stands, after only a short time, ALB was found distributed throughout the forests. These patterns along with potential annual dispersal distances of 100 m up to 2600 m (Bancroft and Smith 2005) suggests that ALB will not likely “disappear into the woodwork” as predicted for northeastern forests (Williams et al. 2004) but rather will continue to spread and feed on the valuable hardwood trees in the region if not successfully eradicated.

Posteradication forest

Changes in forest communities can result directly from an invasion or indirectly from efforts to control the introduction. Eradication efforts that consist of tree removals occurred at both Bovenzi and Delaval where all *Acer* spp. and some other host species were chipped and left on site. Data from pre-eradication stands offer some insight into the residual forest remaining at each site. The removal of host trees from these stands resulted in drastically different residual stand conditions. Basal area was decreased by 35% and the number of stems reduced by 50% in Bovenzi, resulting in a much more open stand dominated by large *Quercus* spp. This change in structure is likely to be long term, especially since all *Acer* stump sprouts were chemically herbicided to prevent ALB from subsequent re-infestation. The impact of host removals was more significant in Delaval, with approximately 73% of basal area and 84% of total stems present at the time of sampling removed during eradication efforts. Delaval is now a stand with few trees spread throughout the area, with much open crown space.

Research and management implications

Because previous ALB infestations occurred in urban settings, little is known on how this insect will behave in natural forests of North America. The two stands in Worcester provided an opportunity to assess ALB behavior and subsequent impacts on tree growth in closed-canopied forests. While caution must be taken in evaluating the data from only two stands, there are some important observations from these forests. First, ALB did not aggressively kill trees. While ALB is estimated to have been in the vicinity of the stands for at least 10 years (Hammel 2008), we observed no signs of trees that were killed outright by this insect. Second, signs of ALB were more common on codominant and dominant trees and this may be an important host selection characteristic along

with tree species. Third, impact on tree growth appears to be negligible in some trees even after infestation for >5 years. Trees in Delaval with many visible exit holes did exhibit reduced radial growth in the last 10 years but still had live crowns. We anticipate that continued ALB presence and feeding in these locations would lead to additional tree damage and decline and eventual tree death.

The estimates of ALB presence in trees have several caveats that must be considered. ALB surveys only provide information on whether the insect is present or absent in a tree and an estimate of number of oviposition sites and exit holes. While a subset of trees in Delaval was intensively sampled for life stage densities, information on attack intensity was not linked to our plot-level data in either location due to rapid eradication efforts. Trees having as little as one oviposition site were considered infested and marked as positive trees that were then tallied during our plot data as ALB-infested. Consequently, the estimate of ALB activity may overestimate their actual tree impact. Certainly, most trees would survive for many years with the low level of ALB activity common in the stands (K.J. Dodds, unpublished data).

It appears that *B. lenta*, *Ulmus* sp., and *F. americana* were not selected as hosts during the initial phase of invasion in these temperate forests, while *A. rubrum*, *A. saccharum*, and *A. platanoides* were favored ALB hosts in forest environments. Further, it appears that *A. rubrum* is preferred and may be particularly vulnerable, even in mixed stands. *Acer rubrum* is a common forest tree, has increased regionally over the last century, is found in a wide variety of habitats from swamps to upland sites, and ranges over most of eastern North America (Abrams 1998). With its large range, *A. rubrum* could provide an easy pathway for ALB into various forest ecosystems of eastern North America.

In conclusion, our results suggest that if ALB is not contained immediately, it could migrate into and be a serious pest of natural forests. Eradication efforts have shifted these forests towards *Quercus-Carya* and *Quercus* mixes, which will likely have cascading impacts on soil processes and ecosystem function without the more labile, calcium-rich foliage from *Acer* spp. (cf. Berg and McLaugherty 2008). Eradication success in such a large area will be challenging, expensive, and will take many years to complete. Since this study was conducted, ALB was found 4.5 km to the northeast in another closed-canopied forest where several hundred trees were subsequently removed. However, complete eradication is critical, as the predicted economic impacts of ALB on urban trees alone in the United States is estimated at >\$600 billion (Nowak et al. 2001), and untold higher values are associated with the billions of precious hardwoods growing in the forest of the eastern United States and the many associated industries.

