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ARTICLE

Phenology of invasive hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae), and the role of resident natural enemies in its population regulation in Nova Scotia, Canada

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Abstract

Adelges tsugae Annand (Hemiptera: Adelgidae), an invasive pest of eastern hemlock, *Tsuga canadensis* (Linnaeus) Carrière (Pinaceae), has been causing widespread tree decline and mortality across southwestern Nova Scotia, Canada, since its detection there in 2017. To gain basic knowledge of its biology in this novel part of its invaded range in eastern North America, we investigated the effect of predation on *A. tsugae* densities and conducted repeated surveys of the resident complex of natural enemies. We found only minimal and incidental predation by generalist arthropod predators, confirming the lack of population regulation by resident natural enemies, including predators of other adelgids. Our results suggest the role of escape from natural enemies in the pest's rapid spread and impact in eastern Canada. In parallel, we tracked the timing of development through the complex life cycle of *A. tsugae* to compare its phenology to that in other invaded regions and to that of the closely related strain native to western North America. We discuss the implications of the local phenology of *A. tsugae* in the context of adopting a classical biological control programme, such as has been implemented in the United States of America, through the redistribution of native specialist predators of *A. tsugae* from British Columbia, Canada.

Introduction

Classical biological control (hereafter, biocontrol) can provide cost-effective, landscape-level control for invasive insect pests in forests (Kenis *et al.* 2019; but see MacQuarrie *et al.* 2016). The release of specialist natural enemies (biocontrol agents) such as predators, parasitoids, or pathogens sourced from the pest's native range aims to regulate invasive populations within the pest's new range. In the long term, biocontrol can offer a self-sustaining complement to other integrated pest management tools, such as chemical or silvicultural control, which may be insufficient in reducing pest damage below economically or ecologically acceptable levels or are not feasible over large areas (Davidson and Rieske 2016; Archer *et al.* 2022). Because biocontrol involves the introduction of nonnative species into the invaded region (Huffaker *et al.* 1976), its

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risks and benefits must be carefully considered before implementation (Abram *et al.* 2024). In cases of shared invasive pests, a biocontrol programme developed and applied in one invaded region can be adapted for use in a similar ecoregion affected by the same pest, along with the benefits of drawing on existing knowledge and expertise (Lyons 2013). However, the ecological context unique to the novel invaded region may warrant additional assessments to ensure the programme's success and efficacy (Stastny *et al.* 2025). For example, predation by the natural enemy complex already present in the newly invaded region may differ from that in other regions, with potential implications for the level of mortality required by the biocontrol agents to achieve pest control, as well as their interactions with the resident natural enemies. The life cycle of the target pest in the newly invaded region relative to its phenology in its native range or in other invaded regions must also be examined to inform the selection and, ultimately, the sourcing and releasing methods of biocontrol agents (Huffaker *et al.* 1976; Crimmins *et al.* 2020; Barker and Coop 2023; Dorman *et al.* 2024). Collectively, this basic research guides the initiation and optimisation of a biocontrol programme and establishes the foundation for further monitoring to evaluate the establishment, spread, and efficacy of biocontrol agents.

A recent damaging invasive forest pest in eastern Canada (Canadian Food Inspection Agency 2017), the hemlock woolly adelgid, *Adelges tsugae* Annand (Hemiptera: Adelgidae), is an aphid-like insect native to Japan and other parts of eastern Asia, as well as to the Pacific Northwest, that threatens hemlock, *Tsuga* spp. Carrière (Pinaceae), in eastern North America (McClure 1987; Orwig *et al.* 2012; Abella 2018). Even before its discovery in eastern Canada, *A. tsugae* had been spreading in the eastern United States of America since the mid-20th century and now occurs in that country from northern Alabama to Maine and west into Kentucky, Michigan, and Ohio (United States Department of Agriculture, Forest Service 2024). This region is marked by widespread decline and mortality of both eastern hemlock, *Tsuga canadensis* (Linnaeus) Carrière, and the endemic Carolina hemlock, *T. caroliniana* Engel (Orwig *et al.* 2012; Limbu *et al.* 2018). An ecological foundation species, eastern hemlock provides specialised habitats for biodiversity (Rohr *et al.* 2009; Ingwell *et al.* 2012) and plays integral roles in nutrient and hydrological cycling, as a frequent component of riparian corridors, and in carbon sequestration (Holmes *et al.* 2010; Li *et al.* 2014). The loss of hemlock due to *A. tsugae* has significant consequences on associated fauna, including fish (Ross *et al.* 2003), amphibians (Siddig *et al.* 2016; Ochs and Siddig 2017), birds (Tingley *et al.* 2002), and mammals (Yamasaki *et al.* 2000; Degrassi 2018). Considerable investments in research and implementation of multiple integrated pest management tactics have been dedicated to mitigating these ecological impacts in the United States of America (Aukema *et al.* 2011; Mayfield *et al.* 2023). Although effective in local or targeted applications, chemical control using systemic neonicotinoid insecticides is feasible only at the scale of select hemlock stands and may pose environmental risks to other organisms (Sweeney *et al.* 2021; Edge *et al.* 2025). Over the last two decades, in particular, biocontrol involving multiple species has been increasingly implemented in integrated pest management programmes to manage *A. tsugae* across forested landscapes in the United States of America (Mayfield *et al.* 2023).

In eastern Canada, *A. tsugae* was first detected in southern Ontario in 2012, where it has since become established in multiple locations (Canadian Food Inspection Agency 2024). In 2017, the pest was discovered in five counties of southwestern Nova Scotia, Canada (where it likely was introduced up to a decade earlier) and has since spread rapidly across the southwestern portion of the province up to and including Halifax County (Canadian Food Inspection Agency 2024). Although detection of incipient populations of *A. tsugae* is difficult, given its cryptic nature and parthenogenetic reproductive process, its invasion in eastern Canada has proceeded at a pace comparable to that observed in the United States of America (MacQuarrie *et al.* 2025), with populations rebounding quickly from near-complete mortality during severe cold spells (MacQuarrie *et al.* 2024). In Nova Scotia, *A. tsugae* has caused significant hemlock decline and mortality in 85 000 ha of forest to date (J.O., unpublished data), suggesting the symptoms and rate of tree impacts are similar to those seen in the northeastern United States of America (Orwig

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et al. 2002). The pest presents a serious threat to hemlock and its ecological and cultural value throughout most of its range in eastern Canada (Emilson *et al.* 2018; Emilson and Stastny 2019). Proactive adoption of the integrated pest management approaches that have been used to manage the pest in the United States of America offers an opportunity to expedite their implementation in Canada, potentially contributing to earlier mitigation of ecological impacts (Emilson *et al.* 2018). However, gaps remain in the basic knowledge of the pest's ecology and life cycle in the recently invaded range.

