

Tree selection and use by the polyphagous xylophage *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in Canada

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Abstract: Two breeding populations of the non-native Asian longhorned beetle (*Anoplophora glabripennis* Motschulsky), a pest of broadleaf trees in its native China, were discovered in Ontario in 2003 and 2013, respectively. Both populations were eradicated by removing all trees injured by the beetle and all uninjured trees deemed at high risk of injury. We used data collected during this removal to study host selection. Signs of *A. glabripennis* injury were observed on 732 stems from seven (i.e., *Acer*, *Salix*, *Populus*, *Betula*, *Ulmus*, *Fraxinus*, and *Tilia*) of the 45 tree genera available. Complete beetle development was confirmed on only the first four of these seven genera. Most signs of injury were on the genus *Acer* and on trees with a diameter at 130 cm above ground ranging between 15 and 40 cm. On most trees, the lowest sign of injury was within 3 m of the ground or within 40% of tree height. Tree height explained 63% of the variance in the location of the lowest sign of injury. Initial attacks were typically near the middle of the tree and expanded both upward and downward with successive attacks over time. We discuss how these findings could improve survey efforts for *A. glabripennis*.

Key words: Asian longhorned beetle, host availability, host range, *Acer*, forest invasive alien pest, urban forest pest, exotic, eradication.

Résumé : Deux populations reproductrices non indigènes du longicorne asiatique (*Anoplophora glabripennis* Motschulsky), un ravageur des essences feuillues en Chine d'où il est originaire, ont été découvertes en Ontario respectivement en 2003 et 2013. Les deux populations ont été éradiquées en éliminant tous les arbres endommagés par le longicorne et tous les arbres non endommagés mais jugés à risque de l'être. Nous avons utilisés les données collectées lors de cette intervention pour étudier la sélection de l'hôte. Des signes de dégâts causés par *A. glabripennis* ont été observés sur 732 tiges appartenant à sept (c.-à-d. *Acer*, *Salix*, *Populus*, *Betula*, *Ulmus*, *Fraxinus*, et *Tilia*) des 45 genres d'arbres pouvant servir d'hôtes. Le développement complet de l'insecte n'a été confirmé que sur les quatre premiers de ces sept genres. La plupart des signes de dégâts ont été observés sur le genre *Acer* et sur des arbres dont le diamètre à 130 cm au-dessus du sol mesurait entre 15 et 40 cm. Sur la plupart des arbres, le signe de dégât le plus bas était situé à moins de 3 m du sol ou 40 % de la hauteur de l'arbre. La hauteur de l'arbre expliquait 63 % de la variance de la localisation du signe de dégâts le plus bas. Les attaques initiales étaient typiquement situées près du milieu de l'arbre et s'étendaient avec le temps vers le haut et vers le bas à la suite d'attaques successives. Nous discutons de la façon dont ces résultats pourraient améliorer les efforts d'inventaire de *A. glabripennis*. [Traduit par la Rédaction]

Mots-clés : longicorne asiatique, disponibilité des hôtes, aire de répartition des hôtes, *Acer*, ravageur forestier exotique invasif, ravageur forestier en milieu urbain, exotique, éradication.

Introduction

A large proportion of non-native terrestrial arthropods that arrive in Canada feed on woody plants (Langor et al. 2009). One of these alien invasive species is the Asian longhorned beetle, *Anoplophora glabripennis* Motschulsky (Coleoptera: Cerambycidae), a polyphagous xylophage of broadleaf trees (Hanks 1999). Since the first discovery of this species outside its native range of China and the Korean Peninsula, in New York City, NY, in 1996, there have been more than 30 outbreaks recorded worldwide (Haack et al. 1996, 2010; Eyre and Haack 2017; Coyle et al. 2021). The number of injured trees in these outbreaks varied between as few as six (e.g.,

Boston, MA) and, as of 2 October 2021, as many as tens of thousands (e.g., 24 203 in Worcester County, MA, and 21 508 in Clermont County, OH (R. Santos, USDA, personal communication)). The main concerns with these outbreaks are that without natural enemies to control its populations, *A. glabripennis* feeding galleries and tunnels in the sapwood and heartwood of injured trees could cause structural weakening, tree mortality, and canopy loss in urban and suburban landscapes (Nowak et al. 2001). Ultimately, *A. glabripennis* could modify the composition and structure of North America's eastern hardwood forest (Dodds and Orwig 2011), which would seriously alter its ecological roles and impact industries such as lumber, maple syrup, and tourism (MacLeod et al. 2002; USDA-APHIS 2008).

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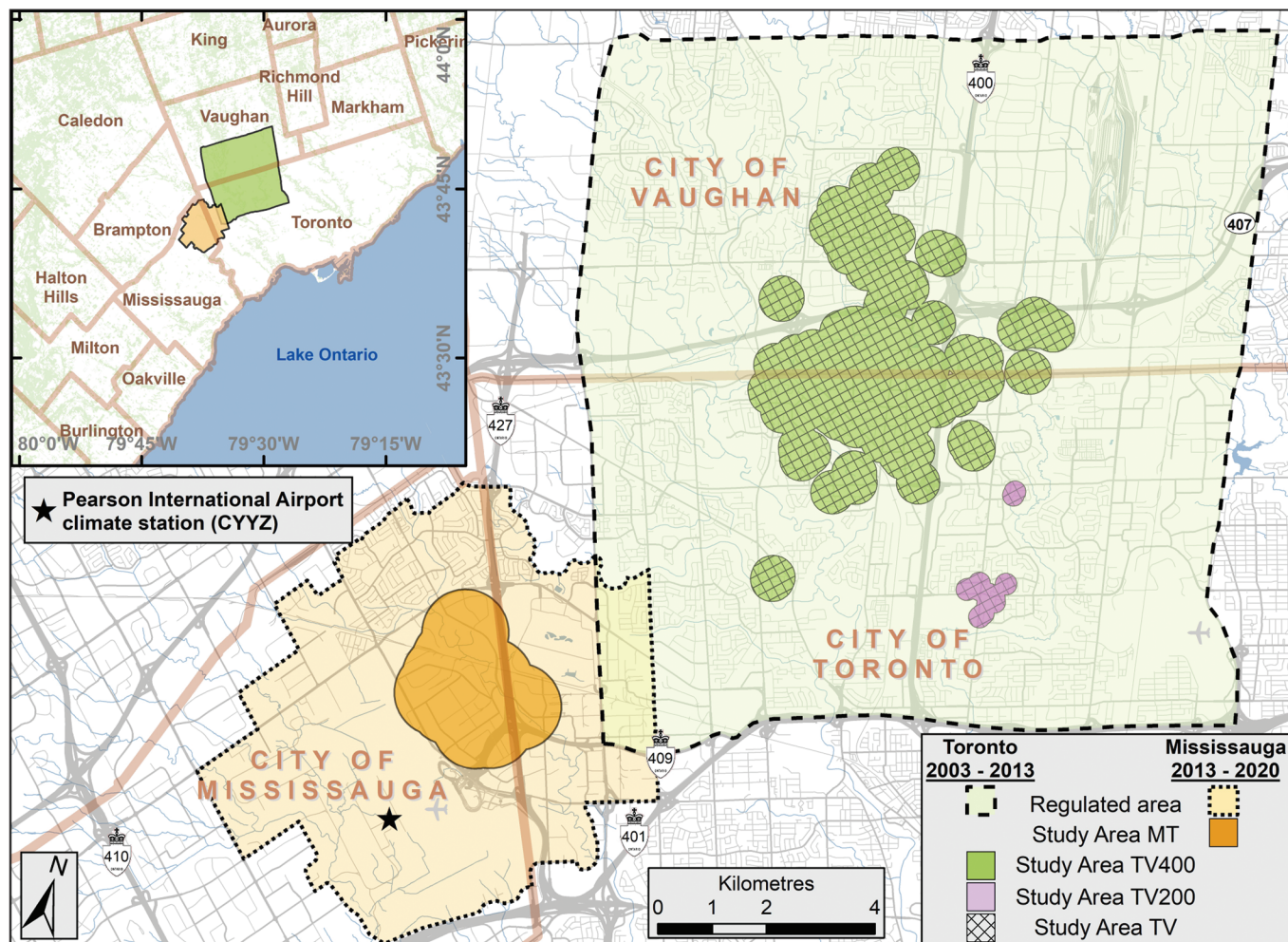
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Fig. 1. Location and extent of *Anoplophora glabripennis* study areas within the regulated areas of the Toronto–Vaughan and Mississauga–Toronto outbreaks and the datasets associated with each study area. Inset shows the boundaries and locations of the Toronto–Vaughan and Mississauga–Toronto regulated areas in the Greater Toronto Area. Base layers from Land Information Ontario (LIO) licensed under the Open Government License — Ontario. Map coordinate system is UTM zone 17 (NAD 83) rotated 17° west. Inset has no rotation.



The Canadian Food Inspection Agency (CFIA), which is responsible for safeguarding food, animals, and plants in Canada, reported the discovery of two outbreaks of *A. glabripennis* in the Greater Toronto Area (GTA; Hopkin et al. 2004). The first outbreak, overlapping the city limits of Toronto and Vaughan (hereinafter Toronto–Vaughan or TV), was publicised on 12 September 2003 (NAPPO 2003), and the second one, which straddled the city limits of Mississauga and Toronto (hereinafter Mississauga–Toronto or MT), on 20 September 2013 (Fig. 1; NAPPO 2013; Turgeon et al. 2015). Delimitation surveys suggested a limited spread of each outbreak; thus, the CFIA determined that eradication was a feasible emergency response to these incursions (CFIA-FPES 2004).

The CFIA's proposed eradication strategy was similar for both outbreaks. Broadly, it consisted of tools to control the beetle's population, survey activities to detect and delimit the outbreaks and assess and monitor the success of control tools, regulatory tools to limit its spread, a recovery program to reduce the impact in affected areas, and an outreach program to educate and keep the public informed and involved (Haack et al. 2010). The control tool was host removal — it targeted all trees with signs of injury as well as those belonging to genera assumed to be at high risk of injury by the beetle (Haack et al. 2010). Detection of trees with characteristic signs (i.e., physical damage caused by an insect) or

symptoms (i.e., response of a tree to insect damage) of *A. glabripennis* injury relied exclusively on a visual inspection of their main stem and branches (Ric et al. 2007).

Knowledge of host range and specificity would be critical to the success of this control strategy (Myers et al. 1998; Myers and Hosking 2002); however, at the time of the initial outbreak, knowledge about *A. glabripennis* hosts outside its native range was limited (Haack et al. 1996; Poland et al. 1998; Nowak et al. 2001). Initial host lists consisted mostly of trees identified to genus and appeared partially inaccurate or incomplete (Lingafelter and Hoebeke 2002; MacLeod et al. 2002), because pest identification on injured trees was not always confirmed (Nowak et al. 2001). Thus, an annotated list of known host trees in the United States (USA), and to a lesser extent, in the beetle's natural range (Nowak et al. 2001; Lingafelter and Hoebeke 2002; MacLeod et al. 2002; Williams et al. 2004) was compiled by Dr. A. Sawyer (USDA-APHIS) and sent by e-mail to Jean J. Turgeon on 14 October 2003 (Turgeon et al. 2016).

The CFIA categorised these tree genera as “suitable” if there was documented evidence that they had hosted *A. glabripennis* to complete development under field conditions (e.g., tree with presence of an emergence hole; Turgeon et al. 2022). As of November 2003, there were 10 genera considered suitable for *A. glabripennis* development in Canada (and thus at high risk of injury): *Acer* L. (Sapindaceae),

Table 1. Radius, extent, tree genera targeted for removal or monitoring, and datasets associated with the Toronto–Vaughan (TV) and Mississauga–Toronto (MT) study areas based on year trees affected by *Anoplophora glabripennis* were discovered.

Study area	Year of discovery	Radius of study area (m)	Extent of study area (ha) ^a	Suitability of trees targeted for removal/monitoring ^b	Dataset
TV	2003–2006	400	1981.6	All [suitable (s), questionable (q), and unknown (u)]	TVa (i.e., TV _{s400} + TV _{q400} + TV _{u400})
	2007	200	82.6	Suitable only	TV _{s200}
	2003–2007	400 and 200	2064.2	Combined suitable (cs)	TVcs (i.e., TV _{s400} + TV _{s200})
MT	2013–2014	800	677.8	Suitable only	MTs

^aValues from table 5 in Turgeon et al. (2022).

^bTree genera in each category of suitability listed in supplementary Table S3¹.

Aesculus L. (Sapindaceae), *Albizia* Durazz. (Fabaceae), *Betula* L. (Betulaceae), *Celtis* L. (Cannabaceae), *Platanus* L. (Platanaceae), *Populus* L. (Salicaceae), *Salix* L. (Salicaceae), *Sorbus* L. (Rosaceae), and *Ulmus* L. (Ulmaceae) (Turgeon et al. 2007; Smith et al. 2009; Haack et al. 2010; Fournier and Turgeon 2017). The remaining tree genera were assumed to represent a lower risk of injury, with suitability characterised as “unknown” if there was no record yet of an injured tree, or “questionable” if records from field observations or laboratory screening tests suggested that egg development alone, or egg and larval development, was possible but unverified under field conditions (Turgeon et al. 2007, 2016).

The CFIA’s eradication responses, which followed a sequence of phases, namely detection, evaluation, response decision, operation, monitoring and review (Hosking 2001), presented great opportunities to document many events and component elements (e.g., origin, host selection, within-tree colonisation, larval behaviour, population spread) of the infestation dynamics of *A. glabripennis* in landscapes outside its native range (Sawyer 2007). Thus, we developed a research program that dovetailed with the CFIA’s operations within each of the two regulated areas established in the GTA and collected information on trees removed and surveyed in each one (Turgeon et al. 2022).

Herein, we report results on plant availability, host selection, and resource utilisation in the outbreaks located in the GTA. More specifically, we (i) assessed abundance, generic richness, and size of available plants; (ii) quantified host acceptance and preference for oviposition; (iii) confirmed host suitability for complete development; and (iv) examined the influence of some tree traits on abundance and location (or host utilisation) of two common signs of injury by *A. glabripennis*: oviposition pits and emergence holes. We compared the observed patterns of host selection and utilisation to those reported for other invasions that occurred outside of the beetle’s native range. Finally, we summarise instances when this knowledge led to adaptive management of these outbreaks. More specifically, we looked at how information on host selection led to changes in the design of survey protocols that improved the efficacy of surveys used during the detection, delimitation, and monitoring phases of this eradication program.

Materials and methods

Terminology

The International Plant Protection Convention (IPPC) and International Standards for Phytosanitary Measures (ISPMs) define an infestation (of a commodity) as the presence in a commodity of a living pest of the plant or plant product concerned (FAO 2018). Not all trees with signs or symptoms of *A. glabripennis* injury contained living specimens (Turgeon et al. 2022). In this study, we referred to trees with assumed signs of *A. glabripennis* of injury as “trees of interest”. These signs were re-examined in a laboratory to confirm the field injury status. We took additional samples from trees injured by *A. glabripennis* to determine their infestation status:

“infested” (contained at least one live *A. glabripennis* specimen), “attacked” (contained only dead specimens of *A. glabripennis* when compared to voucher specimens), or “suspect” (contained only signs and symptoms deemed characteristic of *A. glabripennis* injury) (Turgeon et al. 2007). Herein, we referred to trees in any of these three categories as “affected”; all other trees of interest and those where no signs could be detected were deemed “unaffected”.

