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ARTICLE

The distribution of the hemlock woolly adelgid (Hemiptera: Adelgidae) in Canada

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Abstract
The hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae), has distinct native and invasive populations in Canada. On the country's west coast, the adelgid is a native insect that feeds on western hemlock, *Tsuga heterophylla* (Rafinesque-Schmaltz) Sargent, and mountain hemlock, *Tsuga mertensiana* (Bongard) Carrière (Pinaceae). In eastern Canada, the adelgid is an invasive species that attacks and kills eastern hemlock, *Tsuga canadensis* (Linnaeus) Carrière (Pinaceae). We obtained all Canadian records of *A. tsugae* in institutional and public databases, developed updated range maps and phenologies for the species in British Columbia and eastern Canada, and developed dispersal estimates for populations in Nova Scotia. In British Columbia, *A. tsugae*'s observed distribution is centred around the Lower Mainland and on Vancouver Island but with populations in the British Columbia Interior and along the Pacific coast that have been poorly explored. In eastern Canada, the adelgid has invaded southern Nova Scotia, portions of the Niagara region in Ontario as far west as Hamilton, and at least one site on the north shore of Lake Ontario. No populations have been found in New Brunswick, Quebec, or Prince Edward Island, Canada. Finally, we estimated the rate of spread in Nova Scotia at 12.6 ± 8.2 to 20.5 ± 27.21 km/year.

Introduction

Hemlock trees, *Tsuga* spp. (Endlicher) Carrière (Pinaceae), are an important component of late-successional forests in eastern and western Canada. Three species of hemlock are native to Canada: *Tsuga heterophylla* (Rafinesque-Schmaltz) Sargent (western hemlock) and *Tsuga mertensiana* (Bongard) Carrière (mountain hemlock), with sympatric distributions in British Columbia, and *Tsuga canadensis* (Linnaeus) Carrière (eastern hemlock), which occurs throughout southern Ontario, southern Quebec, and the Maritime provinces (Figs. 1, 2, and 3). Hemlocks are long-lived, shade-tolerant tree species that typically grow in cool, moist environments and on a wide variety of soil types and origins. In British Columbia, *T. heterophylla* grows in association with many other tree species and understorey shrubs and is often an indicator of climax or

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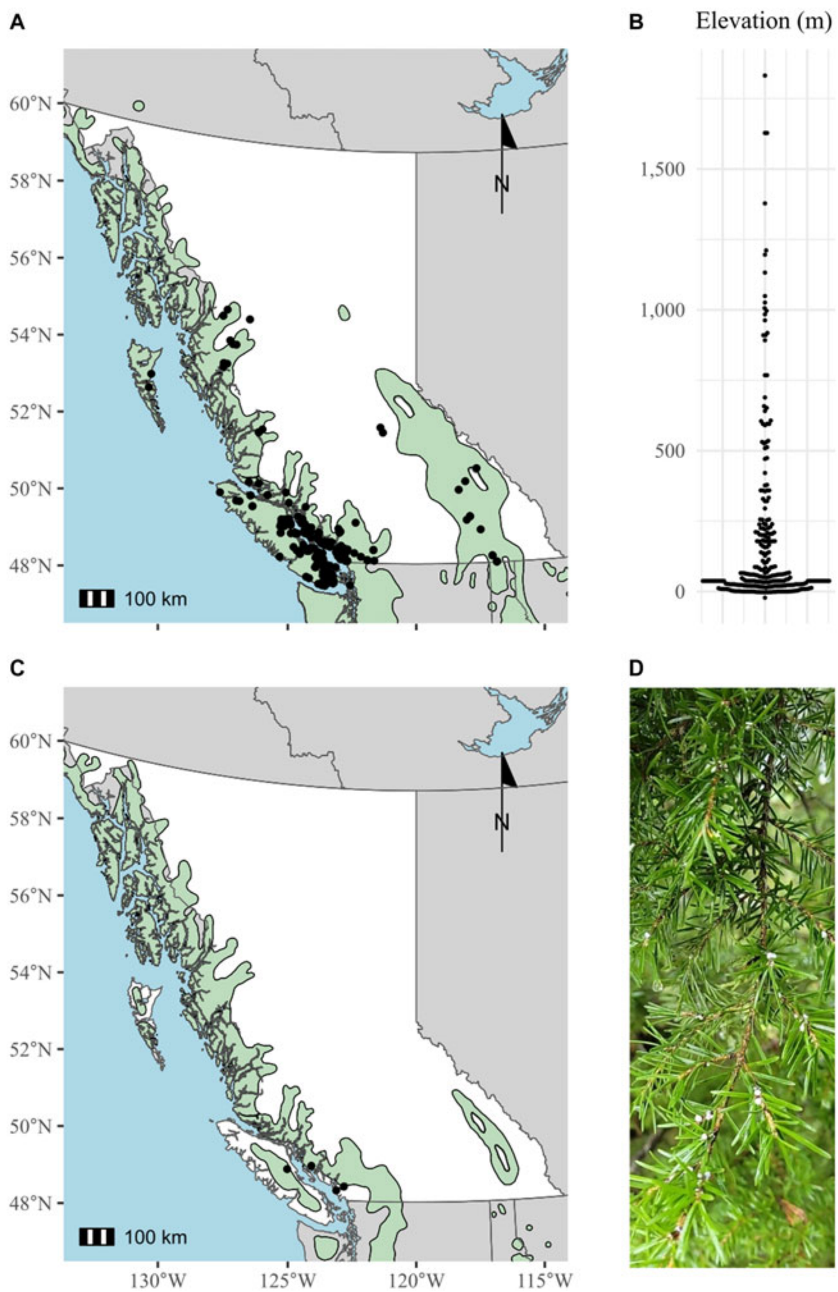

Figure 1. **A**, Recorded observations (circles) in British Columbia, Canada, of *Adelges tsugae* on *Tsuga heterophylla* or unspecified *Tsuga* sp. and **B**, elevation (in metres above sea level) at which *A. tsugae* was observed. Records of *A. tsugae* on **C**, *Tsuga mertensiana*, and an image of *A. tsugae* on **D**, *T. mertensiana* at Mt Seymour Ski Resort, British Columbia. Green shaded areas in **A** and **C** show the distribution of each host tree species from Fryer (2018). Data sources for *A. tsugae* observations are noted in the text; map data from Natural Earth (https://www.naturalearthdata.com); photo credit: T. Kimoto.

