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Effect of a severe cold spell on overwintering survival of an invasive forest insect pest

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ABSTRACT

Cold temperatures can play a significant role in the range and impact of pest insects. Severe cold events can reduce the size of insect outbreaks and perhaps even cause outbreaks to end. Measuring the precise impact of cold events, however, can be difficult because estimates of insect mortality are often made at the end of the winter season. In late January 2023 long-term climate models predicted a significant cold event to occur over eastern North America. We used this event to evaluate the immediate impact on hemlock woolly adelgid (*Adelges tsugae* Annand) overwintering mortality at four sites on the northern edge of the insects invaded range in eastern North America. We observed complete mortality, partial mortality and no effects on hemlock woolly adelgid mortality that correlated with the location of populations and strength of the cold event. Our data showed support for preconditioning of overwintering adelgids having an impact on their overwintering survival following this severe cold event. Finally, we compared the climatic conditions at our sites to historical weather data and previous observations of mortality in Nova Scotia. The cold event observed in February 2023 resulted in the coldest temperatures observed at these sites, including the period within which hemlock woolly adelgid invaded, suggesting cold conditions, especially under anthropogenic climate forcing, may not be a limiting factor in determining the ultimate northern range of hemlock woolly adelgid in eastern North America.

Introduction

In North America cold temperatures constrain the range and impact of native forest pests like the mountain pine beetle (Bleiker and Smith 2019), southern pine beetle (Lesk et al., 2017) and spruce budworm (Gray 2007); and introduced forest pests like the spongy moth (Régnière et al., 2008) and emerald ash borer (Cuddington et al., 2018). Our understanding of the impact of cold is informed by either measuring survival in populations at the end of winter (e.g., Trotter and Shields 2009) or measuring supercooling points of individuals under laboratory conditions (e.g., Duell et al., 2022) both of which have proved useful in making predictions about short and long-term behaviour of insect pest populations, particularly under climate change (Safranyik et al., 2012; Weed et al., 2013; MacQuarrie et al., 2019). Insect populations, however, are also subject to stochastic extreme weather events that, while well characterized, are not usually included in models. Estimating how populations are impacted in the short term can assist with deciding treatment and monitoring regimes in the following year. These short-term estimates can also allow the calibration of models against real world observations.

The hemlock woolly adelgid (*Adelges tsugae*) is an invasive forest insect in eastern North America. Hemlock woolly adelgid is also found in western North America where it is a native species but not a significant forest pest. By contrast, in eastern North America it has been responsible for significant eastern hemlock (*Tsuga canadensis*) mortality over the past 70 years, resulting in ecological and economic impacts on forests (Emilson et al., 2018). Hemlock woolly adelgid was introduced to North America from Japan (Havill et al., 2006; Havill et al., 2016) and was first

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detected in Virginia in the 1950s (McClure 1987). Since then, it spread throughout most of the range of eastern hemlock in the United States (Morin et al., 2009; Fitzpatrick et al., 2012). The insect was first detected in Ontario, Canada in 2012, though these populations were eradicated (NAPPO 2012, 2014). Subsequent detections of large, well established populations were made in Nova Scotia in 2017 and in southern Ontario in 2019 and, as of 2023, the insect had spread to most of the south-western part of Nova Scotia, parts of the Niagara Peninsula of Ontario and one site on the north shore of Lake Ontario (CFIA 2023).