Hemlock in the eastern United States of America (and, presumably, eastern Canada) is highly susceptible to *A. tsugae* due to a lack of specialist predators of *A. tsugae* (McClure 1987; Wallace and Hain 2000) and tree resistance (Oten *et al.* 2014; but see Kinahan *et al.* 2020). Interestingly, *A. tsugae* also exists as a distinct, native strain in the Pacific Northwest, where it causes minimal damage to hemlock (McClure 1987; Havill *et al.* 2016). In that region, top–down regulation by native predators has been invoked as a significant driver of population dynamics of *A. tsugae* (Mausel *et al.* 2017; Crandall *et al.* 2022). Beginning in 1992, long-term management of the invasive *A. tsugae* has centred on the releases of multiple species of specialist predators from its native ranges, including Japan, China, and the Pacific Northwest (Havill *et al.* 2016; Mayfield *et al.* 2023). This biocontrol programme was preceded by research that demonstrated that population regulation by resident natural enemies in the invaded range in the eastern United States of America was insufficient (McClure 1987; Montgomery and Lyon 1995; Wallace and Hain 2000). The rapid spread and impacts of *A. tsugae* on hemlock in Nova Scotia strongly imply a similar lack of population regulation by resident natural enemies, but this has not been investigated.

A critical factor in the effectiveness of a biological control programme is the synchronisation of the biological control agents' development with that of the target pest in the invaded range (Godfray *et al.* 1994; Van Nouhuys and Lei 2004; Hicks *et al.* 2007; Abell *et al.* 2016). Quantification of the target's development in the invaded range is essential because the timing and duration of various life stages may vary from those observed in the insect's native range (Wolkovich and Cleland 2011). Leading to its biocontrol programme in the United States of America, the phenology of *A. tsugae* was examined extensively both in the Pacific Northwest (hereafter, "native range" for the purposes of this paper) and in the eastern United States (McClure 1987; Gray and Salom 1996; Zilahi-Balogh *et al.* 2003; Joseph *et al.* 2011; Dietschler *et al.* 2024). However, given the distinct climate of the invaded areas in Nova Scotia, the timing of *A. tsugae* life stages can be expected to differ from those reported elsewhere. These differences in phenology can have important implications for several components of integrated pest management, including monitoring, regulation, and active management. For instance, information on pest phenology helps substantiate regulatory actions by identifying high-risk periods, such as when mobile crawler stages are present. Similarly, control treatments must be applied during the appropriate developmental stage to exert population regulation, particularly in the case of biological control that uses specialist predators and parasitoids (Gray 2016; Crimmins *et al.* 2020; Barker and Coop 2023). Monitoring of the pest's development also offers insights into its population factors, such as those associated with mortality and growth, and interactions with the host tree and native fauna. Accurate phenological information on *A. tsugae* in Nova Scotia is therefore essential for the selection, sourcing, and release of specialist natural enemies in this region, as well as for informing effective regulatory parameters on movement.

Here, we present the results of a multi-year study evaluating three objectives to gain foundational knowledge about *A. tsugae* in its novel invaded range in Nova Scotia. We conducted a series of field experiments with caged hemlock branches that excluded potential resident predators to evaluate their effects on the mortality of *A. tsugae*. In parallel, we characterised the existing complex of resident natural enemies by sampling infested hemlock foliage at different periods in *A. tsugae* development in heavily infested hemlock stands. Finally, we collected detailed information on the development of *A. tsugae* in Nova Scotia over multiple years. Our objectives were (1) to determine whether resident natural enemies in Nova Scotia are regulating *A. tsugae*

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populations, (2) to identify natural enemies within this complex, and (3) to provide phenological information to guide the sourcing and release of biocontrol agents.

Methods

Study system

In eastern North America, the annual life cycle of *A. tsugae* consists of two parthenogenetic generations (sistens, progrediens), each developing through three stages (egg, four nymphal instars, and adult). For most of its life, the insect lives permanently attached to twigs inside a secreted waxy covering called an ovisac, where the adelgid lays its eggs (McClure 1987). In the spring, hatched sistens crawlers (first-instar nymphs) settle on new shoots and enter a summer diapause before resuming feeding and development in autumn. These nymphs continue development over winter and mature in early spring, when the sistens adults lay eggs. Mobile nymphs ("crawlers" of the progrediens generation) that hatch from these eggs actively search for feeding sites near the base of the needles on the previous year's shoots. Progrediens crawlers are capable of long-distance dispersal at this time of year, including on migrating birds (Russo *et al.* 2019). In its native range, significant *A. tsugae* mortality by predatory insects occurs mostly during the adult and egg stages (Mausel *et al.* 2017; Crandall *et al.* 2022; McAvoy *et al.* 2024). In eastern North America, *A. tsugae* can suffer considerable mortality during summer aestivation (McAvoy *et al.* 2017) and especially in winter, following rapid and extreme temperature fluctuations (Trotter and Shields 2009; MacQuarrie *et al.* 2024). At high infestations on *T. canadensis*, densities of *A. tsugae* are physically limited by the availability of preferred feeding locations along available shoots, leading to increasing density-dependent mortality of neonates in both generations, with a progressive reduction in new shoot production as the tree declines (Sussky and Elkinton 2014).

Study sites

The present study was carried out at several sites in southwest Nova Scotia from 2018 to 2022 (Table 1). The sites had advanced infestations of *A. tsugae* (*i.e.*, 50% or more of trees showing decline symptoms characteristic of *A. tsugae* infestation), with ovisac densities on branches being either moderate or higher (*i.e.*, $>$ 1 ovisac per cm of twig length). Sites were chosen based on the availability of hemlock branches within 2 m of the ground. All stand types were composed of more than 25% hemlock ($>$ 20 cm diameter at breast height) and consisted of other trees typical of the Acadian Forest Region, including *Quercus rubra* Linnaeus (Fagaceae), *Fagus grandifolia* Ehrhart (Fagaceae), *Acer rubrum* Linnaeus (Sapindaceae), *Pinus strobus* Linnaeus (Pinaceae), *Larix laricina* (Du Roi) K. Koch (Pinaceae), *Picea rubens* Sargent (Pinaceae), and *Abies balsamea* (Linnaeus) (Miller) (Pinaceae).