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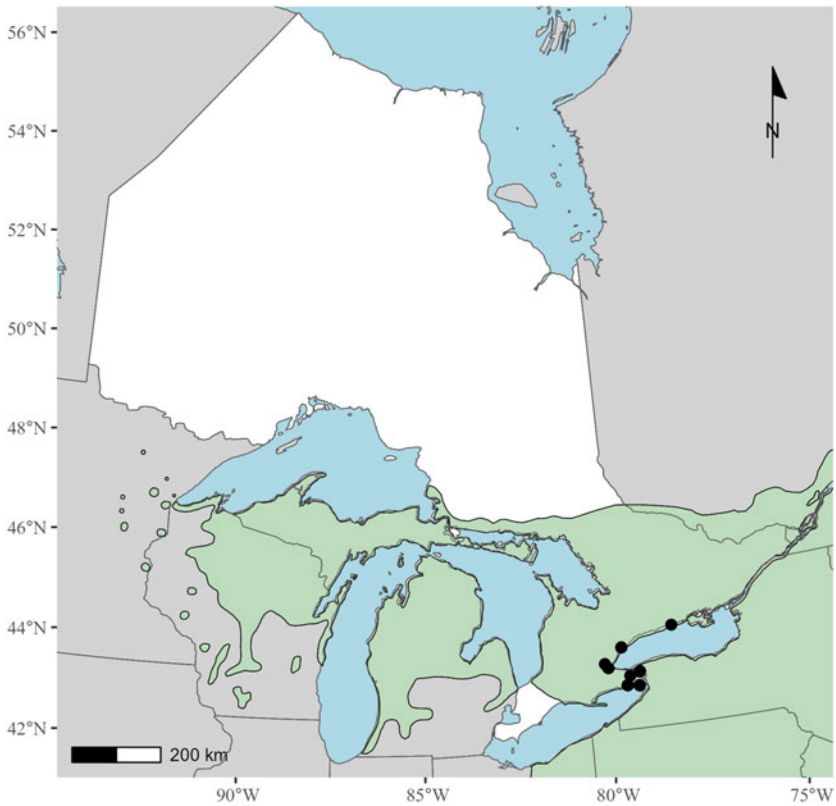

Figure 2. Recorded observations (circles) of *Adelges tsugae*, as of 2023, in Ontario, Canada, and the range (green) of *Tsuga canadensis*. Data sources for *A. tsugae* observations are noted in the text; distribution of *T. canadensis* from Fryer (2018); map data from Natural Earth (https://www.naturalearthdata.com).

near-climax communities. It can be found from sea level to more than 2000 m above sea level, whereas *T. mertensiana* occurs in the subalpine zone in British Columbia, between 900 and 2500 m above sea level, and grows best in sheltered, mixed-species stands with northern exposure. The altitudinal range of both species, however, is also influenced by latitude. In the east, *T. canadensis* typically grows on acidic, moist soils with good drainage found from sea level to 730 m above sea level, and well-developed stands often have little understorey. *Tsuga canadensis* is a major component of four forest types, either as the dominant species or in association with eastern white pine, *Pinus strobus* Linnaeus (Pinaceae), yellow birch, *Betula alleghaniensis* Britton (Betulaceae), or yellow poplar, *Liriodendron tulipifera* Linnaeus (Magnoliaceae), American beech, *Fagus grandifolia* Ehrhart (Fagaceae), red spruce, *Picea rubens* Sargent (Pinaceae), and sugar maple, *Acer saccharum* Marshall (Sapindaceae), on upland sites (summarised from Godman and Lancaster (1990), Means (1990), and Packee (1990)). In eastern Canada, the abundance of *T. canadensis* has been reduced by as much as 80% since European colonisation and now comprises less than 4% of forest cover in its previous range (Loo and Ives 2003; Emilson *et al.* 2018). This change is mostly due to conversion of land to agriculture and other uses and to the preference for early-successional tree species in commercial forestry. What hemlock remains has high ecological and social value in eastern Canada (Parker *et al.* 2023). In western Canada, hemlock retains much of its original range and provides ecological benefits in riparian ecosystems, but the species is also a significant component of coastal and subalpine forests, where it is a commercially important species.