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References

- Abrams, M.D. 1998. The red maple paradox. *Bioscience*, **48**(5): 355–364. doi:10.2307/1313374.
- Bancroft, J.S., and Smith, M.T. 2005. Dispersal and influences on movement for *Anoplophora glabripennis* calculated from individual mark-recapture. *Entomol. Exp. Appl.* **116**(2): 83–92. doi:10.1111/j.1570-7458.2005.00320.x.
- Bancroft, J.S., Smith, M.T., Chaput, E.K., and Tropp, J. 2002. Rapid test of the suitability of host-trees and the effects of larval history on *Anoplophora glabripennis* (Coleoptera: Cerambycidae). *J. Kans. Entomol. Soc.* **75**(4): 308–316.
- Berg, B., and McLaugherty, C. 2008. Plant litter: decomposition, humus formation, carbon sequestration. 2nd ed. Springer-Verlag, Berlin.
- Bohlen, P.J., Scheu, S., Hale, C.M., McLean, M., Migge, S., Groffman, P.M., and Parkinson, D. 2004. Non-native invasive earthworms as agents of change in northern temperate forests. *Front. Ecol. Environ.* **2**(8): 427–435. doi:10.1890/1540-9295(2004)002[0427:NIEAAO]2.0.CO;2.
- Bunn, A.G. 2008. A dendrochronology program library in R (dplR). *Dendrochronologia*, **26**(2): 115–124. doi:10.1016/j.dendro.2008.01.002.
- Campanella, T.J. 2003. Republic of shade: New England and the American elm. Yale University Press, New Haven, Conn.
- Chittick, W.F. 2003. The Worcester Tornado, June 9, 1953. William F. Chittick, Bristol, R.I.
- Davidson, C.B., Gottschalk, K.W., and Johnson, J.E. 1999. Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. *For. Sci.* **45**(1): 74–84.
- DiGregorio, L.M., Krasny, M.E., and Fahey, T.J. 1999. Radial growth trends of sugar maple (*Acer saccharum*) in an Allegheny northern hardwood forest affected by beech bark disease. *J. Torrey Bot. Soc.* **126**(3): 245–254. doi:10.2307/2997279.
- Dodds, K.J., de Groot, P., and Orwig, D.A. 2010. The impact of *Sirex noctilio* in *Pinus resinosa* and *Pinus sylvestris* stands in New York and Ontario. *Can. J. For. Res.* **40**(2): 212–223. doi:10.1139/X09-181.
- Galford, J.R. 1984. The locust borer. Forest Insect & Disease Leaflet 71. U.S. Department of Agriculture, Forest Service, Northern Area State and Private Forestry, Broomall, Pa.
- Gandhi, K.J.K., and Herms, D.A. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol. Invasions*, **12**(2): 389–405. doi:10.1007/s10530-009-9627-9.
- Goyer, R.A., Lenhard, G.J., and Strom, B.L. 2004. The influence of silhouette color and orientation on arrival and emergence of Ips pine engravers and their predators in loblolly pine. *For. Ecol. Manage.* **191**(1–3): 147–155. doi:10.1016/j.foreco.2003.11.012.
- Haack, R.A., Bauer, L.S., Gao, R., McCarthy, J.J., Miller, D.L., Petrice, T.R., and Poland, T.M. 2006. *Anoplophora glabripennis* within-tree distribution, seasonal development, and host suitability in China and Chicago. *Great Lakes Entomol.* **39**(3–4): 169–183.