As hemlock woolly adelgid has expanded its range northwards several studies have assessed its overwintering cold tolerance. Early work showed that hemlock woolly adelgid did not survive below −25 to −30 °C, that insects in late winter had lower survival than insects collected in mid-winter and that insects from the southern part of the invaded range survived at lower rates than insects from the northern, colder, parts of the range (Parker et al., 1998; Parker et al., 1999; Skinner et al., 2003) and that survival was correlated with changes in the heamocyte composition of overwintering insects (Gouli et al., 2000). Overwintering mortality in populations can range from 0 to 100 % depending on where populations are sampled and the intensity of winter at a given site (Shields and Cheah 2005; Paradis et al., 2007; Trotter and Shields 2009; McAvoy et al., 2017) and common garden experiments suggest that adaptation to colder winter temperatures is occurring as the species moves northwards (Butin et al., 2005; Lombardo and Elkinton 2017). Supercooling points of hemlock woolly adelgid also vary among seasons and years in populations of hemlock woolly adelgid from the same location (Elkinton et al., 2017; Lombardo and Elkinton 2017) with the lowest supercooling points of below −25 °C observed for populations from Massachusetts in February of 2015 (Elkinton et al., 2017). These combined observations have led to the development of a hypothesis that cold tolerance of hemlock woolly adelgid is influenced by the conditions it experiences prior to experiencing a cold event (McAvoy et al., 2017), a phenomena sometimes called 'preconditioning'.

With increased anthropogenic climate forcing, the duration and severity of the cold spells at mid-latitudes has decreased (Lu et al., 2018). Climate change-induced Arctic amplification may also weaken the jet stream at mid-latitudes, leading to more important 'wavy' patterns in the Northern hemisphere (Francis and Vavrus 2012). In winter, such patterns could result in the occasional intrusions of cold polar airmasses into more southern areas (Francis and Vavrus 2012). Areas in southern Canada and the northern United States can experience significant, and often rapid, drops to temperatures below −25 °C or −30 °C when these intrusions occur over North America. Previous events have correlated with significant mortality in populations of hemlock woolly adelgid in 2014 and 2016 (Lombardo and Elkinton 2017; Tobin et al., 2017). Severe cold spell events, however, are unpredictable over the time scales used in distribution models for hemlock woolly adelgid, even though they can have significant effects on predicting long-term population stability (Paradis et al., 2007; Tobin et al., 2013). These events also provide an opportunity to test the predictions of survival models against real-time weather conditions.

In early February 2023, North America experienced a short-lived but significant cold spell event (NOAA NCEI 2023). On February 3rd and 4th, a cold front swept the northeastern part of the continent, bringing very strong northerly winds and an Arctic air mass with temperatures below −30 °C and even −40 °C as to southern Ontario (ECCC 2023b) and the northeastern US (NOAA NCEI 2023) (Figure S1). Notably, daily record lows were widespread in southeastern Canada and New England during this time period. Minimum temperatures (T_{min}) associated with this cold spell were at least 5 °C colder than the average extreme T_{min} for February for a large swath of southeastern Canada, which represents *a* > 2 standard deviation anomaly compared with the 1991–2020 reference period (ESCER 2023). This event was predicted by weather observations and predictive models approximately 1 week before the event occurred i.e., Environment and Climate Change Canada's (ECCC) Global Determinist Prediction System (ECCC 2023a), the European Centre for Medium-Range Weather Forecasts (2023), and the United States' Global Forecast System (NOAA 2023).

Given the strong agreement among the long-term weather model predictions, we recognized that this was a unique opportunity to assess the instantaneous effect of a severe cold spell event on hemlock woolly adelgid mortality. Therefore, we designed a study to quantify mortality at infested sites in Canada by measuring survival immediately before and immediately after the event. We then compared this short-term mortality to seasonal observations of hemlock woolly adelgid mortality from Nova Scotia from the previous 4 winters.

Methods

We sampled four locations with known infestations of hemlock woolly adelgid 1 or 2 days prior to the predicted cold spell event, and then again 4 or 12 days after the event occurred (Fig. 1). Two sites were located in the province of Nova Scotia, Canada near Annapolis Royal (44.7354; −65.4470) and Mersey River (44.4788; −65.2217) and a third site was located in Ontario, Canada near Wainfleet (42.8815, −79.4248) (Fig. 2). A fourth site near Grafton, Ontario (43.9779, −78.0317; Fig. 2), could not be sampled before the cold event, but was sampled ca. 4 weeks afterwards.