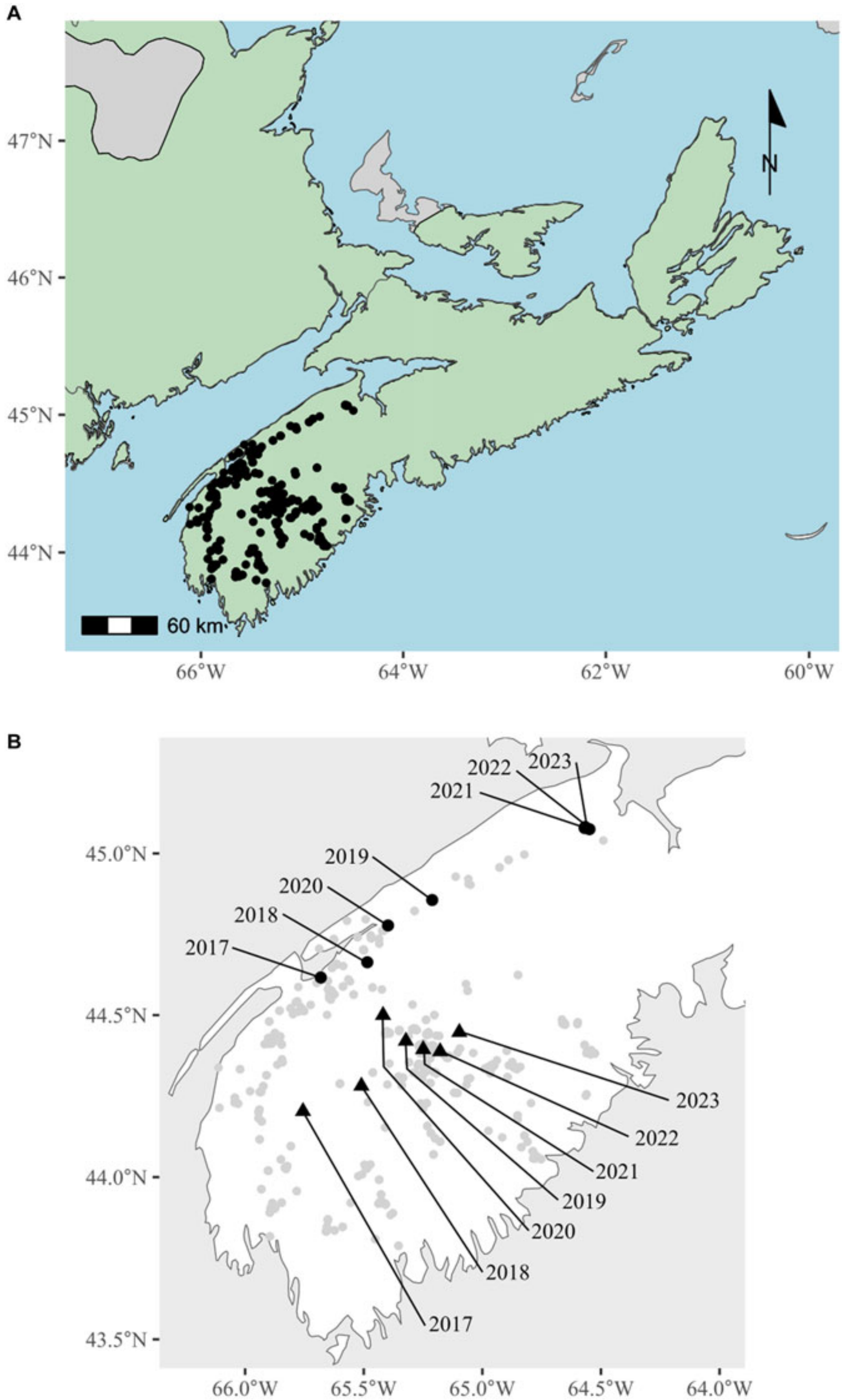

Figure 3. **A**, Recorded observations (circles) of *Adelges tsugae* as of 2023 in Nova Scotia, Canada, and the range (green) of *Tsuga canadensis*; **B**, the locations of population centroids each year since 2017 (triangles) and northernmost observation each year (black circles) in southern Nova Scotia; grey circles show the location of *A. tsugae* records, as seen in **A**. Data sources for *A. tsugae* observations are noted in the text; distribution of *T. canadensis* from Fryer (2018); map data from Natural Earth (https://www.naturalearthdata.com).

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In the eastern United States of America, *T. canadensis* and *Tsuga caroliniana* Engelman (Carolina hemlock) have been under threat from *Adelges tsugae* Annand (Hemiptera: Adelgidae), the hemlock woolly adelgid, for at least the past 70 years. This invasive species was first discovered at a private arboretum in Richmond, Virginia, United States of America in the 1950s and has been spreading in the eastern range of hemlock in the United States since the 1960s. The insect was likely introduced from Japan (Havill *et al.* 2006, 2016a), possibly on infested Japanese hemlocks intended for horticultural planting. In the late 1980s, *A. tsugae* gained prominence as a significant invasive species when hemlock mortality was observed in the mid-Atlantic states (McClure 1987, 1989). Spread of the insect has been slow, estimated at 5–20 km per year (Morin *et al.* 2009; Turner *et al.* 2011; Fitzpatrick *et al.* 2012; Goldstein *et al.* 2019), and its spread is likely facilitated locally by wind and mammals (McClure 1990; Turner *et al.* 2011) and over long distances by migrating birds and the movement of infested wood or plants (McClure 1990; North American Plant Protection Organization 2012; Russo *et al.* 2016, 2019). The northwards spread of *A. tsugae* had been thought to be constrained by cold winter temperatures that limit the insect's survival (Parker *et al.* 1998, 1999; Skinner *et al.* 2003), but recent research has shown that the adelgid's overwintering cold tolerance could facilitate northwards spread (Paradis *et al.* 2008; Elkinton *et al.* 2017; Lombardo and Elkinton 2017). This hypothesis was supported by detections of infestations in coastal Maine, Vermont, upstate New York, United States of America, and in Ontario and Nova Scotia, Canada (CFIA 2012, 2017; Hemlock Woolly Adelgid National Initiative 2024; Nova Scotia Department of Lands & Forestry and Nova Scotia Department of Environment and Climate Change 2024). Recent modelling suggests that under both present and future climate scenarios, some, if not all, of the range of *T. canadensis* in Canada is at risk of invasion by *A. tsugae* (McAvoy *et al.* 2017; Ellison *et al.* 2018; Kantola *et al.* 2019; Cornelsen *et al.* 2024). In the eastern United States of America, infested *T. canadensis* trees die within 4–15 years following initial *A. tsugae* attack, and within-stand mortality can exceed 90% (McClure 1991; Orwig and Foster 1998; Eschtruth *et al.* 2013). *Adelges tsugae* is therefore thought to have the potential to have significant negative impacts on eastern Canada's remaining hemlock forests (Emilson *et al.* 2018; Parker *et al.* 2023).

Adelges tsugae, albeit invasive in eastern North America, is an endemic, native species in western North America. The insect also has a complex life cycle that differs somewhat between the invasive eastern population and the native western populations.

In the eastern population, the insect overwinters in the nymphal stage of the sistens generation and becomes active in very early spring when it transitions to the adult stage. These adult insects are parthenogenic and produce eggs of the progrediens generation. These eggs hatch a mobile, crawler stage that seeks out feeding sites on the previous year's hemlock growth, where the adelgids transition to nymphs, settle, and either become sessile adults or transition into a winged, asexual stage called sexuparae. The sexuparae attempt to fly to an alternate host, *Picea torano* (Siebold ex. K. Koch) (Pinaceae), and establish the sexual, sexuales generation, but because *P. torano* does not grow in North America, the sexuales generation does not establish or produce offspring. The time when progrediens nymphs are active on foliage also roughly corresponds to the timing of spring bird migration in eastern North America, and so this stage is the most likely to be dispersed to uninfested stands. The adult progredientes eventually produce eggs of the sistens generation *via* parthenogenesis. The eggs hatch in mid-summer, and the crawlers that emerge from these eggs move to the new shoots of the host tree, settle, and enter a period of summer aestivation as young nymphs. Aestivation is broken in late summer or early fall, and the insects feed before overwintering. During the sessile portions of its life cycle, the insect produces a white, waxy wool-like covering to protect itself (Fig. 1D); the insect is named for this coating.

The western population of *A. tsugae* is genetically distinct from the eastern population and likely originated *via* the insect's natural spread during the time North America and Asia were connected (Havill *et al.* 2006, 2016a), not as the result of recent invasion. This long residency in western North America has resulted in changes to the biology of *A. tsugae* – most notably, the

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preference for one-year-old twigs, the almost complete loss of the sexuparae stage, and the discarding of *Picea* spp. as alternate hosts. Perhaps more importantly, the long residency has permitted *A. tsugae* and *Tsuga* spp. to co-evolve, and a suite of natural enemies that appears to regulate the insect's populations has emerged (Crandall *et al.* 2022). Similar control mechanisms have not been observed for the eastern North American populations, which contributes to *A. tsugae*'s success as an invasive species in the continent's east (Wallace and Hain 2000; Mayfield *et al.* 2023).

The range of *A. tsugae* in western Canada is not well documented but is assumed to be similar to those of *T. heterophylla* and *T. mertensiana*. Records exist in the iNaturalist database (www.iNaturalist.com) and Havill *et al.* (2016a), who included four records from British Columbia, three of which are from the Lower Mainland and one of which is from Vancouver Island. According to a fifth record from the west coast, *A. tsugae* has also been found on Prince of Wales Island very near to the Canadian border with Alaska, United States of America. These published records are incomplete; however, *A. tsugae* is known to inhabit other areas of British Columbia. For example, *A. tsugae* and its natural enemies have been documented from other parts of Vancouver Island (Zilahi-Balogh *et al.* 2003a, 2003b) that are not documented in Havill *et al.* (2016a).