As mentioned above, the control strategy consisted of removing all affected trees and all those deemed at high risk. High-risk trees were those of a suitable genus that were within a fixed radius of an affected tree. We defined the treatment buffer or radius around each affected stem as the “affected area”.

We characterised a tree as “accepted” when we observed an oviposition pit in the bark and found an egg (live or dead) or any other sign suggesting complete (e.g., emergence hole) or incomplete (e.g., feeding gallery under the bark or tunnel into the wood) larval development had occurred under that pit.

Finally, many of the trees removed or surveyed during these two outbreaks had multiple main stems originating from one root system. The CFIA reported the number of trees removed or monitored (Turgeon et al. 2022), but also recorded the number of stems for each tree. Herein, we always refer to the number of stems.

Study areas

We defined a study area as the affected area in each outbreak plus areas around suspect trees that were monitored (either to 200, 400, or 800 m). There were two study areas: one associated with each outbreak (Fig. 1; supplementary text S1¹).

Adaptive management led the CFIA to adjust its data collection methodology both during the Toronto–Vaughan eradication and between the Toronto–Vaughan and Mississauga–Toronto eradications. These adjustments included (i) changes to the radius of an affected area from 400 m (2003–2006) to 200 m (2007) for the Toronto–Vaughan study area and to 800 m for the Mississauga–Toronto study area (2013); (ii) a reduction in the number of high-risk genera targeted for removal/monitoring; and (iii) an increase in the number of suitable genera targeted for monitoring. When the CFIA reduced the size of the affected area from 400 to 200 m, it also stopped recording data on stems from genera of questionable or unknown suitability. Thus, trees were grouped based on discovery year (Turgeon et al. 2022), which led to the creation of a number of datasets (Table 1; Fig. 1).

Data collection

Details on specific procedures and the type of information collected while removing or inspecting trees during the delimitation, operation or monitoring phases of these eradication programs have been documented previously (Turgeon et al. 2010, 2016, 2022), and thus, are only summarised in supporting documentation (supplementary text S2¹).

¹Supplementary material available with the article at <https://doi.org/10.1139/cjfr-2021-0244>.

Table 2. Number of main stems in each of three datasets by arbitrary category of plant suitability, and richness of families, genera, and species available to, and affected by, *Anoplophora glabripennis* during outbreaks discovered in Ontario, Canada.

Outbreaks Dataset ^a Suitability	No. of stems	Available			Affected		
		Families (n)	Genera (n) ^b	Species (n)	Families (n)	Genera (n)	Species (n)
Toronto–Vaughan outbreak (2003–2013)							
Dataset TVa							
Suitable (TV _{s400})	93 006	7	9	59	4	5	14
Questionable (TV _{q400})	43 324	8	11	34	2	2	2
Unknown (TV _{u400})	13 118	17	24	38	0	0	0
Total	149 448	24	44	131	6	7	16
Dataset TVcs							
Suitable (TV _{s400} and TV _{s200})	96 577	7	9	62	4	5	15
Mississauga–Toronto outbreak (2013–2020)							
Dataset MTs							
Suitable	17 762	8	11	33	2	2	3
Combined outbreaks	170 781	24	45	138	6	7	17

^aContent of datasets is given in Table 1.

^bNumber of suitable genera available in datasets TVa and TVcs (9) differed from that of dataset MTs (11) because of a change in policy on suitability.

See text for more details.

Analyses

We removed as part of treatment, or monitored during intensive surveys carried out over several years, 178 237 stems of broadleaf trees and shrubs from the combined study areas of the Toronto–Vaughan and Mississauga–Toronto regulated areas (Turgeon et al. 2022). From the current study, we discarded stems without a diameter at 130 cm above ground (D_{130} ; Brokaw and Thompson 2000; ($n = 5082$)), stems that were dead from causes other than *A. glabripennis* ($n = 1693$), and all stems without a valid genus ($n = 1188$), leaving 170 781 stems for analysis (Table 2).

We calculated percentage of oviposition pits or emergence holes within each genus, species or D_{130} class on a per stem basis by dividing the number of pits or holes for a given species, genus or D_{130} class by the total number found among affected stems. We defined D_{130} classes arbitrarily in 5 cm increments.

We calculated the basal area (BA, m²) of each stem using the following equation:

$$(1) \quad BA = \pi \left(\frac{D}{2} \right)^2 / k$$

where D is D_{130} in centimetres, and k is a constant (10 000) needed to convert cm² into m². BA is presented in units of m² per hectare of study area.

We calculated relative basal area (RBA) using the following equation:

$$(2) \quad RBA = \left(\frac{BA_x}{BA_t} \right) \times 100$$

where BA_x is the basal area of a genus or species per hectare and BA_t is the total basal area of the study area per hectare.

We calculated relative density (RD) using the following equation:

$$(3) \quad RD = \left(\frac{S_x}{S_t} \right) \times 100$$

where S_x is the number of stems per hectare of a genus or species and S_t is the respective total number of stems per hectare in the study area.

We calculated importance value (IV; Dodds and Orwig 2011) using the following equation:

$$(4) \quad IV = \frac{(RBA + RD)}{2}$$

We employed chi-squared analyses to test for differences between observed *A. glabripennis* attack frequencies and expected attack frequencies for different genera, species within the genus *Acer*, and D_{130} classes. We used an omnibus chi-squared statistic to test overall significance for each frequency table; we tested significance of individual frequency table cells using cell-specific chi-squared values with one degree of freedom (Shan and Gerstenberger 2017). We used a Simes correction to adjust the significance cut-off value (i.e., $p = 0.05$) to account for multiple tests (Simes 1986). Classes of D_{130} were ordinal, thus we used a Cochran–Armitage test to test for a linear trend in attack rate across classes. We examined potential interactions between D_{130} and tree genus using a 2-way chi-squared analysis. Differences in D_{130} between suitability classes and between affected versus unaffected stems, as well as differences in abundance of oviposition pits and emergence holes between genera, species and D_{130} classes, were examined using Kruskal–Wallis (H) tests with post-hoc Dwass, Steel, Critchlow–Fligner pairwise comparison tests. We carried out these analyses using SAS software (SAS Institute Inc. 2015). Regressions were performed in Microsoft Excel version 2016 (Microsoft 2015). We report averages as mean \pm SE.

Results

Plant availability

Toronto–Vaughan study area (TV)

We based our assessment of plant availability in this study area on dataset TVa because it contained data on all genera of broadleaf trees inventoried in that study area, irrespective of suitability. Dataset TVcs contained only data on suitable genera. However, we presented data on diversity, density, basal area and D_{130} of available stems from both datasets to show their similarities in general trends to those derived from suitable stems in dataset TVa (Tables 3 and 4; supplementary Tables S3, S4¹).

Richness

Our operational requirement was to identify each stem removed or monitored to the genus level. The percentage of stems identified to species varied among categories of suitability and genera. For example, we identified about 73% of the suitable stems to species compared to about 9% of those with unknown or questionable

Table 3. Density, basal area, and mean diameter at 130 cm above ground (D_{130}) of main stems from each of three arbitrary categories of plant suitability and all suitable genera available to, and affected by, *Anoplophora glabripennis* in the Toronto–Vaughan study area (dataset TVa) together with their respective relative density (RD), relative basal area (RBA), and importance value (IV).

Suitability Genus	Available stems						Affected stems							
	D_{130} (mean ± SE)	Density ^a (stems/ha)	RD (%)	BA (m ² /ha)	RBA (%)	IV	Affected (%) ^b	% ^c of genus affected	D_{130} (mean ± SE) ^d	Density (stems/ha)	RD (%)	BA (m ² /ha)	RBA (%)	IV
Suitable (9 genera^e)														
<i>Acer</i>	10.38±0.05	27.871	36.95	0.5247	45.53	41.24	90.4	1.0	20.05±0.48*	0.286	0.38	0.0119	1.03	0.71
<i>Aesculus</i>	10.69±1.03	0.094	0.13	0.0023	0.20	0.16	0.0	—	—	—	—	—	—	—
<i>Betula</i>	12.49±0.17	1.271	1.68	0.0227	1.97	1.83	1.9	0.5	11.38±1.51	0.006	0.01	0.0001	0.01	0.01
<i>Celtis</i>	8.54±0.66	0.035	0.05	0.0003	0.02	0.04	0.0	—	—	—	—	—	—	—
<i>Platanus</i>	26.87±3.97	0.015	0.02	0.0013	0.12	0.07	0.0	—	—	—	—	—	—	—
<i>Populus</i>	7.71±0.12	3.454	4.58	0.0449	3.90	4.24	3.0	0.3	31.41±5.66*	0.010	0.01	0.0012	0.10	0.06
<i>Salix</i>	5.98±0.08	8.816	11.69	0.1092	9.48	10.58	3.8	0.1	25.04±2.24*	0.012	0.02	0.0007	0.06	0.04
<i>Sorbus</i>	9.87±0.35	0.321	0.43	0.0044	0.38	0.40	0.0	—	—	—	—	—	—	—
<i>Ulmus</i>	10.36±0.11	5.059	6.71	0.0868	7.53	7.12	0.5	<0.1	27.20±9.45*	0.002	<0.01	0.0001	0.01	0.01
Subtotal	9.41±0.04	46.936	62.23	0.7967	69.13	65.68	99.7	0.7	20.05±0.48*	0.315	0.42	0.0140	1.21	0.82
Questionable (11 genera^f)														
Subtotal	9.20±0.05	21.864	28.99	0.3064	26.59	27.79	0.3	— ^c	22.45±0.75*	0.001	<0.01	<0.0000	<0.01	<0.01
Unknown (24 genera^f)														
Subtotal	6.16±0.07	6.620	8.78	0.0493	4.28	6.53	0.0	—	—	—	—	—	—	—
Total	9.07±0.03	75.419	100.00	1.1524	100.00	100.00	100.0	0.4	20.46±0.48*	0.316	0.42	0.0140	1.22	0.82

^aThe extent of study area and number of available stems for dataset TVa is given in Tables 1 and 2, respectively.

^bThe number of affected stems in dataset TVa that could be assessed, irrespective of suitability, was 627.

^cThe numbers of available and affected stems for each genus and those identified to species are given in supplementary Table S3¹.

^dAn asterisk (*) indicates this value is significantly different from mean D_{130} of unaffected stems of the same genus or suitability category (shown in supplementary Table S3¹), based on a Kruskal–Wallis test with a significance cut-off of $p = 0.05$.

^eThere was no stem of the genus *Albizia*.

^fTree genera in each category of suitability are listed in supplementary Table S3¹.

Table 4. Density, basal area, and mean diameter at 130 cm above ground (D_{130}) of main stems for suitable genera available to, and affected by, *Anoplophora glabripennis* in the Toronto-Vaughan study area (dataset TVCs) together with their respective relative density (RD), relative basal area (RBA), and importance value (IV).

Suitability Genus	Available stems				Affected stems				RD (%)	BA (m ² /ha)	RBA (%)	IV	RD (%)	BA (m ² /ha)	RBA (%)	IV	
	D_{130} (mean ± SE)	Density ^a (stems/ha)	Density ^a (stems/ha)	% of genus affected	D_{130} (mean ± SE) ^d	Density (stems/ha)	% of genus affected	% of genus affected									
Suitable (9 genera)																	
<i>Acer</i>	10.62±0.05	27.978	59.80	0.5549	65.52	62.66	90.4	1.0	20.58±0.48*	0.287	0.613	0.0126	1.49	1.05	—	—	—
<i>Aesculus</i>	11.02±0.99	0.095	0.20	0.0023	0.28	0.24	0.0	—	—	—	—	—	—	—	—	—	—
<i>Betula</i>	12.56±0.17	1.233	2.64	0.0223	2.63	2.63	1.8	0.5	11.38±1.51	0.006	0.012	0.0001	0.01	0.01	—	—	—
<i>Celtis</i>	8.54±0.66	0.034	0.07	0.0003	0.03	0.05	0.0	—	—	—	—	—	—	—	—	—	—
<i>Platanus</i>	26.87±3.97	0.014	0.03	0.0013	0.15	0.09	0.0	—	—	—	—	—	—	—	—	—	—
<i>Populus</i>	7.81±0.13	3.335	7.13	0.0447	5.27	6.20	2.9	0.3	31.41±5.66*	0.009	0.020	0.0011	0.13	0.08	—	—	—
<i>Salix</i>	6.12±0.09	8.507	18.18	0.1144	13.51	15.85	4.4	0.2	36.50±5.22*	0.014	0.030	0.0023	0.27	0.15	—	—	—
<i>Sorbus</i>	9.93±0.33	0.346	0.74	0.0048	0.57	0.65	0.0	—	—	—	—	—	—	—	—	—	—
<i>Ulmus</i>	10.69±0.11	5.224	11.21	0.1019	12.03	11.62	0.5	<0.1	27.20±9.45*	0.001	0.003	0.0001	0.01	0.01	—	—	—
Total	9.66±0.04	46.787	100.00	0.8468	100.00	100.00	100.0	0.7	21.46±0.54*	0.317	0.678	0.0162	1.91	1.30	—	—	—

^aThe extent of study area and number of available stems for dataset TVCs is given in Tables 1 and 2, respectively.

^bThe number of affected stems from suitable genera that could be assessed in dataset TVCs was 655.

^cThe numbers of available and affected stems for each genus and those identified to species are given in supplementary Table S4¹.

^dAn asterisk (*) indicates this value is significantly different from mean D_{130} of unaffected stems of the same genus or suitability category (shown in supplementary Table S3¹), based on a Kruskal-Wallis test with a significance cut-off of $p = 0.05$.

^eThere was no stem of the genus *Albizia*.

suitability. Also, due to taxonomic complexities, we identified 17% of *Salix* stems to species compared to 88% for *Acer*.

In this study area, based on dataset TVa, there were broadleaf trees and shrubs from 44 genera and 24 families (Table 2). The numbers of families and genera of stems with unknown suitability was about twice that of suitable stems or of those of questionable suitability. We identified at least 59 species from only nine of the 10 genera and seven families categorised as suitable in Canada in 2003. We did not find any stem of the suitable genus *Albizia* in this study area (Table 3). Stems of the genus *Cercidiphyllum* Siebold and Zuccarini (Cercidiphyllaceae) were present in the quarantine area between 2003 and 2006, but were categorised as unknown suitability until 2011, when reclassified as suitable (Turgeon et al. 2016). We found the same number of suitable families and genera in dataset TVcs as in dataset TVa (Table 2).

Importance

The study area in dataset TVa contained 149 448 stems of broadleaf trees and shrubs (Table 2). Most of these stems (93 006) were of suitable genera. The remaining stems were of genera with questionable or unknown suitability. The study area in dataset TVcs contained 96 577 stems from suitable genera (Table 2).

This study area had a density of 75 stems/ha and a BA of about 1.2 m²/ha (Table 3). The density of suitable hosts was 47 stems/ha, with a relative density (RD) of 62%. Densities of genera with questionable and unknown suitability were 22 and 7 stems/ha, with RD values of 29% and 9%, respectively.

Acer was the genus with the highest RD (37%) followed by *Prunus* L. (Rosaceae), a genus with questionable suitability, and *Salix*, a suitable genus (Table 3; supplementary Table S3¹). There were 12 genera with RD values ranging between 1%–10%. For the remaining 29 genera, RD was ≤1%. Of stems identified to species in dataset TVa, *Acer negundo* L. had the highest RD (18%) followed by *Acer platanoides* L., *Acer saccharum* Marshall, and *Ulmus pumila* L. (supplementary Table S3¹).