Each sample consisted of a 1 branch tip removed from each of 10 trees. Each branch tip contained at least 10 shoots from the previous growing season. We collected all branches by hand from the lower crown of the tree using hand-held clippers and placed them in individual zipper-top bags. We sampled each tree twice – once before the cold spell event and again after the cold spell event – to control for the effect of inter-tree variation in population sizes and potential tree level effects on survivability (Parker et al., 1999). After sampling, all branch tips were packed in coolers and then transported to Natural Resources Canada Canadian Forest Service insect quarantine laboratories at either the Atlantic Forestry Centre in Fredericton, New Brunswick or the Great Lakes Forestry Centre in Sault Ste. Marie, Ontario. The samples were stored at 4–6 °C until they were processed, and all samples were processed 7–40 days after collection (mean = 18 ± 8 days).

We measured the effect of the cold spell event on hemlock woolly adelgid mortality by counting the number of live adelgid sistens on the 'before' and 'after' samples. Hemlock woolly adelgid has a complex lifecycle with two generations per year alternating between a progrediens and sistens form, and as well it reproduces asexually (McClure, 1989). It overwinters in the sistens stage and resumes activity in late winter or early spring. For each branch we randomly selected 10 new shoots (i.e., 2022 growth) on each branch tip and then, beginning at the growing tip and using a dissecting microscope, assessed the status of the first 25 individuals that were encountered on each shoot following directions in McAvoy and Salom (2019) and McAvoy et al. (2017) . Briefly, we examined the size of each insect, firmness of the integument when probed, and the quality of the wool produced by the insect to determine if the insect was alive or dead. We also measured the length of each new shoot. We then expressed the survival of the hemlock woolly adelgid population on each branch as the total number of live adelgid divided by the total number of adelgid that were found on the 10 shoots.

Weather data: We obtained hourly weather data from ECCC weather stations in Nova Scotia and Ontario. For each sample site we identified the closest weather station with hourly weather data using tools in the weathercan library (LaZerte and Albers 2018) for the R statistical computing environment (R Core Team 2019). For the Grafton, Ontario; Wainfleet, Ontario and Mersey River, Nova Scotia sites the closest weather stations with hourly weather data were located 11.5, 12.5 Km and 8.9 Km away, respectively. All distances were estimated using tools in the weathercan library. For the Annapolis Royal site, the closest weather station was 42 Km away and was the same station as the one closest to the Mersey River site. That weather station is located in Nova Scotia's interior, as is the Mersey River site. The Annapolis Royal site, however, is situated in Nova Scotia's Annapolis Valley near the Bay of