Predator exclusion experiments

To evaluate the role of predation by resident natural enemies on *A. tsugae* in Nova Scotia, we conducted predator exclusion experiments using mesh sleeve cages (1.5 m length, 150-μ mesh) around infested hemlock branches (~1 m length; Wallace and Hain 2000). The experiment was repeated in two consecutive years (2020 and 2021) at three sites (Sissiboo, Weymouth Falls, and Wentworth Lake; Table 1) and in 2022 at three new sites. In 2022, we changed experimental locations (Table 1) because of widespread hemlock decline caused by *A. tsugae* at the 2020–2021 study sites. In all experiments, we paired caged hemlock branches with open (uncaged) branches; each pair of branches was located on the same tree or on trees within 3 m of each other. Before installing the sleeve cages in early spring or late fall, we shook the branch to dislodge potential predators, then sealed the cage around the base of the branch using a plastic zip-tie.

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Table 1. Sites used for sampling of *Tsuga canadensis* foliage infested with *Adelges tsugae* in southwest Nova Scotia. We carried out beat sheet or beat net sampling (Beat sheet, Net) and sleeve cage (sleeve) studies at various sites. PT, start of the sleeve cage study, where a pretreatment sample was taken off each branch. Otherwise, collections were carried out on the month and day (for the same month) indicated below.

Site (abbreviation)	Coordinates: latitude, longitude	Year	Study	Collection
Annapolis Royal (AR)	44.701735°, −65.487239°	2022	Sleeve cage	March PT, late April, mid-May, 7 July, 20 July
Bear River (BR)	44.606310°, −65.677311°	2018–2020	Branch collection (phenology)	February (once); March, April, September, October (biweekly); May to August (weekly); November (once)
		2020	Beat sheet[§]	June, July
Bloody Creek (BC)	44.816179°, −65.305286°	2022	Sleeve cage	March PT, late April, mid-May, 7 July, 20 July
Sissiboo River Dam (SD)	44.432382°, −65.869206°	2018–2020	Branch collection (phenology)	February (once); March, April, September, October (biweekly); May to August (weekly); November (once)
		2020	Sleeve cage	March PT, October[*]
		2021	Beat sheet	March, April, May
Kejimkujik (K)	44.404975°, −65.249838°	2020	Beat net	June, July
		2021	Beat net	April
MacKay Lakes (ML)	43.923872°, −65.417665°	2020	Beat sheet	November
		2022	Sleeve cage	March PT, late April, mid-May, 7 July, 20 July
Sissiboo “F” (SF)	44.439053°, −65.882868°	2020	Sleeve cage	March PT, October[*]
		2020	Beat sheet[§]	April, May, June, July, October
		2021	Sleeve cage	October 2020 PT, late April, mid-May, 10 July, 21 July
		2021	Beat sheet	March, April, May, July
Ten Mile Lake (TML)	44.186444°, −64.833390°	2020	Beat sheet	November

(*Continued*)

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Table 1. (*Continued*)

Site (abbreviation)	Coordinates: latitude, longitude	Year	Study	Collection
Weymouth Falls (WF)	44.420223°, −65.878250°	2020	Sleeve cage	March PT, October*
		2020	Beat sheet	October
		2021	Sleeve cage	October 2020 PT, late April, mid-May, 10 July, 21 July
		2021	Beat sheet	July
Wentworth Lake§ (WL)	44.182221°, −65.942225°	2019, 2020	Branch collection (phenology)	February (once); March, April, September, October (biweekly); May to August (weekly); November (once)
		2020	Sleeve cage	March PT, October*
		2020	Beat sheet§	Late April, mid-May, mid-June, July, October
		2021	Sleeve cage	October 2020 PT, late April, mid-May, 10 July, 21 July 2021
		2021	Beat sheet	March, April, May, July

§Samples were pooled by site for the April, May, June, and July collections.
*Due to COVID-19 travel restrictions, only an October collection was possible in 2020 following the March 2020 setup.

All experiments began with a pretreatment assessment of the initial density of live *A. tsugae* (third-instar nymphs in fall and fourth-instar nymphs in spring) on all branches before installing cages in late fall or early spring each year. After cage installation, we sampled all branches four distinct times during the spring and summer months: twice during each of the predicted peaks of progrediens and sistens egg stages, respectively, at two- to three-week intervals except in 2020 (see next paragraph).

In November 2019, we selected 20, 30, and 15 pairs of branches that were moderately to heavily infested by *A. tsugae* (*i.e.*, three or more ovisacs per centimetre of twig) at each of the three sites, respectively. In the spring and summer of 2020, COVID-related travel restrictions prevented twig sampling during the peak oviposition periods. Instead, we sampled in March and October of 2020 (when this year's experiment ended). In late March 2021, we set up 10 pairs of branches at the same sites but selected new trees with lower densities of *A. tsugae* (*i.e.*, ≤ 1 ovisac per centimetre of twig length) because we found that selecting more heavily infested branches resulted in branch dieback in both treatments by the end of the 2020 season. In 2021, COVID-related travel restrictions necessitated site visits by a local contractor (Mersey Tobeatic Research Institute, Caledonia, Nova Scotia), who subsampled branches haphazardly by removing a subterminal twig at the appropriate sampling times and shipping them to the Atlantic Forestry Centre quarantine laboratory (Natural Resources Canada, Canadian Forestry Service; Fredericton, New Brunswick, Canada) for processing.

In 2022, we set up 11, 12, and 15 pairs of branches at the Bloody Creek, Annapolis Royal, and McKay Lakes sites, respectively. In all three years, we collected a twig sample (25 cm length) from all branch tips. Except as noted above, we collected twig samples before treatment and twice (*i.e.*, 2–3 weeks apart) during the peak oviposition period of the *A. tsugae* sistens and progrediens adult stages. Twig samples were kept at 4 °C until they could be processed, usually within 2–4 weeks of collection, except in 2020 (within two months of collection, due to COVID-related work restrictions).

