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Cold tolerance of the invasive larch casebearer and implications for invasion success

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Abstract

1 Larch casebearer became established in North America in the late 1800s. Cold temperatures are considered a limiting factor for the insect's range, yet the cold hardiness of larch casebearer has never been quantified.
2 We investigated (i) larval survival after acute and prolonged exposure to subzero temperatures and (ii) supercooling points (i.e. temperatures causing the onset of freezing) of overwintering and active larvae from November 2015 to April 2017.
3 We developed models linking exposure temperatures to survival and evaluated them with larvae from field conditions. Historical minimum temperature data were used to estimate changes in survival across time at a site in northern Minnesota.
4 The cold tolerance of larch casebearer changed significantly with season: both lower lethal temperatures and supercooling points were lowest in mid-winter and highest in spring and autumn. For example, 50% survival was estimated after acute exposure to a mean ± SE temperature of −28.9 ± 1.77 °C in October, −40.8 ± 0.77 °C in January and −27.8 ± 1.00 °C in April.
5 A model predicting survival using supercooling points provided conservative estimates of overwintering survival because it overestimated survival by approximately 4% and 8% in 2016 and 2017, respectively.
6 Analysis of climate data suggested that overwintering survival could have increased significantly over the previous half century.

Keywords Climate change, *Coleophora laricella*, lower lethal temperature, outbreak dynamics, supercooling.

Introduction

Larch casebearer *Coleophora laricella* Hübner (Lepidoptera: Coleophoridae) is native to Europe, where it defoliates European larch *Larix decidua* Mill. It was first detected in North America in Northampton, Massachusetts, in the late 1800s, defoliating planted European larch (Hagen, 1886), although it eventually spread throughout most of the range of eastern larch *Larix laricina* (Du Roi) K. Koch (Ryan *et al.*, 1987). Subsequent to a new detection in Idaho in 1957, the insect spread throughout most of the range of western larch *Larix occidentalis* Nutt. (Denton, 1979; Tunnock & Ryan, 1985). Moths emerge throughout summer and oviposit individual eggs onto larch needles. Larvae mine the needles for the first and second instar, eventually constructing cases by inhabiting mined needles (Herrick, 1911). After molting into third instars, larvae attach cases to twigs on host trees and enter diapause to overwinter (Ryan, 1975). In spring, larvae molt into the fourth instar, resume feeding and pupate inside their cases attached to host foliage. Larvae enlarge their cases with silk or construct new cases out of needles (Bucheli *et al.*, 2002). Larval feeding in the spring causes the most damage to host trees. Defoliation can decrease the growth of host trees (Tunnock *et al.*, 1969), predispose trees to attack from fungi or other secondary agents (Tunnock *et al.*, 1969; Benoit & Blais, 1988) and/or kill trees in multiyear infestations (Craighead, 1950; Dowden, 1957).

Subsequent to invasion by larch casebearer in North America, an importation biological control programme was initiated and considered to be a success in both eastern and western larch forests (Graham, 1948; Webb & Quednau, 1971; Otvos & Quednau, 1981; Ryan, 1990, 1997). The imported parasitoids *Agathis pumila* Ratzeburg (Hymenoptera: Braconidae) and *Chrysocharis laricinellae* Ratzeburg (Hymenoptera: Eulophidae) appeared to

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be efficacious and were distributed throughout most of the introduced range of larch casebearer (Quednau, 1970; Miller-Pierce *et al.*, 2015). In eastern larch forests, *A. pumlia* appeared to be the most important control agent (Quednau, 1970). In western larch forests, *A. pumila* was identified as the most important mortality factor for larch casebearer (Ryan, 1986, 1997). The establishment of natural enemies was associated with significant declines in larch casebearer populations. For example, defoliation in western larch forests of Oregon and Washington was reduced to sporadic occurrences until 1997 (Ward & Aukema, 2018). Aerial surveys in eastern larch forests of Minnesota did not detect defoliation until 2000 (Ward & Aukema, 2018).