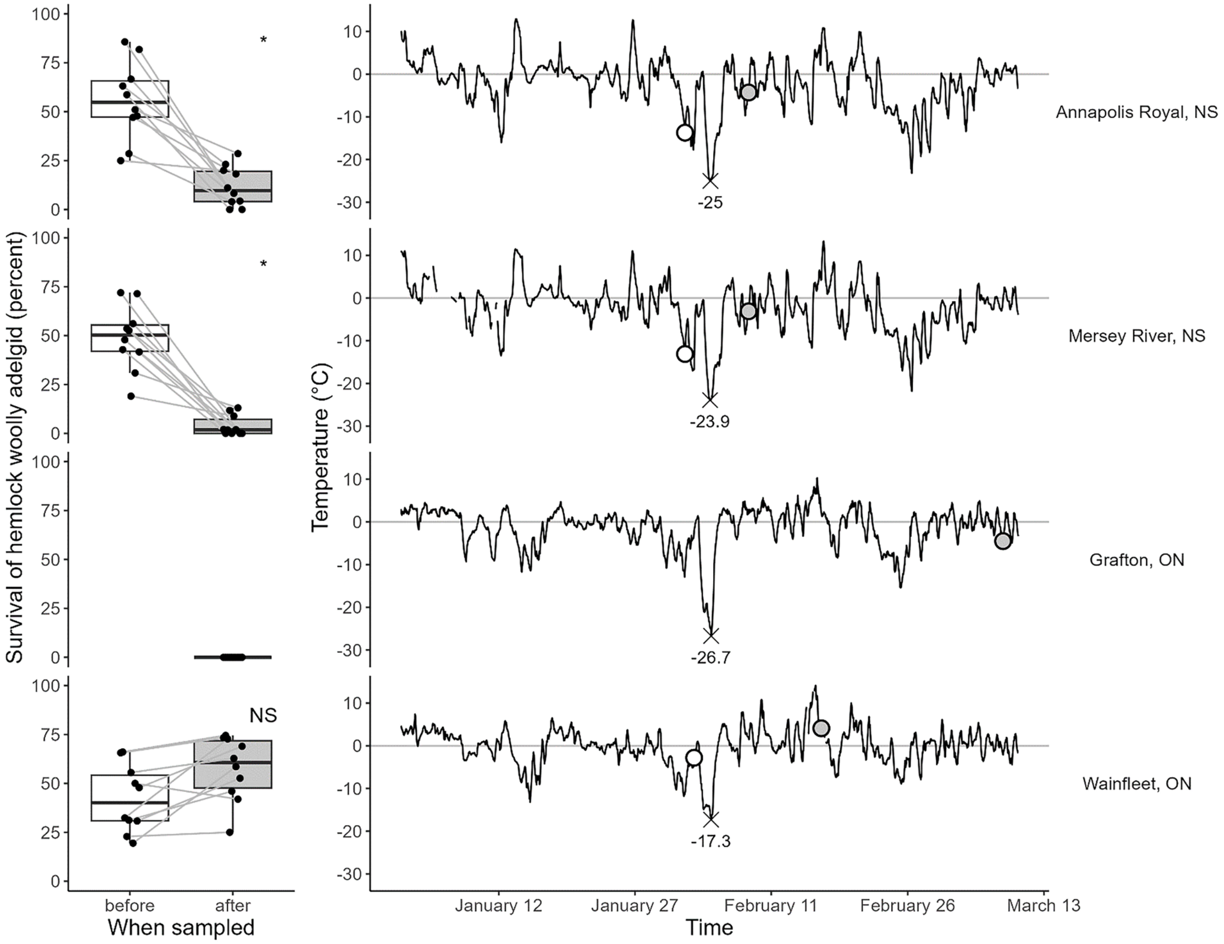

Fig. 1. Survival of live hemlock woolly adelgid on shoots at four sites in eastern Canada before (white) and after (grey) a cold spell event in February 2023 (left) and observed temperatures at the same sites between 1 January and 10 March 2023 (right). In survival plots, boxes show the mean (thick black line) and 25th and 75th percentiles, whiskers are 1.5 times the distance between the 1st and 3rd quartiles of the data; star (*) indicates a statistically significant difference between the before and after samples and thin black lines join observations from the same trees. In the temperature plots circles show the sampling days at each site before (white) and after (gray), and the lowest observed temperature (denoted with X).