- Haack, R.A., Hérard, F., Sun, J., and Turgeon, J.J. 2010. Managing invasive populations of Asian longhorned beetle and citrus longhorned beetle: a worldwide perspective. *Annu. Rev. Entomol.* **55**(1): 521–546. doi:10.1146/annurev-ento-112408-085427. PMID:19743916.
- Haavik, L.J., Fierke, M.K., and Stephen, F.M. 2010. Factors affecting suitability of *Quercus rubra* as hosts for *Enaphalodes rufulus* (Coleoptera: Cerambycidae). *Environ. Entomol.* **39**(2): 520–527. doi:10.1603/EN09271. PMID:20388283.
- Hammel, L. 2008. 97 Beetle find is confirmed. Worcester Telegram & Gazette, 16 September 2008, Worcester, Mass.
- Hérard, F., Ciampitti, M., Maspero, M., Krehan, H., Benker, U., Boegel, C., Schrage, R., Bouhot-Delduc, L., and Bialooki, P. 2006. *Anoplophora* species in Europe: infestations and management processes. *EPPO Bull.* **36**(3): 470–474. doi:10.1111/j.1365-2338.2006.01046.x.
- Hérard, F., Maspero, M., Ramualde, N., Jucker, C., Colombo, M., Ciampitti, M., and Cavagna, B. 2009. *Anoplophora glabripennis* infestation (Col.:Cerambycidae) in Italy. *EPPO Bull.* **39**(2): 146–152. doi:10.1111/j.1365-2338.2009.02286.x.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bull.* **43**: 69–78.
- Hu, J., Angeli, S., Schuetz, S., Luo, Y., and Hajek, A.E. 2009. Ecology and management of exotic and endemic Asian longhorned beetle *Anoplophora glabripennis*. *Agric. For. Entomol.* **11**(4): 359–375. doi:10.1111/j.1461-9563.2009.00443.x.
- Jones, B. 2011. The Asian long-horned beetle: hopefully not coming to a neighborhood near you — guest blog. *Scientific American*. Available at <http://www.scientificamerican.com/blog/post.cfm?id=the-asian-longhorned-beetle-hopeful-2011-03-17>.
- Keena, M.A. 2002. *Anoplophora glabripennis* (Coleoptera: Cerambycidae) fecundity and longevity under laboratory conditions: comparison of populations from New York and Illinois on *Acer saccharum*. *Environ. Entomol.* **31**(3): 490–498. doi:10.1603/0046-225X-31.3.490.
- Lingafelter, S.W., and Hoebeke, E.R. 2002. Revision of *Anoplophora* (Coleoptera: Cerambycidae). *Entomological Society of Washington*, Washington, D.C.
- McCann, J.M., and Harman, D.M. 1990. Influence of the intrastand position of black locust trees on attack rate of the locust borer (Coleoptera, Cerambycidae). *Ann. Entomol. Soc. Am.* **83**(4): 705–711.
- Moericke, V., Prokopy, R.J., Berlocher, S., and Bush, G.L. 1975. Visual stimuli eliciting attraction of *Rhagoletis pomonella* (Diptera: Tephritidae) flies to trees. *Entomol. Exp. Appl.* **18**(4): 497–507. doi:10.1111/j.1570-7458.1975.tb00428.x.
- Morewood, W.D., Neiner, P.R., McNeil, J.R., Sellmer, J.C., and Hoover, K. 2003. Oviposition preference and larval performance of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in four eastern North American hardwood tree species. *Environ. Entomol.* **32**(5): 1028–1034. doi:10.1603/0046-225X-32.5.1028.
- Morewood, W.D., Hoover, K., Neiner, P.R., McNeil, J.R., and Sellmer, J.C. 2004a. Host tree resistance against the polyphagous wood-boring beetle *Anoplophora glabripennis*. *Entomol. Exp. Appl.* **110**(1): 79–86. doi:10.1111/j.0013-8703.2004.00120.x.
- Morewood, W.D., Neiner, P.R., Sellmer, J.C., and Hoover, K. 2004b. Behavior of adult *Anoplophora glabripennis* on different tree species under greenhouse conditions. *J. Insect Behav.* **17**(2): 215–226. doi:10.1023/B:JOIR.0000028571.52739.50.
- Nehme, M.E., Keena, M.A., Zhang, A., Baker, T.C., and Hoover, K. 2009. Attraction of *Anoplophora glabripennis* to male-produced pheromone and plant volatiles. *Environ. Entomol.* **38**(6): 1745–1755. doi:10.1603/022.038.0628. PMID:20021771.
- Newton, W.G., and Allen, D.C. 1982. Characteristics of trees damaged by sugar maple borer, *Glycobius speciosus*. *Can. J. For. Res.* **12**(4): 738–744. doi:10.1139/x82-112.
- North American Plant Protection Organization Phytosanitary Alert System. 2010. Asian longhorned beetle, *Anoplophora glabripennis* — confirmed in Suffolk County, Massachusetts; portions of Suffolk and Norfolk counties added to quarantine area. Posted on 19 July 2010. Available at <http://www.pestalert.org/oprDetail.cfm?oprID=439> [accessed 22 March 2011].
- Nowak, D.J., Pasek, J.E., Sequeira, R.A., Crane, D.E., and Mastro, V.C. 2001. Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in the United States. *J. Econ. Entomol.* **94**(1): 116–122. doi:10.1603/0022-0493-94.1.116. PMID:11233100.
- Orwig, D.A., and Foster, D.R. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. *J. Torrey Bot. Soc.* **125**(1): 60–73. doi:10.2307/2997232.
- Orwig, D.A., Cobb, R.C., D'Amato, A.W., Kizlinski, M.L., and Foster, D.R. 2008. Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests. *Can. J. For. Res.* **38**(4): 834–843. doi:10.1139/X07-196.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., and Goldwasser, L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, **1**(1): 3–19. doi:10.1023/A:1010034312781.
- Pederson, N.A. 2005. Climatic sensitivity and growth of southern temperate trees in the eastern US: implications for the carbon cycle. Ph.D. dissertation, Columbia University, New York.
- Peterson, A.T., and Scachetti-Pereira, R. 2004. Potential geographic distribution of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in North America. *Am. Midl. Nat.* **151**(1): 170–178. doi:10.1674/0003-0031(2004)151[0170:PGDOAG]2.0.CO;2.
- Prokopy, R.J., and Owens, E.D. 1983. Visual detection of plants by herbivorous insects. *Annu. Rev. Entomol.* **28**(1): 337–364. doi:10.1146/annurev.en.28.010183.002005.
- R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN3-900051-07-0. Available at <http://www.R-project.org>.
- Sawyer, A. 2011. Asian longhorned beetle: annotated host list. USDA-APHIS-PPQ, Center for Plant Health Science and Technology, Otis Laboratory. Available at http://www.aphis.usda.gov/plant_health/plant_pest_info/asian_lhb/downloads/hostlist.pdf [accessed 5 June 2011].
- Simberloff, D., and Rejmánek, M. 2011. *Encyclopedia of biological invasions*. University of California Press, Berkeley and Los Angeles, Calif.
- Smith, D.M. 1986. *The practice of silviculture*. John Wiley & Sons, Inc., New York.
- Smith, M.T. 1999. The potential for biological control of Asian longhorned beetle in the U.S. *Midwest Biol. Control News*, **6**: 1–7.
- Smith, M.T., Bancroft, J., and Tropp, J. 2002. Age-specific fecundity of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on three tree species infested in the United States. *Environ. Entomol.* **31**(1): 76–83. doi:10.1603/0046-225X-31.1.76.
- Smith, M.T., Turgeon, J.J., de Groot, P., and Gasman, B. 2009. Asian longhorned beetle *Anoplophora glabripennis* (Motschulsky): lessons learned and opportunities to improve the process of eradication and management. *Am. Entomol.* **55**(1): 21–25.
- Solter, L.F., Keena, M., Cate, J.R., McManus, M.L., and Hanks, L.M. 2001. Infectivity of four species of nematodes (Rhabditioidea: Steinernematidae, Heterorhabditidae) to the Asian longhorn beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae). *Biocontrol Sci. Technol.* **11**(4): 547–552. doi:10.1080/09583150120067580.
- Timms, L.L., Smith, S.M., and de Groot, P. 2006. Patterns in the within-tree distribution of the emerald ash borer *Agilus*