For all twig samples, we counted the number of ovisacs on the 12 most distal current-year (new growth) shoots or one-year-old twigs per branch, or until approximately 100 ovisacs had been counted. We also measured the length of each twig to determine the density of intact ovisacs containing live *A. tsugae* per centimetre of twig length. Outside of the egg periods of *A. tsugae*, we differentiated between live and dead *A. tsugae* nymphs based on movement (*i.e.*, leg movement or peristalsis). To facilitate this assessment, samples were placed at room temperature the night before being processed. During the egg periods of *A. tsugae*, we recorded any adult that was moving or had produced eggs in an intact ovisac as "live." We counted the total live *A. tsugae* on a subsample of the branch tips in 2020 (*i.e.*, sistens sample 3) and in 2021 (*i.e.*, sistens sample 1). Only replicates with intact (undamaged) cages at the time of assessment were included in the analyses.

Because the level of infestation affects tree growth, the relative health of the sampled branches varied among trees. For example, some branch tips had ample new shoots, whereas others had none. When adelgids settle on portions of twigs that are older than the preferred current growth, their survival is significantly decreased (McClure 1991). For this reason, from all clippings, we sampled ovisacs from current-year shoots, with a supplementary assessment of the previous year's (*i.e.*, one-year-old) twigs if new growth was not available.

Surveys of natural enemies

We employed two complementary methods to examine the diversity and abundance of natural enemies found on *A. tsugae*–infested hemlock foliage in southwest Nova Scotia. The first method relied on dissection of ovisacs on branches collected from the open treatment during the predator exclusion experiment, allowing for detection of arthropods (including immature life stages or puparia) present on the twigs (entire sample) or directly in association with *A. tsugae* ovisacs

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(12 most distal current-year – new growth – shoots or one-year-old twigs, inspecting up to approximately 100 ovisacs; see above). The second method involved beating foliage to dislodge and collect arthropods several times throughout the year, as described below. Samples of potential natural enemies were put in 95% ethanol until they could be identified.

Beat sheet sampling

This method consisted of placing a 1-m^2 beat sheet underneath two hemlock branch tips (~1 m^2 of foliage) per tree and vigorously striking the top surface of the branch tips 5–6 times with a PVC rod to dislodge any arthropods present on this foliage (Mausel *et al.* 2010). However, on one occasion, branches at two sites were sampled using a sleeve cage, instead of a sheet (Wallace and Hain 2000), wherein we enclosed the distal 1 m of a branch within a mesh sleeve (1.5 m in length, sampling about 0.5 m^2 of foliage) and then vigorously shook the branch for 30 seconds to dislodge any arthropods. We collected the arthropods found on the sheet or in the sleeve cage, placing them in 41-mL glass vials filled with 95% ethanol.

Sampling took place at each site several times per year for a two-year period (Table 1). On each visit, we sampled between 10 and 30 trees and from two to four branch tips from each tree, or approximately 2 m^2 of hemlock foliage. Samples from Bear River, Sissiboo, and Wentworth Lake in the spring and summer of 2020 were pooled among trees. In the laboratory, we sorted the samples to species where possible, targeting the Coleoptera, Hemiptera, Diptera, Hymenoptera, and Neuroptera because these groups contain most of the natural enemies that may feed on *A. tsugae* in eastern North America (Montgomery and Lyon 1995; Wallace and Hain 2000; Wantuch *et al.* 2019). In addition to the native *Laricobius rubidus* Leconte (Coleoptera: Derodontidae), we focused on checking for the presence of any specialised adelgid or aphid predators, which we identified to species level where possible, that could be expected to adopt this novel prey, such as coccinellids (Coleoptera) and silver fly larvae (Chamaemyiidae).

Adelgid phenology

The study was conducted at three *A. tsugae*–infested hemlock stands of similar size, species composition, and infestation severity within the western counties of Nova Scotia: Sissiboo, Bear River, and Wentworth Lake Municipal Park (Table 1) in 2019 and 2020. Sites were spread across southern Nova Scotia and encompassed different climatic conditions. Each site was sampled once in November and in February, biweekly in March, April, September, and October, and weekly from May to August each year, according to anticipated transitions in insect development as have been observed in the northeastern United States of America (Connecticut; McClure 1987). At each site and for each sampling date, one branch tip (45 cm length) with *A. tsugae* was collected from each of 10 randomly selected hemlock trees. All samples were processed the following day. At each visit, up to 50 adelgids per branch tip were examined while focusing on the most current growth available at the time (*i.e.*, up to 500 adelgids per site per visit). The observations were pooled across branches for each site and averaged among sites for each time point.

Statistical analysis

We fit a negative binomial generalised mixed effect linear model (function *glmer.nb* in R) to compare differences in the density of live, intact *A. tsugae* ovisacs as the response variable, using branch treatment (caged; open) as a fixed factor and *site* as a random effect in the model. We analysed each year and collection period separately due to changing protocols for the assessment of twigs as described above; in all cases, analyses for the current-year and previous-year shoots were separate. We fit and tested the assumptions of our models by examining residual plots and dispersion parameters of our models, as described in Zuur *et al.* (2009). Analyses were carried out

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Table 2. Effect of the experimental exclusion of predators on the density of live, intact *Adelges tsugae* ovisacs on current-year shoots of *Tsuga canadensis*, comparing branch tips enclosed in sleeve cages *versus* open (uncaged) branch tips (treatment) over multiple sites and sampling periods from 2020 to 2022. Each sampling period was analysed separately (see text for details). Pretreatment samples denote the initial *A. tsugae* density before branch caging. See Table 1 for details on the timing of sampling. *In 2020, sistens sample 3 involved one-year-old twigs instead, due to a lack of current growth.

Response variable: density of live, intact ovisacs				
Year	Sample	*d.f.*	c^2	$P > c^2$
2020	Sistens pretreatment	1,105	2.20	0.14
	Sistens sample 3	1,13	0.01	0.91
	Sistens sample 3*	1,112	2.68	0.10
2021	Sistens pretreatment	1,57	2.85	0.09
	Sistens sample 1	1,50	0.01	0.99
	Sistens sample 2	1,46	0.01	0.91
	Progrediens sample 1	1,32	0.63	0.43
	Progrediens sample 2	1,53	2.87	0.09
2022	Sistens pretreatment	1,71	0.24	0.62
	Sistens sample 1	1,68	3.29	0.07
	Sistens sample 2	1,67	0.45	0.50
	Progrediens sample 1	1,52	0.28	0.59
	Progrediens sample 2	1,71	0.05	0.83

in the R statistical computing environment, version 3.4.3 (R Core Team 2017). The glmer.nb model was fit using functions in the mass package (Venables and Ripley 2002). Means were separated using functions in the emmeans package (Lenth 2023).