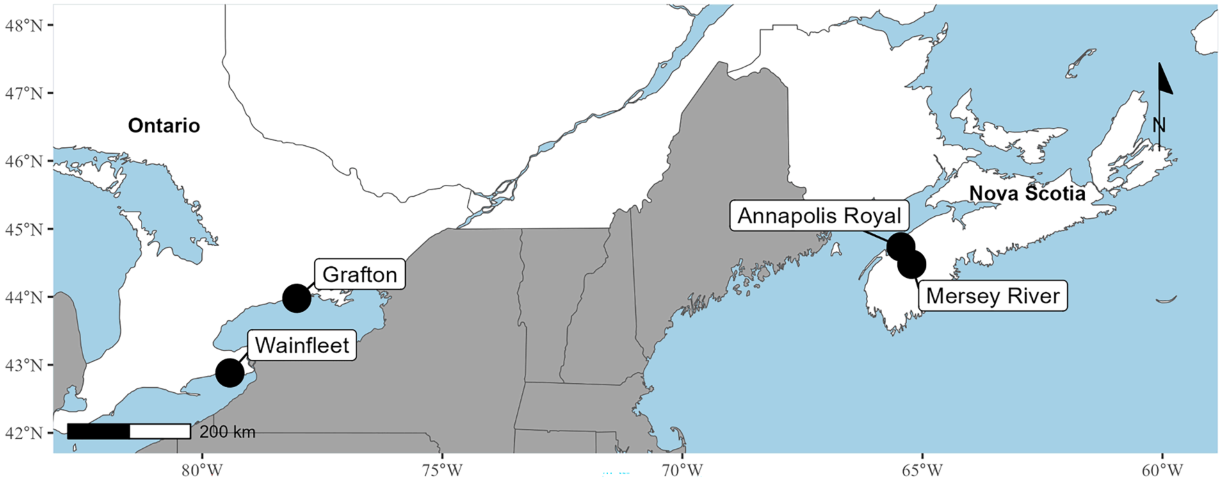

Fig. 2. Location of four sites in eastern Canada where hemlock woolly adelgid mortality was assessed following a cold spell event in February 2023.

Fundy coast. We therefore selected a weather station at Greenwood Nova Scotia, 49 Km from the sampling site in Annapolis Royal, because it is also located in the Annapolis Valley and we assumed the temperatures it recorded would be more representative of the temperatures experienced by the hemlock woolly adelgid population at Annapolis Royal. We checked our assumption by comparing the observed temperatures at Greenwood to those recorded by an independent agricultural weather station located near the Annapolis Royal site (NSFGA

2023). The temperature traces for January, February and March for Greenwood (Fig. 1) were essentially identical to those from the agricultural weather station (data not shown) and so we used the data from the Greenwood station as it allowed a comparison of historical trends, which the agricultural weather station did not.

As some weather stations had rather short periods of record, we also used ERA5 data to further compare this event with the historical climatology (1950–2023) of each site. ERA5 is a state-of-the-art global atmospheric reanalysis database developed by the European Centre for Medium-Range Weather Forecasts (2023), that provides detailed historical weather and climate data, including temperature, precipitation, wind, at various geopotential heights and on a global scale, spanning from 1950 to present at a 0.25° x 0.25° resolution.

Nova Scotia hemlock woolly adelgid mortality: We compared mortality immediately after the cold spell to a data set of hemlock woolly adelgid sistens mortality estimates from Nova Scotia from the winter of 2022–2023 and the previous 4 winters. These data consist of counts of sistens mortality from samples collected in late March in each year from 2 sites (2019), 3 sites (2020, 2021) or 9 sites (2022, 2023). At each site 5 or 10 trees were randomly sampled and one or two 30 cm branches were removed from each tree. These branches were then taken to a laboratory and up to 10 new shoots (from the previous year) were examined from each branch. On each shoot the number of live and dead sistens was recorded. From these measures an estimate of percent mortality for the site was determined. We averaged these values for all sites in all years to estimate the recent trend in overwintering mortality in Nova Scotia.

Analysis: We used a Student's one-sided paired T-test to determine if survival of hemlock woolly adelgid in paired samples taken after the cold spell event was lower than survival before the cold spell event. We completed independent analyses for each sample site with before and after data (Annapolis Royal, Mersey River, Wainfleet); no analyses were done with the Grafton data as there were no live insects found (see below). We computed an estimated sistens mortality rate (i.e., the proportion of sistens dead in a given sample) for each population using equation 2 from McAvoy et al. (2017) using values derived from the ECCC weather data. All analyses were done using tools in the stats library in R (R Core Team, 2019). Data and analytical code are available see: MacQuarrie et al. (unpublished).

Results

The percent survival of live hemlock woolly adelgid populations was lower at two of three sites after the cold spell event (Fig. 1). We observed hemlock woolly adelgid populations on trees at Annapolis Royal and Mersey River that had lower survival after the cold spell (Annapolis Royal $t = -5.6571$, df = 9, $p = 0.0002$; Mersey River $t = -7.2567$, df = 9. $p < 0.0001$). There was no statistically significant difference in survival estimates at the Wainfleet site ($t = 3.1593$, df = 9, $p = 0.9942$; Fig. 1). In all sites survival up until early February was estimated to be approx. 50–60 %, but dropped to between 3 and 11 % at the Nova Scotia sites (Fig. 1). This reduction in survival equated to an average 43 % reduction in survival in the Annapolis Royal population and an 44 % reduction in survival in the Mersey River population. All hemlock woolly adelgid in the samples from the Grafton site were dead.