Available suitable stems had a BA of 0.8 m²/ha and an RBA of 69% (Table 3). The BA and RBA of stems with questionable suitability were 0.3 m²/ha and 27%, whereas those of stems with unknown suitability were 0.05 m²/ha and 4%, respectively.

Of all available genera, *Acer* had the highest RBA (46%). *Salix*, *Ulmus*, and *Prunus* had RBAs between 5% and 10% (Table 3; supplementary Table S3¹). There were 10 genera with RBA values ranging between 1% and 5% (supplementary Table S3¹). RBA for each remaining genus was <1%. Of the stems identified to species, *A. platanoides*, *A. negundo*, and *A. saccharum* had the highest RBA values at 13%, 12%, and 7% (supplementary Table S3¹), respectively.

Overall, IV of available genera differed slightly from that reported for RD. *Acer* remained the genus with the highest IV. The genera *Salix* and *Prunus* traded places, with *Salix* becoming the second most important and *Prunus* third (Table 3; supplementary Table S3¹). *Acer negundo* had the highest IV followed by *A. platanoides* and *A. saccharum* (supplementary Table S3¹).

Size

Based on TVa, stem D_{130} in this study area varied between 0.1 and 156 cm. Stem size differed significantly among suitability categories (Table 3; $F = 549.3$; $p < 0.0001$). Specifically, based on a Kruskal-Wallis test with Dwass, Steel, Critchlow-Fligner pairwise comparison tests, suitable stems (9.41 cm) were significantly larger than stems of questionable suitability (9.20 cm), which in turn were significantly larger than stems of unknown suitability (6.16 cm).

Stem D_{130} also varied widely among genera within each category of suitability. For example, average D_{130} of stems of suitable genera varied between 5.98 cm for *Salix*, a genus with many shrub-sized species, and 26.87 cm for *Platanus* (Table 3). Average D_{130} of stems with questionable suitability varied between 1.88 cm on *Hibiscus* L. (Malvaceae) and 19.58 cm on *Quercus* (supplementary Table S3¹). Similarly, average D_{130} of stems with unknown suitability varied

between 1.91 cm on *Sambucus* L. (Adoxaceae) and 21.29 cm on *Zelkova* Spach (Ulmaceae). For most multispecies-genera, stem D_{130} also varied widely among species.

Distribution of the percentage of stems among our arbitrary classes of D_{130} followed the same pattern for all three categories of host suitability (Fig. 2A). The highest percentage of available stems was associated with $D_{130} < 5$ cm; over 60% of all stems were < 10 cm in diameter.

Mississauga–Toronto study area

In this study area, the CFIA removed only stems from all four suitable high-risk genera. Specialists performed a minimum of three surveys over a minimum of 5 years on all stems of the remaining eight suitable genera that represented a moderate risk of injury (Fournier and Turgeon 2017).

Richness

We recorded the presence of plants from 11 of the 12 genera considered suitable in Canada in 2013; there were no *Albizia* (Table 5). We identified to species 38% of all suitable stems in the study area. This percentage varied between 0% for the genera *Koelreuteria* and *Sorbus*, and 88% for *Cercidiphyllum* (supplementary Table S5¹). This resulted in a lower species richness than in datasets TVa and TVcs (supplementary Tables S3, S4¹, respectively).

Importance

Based on dataset MTs, we inventoried 17 762 stems of suitable broadleaf trees in the study area of this outbreak (Table 2). The density of suitable stems was 26.2 stems/ha (Table 5). The genus *Acer* had the highest RD (65%) of all stems categorised as suitable followed, in decreasing order of importance, by *Salix*, *Populus*, and *Ulmus*. RD for all remaining suitable genera was $< 1\%$. The species with the highest RD among suitable stems identified to species were *Acer negundo* (22%) and *A. platanoides* (5%; supplementary Table S5¹).

BA for all suitable stems was 0.7 m²/ha, with *Acer* having the highest RBA (63%; Table 5). Of those identified to species, *Acer negundo*, *A. platanoides*, *Acer saccharinum* L., and *A. saccharum* represented 17%, 11%, 6%, and 5% of the RBA, respectively (supplementary Table S5¹).

Acer was the genus with the highest IV followed by *Salix*, *Populus*, and *Ulmus* (Table 5). The species with the highest IV was *A. negundo* followed by *A. platanoides*, *A. saccharinum*, and *A. saccharum* (supplementary Table S5¹).

Size

Overall, D_{130} of suitable stems in this study area varied between 1 and 210 cm, averaging 11.94 cm (Table 5). Stem diameter also varied widely among suitable genera. For example, average stem D_{130} varied between 8.00 cm ($n = 1$) for *Koelreuteria* and 16.94 cm for *Aesculus*.

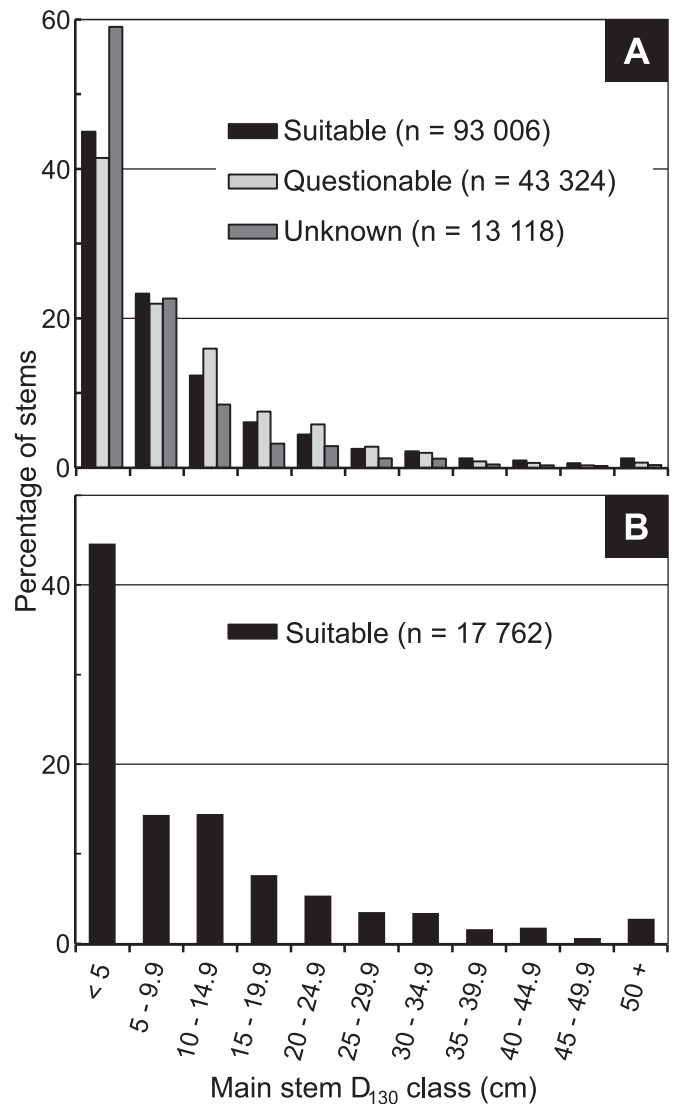
The percentage of suitable stems in each class of D_{130} varied greatly. The < 5 cm class had the highest percentage of stems. Nearly 60% of stems were < 10 cm in D_{130} (Fig. 2B).

Plant selection

Toronto–Vaughan study area

We based our assessment of plant selection by *A. glabripennis* in this study area on dataset TVcs rather than dataset TVa to ensure our analyses would include as many of the affected stems as possible. Dataset TVcs contained data on all but the two affected stems with questionable suitability (e.g., *Fraxinus excelsior* L. (Oleaceae) and *Tilia cordata* Mill. (Malvaceae); supplementary Tables S3, S4¹); information on these two stems had been published already (Turgeon et al. 2016). Also excluded from dataset TVcs were 25 affected stems that were destroyed before D_{130} measurements

Fig. 2. Percentage of stems available per category of host suitability to *Anoplophora glabripennis* among arbitrary classes of diameter at 130 cm above ground (D_{130}) in the Toronto–Vaughan (A; dataset TVa) and Mississauga–Toronto (B; dataset MTs) outbreaks. NOTE: Tree genera in each category of host suitability in datasets TVa and MTs are listed in supplementary Tables S3 and S5¹, respectively.



could be obtained. Thus, we based our analysis of plant selection on 655 of the 682 stems affected in this study area (Table 4).

Richness

Anoplophora glabripennis selected and accepted plants from only five of the nine suitable genera (four out of seven families) of broadleaf trees available in this study area (Tables 2 and 3). We identified 15 suitable species as selected by *A. glabripennis* (Table 2).

Ninety percent of suitable stems selected were of the genus *Acer* (Table 4). We found evidence of acceptance on only 8 of the 17 species of *Acer* available (Table 6). Almost 60% of all affected stems were *A. platanoides* and 65% of the affected *Acer* stems were *A. platanoides* (supplementary Table S4¹).

At the time we discovered the last affected stem, *A. glabripennis* had selected about 1% of all suitable stems present in this study area. The proportion of stems selected in the study area varied among selected genera (Table 4): it was $< 0.1\%$ for *Ulmus* stems, but

Table 5. Density, basal area, and mean diameter at 130 cm above ground (D_{130}) of main stems for suitable genera available to, and affected by, *Anoplophora glabripennis* in the Mississauga-Toronto study area (dataset MTs) together with their respective relative density (RD), relative basal area (RBA), and importance value (IV).

Suitability Genus	Available stems						Affected stems								
	D_{130} (mean ± SE)	Density ^a (stems/ha)	RD (%)	BA (m ² /ha)	RBA (%)	IV	Affected (%) ^b	% ^c of genus affected	D_{130} (mean ± SE) ^d	Density (stems/ha)	RD (%)	BA (m ² /ha)	RBA (%)	IV	
Suitable (11 genera^e)															
<i>Acer</i>	12.82 ± 0.12	16.986	64.82	0.4371	62.94	63.88	97.7	0.37	18.20 ± 1.39*	0.063	0.242	0.0021	0.296	0.269	
<i>Aesculus</i>	16.94 ± 1.95	0.024	0.09	0.0006	0.09	0.09	0.0	—	—	—	—	—	—	—	
<i>Betula</i>	17.13 ± 1.09	0.186	0.71	0.0065	0.93	0.82	0.0	—	—	—	—	—	—	—	
<i>Celtis</i>	10.46 ± 0.65	0.068	0.26	0.0007	0.10	0.18	0.0	—	—	—	—	—	—	—	
<i>Cercidiphyllum</i>	9.25 ± 0.41	0.012	0.05	0.0001	0.01	0.03	0.0	—	—	—	—	—	—	—	
<i>Koelreuteria</i>	8.00 ± 0.00	0.001	0.01	<0.0001	<0.01	<0.01	0.0	—	—	—	—	—	—	—	
<i>Platanus</i>	11.88 ± 1.88	0.047	0.18	0.0009	0.13	0.16	0.0	—	—	—	—	—	—	—	
<i>Populus</i>	9.11 ± 0.24	3.271	12.48	0.0538	7.75	10.11	0.0	—	—	—	—	—	—	—	
<i>Salix</i>	10.58 ± 0.38	4.175	15.93	0.1694	24.39	20.16	2.3	0.04	30.00 ± 0.0	0.001	0.006	<0.0001	<0.001	0.003	
<i>Sorbus</i>	8.68 ± 1.23	0.028	0.11	0.0002	0.03	0.07	0.0	—	—	—	—	—	—	—	
<i>Ulmus</i>	11.43 ± 0.32	1.407	5.37	0.0252	3.63	4.5	0.0	—	—	—	—	—	—	—	
Total	11.94 ± 0.10	26.205	100.00	0.6945	100.00	100.00	100.0	0.2	18.47 ± 1.39*	0.065	0.248	0.0021	0.296	0.272	

^aThe extent of study area and number of available stems for dataset MTs is given in Tables 1 and 2, respectively.

^bThe number of affected stems from suitable genera in dataset MTs that could be assessed was 44.

^cThe numbers of available and affected stems for each genus and those identified to species are given in supplementary Table S5¹.

^dAn asterisk (*) indicates this value is significantly different from mean D_{130} of unaffected stems of the same genus or suitability category (shown in supplementary Table S3¹), based on a Kruskal-Wallis test with a significance cut-off of $p = 0.05$.

^eThere was no stem of the genus *Albizia*.

Table 6. Density, basal area and mean diameter at 130 cm above ground (D_{130}) of main stems of *Acer* spp. available to and affected by *Anoplophora glabripennis* in the Toronto–Vaughan study area (dataset TVCs) together with their respective relative density (RD), relative basal area (RBA), and importance value (IV).

<i>Acer</i> species	Available stems						Affected stems								
	D_{130} (mean ± SE)	Density ^a (stems/ha)	RD (%)	BA (m ² /ha)	RBA (%)	IV	Affected (%) ^b	% of <i>Acer</i> sp. affected	D_{130} (mean ± SE) ^d	Density (stems/ha)	RD (%)	BA (m ² /ha)	RBA (%)	IV	
<i>A. campestre</i>	13.64±1.71	0.016	0.03	0.0003	0.04	0.04	0.2	3.1	25.50±1.39	<0.001	0.001	<0.0001	<0.01	<0.01	
<i>A. circinatum</i>	1.00±1.95	0.019	0.04	<0.0001	<0.01	0.02	0.0	—	—	—	—	—	—	—	
<i>A. ginnala</i>	4.31±1.09	0.816	1.74	0.0025	0.29	1.02	1.4	0.5	7.89±0.70*	0.004	0.009	<0.0001	<0.01	0.01	
<i>A. glabrum</i>	1.00±0.00	<0.001	<0.01	<0.0001	<0.01	<0.01	0.0	—	—	—	—	—	—	—	
<i>A. griseum</i>	12.40±1.63	0.010	0.02	0.0002	0.02	0.02	0.0	—	—	—	—	—	—	—	
<i>A. negundo</i>	7.86±0.05	13.201	28.22	0.1328	15.68	21.95	15.0	0.4	12.55±0.69*	0.047	0.101	0.0008	0.09	0.10	
<i>A. nigrum</i>	15.26±0.56	0.268	0.57	0.0085	1.01	0.79	0.2	0.2	9.80±0.00	<0.001	0.001	<0.0001	<0.01	<0.01	
<i>A. palmatum</i>	4.44±0.11	0.479	1.02	0.0012	0.14	0.58	0.0	—	—	—	—	—	—	—	
<i>A. pensylvanicum</i>	2.44±1.87	0.006	0.01	<0.0001	<0.01	0.01	0.0	—	—	—	—	—	—	—	
<i>A. pictum</i>	1.64±0.14	0.100	0.21	0.0001	0.01	0.11	0.0	—	—	—	—	—	—	—	
<i>A. platanoides</i>	13.59±0.11	6.198	13.25	0.1678	19.82	16.53	58.6	3.0	21.08±0.49*	0.186	0.398	0.0078	0.92	0.66	
<i>A. pseudoplatanus</i>	11.39±2.86	0.009	0.02	0.0002	0.02	0.02	0.0	—	—	—	—	—	—	—	
<i>A. rubrum</i>	15.91±0.55	0.363	0.78	0.0137	1.61	1.19	2.6	2.3	21.88±2.65*	0.008	0.018	0.0004	0.05	0.03	
<i>A. saccharinum</i>	25.53±0.53	0.758	1.62	0.0646	7.63	4.62	5.3	2.2	29.65±3.60	0.017	0.036	0.0018	0.21	0.12	
<i>A. saccharum</i>	15.56±0.20	2.462	5.26	0.0847	10.00	7.63	7.2	0.9	28.59±2.08*	0.023	0.049	0.0018	0.21	0.13	
<i>Acer</i> sp.	10.69±0.17	3.240	6.93	0.0769	9.08	8.00	0.0	—	—	—	—	—	—	—	
<i>A. spicatum</i>	11.00±0.00	<0.001	<0.01	<0.0001	<0.01	<0.01	0.0	—	—	—	—	—	—	—	
<i>A. × freemanii</i>	19.67±1.74	0.031	0.07	0.0014	0.17	0.12	0.0	—	—	—	—	—	—	—	
Total	10.62±0.05	27.978	59.80	0.5549	65.52	62.66	90.4	1.0	20.58±0.48*	0.287	0.613	0.0126	1.49	1.05	