Results

Predator exclusion experiments

In all three years, the initial, pretreatment density of live *A. tsugae* on new shoots did not differ significantly between caged and open branch tips (Table 2; Fig. 1). In 2020, the density of live *A. tsugae* (sistens generation) remained similar between the two treatments for the October sampling period (sample 3). Likewise, at the four sample periods in both 2021 and 2022, the density of live, intact ovisacs on caged branches was similar to those on open branches (Table 2; Fig. 1). We also did not detect differences in density of live *A. tsugae* between the treatments on one-year-old twigs on the branch tips (Supplementary material, Fig. S1).

Surveys of natural enemies

Ovisac dissections. We did not find any adult life stages of natural enemies during branch dissections, and we found very few immature specimens. For example, we found 2, 32, and 4 fly larvae in 2020, 2021, and 2022, respectively, including from the caged branches. Most of these larvae (29 of 38) were collected during the *A. tsugae* sistens egg stage in summer, with the remainder collected during the progrediens egg stage in spring. Six of 38 specimens were identified using DNA barcodes (see Havill *et al.* 2018): these comprised five *Aphidoletes* spp. Kieffer (Diptera: Cecidomyiidae) and one *Scaptomyza* sp. Hardy (Diptera: Drosophilidae) (Nathan Havill, personal communication). The DNA

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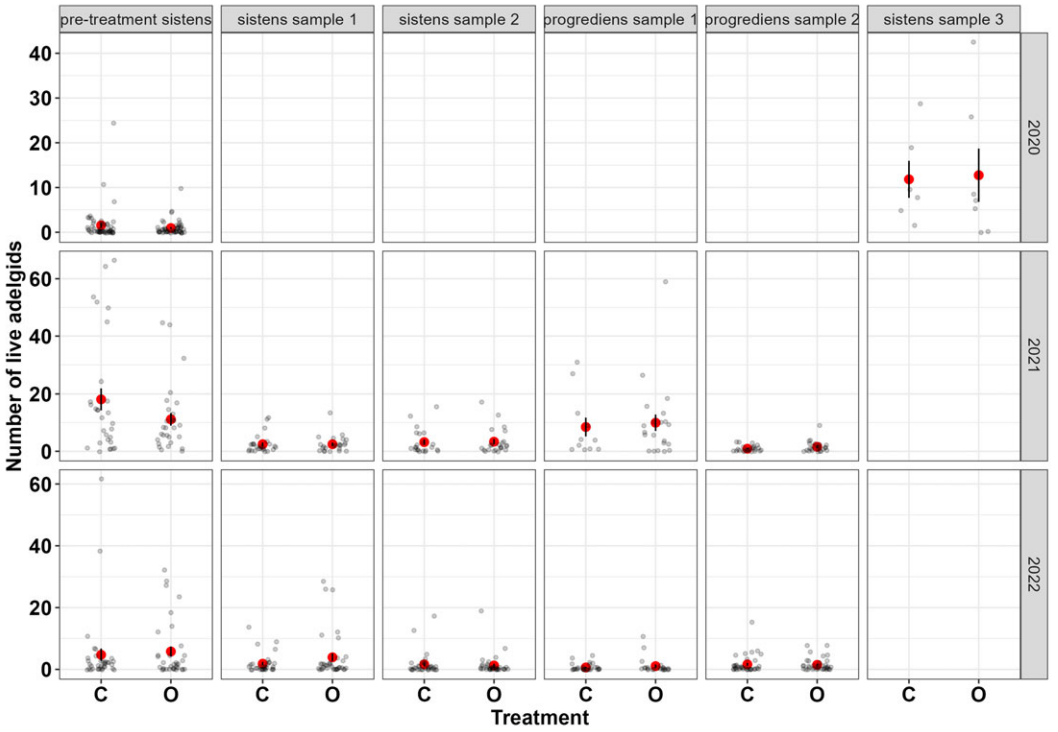


Figure 1. Density (number of intact ovisacs containing live *A. tsugae* per 10 cm of shoot ± standard error) of live, intact *Adelges tsugae* ovisacs at six sampling points in 2020–2022 on *Tsuga canadensis* branches in southwest Nova Scotia, Canada, comparing caged (C) branches that excluded predators *versus* open (O) branches. Grey dots show raw density (jittered for visualisation) per branch tip. Timing of sampling: March for pretreatment sistens in 2020 and March in 2021 and 2022; May and June for sistens samples 1 and 2; July for progrediens samples 1 and 2; October for sistens sample 3. See text for details.

barcoding for the remaining 32 was not successful because of DNA degradation. Four of the *Aphidoletes* spp. collected in 2021 and identified *via* molecular methods were entered into GenBank (National Center for Biotechnology Information; https://www.ncbi.nlm.nih.gov/genbank/) with the following sequences: PV563528, PV563529, PV563530, and PV563531. The remaining *Aphioletes* sp. was not assigned a GenBank number at the time of processing, and the *Scaptomyza* sp. was excluded because this genus does not include predators.

Beat sheet sampling. We recovered approximately 2653 arthropod specimens from beat sheet sampling during 2020 and 2021 (Table 3; Fig. 2). Of these, approximately 77% were spiders, with the remainder (~23%) being insects. Coleoptera and Diptera represented 1.7% and 15.8% of the total arthropods collected, respectively, when data were pooled from 2020 and 2021, whereas Hymenopterans and Neuropterans represented 3.24% and less than 1%, respectively. Our surveys did not detect any specialist predators of adelgids, such as the nonnative *Laricobius erichsonii* Rosenhauer (Coleoptera: Derodontidae) released repeatedly in the mid-1900s to control the introduced balsam woolly adelgid, *Adelges piceae* (Ratzeburg), or *Laricobius rubidus* LeConte, a native predator of the native pine bark adelgid, *Pineus strobi* (Hartig) (Hemiptera: Adelgidae) (Clark and Brown 1958; Zilahi-Balogh *et al.* 2005). We did not detect any adult chamaemyiids, which in their larval stage are also native predators of *P. strobi*. Of the notable generalist predators

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Table 3. List of insect predators collected using beat sampling (sheet or net) in eastern hemlock stands infested by *Adelges tsugae* in southwestern Nova Scotia, Canada, in 2020 and 2021. Site locations (see Table 1 for coordinates) are listed using the following abbreviations: WL, Wentworth Lakes; SF, Sissiboo "F"; ML, MacKay Lakes; SD, Sissiboo Dam. Asterisk denotes a specimen that was in larval form at the time of collection; all others were adults; "*n*" indicates the number of individuals (adults or larva/nymph) collected on the date of sampling.