Since 1997 in Oregon/Washington and 2000 in Minnesota through 2016, between 40–32 000 hectares of defoliation of larch have been detected each year (except 2014 in OR/WA), with no definitive explanation for what is facilitating these outbreaks (Ward & Aukema, 2018). Cold, wet springs have been implicated as significant mortality factors for larch casebearer, although population regulation in such springs may be a result of competition for foliage from fungi rather than temperature (Tunnock & Ryan, 1985). Historically, before the establishment of *A. pumila*, mortality during the needle mining stage and disappearance of overwintering larvae were regarded as the most important events affecting demography (Ryan, 1986, 1990, 1997). These results suggest that mortality from cold temperatures and/or winter predation may play a role in regulating the abundance of larch casebearers on the landscape. Cold temperatures have been implicated in limiting the northern and elevational limits of the invaded range, despite the apparent ability of some larch casebearers to survive January temperatures around −40 °C (Shepherd & Ross, 1973). Larch casebearer has not yet been reported on alpine larch *Larix lyallii* Parl., a high elevation larch in western North America, where temperatures at some locations can be as low as −57 °C (Arno & Habeck, 1972; Tunnock & Ryan, 1985).

Changes in winter temperatures and associated overwintering survival have been implicated in altering patterns of outbreaks and range limits of several insect species (Crozier, 2003, 2004; Battisti *et al.*, 2005; Jepsen *et al.*, 2008; Hoch *et al.*, 2009; Lesk *et al.*, 2017). Forecasting such changes in survival in response to climate change is important for managing natural resources (Volney & Fleming, 2000; Walther *et al.*, 2002; Estay *et al.*, 2009). In the present study, we investigated the lower lethal temperatures and supercooling points for active/feeding and overwintering larch casebearer larvae from autumn to spring across 2 years. The first aim of the study was to quantify changes in the cold tolerance of larch casebearer associated with season and status (active versus diapausing). We hypothesized that larvae would be most cold hardy in mid-winter and the least cold hardy in autumn and spring when larvae are entering or terminating diapause respectively. We also conducted a lower lethal time study aimed at determining whether exposure length interacts with temperature to moderate survival. Correlation of temperatures with cold tolerance metrics may provide reliable estimates of distributional limits, as has been demonstrated with *Drosophila* spp. (Andersen *et al.*, 2015). Thus, the final aim of the present study was to develop a model linking minimum temperatures to annual survival using laboratory derived cold tolerance metrics. We used this model to reconstruct overwintering survival based on climate data in northern Minnesota, U.S.A. We hope that these investigations will provide insight into potential changes in overwintering survival in Minnesota, clarify the role of overwintering survival in outbreaks of larch casebearer and enable forecasting of range limits under global climate change scenarios.

Materials and methods

Insects

Several collections of larval larch casebearers were conducted from eastern larch at a single site near Jacobson, Minnesota (46.9972°N, 93.1092°W). Unless otherwise specified, all larvae assayed originated from the Jacobson site. Larvae were also collected from two additional sites near Floodwood, Minnesota (46.9686°N, 92.9916°W) and McGregor, Minnesota (46.6443°N, 93.3156°W), 10 and 42 km from Jacobson, respectively. These additional collections were conducted to determine whether cold tolerance metrics of larch casebearer varied among locations. Site locations are depicted in Fig. 1. Collections and cold tolerance assays were conducted from November 2015 to April 2017.

Several collections of overwintering and active larvae were conducted. 'Overwintering' in the context of the present study refers to inactive larvae attached to branches via a silken plug and includes larvae in diapause and larvae that had either recently attached to or were close to detaching from twigs in autumn and spring, respectively. For overwintering larvae, we were not able to confirm whether a larva was in a true diapause, and so the term 'overwintering' is used in place of diapause throughout. Active larvae were also collected when available in autumn and spring, and so 'active' refers to larvae that had not yet attached to the twig in autumn or that had detached in spring. During autumn and spring, both overwintering and active larvae co-occurred on larch twigs and were easily differentiated because the former were attached directly to twigs with a silken plug that completely sealed one end of the case and the latter were attached to foliage and moved when contacted.

For each trial in November 2015 to October 2016, a minimum of 12 eastern larches was randomly selected from a stand and live twigs with larvae within 2 m of the ground were collected. When only overwintering larvae were collected (late autumn to early spring), twigs were placed into a well-ventilated plastic container (46 × 31.1 × 17.8 cm) and stored inside a wooden, roofless cold frame abutting a greenhouse on the University of Minnesota campus (44.9886°N, 93.1801°W). When active larvae were present in autumn and spring, twigs were placed in 1-L glass jars with 300–500 mL of tap water in the bottom to prevent desiccation of foliage. Glass jars and twigs were stored outside in the cold frame. For assays taking place in or after November 2016, overwintering larvae were collected in early November from 60 trees (two twigs per tree) and stored outside as described above. For trials taking place before November 2016, larvae were assayed within 1 week of the field collection date. For trials in November 2016 and onwards, larvae were assayed from 1 week to several months after field collection. For all cold tolerance assays, larvae were not removed from twigs until immediately before use.