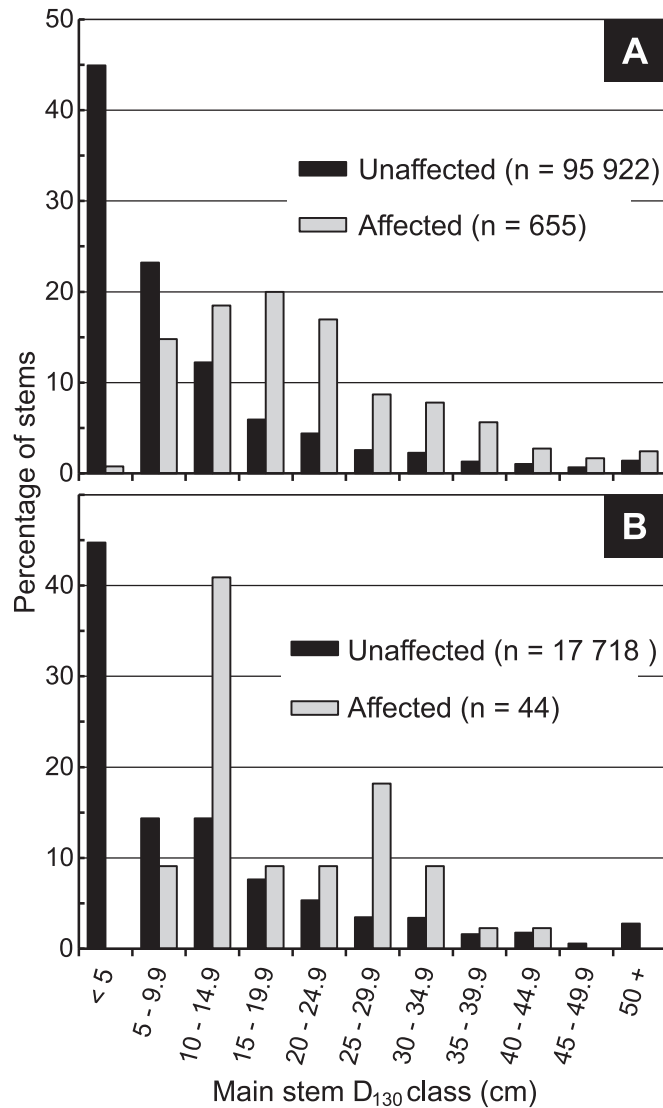
^aThe extent of study area and number of available stems for dataset TVCs is given in Tables 1 and 2, respectively.

^bThe numbers of affected stems from suitable genera and of affected *Acer* spp. that could be assessed in dataset TVCs were 655 and 592, respectively.

^cThe numbers of available and affected stems for other species are given in supplementary Table S4¹.

^dAn asterisk (*) indicates this value is significantly different from mean D_{130} of unaffected stems of the same species or suitability category (shown in supplementary Table S3¹), based on a Kruskal–Wallis test with a significance cut-off of $p = 0.05$.

Fig. 3. Percentage of *Anoplophora glabripennis* affected and unaffected stems of suitable genera in each arbitrary class of stem diameter at 130 cm above ground (D_{130}) in the Toronto–Vaughan (A; dataset TVs) and Mississauga–Toronto (B; dataset MTs) study areas. Note: Suitable genera in each outbreak are listed in Tables 4 and 5.



1% for *Acer*. A chi-squared analysis indicated that suitable genera were not selected in accordance with their availability ($\chi^2 = 264.8$, $p < 0.0001$). Specifically, *Acer* ($\chi^2 = 102.4$, $p < 0.0001$) was selected far more than expected by chance alone, whereas *Salix* ($\chi^2 = 68.2$, $p < 0.0001$), *Ulmus* ($\chi^2 = 67.5$, $p < 0.0001$), and *Populus* ($\chi^2 = 16.4$, $p < 0.0001$) were selected less than expected.

Selection also varied among stems identified to species (Table 6). Within the genus *Acer*, species were not selected according to availability ($\chi^2 = 584.6$, $p < 0.0001$); *Acer platanoides* ($\chi^2 = 374.5$, $p < 0.0001$), *Acer saccharinum* ($\chi^2 = 15.7$, $p < 0.0001$), and *Acer rubrum* ($\chi^2 = 7.9$, $p = 0.005$) were selected more than expected, whereas *Acer negundo* ($\chi^2 = 150.3$, $p < 0.0001$) and *Acer palmatum* ($\chi^2 = 11.5$, $p = 0.0007$) were selected less than expected. We could not identify with certainty most of the *Salix* spp. stems that were affected (supplementary Table S4¹).

Importance

The density of affected stems was 0.32 suitable stems/ha. *Acer* was the genus with the highest density (0.29 stems/ha) followed in

decreasing order by *Salix*, *Populus*, *Betula*, and *Ulmus* (Table 4). The RD of affected stems from these genera followed the same order.

Affected *Acer platanoides* stems had the highest RD (0.40%) of all species identified within the study area. This RD was much higher than that associated with affected stems of *A. negundo*, *A. saccharum*, and *A. saccharinum* (Table 6). These four species all had higher RD of affected stems than that of *Salix* not identified to species. All remaining species had affected stems that accounted for RD of 0.03% or lower (supplementary Table S4¹).

At the time this outbreak was declared eradicated, affected stems had a BA of 0.0162 m²/ha. *Acer* had the highest RBA (2%) followed by *Salix*, *Populus*, *Ulmus*, and *Betula* (Table 4). Affected stems of *Acer platanoides*, *A. saccharinum*, and *A. saccharum* represented 0.9%, 0.2%, and 0.2% of the BA, respectively (Table 6). All other affected species had an RBA of <0.1% (supplementary Table S4¹). The IV of affected genera (Table 4) or of *Acer* species (Table 6) followed the same ranking as those of the RBA. Again, that of *Salix* spp. came after *A. saccharum*.

Size

The total tree height of affected stems in this study area varied between 1.7 and 27.6 m, averaging 8.8 m, whereas D_{130} varied between 3.9 cm (*Acer negundo*) and 125.6 cm (*Populus deltoides* W. Bartram ex Marshall), averaging 21.46 cm (Table 4). Kruskal–Wallis tests indicated that, for all suitable genera other than *Betula*, the average D_{130} of affected stems was significantly greater than that of unaffected stems (Table 4; supplementary Table S4¹). Concomitant with this difference in mean diameter was a different frequency distribution among class sizes. There were many more small-unaffected stems than those affected (Fig. 3A); about 45% of unaffected stems from the five suitable affected genera were <5 cm in diameter compared to <1% for affected stems.

A chi-squared analysis confirmed that D_{130} classes of suitable trees were not attacked in accordance with their availability ($\chi^2 = 1103.8$, $p < 0.0001$). Specifically, the <5 cm ($\chi^2 = 285.5$, $p < 0.0001$) and the 5–10 cm ($\chi^2 = 18.5$, $p < 0.0001$) size classes were selected less than expected by chance alone. All size classes ≥ 10 cm were selected significantly more than expected. Furthermore, a Cochran–Armitage trend test, which is appropriate for ordinal data such as the D_{130} classes used here, indicated that there was a significant overall increase in attack rate as diameter increased ($T = 28.9$, $p < 0.0001$); however, closer examination of the percentage of stems attacked in each size class indicated that preference for larger stems may plateau — or even drop off — at D_{130} classes ≥ 40 cm (Fig. 4A).

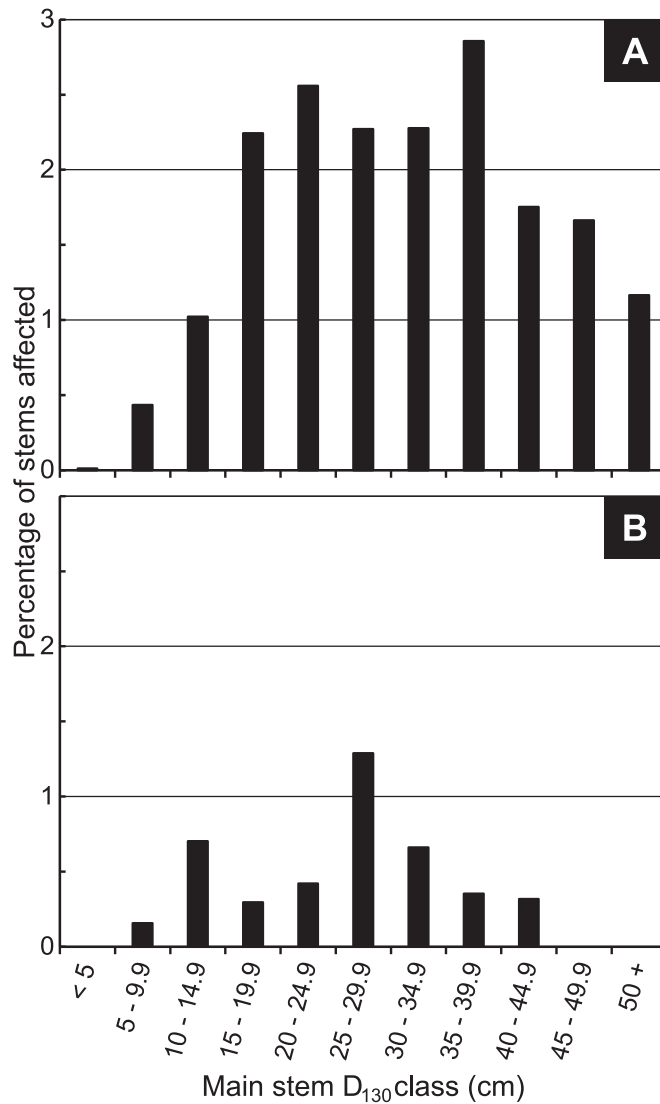
Size–genus interaction. For this analysis, we employed a 2-way χ^2 test. Our datasets contained a large number of potential size–genus combinations; to reduce the number of contingency table cells with low counts, we included only the five affected suitable genera and five D_{130} classes (<10, 10–20, 20–30, 30–40, and >40 cm) in the analysis. The results supported the main findings from the single variable analyses — namely a preference for *Acer* and an avoidance of trees with $D_{130} < 10$ cm (Table 7). However, other details emerged, including a preference for *Populus* in the 20–30 cm D_{130} class, a preference for *Salix* at $D_{130} > 40$ cm, and a reduced, but statistically significant, preference for *Acer* in the largest size class.

We further examined potential interactions by generating separate D_{130} histograms for *Acer* versus all other genera combined (Figs. 5A and 5C). These figures showed similar size selection patterns by *A. glabripennis* for both groups, though selection of stems >40 cm appeared somewhat stronger in the non-*Acer* genera than in *Acer*.

Use — signs of injury

Oviposition pits were the most common signs we observed when examining stems for evidence of *A. glabripennis* injury. Of the 655 affected stems we retained, 644 were suitable for the analyses on signs of oviposition and emergence.

Fig. 4. Percentage of stems from suitable genera ($n = 96753$) that were affected by *Anoplophora glabripennis* in each arbitrary class of stem diameter at 130 cm above ground (D_{130}) in the Toronto–Vaughan (A; dataset TVCs) and Mississauga–Toronto (B; dataset MTs) study areas. Note: Suitable genera affected are listed in Tables 4 and 5.



Signs of oviposition. We observed oviposition pits on 97% of the 644 affected stems from suitable genera. Overall, about 1% of all suitable stems present in the study area were affected (Table 4). Over 90% of affected stems with pits were of the genus *Acer* and 60% were *A. platanoides* (Table 8). The D_{130} of stems with pits ranged between 3.9 cm (*Acer negundo*) and 125.6 cm (*Populus deltoides*). The percentage of all affected stems with pits was lowest (1%) on stems with a $D_{130} < 5$ cm and highest (20%) on stems of 15–20 cm (Fig. 6A). Most stems with pits (85%) had a $D_{130} \geq 10$ cm. All D_{130} classes between 5 and 25 cm contained between 14% and 20% of the stems with pits. The percentage of affected stems with pits in all other classes was <9%.

Based on dataset TVCs, we inventoried 47 763 pits in this study area (Table 8). The relative abundance of pits varied among affected tree genera and species, and D_{130} classes. We found 96% of these pits on *Acer* spp. and most (62%) were on *Acer platanoides*. Chi-squared tests confirmed that pits were not distributed in accordance with genus availability ($\chi^2 = 26627$, $p < 0.0001$).

Table 7. Pearson chi-squared (χ^2) statistics associated with various combinations of suitable tree genera affected by *Anoplophora glabripennis* and classes of diameter at 130 cm above ground (D_{130}) within the Toronto–Vaughan (ON) study area (dataset TVCs).

Study area genus	D_{130} class (cm)				
	<10	10–20	20–30	30–40	>40
Toronto–Vaughan (2003–2013)					
<i>Acer</i>					
Stems available	36 762	11 800	4662	2465	2063
Stems selected	97	231	151	80	33
χ^2	<u>–95.3</u>	<u>278.7</u>	<u>443.5</u>	<u>235.7</u>	<u>25.2</u>
<i>Betula</i>					
Stems available	1075	1011	338	90	31
Stems selected	4	7	1	0	0
χ^2	–1.5	0	–0.8	–0.6	–0.2
<i>Populus</i>					
Stems available	5304	969	281	177	153
Stems selected	0	5	8	3	3
χ^2	<u>–36.4</u>	–0.4	<u>19.2</u>	2.6	3.6
<i>Salix</i>					
Stems available	14 593	1562	675	307	424
Stems selected	1	8	7	5	8
χ^2	<u>–98</u>	–0.7	1.2	4	<u>8.9</u>
<i>Ulmus</i>					
Stems available	7073	2130	807	452	363
Stems selected	0	1	1	0	1
χ^2	<u>–48.5</u>	<u>–12.7</u>	–3.7	–3.1	–0.9

Note: Positive χ^2 values indicate preference; negative values indicate avoidance. Bold underlined values are statistically significant at $p = 0.05$ with a Simes correction for multiple comparisons.