Order	Family	Species	Site	Date (dd Month yyyy)	*n*
Coleoptera	Coccinellidae	*Harmonia axyridis* (Pallas)	WL	20 July 2020	2
Coleoptera	Coccinellidae	*H. axyridis*	WL	20 July 2020	2*
Coleoptera	Coccinellidae	*H. axyridis*	SF	21 July 2020	3
Coleoptera	Coccinellidae	*H. axyridis*	WL	29 October 2020	5
Coleoptera	Coccinellidae	*H. axyridis*	ML	6 November 2020	1
Neuroptera	Chrysopidae		SD	20 July 2020	1*
Neuroptera	Chrysopidae		WL	20 July 2020	4
Coleoptera	Coccinellidae	*H. axyridis*	WL	20 July 2020	1
Coleoptera	Coccinellidae	*H. axyridis*	WL	21 July 2020	2*
Coleoptera	Coccinellidae	*H. axyridis*	SF	21 July 2020	3
Neuroptera	Chrysopidae		WL	20 July 2020	1*
Neuroptera	Chrysopidae		WL	20 July 2020	2
Neuroptera	Chrysopidae		SD	21 July 2020	1

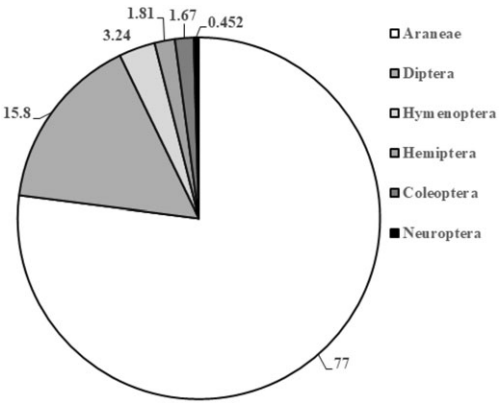


Figure 2. Arthropods with eastern hemlock (*Tsuga canadensis*) foliage infested with *Adelges tsugae* during beat sampling in southwest Nova Scotia, Canada, during 2020 and 2021. Numbers represent the percentage of total arthropods ($n = 2653$) collected using beat sampling (beat sheet or beat net).

reported from *A. tsugae* population surveys in the United States of America (*e.g.*, McClure 1987; Montgomery and Lyon 1995; Wallace and Hain 2000), we recovered only *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) ($n = 11$; Table 3; Supplementary material, Table S1), and several chysopids (Neuroptera) ($n = 10$; Table 3; Supplementary material, Table S1).

Adelgid phenology

The patterns observed in the timing of development were generally consistent between the 2019 and 2020 datasets; because of this, to better highlight regional phenology, we amalgamated all data into

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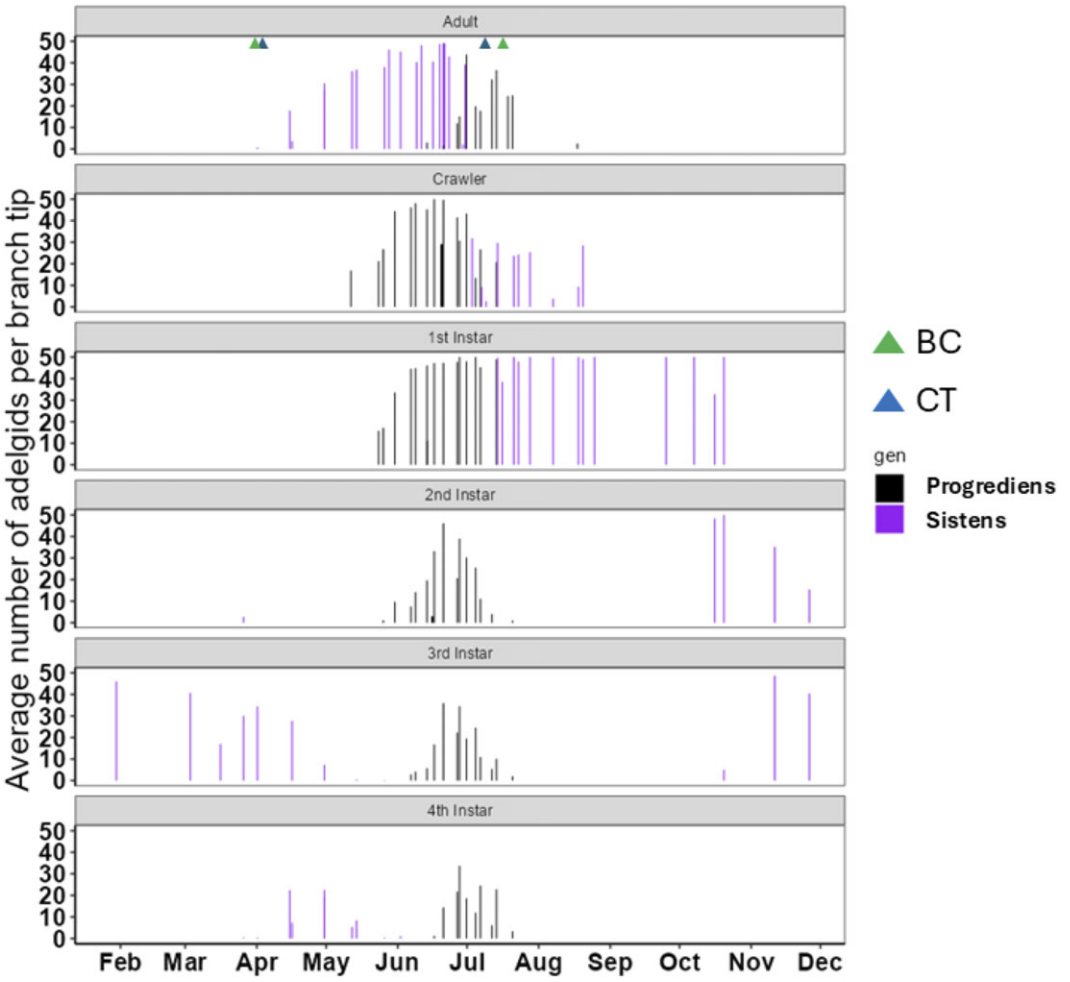