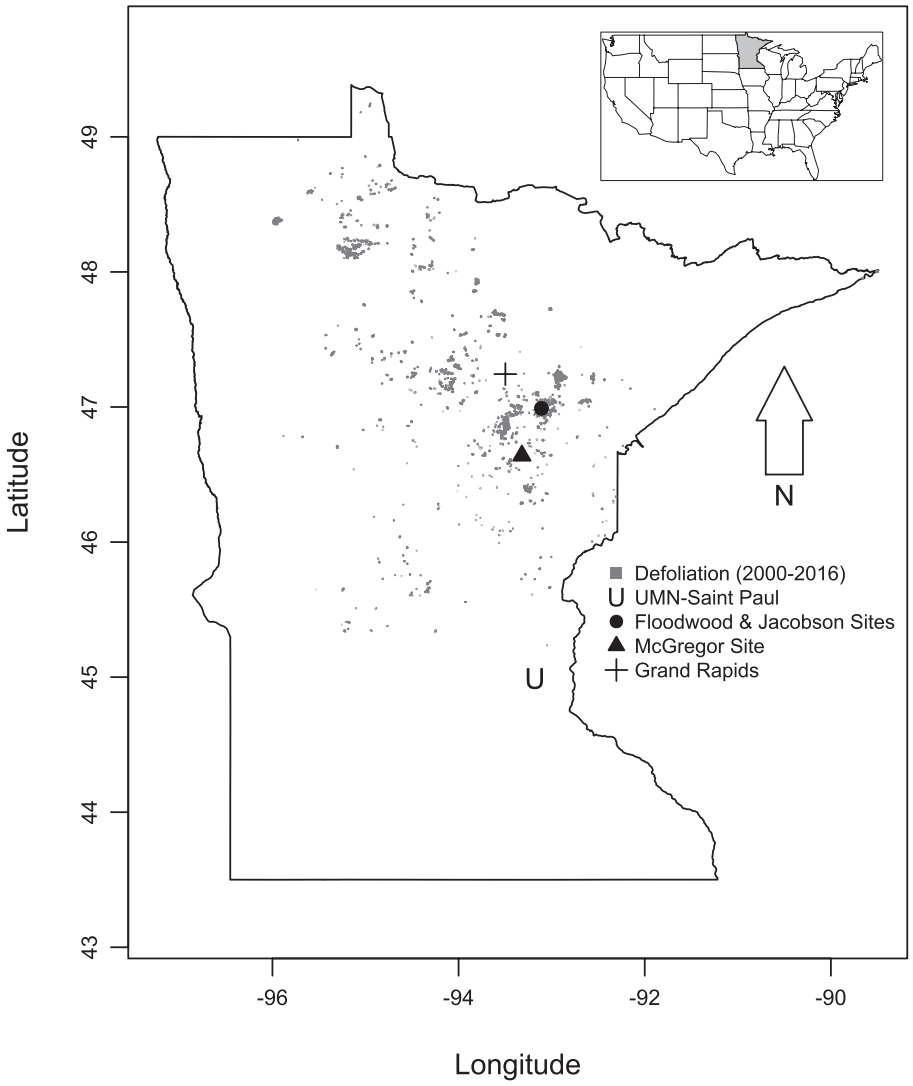

Figure 1 Proximity of collection sites for larch casebearer in Minnesota, U.S.A., to areas of eastern larch, *Larix laricina*, defoliated by larch casebearer as detected via aerial surveys (2000–2016). The Floodwood and Jacobson sites are within 10 km.

Lower lethal temperatures

We were interested in estimating lower lethal temperatures (i.e. expected mortality given acute exposure to a specific temperature) from autumn through spring. Larvae were assayed for lower lethal temperatures every 2–3 months in 2015–2016 and every 2–3 weeks in 2016–2017. For each trial across the entire study, larvae were carefully removed from twigs or foliage using forceps, placed into the bottom of a 1.5-mL microcentrifuge tube, and randomly assigned to an exposure temperature below 0 °C (range 0 to −60 °C). Each microcentrifuge tube was sealed with a customized plastic dowel fit with an O-ring through which a 0.127-mm diameter (36 AWG) type-T copper-constantan thermocouple, accurate to ±0.17 °C, was threaded (Stephens *et al.*, 2015). When active larvae were assayed, the microcentrifuge tubes were fitted with a small piece of cotton to ensure larvae remained near the thermocouples. Thermocouples were adjusted to contact larvae in the bases of tubes. Sixteen larvae were assayed at a time. The entire apparatus was cooled in one of two ways. For the first set-up, each apparatus was placed individually into the centre of a 20-cm polystyrene cube and then in a freezer at −80 °C. Polystyrene cubes were calibrated to cool at a rate of −1 °C/min (Carrillo *et al.*, 2004; Stephens *et al.*, 2015). Under the second set-up, each apparatus was placed into a 18 × 150 mm (outer diameter × length) Kimax glass test tube inside a cooling bath of silicon 180 oil (A40; Thermo Fisher Scientific, Waltham, Massachusetts) and cooled at approximately −1 °C/min (Cira *et al.*, 2016). Cooling rates for the freezer and cooling bath are provided in Supporting information, File S1. The −80 °C freezer was used for all larvae except for assays conducted in April 2015 because the chiller bath could only cool to −40 °C.