Since 2012, a series of introductions and detections of *A. tsugae* have occurred in eastern Canada, most notably in southern Nova Scotia in 2017. Location data of pest detections are critical to understand the potential for *A. tsugae* range expansion and for assessing its risk to *T. canadensis* in eastern Canada. These data would also allow validation of predictions from models for climatic suitability that have been developed based on populations from eastern United States of America. Information about these detections has not been consolidated, and only basic information on the detections and no data on spread are provided in annual reports (*e.g.*, CFIA 2012). It is also important to consolidate this information because, in eastern Canada, *A. tsugae* is considered an invasive pest and so is regulated by the Canadian Food Inspection Agency (CFIA) under the authorities of the *Plant Protection Act and Regulations* (1990). As part of this regulation, the CFIA identifies the specific areas of Canada and the United States of America where *A. tsugae* is established and outlines the movement requirements for *A. tsugae*'s host material to and from these regulated areas. The CFIA also has an obligation to international trading partners to conduct surveillance activities for *A. tsugae* within unregulated areas of Canada to provide data in support of CFIA's declarations of pest freedom for commodities originating from areas where the pest is not known to occur. Once a new find of *A. tsugae* is identified within an area of Canada where the pest was not known to exist, the CFIA is required to take regulatory action to mitigate the immediate risk of artificial spread. At the same time, the CFIA conducts delimitation surveys to assess the overall size and severity of the infestation and determine response options. The response may involve implementing controls to eradicate the population or the establishment of larger regulated areas to mitigate the risk of spread from the area.

Herein, we accumulate all records of *A. tsugae* in Canada. We use these data to clarify the insect's present distribution in British Columbia and to understand the insect's spread in eastern Canada. We show that the adelgid's occurrences in British Columbia suggest that many areas are underexplored for *A. tsugae* and its associated natural enemies. We also show that contemporary invasive populations in eastern Canada are spreading at rates consistent with those observed in the eastern United States of America.

Methods

We used published and unpublished records of collections of *A. tsugae* from a variety of sources to determine its range in Canada.

Specimen data records for *A. tsugae* from western Canada were extracted from institutional and publicly available databases. We obtained collection records of the Canadian Forest Insect and

Disease Survey (FIDS), held within the Forest Invasive Alien Species Document Library (Natural Resources Canada 2023). These records document observations of insects or damage reported as part of annual forest health surveys done in Canadian forests by the Canadian Forest Service from 1936 to 1994. We also included pre-1936 records from the FIDS database that originate from earlier surveys (Van Sickle *et al.* 2001). Records from FIDS include host records, so we included that information as well. In general, records within FIDS are a combination of observations of forest pest presence and activity and specific surveys of notable pest events (*i.e.*, outbreaks) conducted by technical staff throughout Canada. The location, intensity, duration, coverage, and goals of each survey often varied from year to year (see Van Sickle *et al.* 2001 for more information). To our knowledge, no specific surveys for *A. tsugae* occurred during the period of the FIDS programme, and as a result, the FIDS data contain only records of where and when the insect was observed or collected.

We supplemented the FIDS data with other records of *A. tsugae* in Canada. We incorporated those in the Global Biodiversity Information Facility (Global Biodiversity Information Facility Secretariat 2023; https://www.gbif.org), which includes records of observations from iNaturalist, and specimen data records from arthropod collections, including the Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada) and the Yale Peabody Museum (New Haven, Connecticut, United States of America; Global Biodiversity Information Facility Secretariat 2023). These data lack host records. We also included records from the Barcode of Life Database (Ratnasingham and Hebert 2007), the Pacific Forestry Centre arthropod reference collection (Natural Resources Canada, Canadian Forest Service, Victoria, British Columbia, Canada), and Havill *et al.* (2016a), which we obtained from Havill *et al.* (2016b), and observations made by the CFIA, the Canadian Forest Service, and Cornell University (Ithaca, New York, United States of America) between 2019 and 2023 in British Columbia during explorations for *A. tsugae* biological control agents (see Celis *et al.* 2022 for information about the Cornell University surveys). Inspection of the resulting combined data suggested that only a small amount of duplication occurs across records from institutional collections, the Barcode of Life database, and Havill *et al.* (2016b) for specimens collected from southern Vancouver Island and the Vancouver region. We also note that early British Columbia records in the FIDS database are often geographically imprecise. The FIDS records report this geographic accuracy, so we limited our examination to records for which the accuracy was at least 20 km.

We obtained records for eastern Canada from the CFIA survey and reporting database (provided by R.N.) and from the Nova Scotia Department of Natural Resources and Renewables (Halifax, Nova Scotia, Canada; provided by J.B.O.). Once an area has been regulated under a CFIA Infested Places Order, the agency ceases its intense surveys within that area: because of this, we augmented the CFIA data with iNaturalist records found within the Global Biodiversity Information Facility. No records for eastern Canada were found in any of the other databases.

Data from the CFIA include the first-detection records for *A. tsugae* in eastern Canada. Year and location information for each first detection is contained in the CFIA's annual survey reports (CFIA 2012, 2013, 2014, 2015, 2016, 2017, 2018, 2019, 2020, 2021, 2022, 2023). For each first-detection record, we describe how the detections were made, based on contemporary records, reports to the CFIA, and our own observations that were not included in the annual survey reports. We also examined the location and yearly distribution of CFIA survey sites for *A. tsugae* in eastern Canada over the same period to evaluate survey effort.

We evaluated the temporal trend in *A. tsugae* collections using data associated with each collection record. For records from British Columbia, we also determined the elevation at which each observation was made by cross-referencing the recorded locations to a digital elevation model of the province. We did this to allow us to examine the geographic and elevation variation in native *A. tsugae* records.

For records from Nova Scotia, we examined the rate of spread for the invasive population from its initial detection location in 2017. We used two methods to evaluate range expansion in Nova

Scotia. For the first method, we used all records from the province and determined the geographic centre of the *A. tsugae* population in each year. These records included those from CFIA inspection data and records from the Global Biodiversity Information Facility, which consisted mostly of records from iNaturalist. We determined the geographic centre of the *A. tsugae* population by first expressing the latitude and longitude for each location where *A. tsugae* was recorded in decimal degrees. We then computed the average latitude and average longitude for all observations from a given year. We refer to this location as the centroid of each population. We then determined the Euclidean distance between centroids from consecutive years, and from these values, we computed the mean displacement of the position of the population's centroid since 2017. We assumed that displacement of the centroid reflected more observations in new locations and, thus, can serve as a proxy for the rate of *A. tsugae* spread. The second approach repeated this analysis but evaluated the northwards spread of the population by examining the average change in Euclidean distance between the most northerly observation in the province in successive years. We report the mean and standard deviation of our estimates.