Figure 3. The occurrence of life stages of *Adelges tsugae* on *Tsuga canadensis* in southwest Nova Scotia, Canada, averaged across multiple sampling sites for 2019 and 2020; see text for details. The adult stage also includes the egg stage. For reference, triangles indicate the midpoints of the observed occurrence of progrediens and sistens egg stages, respectively, in Connecticut, United States of America (CT; invaded range) and British Columbia, Canada (BC; native range), as reported in McClure (1987) and Zilahi-Balogh *et al.* (2003).

one visualisation (Fig. 3). Adult sistens with eggs (Fig. 3, purple bars) were observed from late April to early July. These eggs gave rise to progrediens crawlers (Fig. 3, black bars), which we observed on foliage from mid-May to mid-July each year. Progrediens developed over a 10-week period, with each instar and adults with eggs overlapping considerably from mid-May to mid-July each year. The sistens crawlers (purple bars) were active from mid-July to late August each year, entering an aestival diapause that lasted until early October. Following this diapause, sistens nymphs developed rapidly in fall, attaining the third-instar stage before the end of December. Adelgids remained as third-instar nymphs until the end of March, when they became fourth-instar nymphs. It took about a month thereafter for adults to appear in the population (Fig. 3). We noted considerable overlap of the egg and crawler stages of the sistens and progrediens generations.

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Discussion

Throughout our predator exclusion experiments, we observed similar densities of live *A. tsugae* in both open and caged branches, suggesting a dearth of resident natural enemies that have adopted the pest as prey. This observed pattern was consistent among years, sites, and collection periods within each year and was similar to findings from the United States of America (McClure 1987; Montgomery and Lyon 1995; Wallace and Hain 2000). Our experiments demonstrate that *A. tsugae* in southwestern Nova Scotia does not experience sufficient predation by resident natural enemies to prevent deleterious effects on hemlock. Indeed, we had to abandon the sites used in 2020 and 2021 due to severe decline of hemlock canopy (including some tree mortality) under increasing *A. tsugae* infestations, and we observed similar dynamics at the sites of our phenological and beat sheet sampling (see below). The lack of natural enemies that prey on the two generations of *A. tsugae* is likely a key factor in the rapid buildup and spread (*i.e.*, 12–13 km per year in Nova Scotia; MacQuarrie *et al.* 2025) of *A. tsugae* and of subsequent damage to hemlock in southwestern Nova Scotia.

Importantly, our surveys of advanced infestations did not detect any specialist native predators on *A. tsugae*, despite our study spanning multiple years and multiple sites to account for spatiotemporal fluctuations of predator populations, as suggested by Wallace and Hain (2000). This result is surprising, given that two adelgid specialist derodontids, *L. rubidus* and *L. erichsonii*, have been recorded from southwest Nova Scotia (Majka 2007), and *A. tsugae* has likely been present in the region for at least a decade (Stastny *et al.* 2024). The pine bark adelgid predator, *L. rubidus*, can complete development on *A. tsugae* and has been found in association with *A. tsugae* populations in the eastern United States of America (Zilahi-Balogh *et al.* 2005; Fischer *et al.* 2015; McAvoy *et al.* 2024); *L. erichsonii* was widely released in Atlantic Canada for biological control of the balsam woolly adelgid (Clark and Brown 1958), although host range information for this species is lacking. Our findings highlight that the absence of specialist natural enemies may partly explain the rapid spread and impacts of *A. tsugae* in Nova Scotia, similar to the circumstances in the eastern United States of America (Wallace and Hain 2000). In contrast, *A. tsugae* appears to be well regulated by predators in the Pacific Northwest (*e.g.*, Lamb *et al.* 2005; Crandall *et al.* 2022).

We report here a few noteworthy observations from our predator exclusion experiment. First, we did occasionally collect larval Diptera foraging in twig samples of caged branches, indicating that female flies managed to oviposit through the mesh or before its installation. We were able to identify these species through molecular diagnostics of six specimens: five of these were *Aphidoletes* spp., and one was *Scaptomyza* sp. Wallace and Hain (2000) had recovered *Aphidoletes* spp. as both adults and larvae in Virginia, United States of America, although numbers of both were low. One species, *Aphidoletes thompsoni* (Möhn), was released in eastern Canada as a biological control agent for *A. piceae* in Nova Scotia in 1966 and 1967, although no measurable effect on *A. piceae* was recorded (Schooley *et al.* 1984). In most instances when we found fly larvae within the cages, it was in areas already sustaining heavy impacts from *A. tsugae*. We did not observe fly larvae preying on live *A. tsugae*. Second, we observed that twig samples from caged branches appeared to be healthier than those from open branch tips. We suspect the cages prevented immigration from *A. tsugae* crawlers dispersing from the canopy and thus greatly reduced the propagule pressure on these replicates. Lastly, when cages were left in place for an extended period (2020), we did not see differences in the density of *A. tsugae* on caged and open branches (Figs. 2 and 3), suggesting that the physical effect of the cages did not have a major influence on the outcomes.

Our surveys of arthropod communities in infested hemlock stands in southwest Nova Scotia, using beat sheet sampling as a complementary method to detect dominant and relatively host-specific natural enemies, yielded primarily generalist and opportunistic predators. The majority (77%) of these were spiders, which are increasingly recognised as an important source of generalist predation of forest insect pests (Riechert 1999; Bowden *et al.* 2023). Although spiders have not yet

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been shown to suppress populations of *A. tsugae*, ascertaining their possible direct or indirect effects (*via* consumption of *A. tsugae* or of biocontrol agents, respectively) may increase our understanding of *A. tsugae* population regulation (Mallis and Rieske 2011). The next most common group of natural enemies that were collected were Diptera (16% of all arthropod specimens), primarily as larvae and adults, but we found no adelgid specialist dipteran or coleopteran predators (< 2.0% of individuals collected). Both *Laricobius rubidus* and *La. erichsonii* are adelgid specialists found in Nova Scotia (Majka 2007), with *La. rubidus* observed to both feed and complete development on *A. tsugae* in both lab and field studies (Zilahi-Balogh *et al.* 2005; Story *et al.* 2012). The most common coleopteran predator that we collected was *H. axyridis*. *Harmonia axyridis*, a ubiquitous, introduced polyphagous predator of aphid and coccid species, has been recovered during *A. tsugae* natural enemy surveys and field experiments in the United States of America (Wallace and Hain 2000; Mausel *et al.* 2008). Although observed to feed on both *A. tsugae* sistens ovisacs and adults (Flowers *et al.* 2005), *H. axyridis*'s regulation of *A. tsugae* populations in field evaluations is minimal (Mausel *et al.* 2008; but see Flowers *et al.* 2006). Similar to other surveys, we recorded the presence of adult lacewings (Neuroptera: Chrysopidae) (McClure 1987; Wallace and Hain 2000), although numbers were low even when compared with the small numbers of other insects collected in 2020 and 2021.