Thermocouples were connected to USB-data loggers and temperatures were recorded once per second with TRACERDAQ PRO (Measurement Computing, Bourne, Massachusetts). Larvae were cooled constantly when in the freezer or cooling bath and were manually removed when they reached their randomly

predetermined exposure temperature; thus, larvae remained at exposure temperatures for < 1 s before being returned to room temperature. During each assay, control larvae ($n = 6–30$) were handled equivalently but kept at room temperature. For assays on overwintering larvae from October to 30 November in each year, larvae were extracted from cases within 24 h of the assays and survival was determined as movement of the legs in response to tactile stimulation via a small brush. Larvae assayed between 1 December and April were placed into growth chambers at 20 °C (LD 18 : 6 h) inside 1.5-mL microcentrifuge tubes with four to six holes poked in the lids and survival was determined by observation of active wandering.

Supercooling points

The supercooling point (i.e. the temperature at which insect body fluids begin to freeze) of individual larvae was measured to determine its utility with respect to predicting overwintering survival. Supercooling points are easier to obtain than lower lethal temperatures, and may be preferred in future studies of larch casebearer if they provide reliable estimates of overwintering survival/mortality. Supercooling points were collected, on average, during every other lower lethal temperature assay. For supercooling assays, larvae were treated equivalently to lower lethal temperature assays but were cooled until an exotherm, indicative of the release of heat as a result of a change from liquid to solid, was observed. Supercooling points were defined as the lowest temperature recorded immediately before the exotherm occurred (Sinclair *et al.*, 2015).

Active versus overwintering larvae

For lower lethal temperature assays that occurred in April to May 2016 and September 2016, active larvae were assayed in addition to overwintering larvae. For the assays in April to May 2016, both fed and starved larvae that were active were assayed. For fed larvae, naturally-activated larvae (i.e. larvae that had broken diapause and were actively wandering) were collected from the plastic storage container in the cold frame, placed onto potted eastern larch trees and assayed after larvae were permitted to feed for a minimum of 24 h. Only larvae that had attached and were feeding were recollected for assays. For comparison, naturally-activated, unfed (starved) larvae from the plastic storage container were collected and assayed the same day as feeding larvae were recollected from trees. Starved and fed larvae were assayed simultaneously. In September 2016, only overwintering and active/feeding larvae were assayed. In April 2017, supercooling points of overwintering and active/starved larvae were investigated in the same manner as described above.

Supercooling points across sites

To quantify how supercooling points of larch casebearer vary among sites, 15–30 larvae per site were collected in early November 2016 from sites near Jacobson, Floodwood, and McGregor, Minnesota (Fig. 1). These additional collections were conducted using the same protocol as described above. Larvae were stored outside of the greenhouse as described above and their supercooling points were measured in January 2017.

Deacclimation

We conducted a study to determine how quickly larch casebearer might deacclimate from the cold tolerant overwintering stage. In January 2017, 80 larvae were placed individually into microcentrifuge tubes with four to six holes poked in each lid. Forty tubes were transferred into a greenhouse (10.5–30.3 °C and 12–43% relative humidity) and the remaining 40 were placed outside into the plastic storage container (−14.2 to 3.7 °C and 54–100% relative humidity). Temperatures and relative humidity in each location were recorded using HOBO Data-loggers (Onset Computer Corporation, Bourne, Massachusetts) and larvae were held under natural photoperiods. The wide range of temperatures in both locations was a result of diurnal variation and general changes across the duration of the study (3 weeks). A subset of larvae were removed and assayed for supercooling points at 1, 3, 6, 13 and 21 days after placement into the respective locations to determine how quickly larvae deacclimate. A maximum of 16 larvae (eight stored in the greenhouse, eight stored outside) was measured per sample day.