All mapping and analyses were done within the R statistical computing environment, version 4.0 (R Core Team 2024), using functions in the *stats* (R Core Team 2024) and *sf* (Pebesma 2018; Pebesma and Bivand 2023) packages. Altitudes were determined in ArcGIS Pro, version 3.0.4 (Environmental Systems Research Institute, Inc. 2011), using either the High-Resolution Digital Elevation Model (Government of Canada 2024) or the Canadian Digital Elevation Model (Government of Canada 2023). The High-Resolution Digital Elevation Model has a higher resolution (1–2 m) but a smaller coverage area than the Canadian Digital Elevation Model does, so we used the Canadian Digital Elevation Model for records that fell outside the High-Resolution Digital Elevation Model's coverage area. *Adelges tsugae* observation records are available from the Barcode of Life Database (Ratnasingham and Hebert 2007), the Forest Invasive Alien Species Document library (Natural Resources Canada 2023), the Global Biodiversity Information Facility (Global Biodiversity Information Facility Secretariat 2023), and Havill *et al.* (2016b). Data from the CFIA and the Nova Scotia Department of Natural Resources and Renewables can be obtained by contacting those agencies.

The ranges of *T. heterophylla*, *T. mertensiana*, and *T. canadensis* were mapped using resources from Fryer (2018). These maps are known to be somewhat imprecise with respect to the range of some tree species, and they do not reflect the abundance of each species. Herein, the maps are used only to show the approximate area within which each tree species can be expected to be found.

Results and discussion

British Columbia

The earliest definitive record of *A. tsugae* in Canada occurs in a May 1938 report indicating that the species was active on *T. heterophylla* in Vancouver, British Columbia (Venables and Hopping 1938; Hopping 1939). Chystal (1916), however, described an insect very similar to *A. tsugae* on *T. heterophylla* in Vancouver's Stanley Park 22 years earlier (see Havill *et al.* 2006 for further discussion). Most observations of *A. tsugae* in British Columbia were made in the 1960s and from the late 1980s to the early 1990s (Fig. 4A). The reasons for the gap from 1970 to approximately 1985 are not apparent, but the abrupt end of records in 1994 corresponds with the end of the FIDS programme and the devolution of forest health surveys to the Canadian provinces.

Adelges tsugae were collected year-round in British Columbia, with most collections made during the summer months (Fig. 4B). The range of *A. tsugae* spans from 48.4° to 55.4° latitude north in British Columbia and from 0 m to 1800 m above sea level (Fig. 1B), with most records reported from the province's coastal region, which corresponds to British Columbia's Coastal Western Hemlock and Mountain Hemlock biogeoclimatic zones (British Columbia Ministry of Forests 1997). Both *T. heterophylla* and *T. mertensiana* are generally restricted to the Pacific coast

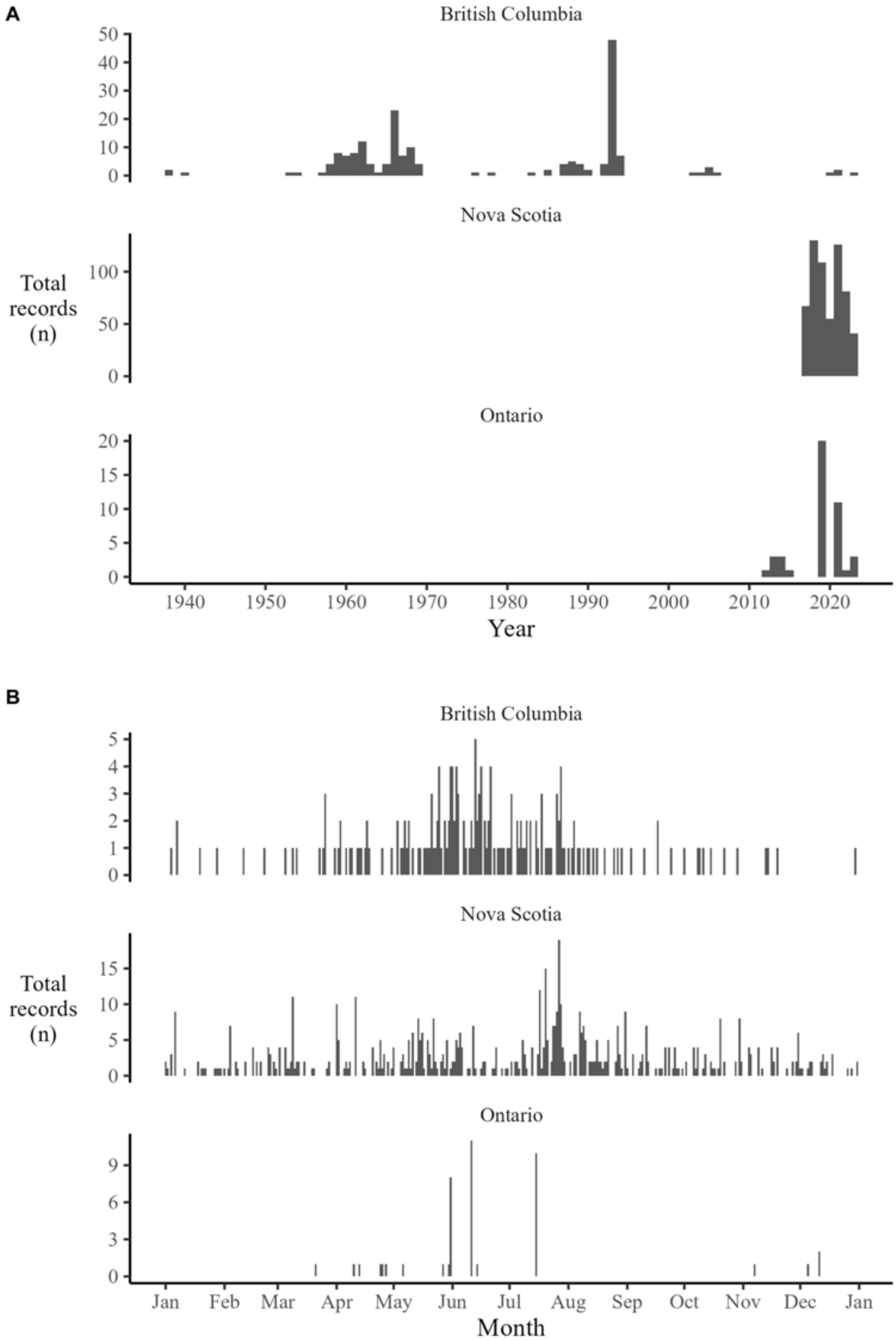

Figure 4. **A**, Historical timing and **B**, within-year phenology of *Adelges tsugae* observations in three Canadian provinces. See text for information on source data.

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in British Columbia, although populations of both species occur in east–central (*i.e.*, the eastern Cariboo, northern Thompson–Nicola, and Columbia–Shuswap regions) and southeastern (*i.e.*, the Kootenays) British Columbia. In general, the southern portion of *T. heterophylla*'s coastal range is well surveyed for *A. tsugae* (Fig. 1A). In comparison, British Columbia's coastal and Interior forests further to the north appear to be relatively undersurveyed. The coastal region is difficult to access, which likely has limited surveys for *A. tsugae* in north–coastal areas and may explain why most observations there appear to follow roads that connect the province's Interior to the Pacific coast. Collections of *A. tsugae* have also been made on Haida Gwaii, British Columbia (Fig. 1A) and on Alaska's Prince of Wales Island (Havill *et al.* 2016b).