- planipennis* (Fairmaire) in young, green-ash plantations of south-western Ontario, Canada. *Agric. For. Entomol.* **8**(4): 313–321. doi:10.1111/j.1461-9563.2006.00311.x.
- Tingley, M.W., Orwig, D.A., Field, R., and Motzkin, G. 2002. Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. *J. Biogeogr.* **29**(10–11): 1505–1516. doi:10.1046/j.1365-2699.2002.00789.x.
- Turgeon, J.J., Ric, J., de Groot, P., Gasman, B., Orr, M., Doyle, J., Smith, M.T., Dumouchel, L., and Scarr, T. 2007. Détection des signes et des symptômes d'attaque par le longicorne étoilé: guide de formation. Service canadien des forêts, Ressources naturelles Canada, Ottawa, Ont.
- Turgeon, J.J., Pedlar, J., de Groot, P., Smith, M.T., Jones, C., Orr, M., and Gasman, B. 2010. Density and location of simulated signs of injury affect efficacy of ground surveys for Asian longhorned beetle. *Can. Entomol.* **142**(1): 80–96. doi:10.4039/n09-049.
- Williams, D.W., Lee, H.-P., and Kim, I.-K. 2004. Distribution and abundance of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in natural *Acer* stands in South Korea. *Environ. Entomol.* **33**(3): 540–545. doi:10.1603/0046-225X-33.3.540.
- Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. *Can. J. For. Res.* **21**(3): 414–416. doi:10.1139/x91-053.
- Yan, X.-F., Li, X.-J., Luo, Y.-Q., Xu, Z.-C., Tian, G.-F., and Zhang, T.-L. 2008. Oviposition preference of *Anoplophora glabripennis* emerging from five host tree species under field conditions. *For. Stud. China*, **10**(1): 23–26. doi:10.1007/s11632-008-0013-y.