Lower lethal time

On 30 December 2015, 72 larvae were placed into 1.5-mL microcentrifuge tubes and into freezers held at 2 °C, −2 °C, −23 °C and −28 °C. Temperatures were again measured using HOBO Data-loggers. Cohorts of 4–10 larvae from each exposure temperature were removed at 20, 24 and 34 days, placed at 20 °C (LD 18 : 6 h) and monitored for survival every 2–3 days. The proportion of larvae activating (i.e. surviving) was recorded.

Field evaluation

We investigated the utility of cold tolerance metrics for predicting survival in the field at two locations: Jacobson in 2016 and Saint Paul in 2017. In 2016, 58 larvae were collected from Jacobson in late March and stored outside for between 1 and 3 weeks in Saint Paul before being transferred into 1.5-mL microcentrifuge tubes and into a growth chamber (20 °C and LD 18 : 6 h). Across April 2017, 29 and 45 larvae from the November 2016 collection were transferred into either 1.5-mL microcentrifuge tubes or Petri dishes (9 × 50 mm polystyrene dishes; Falcon Labware, Oxnard, California), respectively. Tubes and Petri dishes were placed into a growth chamber (20 °C and LD 18 : 6 h). In both years, larvae were monitored for survival every 2–3 days for several months after transfer. Two estimates of survival were obtained: one for survival to March 2016 at Jacobson and the other for survival to April 2017 in Saint Paul.

Expected survival at the overwintering locations of Jacobson and Saint Paul was quantified and compared with observed mortality in 2016 and 2017, respectively. We defined an 'insect year' such that 1 October 2015 to 30 April 2016 would be insect year 2016 because mortality in October to December will affect insect pressure in spring the next year. Daily minimum

Table 1 Month-specific logistic regression models linking the survival of larch casebearer larvae to coldest, acute exposure temperature (0 °C to −60 °C)

Month	*n*	Intercept (mean ± SE)	Temperature (°C) (mean ± SE)	LT_{50}[a]
October	48	6.881 ± 1.932**	0.238 ± 0.070**	−28.90
November	160	13.349 ± 2.457***	0.359 ± 0.064***	−37.19
December	30	8.368 ± 2.779*	0.230 ± 0.074*	−36.35
January	201	10.255 ± 1.620***	0.252 ± 0.038***	−40.77
February[b]	61	10.892 ± 3.610*	0.277 ± 0.088*	−39.34
March[c]	96	5.914 ± 1.440***	0.189 ± 0.042***	−31.31
April	201	5.609 ± 0.814***	0.202 ± 0.028***	−27.79

Data were collected from November 2015 to April 2017 in Minnesota, U.S.A. Data within a month were combined across years because annual variation was statistically insignificant.

All models followed the general eq $P(\text{Larva survives}) = 1/(1 + \exp[-(\text{intercept} + \beta_1 \times \text{temperature})])$.

[a] LT_{50}, temperature required to kill 50% of individuals.

[b] Included larvae assayed between 1 February and 3 March.

[c] Included larvae assayed between 4 March and 31 March.

*$|Z| \geq 1.96$, $P \leq 0.05$.

**$|Z| \geq 3.30$, $P \leq 0.001$.

***$|Z| \geq 3.90$, $P \leq 0.0001$.

temperatures from weather stations near Floodwood and on the Saint Paul campus of the University of Minnesota were obtained for insect years 2016 and 2017, respectively, from the National Oceanic and Atmospheric Administration (NOAA, 2017). Weather stations were within 20 km of Jacobson and 1 km of Saint Paul. For predictions of survival using lower lethal temperature models, we obtained the absolute minimum temperature during the overwintering stage and the month in which it occurred. The minimum temperature was then entered into a month-specific lower lethal temperature model (see Statistical analyses) to generate an estimate of survival. Accordingly, if the coldest day in the insect year occurred in December, then the lower lethal temperature model for December would be used to estimate overwintering survival.