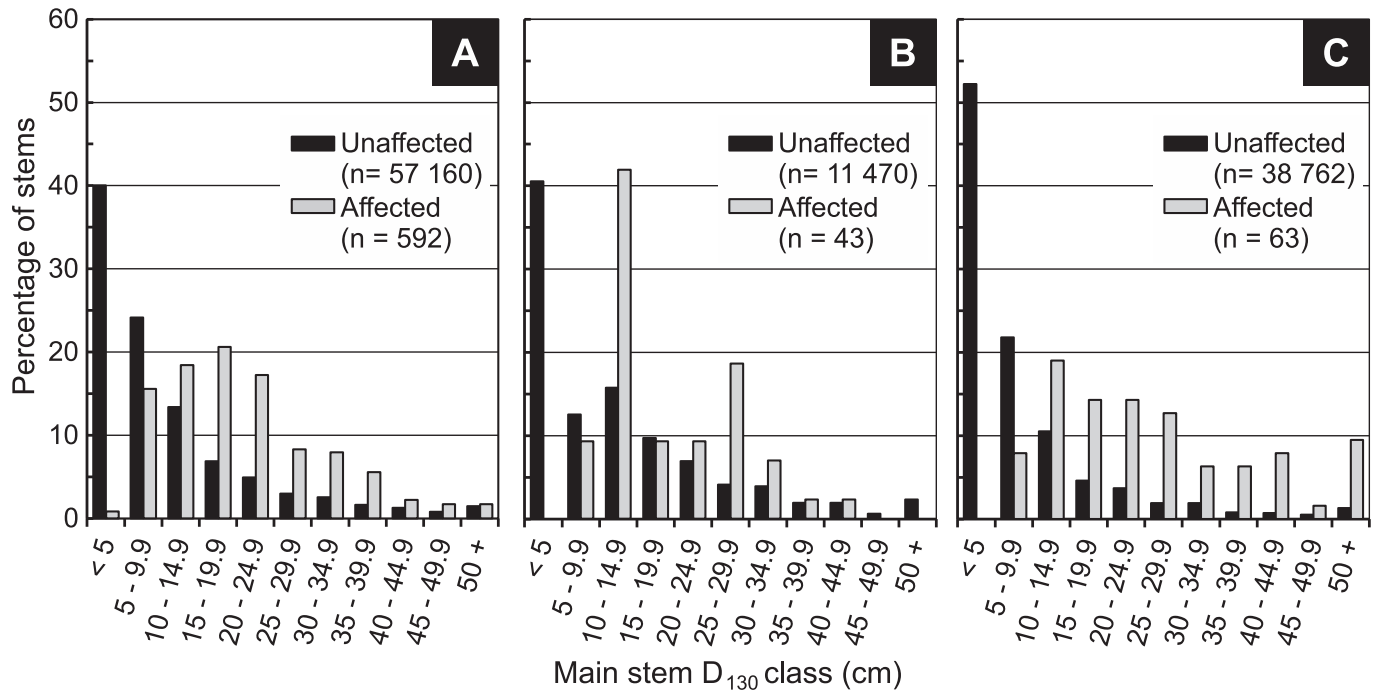
Specifically, the genus *Acer* had more pits than expected ($\chi^2 = 10673$, $p < 0.0001$), whereas all remaining genera had less pits than expected by chance alone. For species within the genus *Acer*, pits were also not distributed according to availability ($\chi^2 = 91513$, $p < 0.0001$), with *A. saccharinum* ($\chi^2 = 41679$, $p < 0.0001$), *A. platanoides* ($\chi^2 = 27632$, $p < 0.0001$), and *A. rubrum* ($\chi^2 = 839$, $p < 0.0001$) having more pits than expected by chance alone.

More than 95% of pits were on stems with a $D_{130} \geq 10$ cm and about 60% of pits were on stems with a D_{130} ranging between 10 and 25 cm (Fig. 6A). The highest percentage of pits (25%) was on stems with a D_{130} of 20–24.9 cm. The percentages of pits found on stems <5 cm and >40 cm were around or below 1%. Oviposition pits were not distributed in accordance with availability of the various D_{130} classes ($\chi^2 = 186536$, $p < 0.0001$). Specifically, mid-sized D_{130} classes ranging from 15–40 cm were selected far more than expected ($\chi^2 = 158288$, $p < 0.0001$), small D_{130} classes (<10 cm) were selected far less than expected ($\chi^2 = 28188$, $p < 0.0001$), whereas the remaining classes were selected approximately as available.

The overall number of pits per affected stem with pits averaged 76.7 and varied among genera (e.g., between 12.9 for *Populus* spp. and 81.5 for *Acer* spp.) and *Acer* species (e.g., between 1 for *A. nigrum* and 275 for *A. saccharinum*) (Table 8). Though substantial, differences in pits per stem were not statistically significant across genera ($H = 7.62$, $p = 0.11$) due to large variance associated with pit numbers (e.g., number of pits on *Acer* stems ranged from 1 to 3829) and small sample sizes for some genera (e.g., $n = 3$ for *Ulmus*). However, there were significant differences between species in the genus *Acer* ($H = 31.29$, $p > 0.0001$), with *A. saccharinum* and *A. negundo* both having significantly more pits than *A. saccharum*. Pits per stem also varied significantly between D_{130} classes ($H = 25.61$, $p = 0.004$), ranging between 4.3 cm on stems <5 cm in diameter and 203.2 cm on stems 35–40 cm.

Signs of emergence. We observed emergence holes on 26% of the 644 affected stems assessed (Table 8). The genus with the most affected stems with holes was *Acer* (91%); 57% of all stems with holes

Fig. 5. Percentage of *Anoplophora glabripennis* affected and unaffected stems of *Acer* species (A, B) and of genera other than *Acer* (C) among arbitrary classes of stem diameter at 130 cm above ground (D_{130}) in the Toronto–Vaughan (A and C; dataset TVCs) and Mississauga–Toronto (B; dataset MTs) study areas.



were *A. platanoides*. The D_{130} of stems with holes ranged between 5.3 cm on *Betula papyrifera* and 113 cm on *Salix* sp. We found stems with holes in all classes of D_{130} except in that of <5 cm (Fig. 7A). The class with the highest percentage of stems with holes was 15–20 cm with 23% of all stems. More than 90% of the stems with a hole had a D_{130} >10 cm. Each of the three classes with a D_{130} between 10 and 25 cm represented >19% of the affected stems with holes.

We recorded the presence of 1839 holes in this regulated area: 98% were on *Acer* spp. (Table 8). Most were on *A. platanoides* (61.6%) and *A. saccharinum* (25.1%). Emergence holes were not distributed according to genus availability ($\chi^2 = 1119$, $p < 0.0001$). The genus *Acer* had significantly more holes than expected ($\chi^2 = 449$, $p < 0.0001$) whereas all other genera had fewer than expected. Within the genus *Acer*, *A. saccharinum* ($\chi^2 = 2997$, $p < 0.0001$), *A. platanoides* ($\chi^2 = 1026$, $p < 0.0001$), and *A. rubrum* ($\chi^2 = 28$, $p < 0.0001$) had significantly more holes than expected based on their availability, whereas *A. negundo* ($\chi^2 = 787$, $p < 0.0001$), *A. saccharum* ($\chi^2 = 83$, $p < 0.0001$), *A. ginnala* ($\chi^2 = 46$, $p < 0.0001$), *A. palmatum* ($\chi^2 = 35$, $p < 0.0001$), and *A. nigrum* ($\chi^2 = 20$, $p < 0.0001$) had fewer holes than expected.

We found >95% of holes on stems with a $D_{130} \geq 10$ cm (Fig. 7A). We found the greatest percentage of holes, 28%, on stems with a D_{130} of 20–25 cm. Four of the six classes between 5 and 40 cm each contained between 13%–28% of the holes. Classes with a $D_{130} < 10$ cm or ≥ 40 cm, each contained <5% of the holes. Emergence holes were not distributed across D_{130} classes in accordance with their availability ($\chi^2 = 8353$, $p < 0.0001$). Similar to pits, significantly more holes than expected were found on stems with D_{130} ranging between 15 and 40 cm ($\chi^2 = 14\,358$, $p < 0.0001$) and significantly fewer holes than expected were associated with smaller (i.e., $D_{130} < 10$ cm) stems ($\chi^2 = 14\,358$, $p < 0.0001$).

The average number of emergence holes per affected stem with holes discovered by the end of this outbreak was 11.0 (Table 8): it was lowest on *A. ginnala* (3.5) and highest on *A. saccharinum* (28.8). The number of holes per stem did not vary significantly across genera ($H = 8.38$, $p = 0.04$), with the genus *Acer* having significantly

more holes than *Betula*. Emergence hole abundance also varied significantly across species within the genus *Acer* ($H = 13.98$, $p = 0.02$); specifically, *A. saccharinum* had significantly more holes than *A. negundo*. The average number of holes per stem with holes varied between 4.8 on stems in the 5–10 cm D_{130} class and 20.8 on stems in the 35–40 cm class; however, this range did not vary significantly between D_{130} classes ($H = 6.33$, $p = 0.71$).

Use — location of signs on main stem

The height above ground of the lowest and highest signs of injury by *A. glabripennis*, whether oviposition, emergence or other type, was available for only 608 of the 644 affected stems with a D_{130} . The height at which the lowest sign of injury by *A. glabripennis* occurred varied between 0.0 m (ground level) and 18.9 m, averaging 2.9 ± 0.1 m. About 65% of all affected stems had their lowest sign of injury within 3 m of the ground and 85% within 5 m (Fig. 8A). We noted a similar pattern when we considered only stems with a $D_{130} \geq 10$ cm. We chose this threshold because these stems represented about 85% of those affected (Figs. 3A and 5A), and where we found about 95% of the pits (Fig. 6A) and holes (Fig. 7A). In addition, stems with a $D_{130} < 10$ cm were still relatively easy to examine completely from the ground. When we expressed the location of a sign as a percentage of tree height, we found that about 90% of the time, the lowest sign was located in the bottom half of the tree (Fig. 8B). Stems with $D_{130} \geq 10$ cm followed the same trend. We are focusing here on the lowest sign of attack as this has the greatest implication for survey methodology; however, the height of the highest sign of injury varied between 0 and 21.8 m, averaging 5.3 m.

The distance between lowest and highest sign of injury varied between 0 and 15.4 m but averaged 2.5 m. There was a positive relationship between both tree height and main stem D_{130} and heights of the lowest and highest signs of injury (Figs. 9A and 9B). Tree height explained 78% of the variation in height of the highest (black diamonds), and 63% of that of the lowest sign of injury (open circles), whereas stem D_{130} explained 52% and 30% of the variation in height recorded for highest (black diamonds) and lowest (open circles) signs of injury, respectively.

Table 8. Relative abundance of stems^a with signs of adult oviposition (pits) and emergence (holes) characteristic of *Anoplophora glabripennis* and relative abundance of these signs per tree species within affected areas of two outbreaks found in Ontario, Canada.

Study area species	Stems with pits (%)	Total pits (%)	Pits/stem (mean ± SE)	Stems with holes (%)	Total holes (%)	Holes/stem (mean ± SE)
Toronto–Vaughan (2003–2013)						
<i>Acer campestre</i>	0.2	0.01	7.0±0.0	0.0	—	—
<i>Acer ginnala</i>	1.4	0.57	30.3±10.5	1.2	0.4	3.5±1.5
<i>Acer negundo</i>	13.6	10.20	57.3±7.7	13.8	5.0	4.0±1.0
<i>Acer nigrum</i>	0.2	0.00	1.0±0.0	0.0	—	—
<i>Acer platanoides</i>	60.0	61.51	78.6±13.6	56.9	61.6	11.9±3.3
<i>Acer rubrum</i>	2.6	2.99	89.3±41.3	3.0	2.9	10.6±5.3
<i>Acer saccharinum</i>	5.3	19.00	275.0±79.6	9.6	25.1	28.8±9.4
<i>Acer saccharum</i>	7.4	2.06	21.4±5.8	6.6	3.1	21.4±5.8
Subtotal Acer	90.7	96.35	81.5±10.5	91.0	98.0	11.9±2.4
<i>Betula papyrifera</i>	1.4	0.30	16.0±9.5	2.4	0.2	1.0
Subtotal Betula	1.4	0.30	16.0±9.5	2.4	0.2	1.0
<i>Populus deltoides</i>	1.6	0.23	11.0±3.6	0.6	0.1	1.0
<i>Populus tremuloides</i>	0.2	0.01	5.0±0.0	0.0	—	—
<i>Populus × canadensis</i>	1.0	0.22	17.3±4.8	0.0	—	—
Subtotal Populus	2.7	0.46	12.9±2.8	0.6	0.1	1.0
<i>Salix alba</i>	0.3	0.08	19.5±5.5	1.2	0.3	2.5±0.5
<i>Salix</i> sp.	4.3	2.71	47.9 ± 4.8	4.8	1.4	3.3±0.8
Subtotal Salix	4.7	2.79	45.9±11.4	6.0	1.7	3.1±0.7
<i>Ulmus americana</i>	0.3	0.09	21.5±20.5	0.0	—	—
<i>Ulmus rubra</i>	0.2	0.01	3.0±0.0	0.0	—	—
Subtotal Ulmus	0.5	0.10	15.3±13.3	0.0	—	—
Total (n)^a	623	47 763		167	1839	
Mississauga–Toronto (2013–2020)						
<i>Acer negundo</i>	73.8	99.15	108.5±53.4	68.8	99.1	92.3±48.4
<i>Acer platanoides</i>	23.8	0.77	2.6 ± 0.8	31.3	0.9	1.8±0.4
Subtotal Acer	97.6	99.91	82.7±40.9	100.0	100.0	64.0±34.5
<i>Salix</i> sp.	2.4	0.09	3.0±0.0	0.0	—	—
Subtotal Salix	2.4	0.09	3.0±0.0	0.0	—	—
Total (n)^a	42	3392		16	1024	

^aTotal number of affected stems adequate for assessment in Toronto–Vaughan and Mississauga–Toronto study areas were 644 and 43, respectively.

There were exponential (lin-log) relationships between the density of pits and the height of signs of injury. The height of the lowest and highest signs, expressed as a percentage of tree height, decreased (i.e., closer to the ground) and increased as oviposition pit density increased, respectively (Fig. 10). Pit abundance explained about 32% of the variation in height of the lowest sign of injury. The percentage of the variation in height of the lowest signs of injury explained by pit density increased slightly if we considered only stems with a $D_{130} \geq 10$ cm ($R^2 = 0.38$; not shown) or just stems of the genus *Acer* ($R^2 = 0.42$; not shown).

Mississauga–Toronto study area

We based our analyses of plant selection by *A. glabripennis* in this regulated area on 44 of the 50 affected stems (Table 5). We excluded six stems with missing D_{130} values.

Richness

In this study area, *A. glabripennis* selected stems from two of the 11 suitable host genera (two out of eight families) available in Canada in 2013 (Table 5). We identified only two of the three suitable species affected (supplementary Table S5¹).

All but one (98%) of the affected stems were of the genus *Acer* (Table 5). We found evidence of acceptance on only two of at least eight species of *Acer* identified in this study area (Table 8). *Acer negundo* and *A. platanoides* represented 73% and 25% of affected stems treated in this area, respectively (supplementary Table S5¹).