The coldest temperatures of the winter of 2022–2023 were recorded at each site in the early hours of February 4th 2023. Hereafter, all times are given in the local time zone (Atlantic standard time for Nova Scotia and Eastern standard time for Ontario) and refer to data from ECCC weather stations. The recorded temperature was −25.0 °C at Annapolis Royal at 3 am and −23.9 °C at Mersey River at 2 am. At Annapolis Royal, temperatures were below −20 °C for 17 h (from 8 pm on 3 February to 1 pm on 4 February) and at Mersey River temperatures were below −20 °C for 14 h (from 9 pm on 3 February to 11 am on 4 February). At Grafton, Ontario temperatures were near or below −20 °C for 24 h beginning at 8 am on 3 February. The temperature warmed to −19.8 °C at 2 pm on 4 February, reaching a daytime high of −19.1 °C at 5 pm, then fell below −20 °C for 15 h (from 6 pm on 3 February to 9 am on 4 February). The coldest temperature recorded at Grafton was −26.7 °C at 4 am on 4 February. At the same time, Wainfleet recorded a low of −16.7 °C. After the cold spell event temperatures at all sites increased to average around the 0 °C mark and remained there for a number of weeks - including the period when the 'after' samples were collected (Fig. 1). A second, less intense, cold event was recorded in late February before sample collections were made at the Grafton site but during this event temperatures did not approach −20 °C (Fig. 1).

A similar drop in temperatures were recorded by ERA5 reanalyses for 3 and 4 February (Figure S2). On a historical perspective, the observed T_{min} were at least colder than the 10th percentile of the 1991–2020 climatology in all sites. Daily record T_{min} were observed for Grafton (−25.9 °C) and Mersey River (−25.8 °C) while Annapolis Royal recorded its all-time record low T_{min} (−25.4 °C) for the historical period (1950–2023) according to ERA5.

The predicted sistens mortality for each population ranged from 55.5 to 93.5 %, based on estimates from McAvoy et al.'s equation 2, which uses the minimum observed temperature (Fig. 1), the number of days with an average temperature below −1 °C and the mean temperature 3 days before the cold event to predict a mortality rate (McAvoy et al., 2017).

Overwintering mortality in Nova Scotia ranged from 46 ± 7.5 % to 57 ± 10.6 % (mean ± 1 s.d.) in the winters of 2018–2019, 2019–2020 and 2020–2021 but was higher in winter 2021–2022 (77 ± 25.0 %) and winter 2022–2023 (93 ± 5.5 %) (Fig. 3).

Discussion

We show that mortality of hemlock woolly adelgid after the cold spell event of February 2023 was significant in those parts of Canada where temperatures dropped below −20 °C in the early morning of 4 February 2023. Hemlock woolly adelgid survival at all sites was approximately the same prior to 4 February (Fig. 1) and consistent with average mortality observed in Nova Scotia between 2019 and 2021 (Fig. 3) suggesting no other significant mortality events had occurred prior to 4 February. Survival after the cold event, however, was reduced in just those sites where temperatures fell below −20 suggesting a strong correlation between the cold spell event and mortality in these populations. Our observations are consistent with predictions from equation 2 in McAvoy et al. (2017) which estimated sistens survival rates of 11 % for Annapolis Royal, 12 % for Mersey River, 6 % for Grafton, and 45 % for Wainfleet based on observed weather data at these sites. Our estimates are also consistent with those taken at the end of winter from a number of sites across southern Nova Scotia (Fig. 3) suggesting that most of the mortality that affected these populations during the winter of 2022–2023 happened on the night of 4 February 2023. Our results are the first to document the effects of winter mortality on hemlock woolly adelgid at the northern edge of its invaded range.