For predictions using supercooling points, we first bootstrapped 1000 samples to obtain estimates of the variance, s_i^2, for each model coefficient $(\widehat{\beta}_0, \widehat{\beta}_1, \widehat{\beta}_2)$ from our quantile regression model employing ordinal day to predict supercooling points (see Statistical analyses). Bootstrap estimates of the variance were obtained by resampling residuals via the lm.boot() command in the simpleboot package in R (Peng, 2008). We then obtained the ordinal day on which the coldest temperature occurred in each insect year. The ordinal day (D, days after September 1) was then entered into our model and 1000 bootstrapped estimates of the supercooling point were generated using:

$$\text{SCP} = \beta_0 + \beta_1 \times D + \beta_2 \times D^2$$

where SCP = estimated median supercooling point, $\beta_0 \sim N\left(\widehat{\beta}_0, s_0^2\right)$, $\beta_1 \sim N\left(\widehat{\beta}_1, s_1^2\right)$ and $\beta_2 \sim N\left(\widehat{\beta}_2, s_2^2\right)$. Each $\widehat{\beta}_i$ was extracted from the quantile regression of supercooling points on ordinal day. This process was repeated 1000 times (i.e. 1000 iterations with 1000 estimated SCPs / iteration). For each iteration, the proportion of estimates (i.e. supercooling points) lower than the observed minimum temperature was recorded as the percentage survivorship. Thus, according to our model, if the supercooling point of a larva was below the minimum temperature, then that larva survived the winter. Of the 1000 estimates of survival, the highest and lowest 2.5% were removed to obtain a confidence interval. The predicted survival in 2016 (Jacobson) and 2017 (Saint Paul) using lower lethal temperature models and the supercooling point model (i.e. four estimates of survival) was then compared with the observed survival at these locations.

Trends in predicted overwintering survival

We obtained temperature data from 1964 to 2016 at a weather station in Grand Rapids, Minnesota (Fig. 1). Daily minimum temperatures were obtained from NOAA. For each insect year, the minimum temperature and the ordinal day (= days after September 1) on which it occurred were obtained. Survival per year was then estimated as described for the supercooling point model (see Field evaluation), which provided more conservative estimates of cold-driven mortality than models based on lower lethal temperatures. (see Results).

Statistical analyses

To model seasonal changes in cold tolerance, we combined data from both years of the study, split the data by month and fit logistic regression models relating survival of larvae to exposure temperature. To homogenize the number of larvae sampled across time, the February model included larvae sampled from 1 February to 3 March and the March model included larvae assayed from 4 March to 31 March. A term for year was also considered as a predictor in each model. The temperature estimated to kill 50% of the population (LT_{50}) was then estimated for each month using the dose.p() function from the MASS package in R (Venables & Ripley, 2002). To determine how supercooling points changed over time, the effect of ordinal day and a quadratic term for ordinal day and year on supercooling points was modelled using quantile regression. Quantile regression models were fit via the quantreg package in R and bootstrapped SEs for regression coefficients were obtained by setting the 'se' argument of the summary() command equal to 'boot' (Koenker, 2018).

For comparisons of lower lethal temperatures by status in April/May 2016, the effects of sampling day (continuous variable; days after 1 September 2015), temperature, status (fed versus starved versus overwintering) and the temperature × status interaction on survival of larvae were assessed using logistic regression. For studies in September 2016, the effects of temperature, status (starved versus overwintering) and their interaction on survival were again assessed using logistic regression. We implemented Tukey's honestly significant difference (HSD) test via the emmeans() command in the emmeans package in R (Lenth, 2018) to compare lower lethal temperatures between active/fed, active/starved and overwintering larvae. Differences in supercooling points between overwintering and active/starved larvae in spring 2017 were compared using simple linear regression.

Variation in supercooling points by site was assessed using analysis of variance. For analysis on deacclimation, supercooling points were modelled as a function of the interaction between length of storage (days, log-transformed) and storage location using analysis of covariance. To determine how exposure time to cold temperatures influenced survival, we investigated the role of days of exposure, temperature and their interaction in the proportion of larvae activating using logistic regression.

For analyses of historical trends in overwintering survival, the role of year in predicted survival at Grand Rapids was modelled using simple linear regression. Proportions of larvae estimated to survive were logit-transformed. Statistical significance for all models was determined using $\alpha = 0.05$ and multiple regression models were reduced by backwards elimination until all variables remaining were significant. Only final models are reported. Analytical assumptions for all general linear models were met as determined via graphical inspection of residuals. All analyses were completed using R (R Core Team, 2018).

Results

Lower lethal temperature

Monthly observations from autumn (i.e. October) to spring (i.e. April) indicated that the lower lethal temperatures decreased going into winter and increased with the onset of spring. That is, larvae were most cold hardy in mid-winter and less cold hardy in autumn and spring. Parameter estimates for each month-specific logistic regression, along with monthly LT_{50} predictions, are provided in Table 1. For example, 50% survival was estimated at a mean ± SE temperature of −28.9 ± 1.77 °C in October, −40.8 ± 0.77 °C in January and − 27.8 ± 1.00 °C in April (Table 1). The term for year was not significant in any monthly model (all $P > 0.05$).