The eastern range of *T. heterophylla* in British Columbia does not appear to have been well surveyed for *A. tsugae* (Fig. 1A). In the southeastern part of the province, *Tsuga* spp. are distributed through the Interior Cedar–Hemlock biogeoclimatic zone and to a lesser extent in the Engelmann Spruce–Subalpine Fir biogeoclimatic zone (British Columbia Ministry of Forests 1996, 1998). The range of *T. heterophylla* in this region is disjunct from that along the Pacific coast but is connected to populations in Oregon, Idaho, and Montana, United States of America. *Tsuga mertensiana* also occurs in this region but over a smaller area (Fig. 1C). About a dozen observations of *A. tsugae* are reported in this part of the province, mostly in the Kootenay region of southeastern British Columbia (Fig. 1A), with no observations in the northern part of the range, and most observations are from the FIDS records. However, *A. tsugae* was found more recently near the community of Likely, British Columbia, and on the southwest side of Quesnel Lake in the Cariboo region (T.K., unpublished data). The southern and lower-elevation areas of this region in British Columbia are plant hardiness zones 5 and 6, whereas the northern and higher-elevation areas are plant hardiness zones 3 and 4 and therefore may not be climatically suitable for successful *A. tsugae* overwintering (*e.g.*, Elkinton *et al.* 2017). The distribution of *Tsuga* spp., and therefore also *A. tsugae*, may thus be limited in this area even though *Tsuga* spp. can grow in wetter parts of the Cariboo region on the western side of the Cariboo Mountains.

Most observations from the FIDS records report *A. tsugae* from *T. heterophylla* or from "*Tsuga* sp." There are, however, records of *A. tsugae* from *T. mertensiana* (Fig. 1C). Some of these records date back to 1966, but recent records of *A. tsugae* on *T. mertensiana* exist at the alpine ski resort on Mt. Washington on Vancouver Island, at Mt. Seymour Ski Resort, Mt. Seymour Provincial Park near Vancouver (Fig. 1D), and at the University of British Columbia's Botanical Garden in Vancouver, and a record of *A. tsugae* on introduced *T. canadensis* is reported at the Malcom Knapp Research Forest in Maple Ridge, British Columbia (T.K., unpublished data). The FIDS data also record *A. tsugae* being collected from Pacific silver fir, *Abies amabilis* (Douglas) Forb (Pinaceae), Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco (Pinaceae), and western redcedar, *Thuja plicata* Donn (Cupressaceae). These observations from non–*Tsuga* spp. hosts represent a minute fraction of records ($n = 3$) and are from beat-sheet collections that could have been contaminated by *A. tsugae* dislodged from neighbouring trees (Natural Resources Canada 2023). These specimens could also have been misidentified. For example, *A. amabilis* hosts *Adelges piceae* (Ratzeburg) (Hemiptera: Adelgidae), and *P. menziesii* hosts *Adelges cooleyi* (Gillette) (Hemiptera: Adelgidae), both of which could have been mistaken for *A. tsugae*.

Alberta, Saskatchewan, and Manitoba

Tsuga heterophylla is recorded in the Rocky Mountains of western Alberta (Moss and Packer 1983) near the edge of its range. Other members of the genus are not native to the Prairie Provinces, and so there are no historical or contemporary records of *A. tsugae* and no surveys are conducted in those three provinces. However, *Tsuga* spp. are likely planted in this region as ornamental trees and would be at risk for infestation if they were exposed to infested material imported from British Columbia, the Pacific Northwest, or eastern North America.

Ontario

Multiple infestations of *A. tsugae* were found in Ontario between 2012 and 2024. In 2012, an *A. tsugae* infestation was discovered on four landscape *T. canadensis* trees (*i.e.,* trees that had been intentionally planted by a homeowner). This infestation was detected by an arborist at a private residence in the Etobicoke district of Toronto and marks the first detection of *A. tsugae* in eastern Canada (Fig. 2). The infested trees were removed, and a visual delimitation survey was performed (Fig. 5A) by assessing all species of *Tsuga* within a 500-m radius of the infested site. In 2013, two additional infested trees were identified on neighbouring properties, and those trees were also removed and destroyed. Delimitation surveys were conducted for five years (2014–2019), and no additional infestations were detected in Etobicoke.

In 2013, *A. tsugae* was found on one *T. canadensis* tree in the Niagara Gorge, in the city of Niagara Falls, during a routine detection survey targeting *A. tsugae* conducted by the CFIA and Canadian Forest Service. The infested tree was cut and burned onsite, and delimitation surveys using visual inspection, sticky card trapping (Fidgen *et al.* 2020), ball sampling (Fidgen *et al.* 2021), and branch sampling were implemented to determine the extent of the infestation. No additional *A. tsugae* infestations were discovered in Niagara Falls. Starting in 2014, follow-up surveys were conducted to verify the efficacy of the control efforts and to guide policy decisions. These surveys were conducted between November and June, and additional infested trees were found in 2014 and 2015 in the Niagara Gorge. These trees were located adjacent to the single tree found in 2013. As in 2013, these infested trees were destroyed onsite. Subsequent delimitation surveys were conducted annually, with no additional infestations detected until 2019.

New infestations of *A. tsugae* have been found in Ontario almost every year since 2019. In 2019, *A. tsugae* infestations were discovered near Wainfleet and in the city of Niagara Falls during routine CFIA *A. tsugae*–detection surveys. The 2019 discovery in Niagara Falls consisted of *A. tsugae* populations on 11 trees (of 92 examined) located downriver of the original 2013 detection site and outside the original delimitation zone. Compared to the single tree found in 2013, this infestation was characterised as being spread out and heavy (N.M., upublished data). No new infestations were reported in Ontario in 2020, but in 2021, *A. tsugae* was detected in Fort Erie *via* a posting made by a user on the iNaturalist website (josbees 2021), leading to additional delimitation and containment measures. In 2022, *A. tsugae* was detected near Pelham, Ontario, during routine CFIA *A. tsugae*–detection surveys and in the township of Alnwick/Haldimand, near Grafton, Ontario, by Canadian Forest Service and University of Guelph (Guelph, Ontario, Canada) researchers who noted evidence of *A. tsugae* on the bark of trees and on branches at eye level while conducting plot assessments in a *T. canadensis* stand (M.G., unpublished data). This detection of *A. tsugae* was confirmed by the CFIA in July 2022. In 2023, populations of *A. tsugae* were found on the grounds of the Royal Botanical Gardens in Hamilton by employees of that facility, in Haldimand County as a result of a community-science project (Invasive Species Centre 2023), and near Lincoln by Ontario Ministry of Natural Resources employees. In early 2024, populations of *A. tsugae* were found in Port Colborne during a routine CFIA detection survey for spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae).