While the population reductions at three sites were significant they do not appear to have been sufficient to eliminate populations. Mortality of 90 % is required to hold hemlock woolly adelgid populations static (Paradis et al., 2007) which does not appear to have occurred in Nova Scotia during the cold event. In other parts of the province, all overwintering mortality was estimated at 93 % (Fig. 3) which would suggest, at best, that populations would be static in 2023. In Grafton we assume mortality was 100 % but follow-up sampling at these sites in the spring and summer of 2023 found evidence of live hemlock woolly adelgid and rejuvenating populations (VD personal observation). Hemlock woolly adelgid populations can establish from as few as one individual (Tobin et al., 2013) and losses suffered by the overwintering sistens generation of hemlock woolly adelgid are replaced by enhanced success of the progrediens generation (Tobin et al., 2017; Crandall et al., 2020). Thus, even with 99 % mortality hemlock woolly adelgid populations, once established, are likely to persist.

Cold events, though, may slow population growth and thus mortality

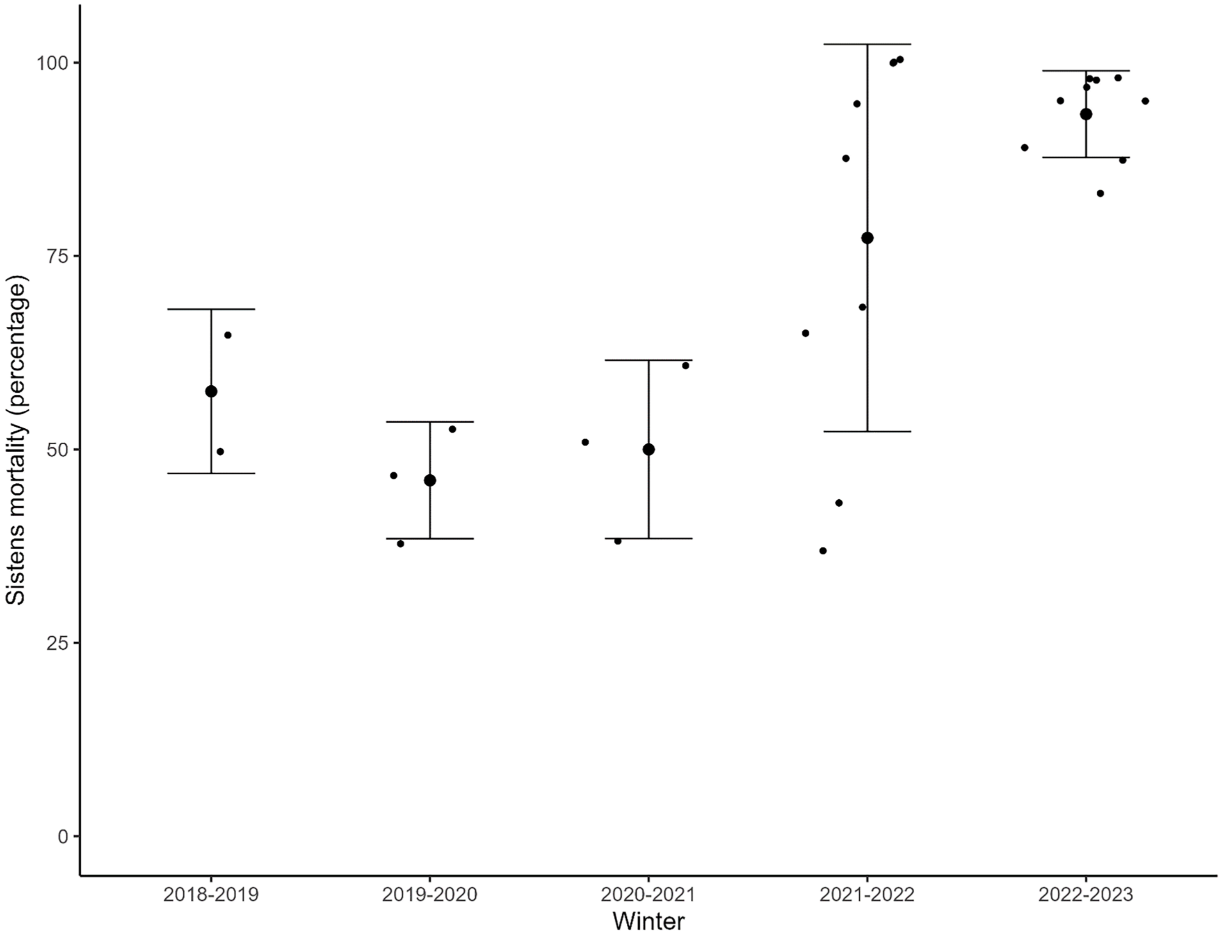

Fig. 3. Mortality (percent) of hemlock woolly adelgid sistens at infested sites in Nova Scotia following winter. Bars show mean and 1 standard deviation.

of hemlock. Equally important may be the frequency and return interval of cold days (Kiefer et al., 2021). All four sites experienced at least one day with −20 °C temperatures since December 2012 (Figure S2) with Wainfleet experiencing 44 days where temperatures dropped that low. This is notable because the Wainfleet infestation when it was discovered in 2019 was well established (CJKM personal observation) which meant it had persisted through two significant cold winters in 2015 and 2018 (Figure S2). By contrast, the Nova Scotia sites have experienced many fewer cold days since 2012 with Annapolis Royal experienced 19 days where temperatures dropped below −20 and Mersey River experiencing 12 days (Figure S2). Indeed, these sites experienced only 1 day below −20 °C between 2016 and 2021, with Annapolis Royal experiencing a historic low on the night of February 4th.