Supercooling points

Median freezing points of larvae changed significantly across the overwintering period but did not vary significantly between years (Fig. 2). Supercooling points were lowest in January and highest in autumn and spring. For example, the median of supercooling points was −44.6 °C (mean ± SE: −44.3 ± 0.3 °C) in January, compared with −37.7 °C (mean ± SE: −36.5 ± 0.6 °C) and − 30.9 °C (mean ± SE: −30.3 ± 0.7 °C) in November and April, respectively.

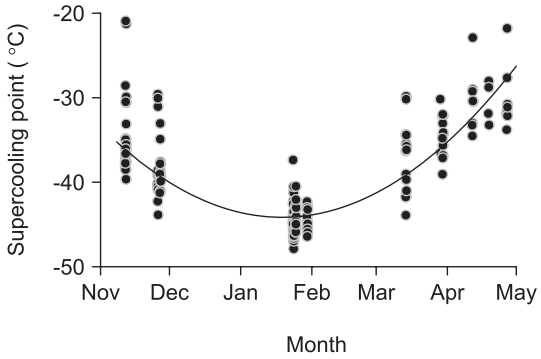

Figure 2 Monthly supercooling points of overwintering larch casebearer larvae in Minnesota, U.S.A. Data are jittered in the *x*-direction. The line is from a quantile regression of the median and follows the equation $y = -10.42\ (\pm 2.26\ \text{SE}) - 0.48\ (\pm 0.0383)\ x + 0.002\ (\pm 0.00014)\ x^2$, where *x* is the number of days after 1 September.

Active versus overwintering larvae

Overwintering larvae co-occurred with active, feeding larvae in autumn and spring; however, overwintering larvae were more cold tolerant than active larvae in both seasons. In April/May 2016, overwintering larvae had significantly lower LT_{50} values than active larvae that were feeding (Tukey's HSD, $Z = 2.50$, $P = 0.0334$) or starved (Tukey's HSD, $Z = 2.37$, $P = 0.0471$). For example, overwintering larvae had a predicted LT_{50} of −28.5 °C compared with −21.0 °C for active and fed larvae (Fig. 3A and Table 2). Larvae that were starved and active were not significantly different from larvae that were fed because starved larvae had an LT_{50} of −20.5 °C (Tukey's HSD, $Z = -0.146$, $P = 0.99$). Sampling day was not significant ($P > 0.05$). In September 2016, the LT_{50} for overwintering larvae was estimated at −28.6 °C compared with −17.4 °C for larvae still feeding (Fig. 3B and Table 2). No statistically significant interactions were found between the variables for status and temperature in analyses of lower lethal temperatures in April/May 2016 and September 2016. Larvae that were active and starved in April 2017 had a mean supercooling point of −20.9 °C, or 9.5 °C warmer than larvae still in the overwintering stage (Fig. 3C and Table 2).

Supercooling points across sites

Supercooling points did not vary significantly among sites ($F_{2,57} = 1.05$, $P = 0.36$). In January, larvae collected from the Floodwood, Jacobson and McGregor sites had mean ± SE supercooling points of −42.8 ± 0.9 °C, −43.9 ± 0.7 °C and −44.0 ± 0.4 °C, respectively.

Deacclimation

Overwintering larch casebearers moved into warmer temperatures began to deacclimate 1 day after transfer (Fig. 4