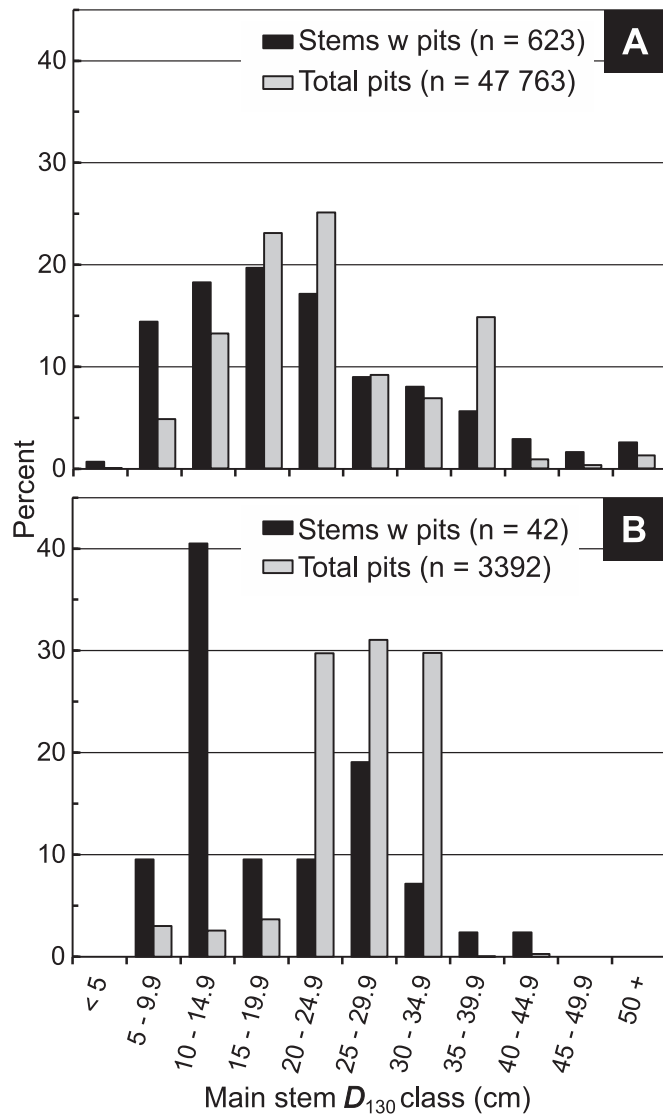
At the time tree removal was completed, *A. glabripennis* had selected about 0.2% of all stems available in the study area, and 0.4% of *Acer* stems available (Table 5). A chi-squared analysis indicated that suitable genera in this study area were not selected in accordance with their availability ($\chi^2 = 21.0$, $p = 0.0222$). Specifically, *Acer* was selected more than expected by chance alone ($\chi^2 = 7.4$, $p = 0.0067$). *Populus* ($\chi^2 = 5.5$, $p = 0.0191$) and *Salix* ($\chi^2 = 5.2$, $p = 0.0232$) were selected less than expected, though these results were of borderline statistical significance when the Simes correction for multiple comparisons was applied. Selections of the remaining genera (e.g., *Betula* and *Ulmus*) were lower than expected, but the differences were not statistically significant. Within the genus *Acer*, and of those identified to species, species appeared to be selected according to availability ($\chi^2 = 9.8$, $p = 0.2805$).

Importance

The density of suitable affected stems was 0.07 stems/ha (Table 5). The genus *Acer* had the highest density at 0.06 stems/ha, and RD at 0.2%. *Acer negundo* had the highest density (0.05 stems/ha) and RD (0.2%) of affected stems (supplementary Table S5¹).

The BA of affected stems was 0.0021 m²/ha. Affected *Acer* spp. had a RBA of 0.3% (Table 5). The ranking of affected *Acer* spp. stems based on RD was the inverse of that based on RBA where *A. platanoides* and *A. negundo* represented 0.2% and 0.1% of the BA, respectively (supplementary Table S5¹). Overall, *A. negundo* had the highest IV.

Fig. 6. Percentages of *Anoplophora glabripennis* affected stems with oviposition pits and of pits in each arbitrary class of stem diameter at 130 cm above ground (D_{130}) in the Toronto–Vaughan (A; dataset TVCs) and Mississauga–Toronto (B; dataset MTs) study areas.

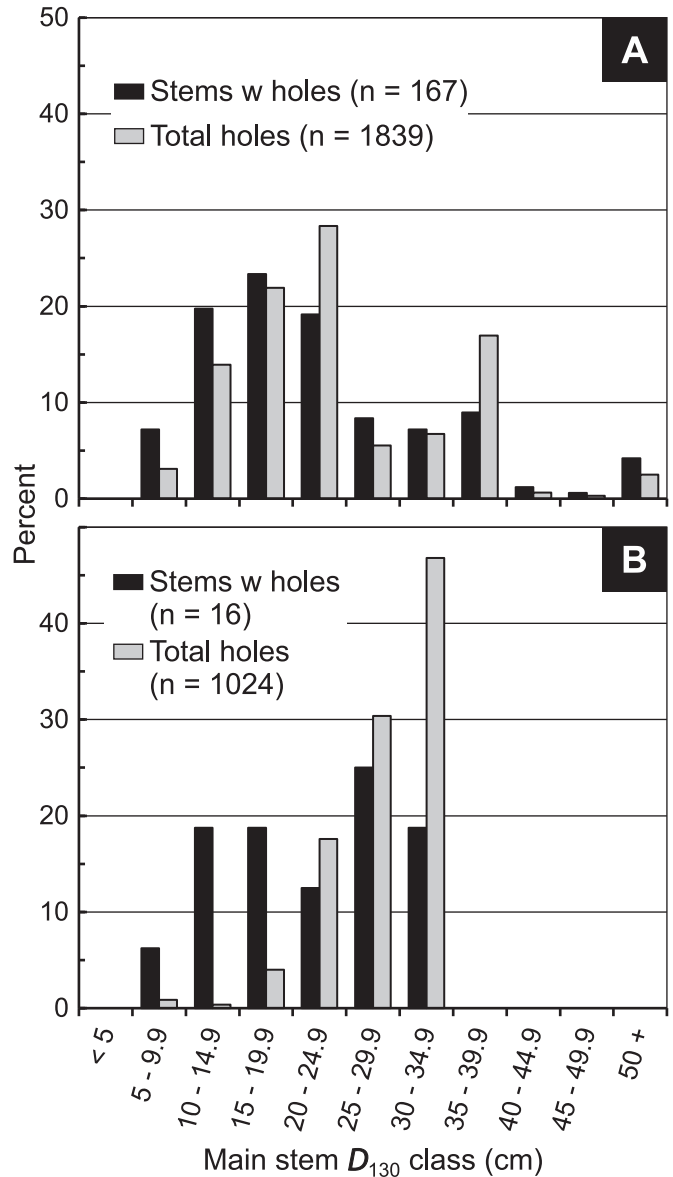


Size

Overall, D_{130} of affected stems in this study area varied between 6.0 and 42.0 cm, averaging 18.5 cm (Table 5). This average D_{130} was greater than that of unaffected stems, 11.9 cm (supplementary Table S5¹). Concomitant with this difference in size is a different frequency distribution of stem diameters (Figs. 3B and 5B). Over 40% of unaffected stems had a D_{130} < 5 cm, compared to 0% for affected stems.

A chi-squared analysis confirmed that D_{130} classes of suitable trees in this outbreak’s study area were not attacked in accordance with their availability ($\chi^2 = 76.3, p < 0.0001$). Specifically, the < 5.0 cm ($\chi^2 = 19.6, p < 0.0001$) D_{130} class was selected significantly less than expected by chance alone. Stems with a D_{130} in class 25–30 cm ($\chi^2 = 27.1, p < 0.0001$) and 10–15 cm ($\chi^2 = 21.3, p < 0.0001$) were selected significantly more than expected, whereas those in the remaining size classes were selected approximately in proportion to availability.

Fig. 7. Percentages of *Anoplophora glabripennis* affected stems with emergence holes and of holes in each arbitrary class of stem diameter at 130 cm above ground (D_{130}) in the Toronto–Vaughan (A; dataset TVCs) and Mississauga–Toronto (B; dataset MTs) study areas.



A Cochran–Armitage trend test indicated that there was a significant overall increase in attack rate as D_{130} increased ($T = 4.0, p < 0.0001$). However, a closer examination of the percentage of stems selected in each size class indicated that preference appeared to peak in the 25–30 cm size class and dropped off slightly after that. The percentage of stems affected varied between 0% and 1% among D_{130} classes with the highest probability of injury recorded on stems with a D_{130} of 25–30 cm (Fig. 4B).

Size–genus interaction. Because there was only one stem other than *Acer* selected in this study area, we could not explore a meaningful size–genus interaction.

Use — signs of injury

Of the 44 affected stems from this study area, we retained 43 for analyses (Table 8), discarding one stem because we had incomplete assessment data. The beetle extensively damaged three

Fig. 8. Percentage of all *Anoplophora glabripennis* affected stems (all stems vs. those with a $D_{130} \geq 10$ cm) among arbitrary classes of height of the lowest sign of injury expressed as metres above ground level (A) or as a percentage of tree height (B) in the Toronto–Vaughan study area (dataset TVCs).

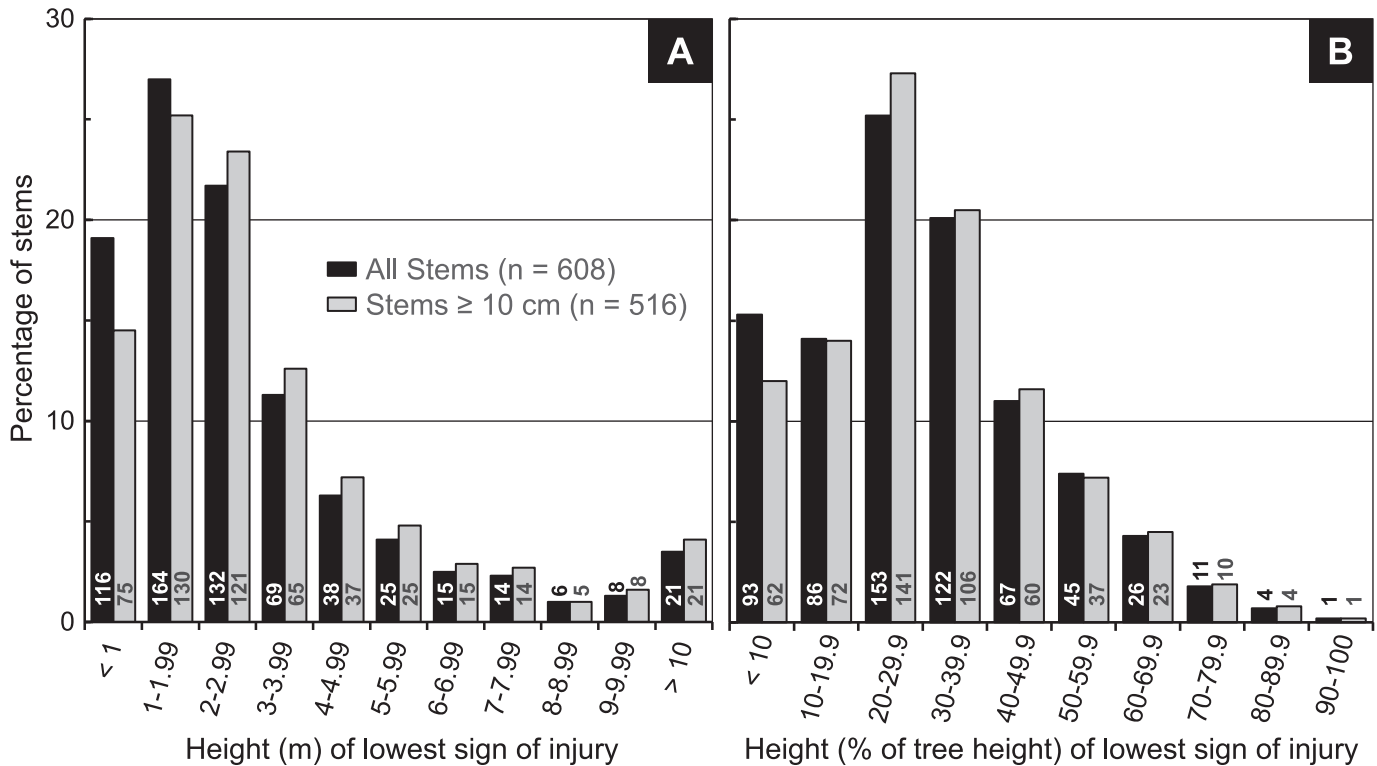
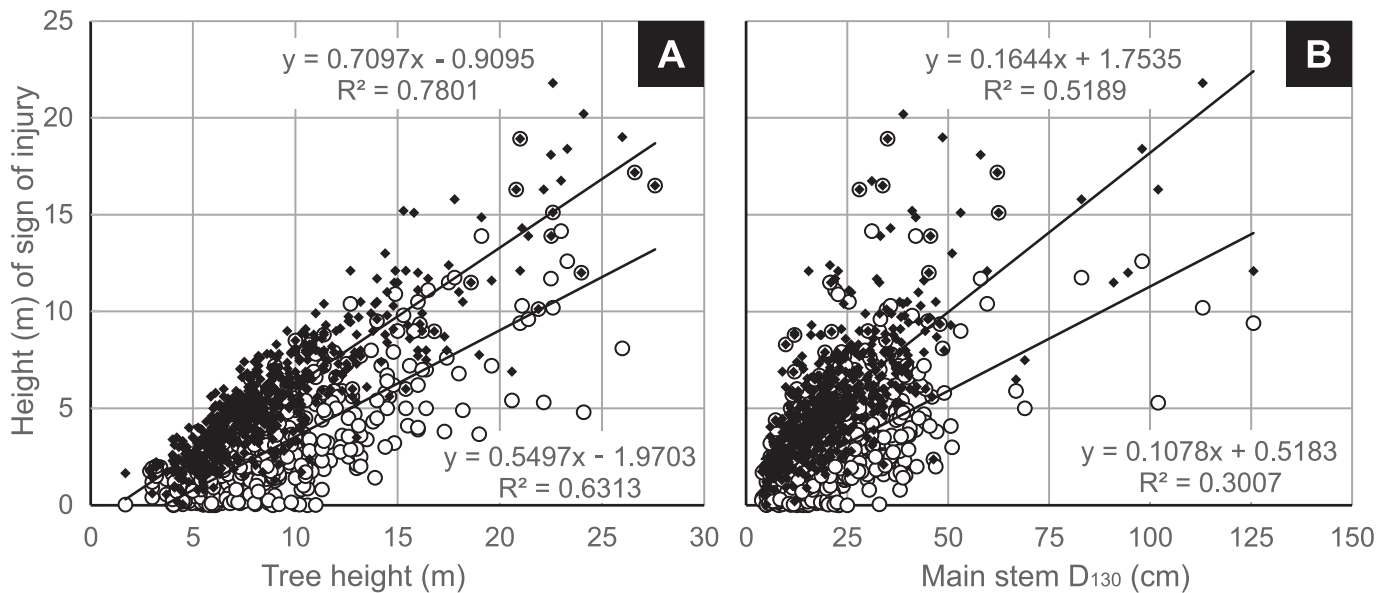


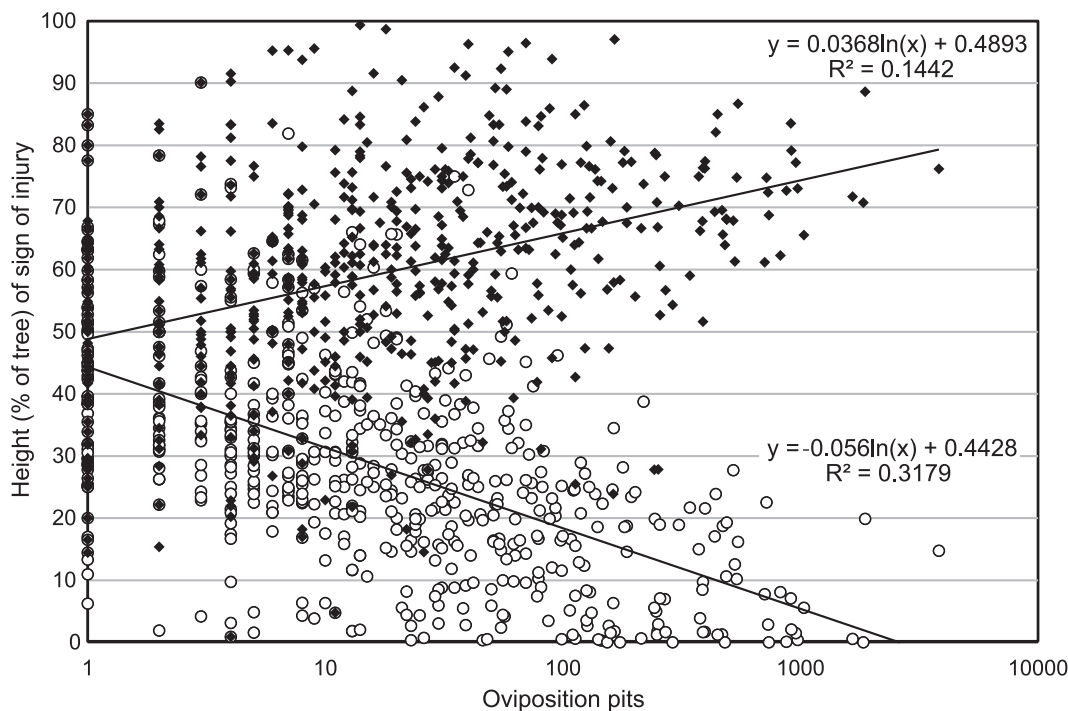
Fig. 9. Relationships between heights of the lowest (\circ) and highest (\blacklozenge) signs of injury on stems affected by *Anoplophora glabripennis* and tree height (A) and diameter at 130 cm above ground (D_{130}) (B) in the Toronto–Vaughan study area (dataset TVCs; $n = 608$).



stems to the point where there were several patches of missing bark, making it impossible to obtain an accurate number of oviposition pits. We stopped counting the number of pits after reaching 1000 on each of these three stems. We used that conservative estimate as the number of pits on each one.