Collectively, these findings are significant because we conducted our surveys at sites with advanced infestations of *A. tsugae*, with high abundances of this alternate prey. On the other hand, its infestations may have displaced native insects, whose predators may not have yet adapted to *A. tsugae* as a prey source or may not have yet increased numerically in response to its availability. Branch sampling that involves rearing out insect material has been used to evaluate *Laricobius* spp. abundance (Mausel *et al.* 2010) and may be more suitable for specialist predators associated with hemlock woolly adelgid ovisacs or for species that are rare or difficult to dislodge. However, in combination with the predators found during sampling of open branches, we conclude, based on our sampling methods, that the resident natural enemy complex in Nova Scotia exerts only minor and incidental predation that does not offset this pest's high population growth rates.

The phenology of an invasive insect is a key factor in its population dynamics and interactions with natural enemies in a new region, with implications for pest management that includes biocontrol (Stastny *et al.* 2025). The most conspicuous difference in the development of *A. tsugae* in Nova Scotia compared to other well-studied invaded regions was the relatively delayed onset of the progrediens egg and crawler stages (Fig. 3), which occurred at least a month later than in the populations found in Virginia (Gray and Salom 1996) and Connecticut (McClure 1987). We suspect that the timing of development in Nova Scotia is similar to that in maritime regions of the northeastern United States of America (*e.g.*, southern Maine, coastal New Hampshire, and Massachusetts), which share the same plant hardiness zones; however, published data on *A. tsugae* phenology in these regions are lacking. The relative asynchrony in development between Nova Scotia and British Columbia (Zilahi-Balogh *et al.* 2003) is unsurprising, given the differences in climate (*i.e.*, plant hardiness zones 5b, 6a, 6b in Nova Scotia *versus* 8a–8b in British Columbia), the role of photoperiod in the phenology of *A. tsugae* (Salom *et al.* 2001), and the fact that the invasive strain originated from Japan (Havill *et al.* 2016). We nonetheless observed similar timing of the peak sistens egg stage and aestivation break between the two regions (Fig. 3; Zilahi-Balogh *et al.* 2003). This phenological match is particularly important because, in British Columbia, it coincides with the aestivation break of one of the region's native specialist predators of *A. tsugae*, the beetle, *Laricobius nigrinus* Fender (Coleoptera: Derodontidae) (Zilahi-Balogh *et al.* 2003), which feeds on developing sistens nymphs. This beetle has been released as a biocontrol agent in eastern North America since 2003 (Mayfield *et al.* 2023), and the developmental synchrony between this predator sourced from coastal British Columbia and *A. tsugae* in its invaded range is critical to its successful establishment (Zilahi-Balogh *et al.* 2003; Mausel *et al.* 2008).

The patterns of development of *A. tsugae* that we observed in Nova Scotia were consistent between 2019 and 2020 and highlight the characteristics of the pest's complex life cycle. Previous

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studies (McClure 1987; Gray and Salom 1996) reported a significant sequential overlap of *A. tsugae* life stages, although outside of the targeted periods for biocontrol. In Virginia, Gray and Salom (1996) found up to 12 different life stages present across multiple sites in late May; in Nova Scotia, we observed a similar overlap, with a maximum of eight life stages co-occurring in June (Fig. 3). Phenological studies previously conducted in Virginia (Gray and Salom 1996), Connecticut (McClure 1987), and in the native range of *A. tsugae* in British Columbia (Zilahi-Balogh *et al.* 2003) show significant yearly fluctuations in *A. tsugae* development, and these may become more pronounced with increased weather stochasticity under climate change. Our study provides baseline phenology data for current climatic conditions and a reference for comparisons with other regions and plant hardiness zones in eastern Canada that are likely to be invaded by the pest in the future.

Multiple strategies are needed to suppress *A. tsugae* infestations to mitigate its continued spread and ecological impacts in eastern North America (Emilson and Stastny 2019; Mayfield *et al.* 2023). Our study highlights the negligible effect of predation by the resident natural enemies associated with *A. tsugae* in Nova Scotia. The lack of population regulation in the pest's invaded range has been invoked as the basis of a biocontrol component of integrated pest management for *A. tsugae*. In the eastern United States of America, efforts to control the invasive pest now involve, to a varying degree, several specialised predators that are phenologically synchronised with its prey: the beetles *Laricobius nigrinus* and *La. osakensis* (Montgomery and Shiyake), and the silver flies *Leucotaraxis argenticollis* (Zetterstedt) and *Le. piniperda* (Malloch) (Diptera: Chamaemyiidae) (Mayfield *et al.* 2023). Except for *La. osakensis,* which is native to Japan, these predators are native to British Columbia and other areas of the Pacific Northwest, where they appear to exert strong population regulation (Crandall *et al.* 2022). A similar biocontrol programme has been recommended to control the invasive *A. tsugae* in eastern Canada (Emilson *et al.* 2018; Emilson and Stastny 2019; Stastny *et al.* 2024), and research is underway to examine the candidate agents' suitability and to optimise their sourcing and releases. Our findings suggest that Nova Scotia is phenologically well suited for the redistribution of *La. nigrinus* from its native populations in British Columbia, but *Leucotaraxis* silver flies are less suitable due to the marked asynchrony between *A. tsugae* eggs in British Columbia and in Nova Scotia. In combination with the existing data from other invaded regions in the United States of America, our study provides baseline information to guide a phased adoption of an existing biocontrol programme to reduce the pest's impacts on eastern hemlock in Canada.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.4039/tce.2025.10018.

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