The ages of the populations discovered in Ontario since 2019 have not been determined. One of us (J.G.F.) surveyed hemlock from the Niagara Gorge to Prescott on the north shore of Lake Ontario in 2008 and found no evidence of infestations in any of the examined sites. We also conducted visual assessments of the infestations near Wainfleet in 2019 (C.J.K.M., J.G.F.) and near Grafton in 2023 (M.G.) that indicated these populations were well established, had been present for several years before detection, and were able to survive severe winter conditions and persist (MacQuarrie *et al.* 2024).

Quebec, New Brunswick, and Prince Edward Island

No detections of *A. tsugae* have been recorded in Quebec, New Brunswick, or Prince Edward Island, Canada, as of 2023. The first recorded CFIA survey for *A. tsugae* in Canada occurred in

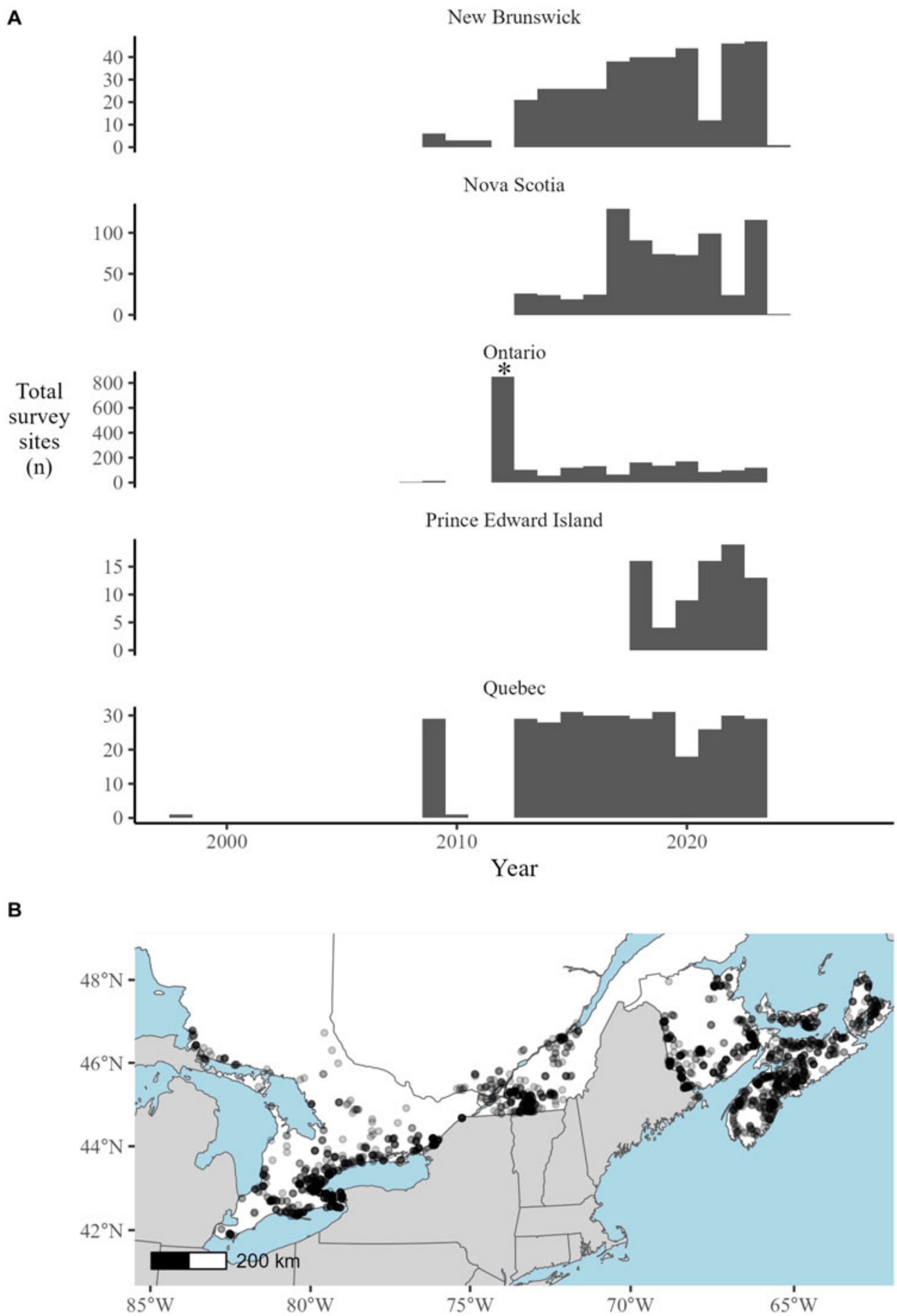

Figure 5. **A**, Number and **B**, location of Canadian Food Inspection Agency (CFIA) *Adelges tsugae* survey sites in eastern Canada, 2008–2024. Regions with a higher density of survey points in **B** have darker shading. The large number of survey sites in Ontario, Canada in 2012 (* in **A**) reflect increased visual survey and delimitation efforts following the first detection in Canada; see text for details.

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Saint-Ignace-De-Stanbridge, Quebec, in 1998, and the province has been regularly surveyed since 2009 (Fig. 5). New Brunswick has also been regularly surveyed since 2009, and surveys in Prince Edward Island began in 2019 (Fig. 5). *Adelges tsugae* occurs in New York, southern Vermont, and southern Maine, United States of America, and could be introduced to New Brunswick and Quebec from those infestations. *Tsuga canadensis* in New Brunswick and Prince Edward Island would be at risk if *A. tsugae* spreads from established populations in southern Nova Scotia (Fig. 3).

Nova Scotia

The first detection in Nova Scotia of *A. tsugae* occurred in 2017 (Fig. 4A) from an arborist's report that was confirmed by the CFIA. Following that initial detection, the CFIA conducted a visual ground survey at 131 sites (Fig. 5), resulting in the detection of the pest in Annapolis, Digby, Yarmouth, Shelburne, and Queens counties (Fig. 3). Additional sites were surveyed by the Nova Scotia Department of Natural Resources and Renewables, Parks Canada, and nongovernmental organisations. No new occurrences of *A. tsugae* were observed beyond those five counties in 2018 and 2019. In 2020, *A. tsugae* was detected in Lunenburg County, and an extensive survey was conducted at 87 sites across Nova Scotia in 2021, with further infestations detected in Kings County. In 2022, CFIA conducted surveys at 66 sites, and no further infestations were identified. In 2023, more infestations were detected in Hants and Halifax counties following reported sightings by a collaborating non-governmental organisation and a homeowner, respectively, that were confirmed by CFIA.