Signs of oviposition. We observed oviposition pits on 98% of the 43 affected stems (Table 8). The genus with most affected stems was *Acer* (98%); most (74%) of the stems were *A. negundo*. The minimum and maximum D_{130} of stems with pits were 6 cm (*A. negundo*) and 42 cm (*A. platanoides*), respectively. The D_{130} class with the greatest

Fig. 10. Semi-log plot of the relationships between height of *Anoplophora glabripennis* lowest and highest signs of injury (LSI (○) and HSI (◆), respectively) as a percentage of total tree height and the abundance/density of oviposition pits on affected stems ($n = 591$) in the Toronto–Vaughan study area (dataset TVCs).



percentage of stems with pits (40%) was 10–15 cm (Fig. 6B). Only one class of D_{130} , 25–30 cm, had between 10% and 20% of the stems with pits; the remaining diameter classes had <9%.

We recorded almost 3400 oviposition pits on these 42 stems with pits (Table 8). The relative abundance of pits differed greatly among affected tree genera and species, and D_{130} classes. Indeed, we found >99% of these pits on *Acer* spp., most (99%) of which were on *A. negundo* (Table 8), and more than 90% were on stems with a D_{130} between 20 and 35 cm. Each of these three classes, 20–25, 25–30, and 30–35 cm, had about 30% of the pits (Fig. 6B). We found no pits on stems in classes <5 cm or ≥ 45 cm. Because of the overwhelming number of pits associated with a small number of genera, species, and size classes, we did not perform statistical analyses on these results.

The average number of pits per affected stem with pits was 80.8 (Table 8). This average number varied among genera: it was highest on *Acer* spp. and lowest on *Salix*. Pit density per stem on *A. negundo* stem was far greater than that on *A. platanoides*.

Signs of emergence. We observed emergence holes on 38% of the 42 affected stems (Table 8). The sole genus with stems with holes was *Acer* and 99% of the holes were on *A. negundo*. The D_{130} of stems with holes varied between 6 and 32 cm (both stems being *A. negundo*). The class with the highest proportion of affected stems with holes was 25–30 cm with 25% of all stems (Fig. 7B). Each of the five D_{130} classes between 10 and 35 cm contained between 10% and 20% of the affected stems with holes.

We recorded over 1000 emergence holes on 16 stems with holes (Table 8). We found >99% of the holes on stems with a $D_{130} \geq 10$ cm (Fig. 7B). We found holes almost exclusively on stems 20–35 cm. We did not find holes on affected stems with a $D_{130} < 5$ cm or ≥ 35 cm. Again, because emergence holes occurred nearly exclusively on mid-sized stems of *A. negundo*, we did not perform statistical analyses on this aspect of the study.

The average number of holes per affected stem with holes was 64.0 (Table 8). This average was highest on *A. negundo* at 92.3.

Discussion

Plant availability

There are few detailed inventories of broadleaf trees available to *A. glabripennis* for oviposition and development during outbreaks outside its native range. Previous studies include those of Haack et al. (2006) in Chicago (IL), Dodds and Orwig (2011) in Worcester (MA), and Straw et al. (2015a) in Paddock Wood, United Kingdom (UK). These studies exhibit important differences from ours with respect to composition and abundance of available broadleaf trees — presumably driven by factors such as geographical location, climate, and varying survey scales and methodologies. Furthermore, the studies have occurred in a variety of landscapes, including light industrial/suburban (current study; Fournier and Turgeon 2017), residential (Chicago; Haack et al. 2006), forest woodlots (Massachusetts; Dodds and Orwig 2011), and agricultural lands (Paddock Wood; Straw et al. 2015a). This wide variation across studies underlines the importance of examining *A. glabripennis* host selection from a range of locations and conditions. The current study contributes to this growing knowledge base. In the following sections, we discuss our findings in relation to this body of previous work.

Richness of families, genera (and sometime species) in our inventory of available plants appeared similar to that reported in Chicago (Haack et al. 2006), but much greater than that in Paddock Wood (Straw et al. 2015a), or in Worcester (Dodds and Orwig 2011). These differences among studies may be partly attributable to the size of the area covered by these assessments or, more specifically, to the number of plants included in these assessments. We based our assessment on about 170 000 trees, all within a 400 m radius of an affected tree in Toronto–Vaughan, whereas Haack et al. (2006) relied on about 540 000 trees included in the 2003 City of Chicago street tree inventory. Whether all species from this inventory were near affected stems is unknown. Dodds and Orwig (2011) determined tree richness in two areas of 40 and

6 ha, respectively, whereas Straw et al. (2015a) based their estimates on broadleaf plants within 100 m of affected plants, which is more closely related to our methodology.

In all studies (e.g., Haack et al. 2006; Dodds and Orwig 2011; Straw et al. 2015a), including ours, there was a wide range of stem diameters available to *A. glabripennis* within affected areas. There were, however, differences in stem diameters included in analyses. Ours included all stems reaching 130 cm above ground in all land uses except woodlots, where we examined plants of all diameters, but only included those with a $D_{130} \geq 10$ cm, which resulted in a slight underestimation of the abundance of small stems and overestimation of larger stems. Dodds and Orwig (2011) and Dodds et al. (2014) only studied trees with a diameter ≥ 7.5 cm whereas Straw et al. (2015a) focused on main stems with a $D_{130} \geq 5$ cm. In Ontario, the range in D_{130} differed greatly among tree species from the same genus and between genera of available trees, irrespective of their category of suitability, likely reflecting differences in growth form among genera.

We did not assess any indices of tree diversity in our study areas; however, Berland and Hopton (2016) tested the hypothesis that communities with higher taxonomic diversity of street trees would exhibit lower vulnerability to *A. glabripennis*. Based on street tree composition and the beetle's host preferences, they estimated that the beetle threatened 36% of the street trees and 47% of total basal area in communities studied, but did not observe a clear connection between taxonomic diversity and beetle vulnerability. Their results demonstrated that relatively high taxonomic diversity in street tree assemblages did not necessarily lead to reduced vulnerability to a polyphagous pest like *A. glabripennis*. Another study comparing the relative abundance of tree genera in 12 eastern North American cities — including three municipalities with *A. glabripennis* outbreaks (i.e., New York, Chicago, and Toronto) — reported that Toronto had the lowest percentage of trees at risk of *A. glabripennis* injury among the cities studied (Raup et al. 2006).

Plant selection

In Ontario, plant selection (presence of oviposition pits) and acceptance (presence of eggs or larvae) for oviposition by *A. glabripennis* was limited to a small number of available families (six of the 24), genera (seven out of 45), and species (16 out of 138, and possibly a few additional *Salix* spp.). These results are consistent with those of Haack et al. (2006), who reported signs of oviposition on only eight of the 20 families and 10 or 11 of the 39 genera available in Chicago; the number of affected species was unreported. Straw et al. (2015a) found a similarly limited selection of hosts in Paddock Wood (three families, five genera, and nine species) and reported that most outbreaks recorded in Europe had similarly low numbers.

The lists of families and genera suitable for complete development in Ontario were even more restricted; we found emergence holes and obtained emerging specimens from logs collected in the field and reared under controlled conditions on only four suitable genera from three families in Toronto–Vaughan, and on only one of the two genera affected in Mississauga–Toronto. Straw et al. (2015a) reported similar results in southern England, where *A. glabripennis* selected for oviposition trees of five genera from three available families, but completed development on only three genera from two families. Numbers of families and genera infested in most European outbreaks were also low (Straw et al. 2015a; Faccoli and Favaro 2016). Whether *A. glabripennis* host range outside its native range is related to the number of years between its arrival into a location and discovery is unknown. Thus, the relatively rapid detection and eradication of *A. glabripennis* outbreaks outside its native range may have limited the range of affected hosts in these locations.

Overall, the numbers of families, genera and species of trees affected in outbreaks outside the native range appeared lower

than those recorded in China (10 families, 14 genera (excluding *Malus* Mill. (Rosaceae) and *Pyrus* L. (Rosaceae) spp.), and 34 tree species; Hu et al. 2009); however, we are uncertain whether the beetle completed development under natural field conditions in all hosts in China. Furthermore, this limited plant selection contrasted sharply with the extensive host lists of more than 100 species on which *A. glabripennis* has been reported to feed, oviposit or complete development, reportedly under field conditions within and outside its native range (Eppo 2013, 2014; van der Gaag and Loomans 2014; Sjöman et al. 2014; Meng et al. 2015). Thus, it might be worthwhile to once again critically review and categorise the suitability of each tree genus/species as a host for *A. glabripennis*.

Diversity and importance

Host family

Our results on plant selection and acceptance showed that Sapindaceae was by far the family most commonly affected by the beetle in Toronto–Vaughan and Mississauga–Toronto. This result is consistent with all other outbreaks reported outside the beetle's native range (Haack et al. 2006; Straw et al. 2015a; Faccoli and Favaro 2016). In Ontario, the second most commonly affected family was Salicaceae, whereas in Chicago and Italy, it was Ulmaceae (Haack et al. 2006; Faccoli and Favaro 2016). The remaining four families of broadleaf trees selected in Toronto–Vaughan for oviposition were the same as those reported in Chicago (Haack et al. 2006). One difference between these two outbreaks, however, was the absence of affected stems in the family Rosaceae in Toronto–Vaughan (Turgeon et al. 2016).

Host genus

In the current study, *A. glabripennis* selected stems from seven genera for oviposition. At the outset of the eradication program, we had categorised five of these genera (i.e., *Acer*, *Betula*, *Populus*, *Salix*, and *Ulmus*) as suitable for complete beetle development and the remaining two (i.e., *Fraxinus* and *Tilia*) as questionable. We could not confirm complete development under field conditions on *Ulmus* spp. because the number of infested stems was so low that we could not obtain verifiable field evidence of complete development; we had to extract the few larval specimens from logs to confirm their identity by comparing them to voucher specimens. The beetle accepted *Fraxinus excelsior* for oviposition, but we found no evidence of larval development, whereas *Tilia cordata* appeared resistant (Turgeon et al. 2016). In New York, the beetle completed development in at least six genera: *Acer*, *Aesculus*, *Betula*, *Populus*, *Salix*, and *Ulmus* (Haack et al. 1997). In Chicago, Haack et al. (2006) reported oviposition on 10 genera (*Acer*, *Aesculus*, *Betula*, *Celtis*, *Fraxinus*, *Malus*, *Pyrus*, *Salix*, *Tilia*, and *Ulmus*), but recorded signs of adult emergence on only seven (*Acer*, *Aesculus*, *Betula*, *Fraxinus*, *Salix*, *Sorbus*, and *Ulmus*). In Paddock Wood, Straw et al. (2015a) reported oviposition on five genera (*Acer*, *Aesculus*, *Betula*, *Populus*, and *Salix*), but complete development on only three (*Acer*, *Populus*, and *Salix*).

Our findings indicated that *A. glabripennis* did not attack tree genera in accordance with their abundance. In both study areas, trees in the genus *Acer* were attacked more than expected, whereas those in the other main suitable genera (*Salix*, *Betula*, *Populus*, and *Ulmus*) were selected either less than expected or in accordance with their availability. This preference for *Acer* spp. is consistent with reports from most outbreaks outside of China (Haack et al. 1996, 1997, 2006; Turgeon et al. 2007; van der Gaag and Loomans 2014; Straw et al. 2015a; Faccoli and Favaro 2016); however, the extent to which *Acer* spp. will be targeted can vary among outbreaks. For example, in the Worcester County and Clermont County outbreaks, the genus *Acer* represented more than 90% of affected stems (J. Ryan, USDA-APHIS, personal communication), whereas in the Paddock Wood, Chicago, and Treviso province (Italy) outbreaks, the proportion of *Acer* stems affected was much lower: 80%, 75%, and 37%, respectively.

The ranking of the remaining genera, with respect to attack rate, differed among outbreaks. In Ontario, the most frequently affected genera after *Acer* were (in decreasing order) *Salix*, *Populus*, *Betula*, and *Ulmus*, whereas in the UK, the order was *Salix*, *Betula*, *Populus*, and *Aesculus* (Straw et al. 2015a). These rankings, however, contrasted noticeably from those reported for Chicago and the Treviso Province, where the genus *Ulmus* followed *Acer*, representing 17% and 29% of affected stems, respectively (Haack et al. 2006; Faccoli and Favaro 2016). In contrast, *Ulmus* comprised only 0.5% of affected stems in Ontario. These differences are difficult to explain given that this genus had relatively comparable IV in these outbreaks. Nonetheless, the low attack rate in Ontario led to the removal of this genus from the list of genera to treat in affected areas in Canada, unless infested (Fournier and Turgeon 2017). *Ulmus*, a common genus in the beetle's native range (Wu and Jiang 1998), is categorised as a good host in the USA and included on the list of genera to treat (Haack et al. 2006; USDA-APHIS-PPQ-CPHST 2015).