A period of preconditioning is associated with increased hemlock woolly adelgid survival in response to cold (Elkinton et al., 2017; Lombardo and Elkinton 2017; McAvoy et al., 2017). When we compare our observed estimates of survival to those from a model that incorporates a term for preconditioning we found generally good correlation between the observed and predicted mortality. Our observed overwintering survival estimates are also consistent with estimates of super cooling points for populations of hemlock woolly adelgid in the northern United States (Elkinton et al., 2017). We had hypothesized that the population at the Wainfleet site would be less cold tolerant as temperatures in that part of Ontario are moderated by Lakes Ontario and Erie, but this proved not to be the case as the insects we examined were able to tolerate temperatures of −17 °C with no apparent mortality. Lake Michigan moderates winter cold temperatures and their effect on hemlock woolly adelgid populations in Michigan (Kiefer et al., 2021). Our data suggest we did not observe similar moderation in the population at Grafton on the north shore of Lake Ontario or the Annapolis Royal site near the Bay of Fundy.

Winter weather can have significant effects on insect populations and the intensity of winter conditions can influence the fate of pest outbreaks. For many forest pests, predictions or observations of overwintering mortality are not incorporated into management decisions (MacQuarrie et al., 2019). For hemlock woolly adelgid, mortality from cold events could be enhanced via the application of chemical insecticides or biological control agents in the following spring, or managers could re-direct planned efforts to areas that did not suffer mortality. Doing so, however, requires incorporating regular overwintering mortality monitoring (e.g., Government of Alberta 2023) into integrated pest management plans for forest pests.

CRediT authorship contribution statement

Chris J K MacQuarrie: Conceptualization, Methodology, Formal analysis, Resources, Data curation, Writing – original draft, Visualization. **Victoria Derry:** Investigation, Writing – review & editing. **Meghan Gray:** Investigation, Data curation. **Nicole Mielewczyk:** Investigation. **Donna Crossland:** Investigation, Writing – review & editing. **Jeffrey B Ogden:** Formal analysis, Investigation, Resources, Writing – review & editing. **Yan Boulanger:** Investigation, Resources, Writing – original draft, Visualization. **Jeffrey G Fidgen:** Conceptualization, Methodology, Investigation, Resources, Data curation, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data and analytical code are available via the Dryad digital repository (MacQuarrie et al., 2024) , see: https://doi.org/10.5061/dryad.5qfttdzcc and https://doi.org/10.5281/zenodo.8363664.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.cris.2024.100077.

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