Observations of *A. tsugae* have been made year-round in Nova Scotia, with an apparent peak in July and August (Fig. 4B). This pattern may occur because many of the records of observations in Nova Scotia in our combined database are drawn from iNaturalist reports. In July and August progrediens-generation ovisacs (*i.e.,* sistens eggs) are typically at their largest size, and as both generations of adults are conspicuous on foliage (*e.g.*, Fig. 1D), a peak in observations during those months may reflect their apparency to the public. This timing may also coincide with more iNaturalist users being active outdoors and submitting reports to the online database. A cursory examination of the iNaturalist database indicates that observations of *A. tsugae* tend to peak in North America during this period (see seasonality map, https://inaturalist.ca/taxa/61513-Adelges-tsugae).

Newfoundland and Labrador, Northwest Territories, Nunavut, and Yukon

Tsuga spp. are not native to Newfoundland and Labrador, Northwest Territories, or Nunavut, but *T. heterophylla* does occur in Yukon's southwestern corner (Figure 1A). No records of *A. tsugae* have been reported from, and no surveys are conducted in, Newfoundland and Labrador or the three northern territories. Any *Tsuga* spp. planted in this region or growing natively would be at risk if exposed to infested material imported from British Columbia, the Pacific Northwest, or eastern North America.

Range expansion in Canada

We estimated an expansion rate of 12.6 ± 8.2 km/year in *A. tsugae* distribution in Nova Scotia, based on the change in the position of the population's centroid, with a northwards expansion rate of 20.5 ± 27.21 km/year (Fig. 3B). The large variability in the northwards expansion rate can be attributed in part to the presence of a new detection of *A. tsugae* in 2021 that was 76.5 km from known 2020 populations. If that 2021 detection is excluded from our calculations, the rate of *A. tsugae* northwards range expansion is 13.4 ± 12.6 km/year. These estimates are consistent with observations of range expansion in the United States of America over longer time scales (Morin *et al.* 2009; Fitzpatrick *et al.* 2012). Northwards expansion in Nova Scotia also appears not to be limited by overwintering conditions (MacQuarrie *et al.* 2024). In Nova Scotia, two infestations appear to be linked with human movement of infested material (J.G.O., unpublished data). That our rates of spread are consistent with those observed elsewhere in the invaded range suggests that a lack of environmental barriers to the pest's spread in Nova Scotia. Our estimates are, however, based on a somewhat rudimentary assessment of spread. A more fine-scale and process-based model of spread in Nova Scotia would help in estimating risk in areas where the insect has yet to be detected.

We lack sufficient information to calculate a rate of expansion for Ontario, but the dispersal of the insect in that province may be limited by forest fragmentation. In the Niagara region and in many other parts of southern Ontario, *T. canadensis* persists in protected areas and in small woodlots (*e.g.,* within conservation areas and parks) embedded within a matrix of urban areas and farmland (Shi *et al.* 2025). Dispersal within this matrix may be more difficult than in the eastern United States of America and Nova Scotia, where forests are more contiguous. This may change, however, should *A. tsugae* infest more of the forests north of Lake Ontario, where *T. canadensis* is more common and forest conditions are like those found in other invaded areas.

Summary and conclusion

Adelges tsugae is perhaps the only insect species in Canada that has distinct native and invasive populations. We have summarised the present state of knowledge on the distribution of both populations of *A. tsugae* in Canada. In British Columbia, the distribution of native *A. tsugae* is well characterised in the Lower Mainland and on Vancouver Island but is poorly surveyed in the province's Interior and along the northern Pacific coast. These undersurveyed areas could host populations of the insect and natural enemies that may be better matched to the climate in eastern Canada than predators native to other parts of the region (*e.g.,* Mausel *et al.* 2011).

The rapid spread of *A. tsugae* and its impacts to *T. canadensis* in eastern Canada imply a lack of regulation by natural enemies native to eastern Canada, similar to that seen in the eastern United States of America (Wallace and Hain 2000; Havill *et al.* 2014). In the eastern United States of America, biological control of *A. tsugae* currently focuses on four predatory species: *Laricobius nigrinus* (Fender) (Coleoptera: Derodontidae), *Laricobius osakensis* Montgomery and Shiyake (Coleoptera: Derodontidae), *Leucotaraxis argenticollis* (Zetterstedt) (Diptera: Chamaemyiidae), and *Leucotaraxis piniperda* (Malloch) (Diptera: Chamaemyiidae). In Washington state, *A. tsugae* is regulated by natural enemies on both native *T. heterophylla* and introduced *T. canadensis* (Crandall *et al.* 2022), which supports the hypothesis that similar regulation can be achieved in eastern North America *via* classical biological control. The four predator species noted above appear to be well suited to conditions in eastern North America and, together, could suppress both the sistens and progrediens generations of *A. tsugae*, although efforts to date have not proved effective at regulating adelgid populations and reducing tree loss (Mayfield *et al.* 2023).

The knowledge generated about *A. tsugae* populations in the present study also suggests additional areas for research in British Columbia. The ecological interactions between *A. tsugae* and *T. mertensiana* have not been explored, and could inform understanding of the host–herbivore dynamics in this system, and may suggest solutions for developing tolerance to *A. tsugae* in *T. canadensis*. The climate tolerances of *A. tsugae* in its native range in western North America, including British Columbia, have also not been assessed, and so the limits of its range in British Columbia can only be speculated. Finally, the natural enemy complex of *A. tsugae*, beyond the four agents presently being exploited for biological control in the United States of America (Mayfield *et al.* 2023), has not been adequately explored in British Columbia. This work could lead to identification of additional natural enemies that play a role in regulating *A. tsugae* populations in western North America. This approach faces challenges, however; specifically, finding and exploiting populations of natural enemies can be difficult. In western North America, *A. tsugae* exists at low densities in forests and rarely kills trees (Furniss and Carolin 1977), which hampers locating natural enemies, although this difficulty is mitigated somewhat in tree plantations and in urban settings, where insect's populations can be larger (Furniss and Carolin 1977; Zilahi-Balogh *et al.* 2003a) and therefore perhaps easier to survey and exploit.

In eastern Canada, *A. tsugae* continues to expand its range in Ontario and Nova Scotia. Our study represents a snapshot of the state of these invasive populations at the end of 2023. The present status of the insect outside of the regulated areas can be determined from information provided by the CFIA and within the regulated areas from tools such as iNaturalist. No climatic boundaries appear to be preventing the insect from infesting most of the Maritime Provinces (Kantola *et al.* 2019; Cornelsen *et al.* 2024; MacQuarrie *et al.* 2024), suggesting *T. canadensis* populations in New Brunswick and Prince Edward Island are at similar risk from the adelgid. The climate in Ontario, however, may prevent the insect from infesting the entire range of hemlock in that province, but those climate barriers may disappear under climate change (Cornelsen *et al.* 2024), as is indicated by recent detections of the insect in the northern part of Michigan's Lower Peninsula, where climate conditions are similar to those of central Ontario. In eastern Canada, improved understanding of, and developing tools to mitigate, the impacts on forest stand structure and composition (Parker *et al.* 2023) and determining the pathways of invasion into and within Canada to optimise future surveys (*e.g.,* Yemshanov *et al.* 2020) and management will be important.

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