There were other notable differences in richness and relative abundance of affected stems between outbreaks. For example, *Aesculus*, considered a preferred host genus in the USA (USDA-APHIS-PPQ-CPHST 2015), was infrequently attacked in the UK, and not at all in Ontario, possibly because of its low RD and RBA. Another noteworthy difference was in the abundance of affected stems of *Fraxinus*. We had categorised the suitability of this genus as questionable prior to the eradication program, reflecting evidence of oviposition in potted trees (Morewood et al. 2003) and complete development under field conditions in Chicago and China (Haack et al. 2006), in combination with an absence of affected trees in New York (Nowak et al. 2001). This genus represented 64 of the 1465 affected stems with evidence of emergence in Chicago, but only 1 (with evidence of larval death) of the 682 affected stems in Toronto–Vaughan, despite having the sixth highest IV of all available genera. These results suggested that *A. glabripennis* did not present a risk to *Fraxinus* spp. in Ontario. Until additional contradictory evidence is obtained, the authors believe that *Fraxinus* should not be included in survey and control operations targeting *A. glabripennis* in Canada. However, species of this genus are still at high risk of attack by *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), another Asian invasive beetle found in North America.

In addition, Haack et al. (2006) reported the discovery in Chicago of one or two trees with oviposition pits from less commonly affected genera (i.e., *Celtis*, *Malus*, *Pyrus*, and *Tilia*) and Faccoli and Favaro (2016) recorded signs of oviposition on nine stems of the genus *Prunus*. We found none on the genera *Celtis*, *Malus*, *Pyrus*, or *Prunus* in Ontario. We did find, however, one *Tilia* with hundreds of signs of oviposition and early instar development. Logs of this tree were kept under rearing conditions for several months, yet no tunneling was observed, suggesting that this genus was unsuitable for complete development (Turgeon et al. 2016). This tree genus, although attacked in some outbreaks, should be considered unsuitable or resistant and used in replanting programs of affected areas, as suggested by Meng et al. (2015). Whether the genus *Prunus* is a true host of *A. glabripennis* as suggested by Sjöman et al. (2014) is debatable given the possibility that some hosts listed in the literature may be misleading. This is because a number of *Anoplophora* species in China have a similar appearance and may have been misidentified (Nowak et al. 2001).

Our study could not clarify the status of *Sorbus* as a suitable genus. We deemed this genus suitable for *A. glabripennis* in 2003, because of the discovery of signs of emergence, not of oviposition, on a single tree in Chicago (Haack et al. 2006; EPPO 2013; van der Gaag and Loomans 2014). All other tree genera listed as infested in Chicago had evidence of oviposition or of oviposition and emergence (Haack et al. 2006). Whether this single tree also had other signs typical of *A. glabripennis* injury is unknown. In Toronto–Vaughan, the few stems with signs of emergence, but

no signs of oviposition, had numerous other signs of injury characteristic of the beetle (some including specimens). Also, the listing of *Sorbus* as a host is based on observations of oviposition pits (USDA-APHIS-PPQ-CPHST 2015; Meng et al. 2015) and emergence in the laboratory. This scenario is somewhat similar to that of the genus *Quercus*. Morewood et al. (2005) reported complete development of *A. glabripennis* in *Quercus* under laboratory conditions, yet there is still no verifiable evidence that it can do so under field conditions. *Quercus* is considered a good genus to use in replanting programs for areas affected by the beetle (Meng et al. 2015).

The control response, namely eradication, to each discovery of *A. glabripennis* in North America or Europe has been the same, although strategies to achieve this goal have differed. Thus, whether plant selection at the genus level in its native range (Lingafelter and Hoebeke 2002; Hu et al. 2009) differs from that in outbreaks outside it, is difficult to assess critically. Nonetheless, it is worth noting that in China, *Populus*, *Salix*, *Ulmus*, and *Acer* represented (their importance differing among authors) the major host genera of *A. glabripennis* (Wu and Jiang 1998) and that the greatest reported damage is associated with the genus *Populus* (Luo et al. 2003; Hu et al. 2009). The establishment of extensive plantations of *Populus* and *Salix* spp. in China as agricultural windbreaks and highway greenbelts may have contributed to this situation (Luo et al. 2003; Williams et al. 2004; Pan 2005; Yin and Lu 2005; Hu et al. 2009; Smith et al. 2009). In a South Korean forest, which contains at least 112 tree species, *A. glabripennis* was found at endemic levels along forest edges predominantly on native species of *Acer* (Williams et al. 2004).

Host species

The list of affected tree species in invaded landscapes continues to expand (Smith et al. 2009; Hu et al. 2009; Meng et al. 2015). In the current study, we identified 16 species across the two outbreak areas as being acceptable hosts for *A. glabripennis*. The identification of oviposition pits on an *Ulmus rubra* tree may represent a new host record for *A. glabripennis*, but the tree was destroyed before determining if it was suitable for complete development under field conditions, as has been shown for several other species of *Ulmus* (Meng et al. 2015). Similarly, we believe the oviposition pits on *Acer campestre* and *Populus × canadensis* represented new host records for these species in North America, but again the number of affected stems was low and there was no evidence of complete development. Both species were reported as infested in Europe (Sjöman et al. 2014) and in garden experiments in China (Wang et al. 2005; Meng et al. 2015).

Our results on tree species selection, when combined with those from other outbreaks, clearly show that the *Acer* species targeted by the beetle will vary among outbreaks, even when similar tree species are available. In the current study, species-level host preferences varied among outbreak areas; *A. platanoides*, *A. saccharinum*, and *A. rubrum* were preferred hosts in the Toronto–Vaughan regulated area, whereas no strong species-level preferences were shown in the Mississauga–Toronto regulated area where only *A. negundo* and *A. platanoides* were attacked. In comparison, the most important host in southern England, despite the presence of a small number of *A. platanoides* and *A. negundo*, was *Acer pseudoplatanus* (Straw et al. 2015a) — a species found in limited abundance in Ontario, but not affected in the current study. In Massachusetts, *A. glabripennis* selected *Acer rubrum* more often than *A. saccharum* or *A. platanoides* (Dodds and Orwig 2011) and performed better on *Acer rubrum* based on holes/pits ratio. We could not calculate this ratio based on live specimens because our affected logs had to be heat-treated in Toronto, thus killing all *A. glabripennis* life stages it contained, before they could be transported for analysis. The *Acer* spp. most commonly attacked in New York included *A. platanoides*, *A. saccharum*, *A. saccharinum*, and *A. pseudoplatanus* (Haack et al. 1996, 1997). In their survey in South Korea, Williams et al. (2004)

observed *A. glabripennis* adults or damage on six *Acer* spp. with the primary hosts being *A. mono* and *A. truncatum*. Given this wide variation in host preference across native and invaded locations, it may be necessary to consider a range of potential hosts during the early stages of new outbreaks. However, host preferences may emerge as the outbreak progresses, allowing for efficiencies in ongoing eradication and monitoring efforts.

Host size

Our results showed that, in both study areas, the average D_{130} of affected stems was significantly larger than that of unaffected stems. Dodds and Orwig (2011) reported a similar pattern in Worcester, but only for trees in the genus *Acer*. Herein, we showed that this difference in D_{130} between affected and unaffected main stems also applied to non-*Acer* genera. Indeed, when combined, the average D_{130} of main stems from affected non-*Acer* genera was larger than that of unaffected stems. However, when not combined, *Betula* is the only genus that showed no difference in D_{130} between affected ($n = 12$) and unaffected ($n = 2533$) main stems.

Using frequency data, we further showed that *A. glabripennis* preferentially attacked medium- and large-sized trees. This finding is consistent with that of Dodds and Orwig (2011) who noted that all trees in Worcester with a diameter greater than 30 cm were infested. In Chicago, about 75% of affected stems had a diameter greater than 20 cm (Haack et al. 2006). The first 1410 infested trees removed in New York included trees in all classes of diameter at breast height between 0 and >150 cm (increments of 15 cm or 6 inches; Haack et al. 1997). In Paddock Wood, the D_{130} of affected main stems varied between 5 and 117 cm, with most having a diameter between 10 and 20 cm (Straw et al. 2015b). Though small stems were generally avoided, our results confirmed that *A. glabripennis* can infest and accept main stems as small as 3–4 cm. These results are consistent with observations in Chicago (Haack et al. 2006), New York (Haack et al. 1997), and Paddock Wood (Straw et al. 2015a). In Ontario, the smallest stem diameter with a sign of emergence was 5 cm, the same as that reported in Paddock Wood (Straw et al. 2015a). Thus, it might be desirable in future outbreaks to define suitability of stems, or high-risk stems, not only based on tree genus, but also on a stem $D_{130} \geq 5$ cm, which would greatly reduce the number of stems to examine and treat.

We found a significant interaction between stem size and genus, which indicated that small stems of most genera were avoided (with the exception of *Betula*) and that the preference for larger stems was strongest for *Acer* — though this preference appeared to wane at large sizes ($D_{130} > 40$ cm). This finding suggests that large, old maple trees may be at less risk of attack, but the relatively limited number of trees at this end of the size spectrum means that this result is best considered tentative.

As pointed out by Berland and Hopton (2016), it is important to keep in mind that this beetle selects larger trees. This is important because larger trees provide more environmental services and benefits than smaller ones (McPherson 2003) and will cost more to treat, using either tree removal or stem injection of insecticides, because such costs are typically based on basal area (Dodds and Orwig 2011).

Our observations also suggest that stem diameter was likely not the only criterion involved in host selection. In Toronto–Vaughan, main stems of the genus *Acer* were more frequently affected despite the presence of other tree genera with unaffected stems of an equal or greater D_{130} . For example, the average D_{130} of unaffected stems of the genus *Platanus* was greater than that of the affected *Acer*, but their IV was much lower than that of *Acer*. Other examples included a few genera of unknown (e.g., *Catalpa*, *Juglans*, and *Zelkova*) or questionable (e.g., *Quercus*, *Robinia*, and *Tilia*) suitability whose average D_{130} of unaffected stems was somewhat comparable (all within 5 cm) to that of affected *Acer* stems. We suspect proximity to an

affected stem and maybe bark thickness or smoothness may play a role in explaining observed infestation patterns.

Abundance of signs

In both outbreaks, signs of oviposition and emergence were distributed similarly with respect to abundance of signs per affected stem (Turgeon et al. 2022) and to D_{130} . We found most pits and holes on main stems with a D_{130} between 15 and 40 cm. Abundance and type of sign is used in the USA to classify beetle infestation within a tree and to identify origin trees (Trotter and Hull-Sanders 2015). Looking at intensity of injury characteristics such as D_{130} of origin trees, at the time of initial attack might provide additional insight, which could improve detectability of infested trees when signs are scarce.

Location of signs

Our study of host colonisation patterns focused on determining the height above ground of the lowest and highest signs of oviposition or emergence, indicating the portion of the tree within which signs were most likely to be found. To our knowledge, this is the first report showing that tree height was a good predictor (and a much better one than D_{130}) of the expected height of the lowest and highest signs of injury and that most of the lowest signs were within 3 m of the ground or 40% of tree height. Our approach differed from that of Haack et al. (2006), who carried out experiments in both China and Chicago on within-tree distribution of oviposition pits, emergence holes, and larvae during the early stages of colonisation, but our results are somewhat consistent with theirs. In China, the initial *A. glabripennis* infestation occurred primarily along the main trunk near the first crown branches, 2–4 m above ground in *Salix* and *Ulmus* but lower in *Populus*. Haack et al. (2006) attributed this difference in distribution among tree genera to differences in branching patterns. In Chicago, they used a slightly different approach cutting a 1-m log from different sections of the trunk and branches of three species of *Acer* and one species of *Fraxinus*. Infestations occurred first in the upper trunk and major crown branches and this colonisation pattern was broadly similar among the four species.

Our results suggest that during the early stages of attack on a tree, *A. glabripennis* aimed for about 50% of tree height and spread upward and downward from there as attack density increased. Information on the colonisation pattern of *A. glabripennis* in general, and the within-tree distribution of signs of injury in particular, are important to acquire because it has the potential to improve detectability of affected trees when conducting visual surveys from the ground, especially when sign density is low (Turgeon et al. 2007; Dodds and Orwig 2011; Straw et al. 2015a). Furthermore, this information will be particularly important during the monitoring phase of eradication, when there is a need to schedule surveys to locate the last few beetle-infested trees and to carry out treatment activities (Haack 2017).

Survey and control implications

At the onset of this eradication program in 2003, there was uncertainty regarding plant selection and the suitability of many tree genera and species for *A. glabripennis* development (Nowak et al. 2001; MacLeod et al. 2002; Turgeon et al. 2016). Thus, this information gap was important because it could directly affect the design, efficacy, duration and cost of eradication (Haack 2017). In recent years, there have been advances in the development of a pheromone- and plant volatile-based trapping program for *A. glabripennis* (Nehme et al. 2010; Wickham et al. 2012; Crook et al. 2014; Hoover et al. 2014; Meng et al. 2014; Nehme et al. 2014). These improvements should lead to increased detectability of new and residual infestations, but until an effective and reliable long-range detection system is available, visual surveys by ground or tree climbing crews will remain the survey and detection methods of choice.

We argue that the visual search for injured trees should not rely solely or mostly on the presence of emergence holes, despite observations by Straw et al. (2015a) showing that detection rates of trees with emergence holes were greater than those of trees without holes. Indeed, in Toronto–Vaughan and Mississauga–Toronto, the abundance of stems with signs of oviposition by *A. glabripennis* was about four times greater than that with signs of adult emergence — and some of the satellite populations of the Toronto–Vaughan outbreak (Fig. 1) and other areas surveyed had no emergence holes at the time of discovery of injured stems, and only low numbers of oviposition pits. Furthermore, the abundance of signs of oviposition was more than 25 times that of emergence in Toronto–Vaughan and at least three times that of emergence in Mississauga–Toronto. Instead, detection of affected trees should be based on the entire gamut of signs (e.g., exposed larval feeding galleries, frass, holes, and patches of hollow bark) or symptoms (e.g., cracks in the bark, exposed oviposition stains, missing bark, sap, callus tissue or branch dieback) of injury (Turgeon et al. 2007; Dodds et al. 2014). Thus, it is critical that inspectors be familiar with, and trained to recognise, all signs and symptoms of *A. glabripennis* injury. Reliance on the array of injuries to identify affected trees should also make it easier to distinguish injuries caused by *A. glabripennis* from those of other species. For example, we found 14 affected stems without a discernable oviposition pit or emergence hole. Examination of other signs and symptoms present on these stems, and intensive sampling of these logs to recover larval specimens, made it possible to attribute these injuries specifically to *A. glabripennis*.

Our findings related to tree taxonomy and size (D_{130}) can help to identify which trees to target during surveys and control operations. For example, it might be desirable to define tree suitability not just based on genus, but also on stem diameter: there was no complete development of *A. glabripennis* on stems with a $D_{130} \leq 5$ cm. The host genus and stem size most often selected, accepted, and suitable for development were *Acer* with a $D_{130} \geq 10$ cm — though there was a suggestion that very large trees ($D_{130} > 40$ cm) may be less attractive. Because the species of *Acer* most often selected varied among outbreaks, detection surveys should focus on trees of the genus *Acer*, rather than a certain species. Furthermore, surveys should focus about halfway up the tree, as early attacks are most likely to occur in this region. These results also served as the basis for the development of survey protocols with different intensities of inspection for high, moderate, and low risk zones within the Toronto–Vaughan regulated area (Fournier and Turgeon 2017) and of surveys of large areas.

Overall, this information should increase the likelihood of detecting affected trees within the landscape, while reducing costs by decreasing the number of tree genera, and thus trees, to examine and (or) treat. Alternatively, knowing whether survey and treatment of all hosts categorised as suitable in Canada (or as preferred and occasional to rare hosts in USA (USDA-APHIS-PPQ-CPHST 2015)) is necessary to achieve eradication, especially in areas where the genus *Acer* represents 90% or more of affected stems, would be an interesting question to explore in future work.

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