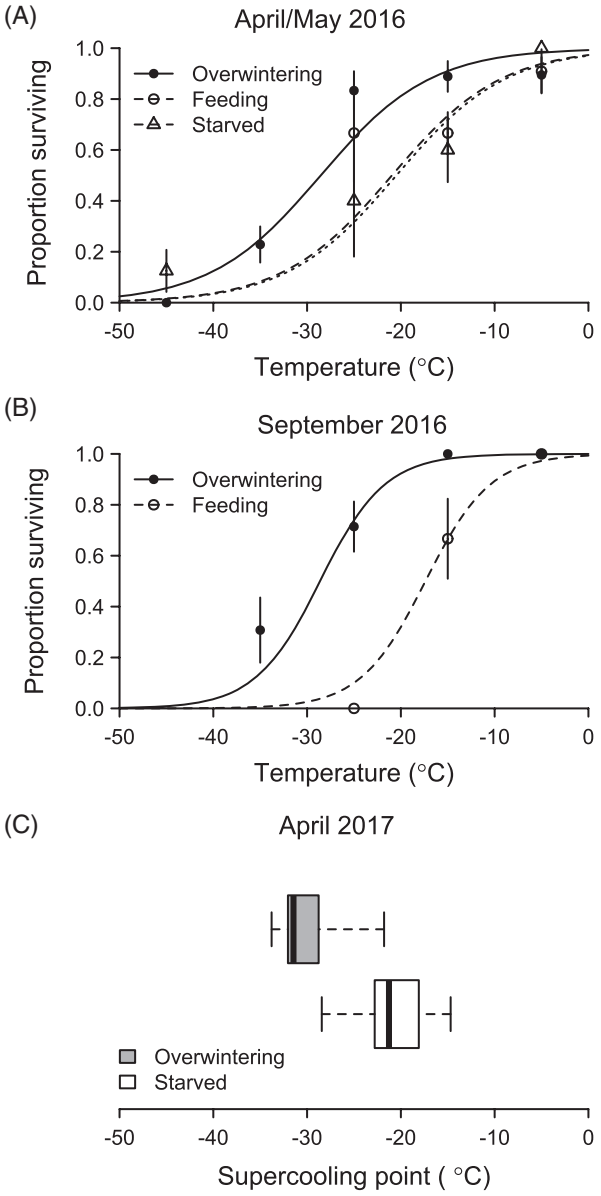

Figure 3 (A) Survival (mean ± SE) of overwintering, feeding and active/starved larch casebearer larvae in April/May 2016 after acute exposure to subzero temperatures. (B) Survival (mean ± SE) of overwintering and feeding larch casebearer larvae in September 2016 after acute exposure to subzero temperatures. (C) Box and whisker plots for supercooling points of overwintering and active/starved larvae in April 2017 (black bar = median; box = interquartile range; whiskers = range). All larch casebearer larvae were sampled from Minnesota, U.S.A. Lines in (A) and (B) are predicted from model coefficients in Table 2.

and Table 2). For example, after 24 h at greenhouse temperatures (10.5–30.3 °C), larvae in the greenhouse had mean ± SE supercooling points of −41.0 ± 0.6 °C compared with −44.9 ± 0.7 °C for larvae stored outside. At 21 days, larvae in the greenhouse had a mean ± SE supercooling point of −30.1 ± 1.5 °C compared with −44.1 ± 0.5 °C for larvae stored outside.

Lower lethal time

Neither temperature, exposure time, nor their interaction moderated survival. Across all treatments, mean ± SE larval survival was 90.3 ± 3.5%. According to our monthly lower lethal temperature models, the expected survival based on acute exposure to −22 °C and − 27 °C in January is 98.9% [95% confidence interval (CI) = 95.3–99.8] and 96.8% (95% CI = 90.4–99.0), respectively. Larvae exposed to −22 °C and − 27 °C for 20–32 days had an observed survival of 93.3% and 76.9%, respectively.

Field evaluation

Predicted survival from lower lethal temperature models (see Materials and methods) underestimated field survival of larvae, whereas our supercooling point model overestimated survival. In insect years 2016 (Jacobson) and 2017 (Saint Paul), a mean ± SE of 94.8 ± 2.9% and 91.9 ± 3.2% of larvae survived the winter when stored in the cold frame, respectively. Using lower lethal temperature models, predicted survival based on minimum temperature exposure was 88.1% (95% CI = 77.1–94.2%) in 2016 and 84.7% (95% CI = 54.7–96.2%) in 2017. Supercooling point models were more conservative, estimating survival of 99.1% (95% CI = 98.5–99.9%) in 2016 and 100.0% (95% CI = 99.8–100.0%) in 2017. Thus, confidence intervals predicted from the lower lethal temperature model fall within one percentage point in 2016 but successfully included observed survival in 2017. The predictions from the supercooling point model were approximately 5–8% higher than the survival we observed, and the observed survival did not fall within model confidence intervals.

Trends in predicted overwintering survival

Across all years, mean ± SE estimated survival was 95.9 ± 1% at the Grand Rapids weather station. The proportion of larvae estimated to survive winter increased from 1964 to present (Fig. 5). For example, on average, approximately 88% of larvae were estimated to survive minimum temperatures in 1965 compared with an average of approximately 98% in 2010.

Discussion

Our lower lethal temperature models estimated a survival approximately 7% lower than was observed in both years, whereas the supercooling point model overestimated survival by up to 8%. Larvae stored outside and transferred into growth chambers may succumb to other mortality factors (e.g. desiccation) in addition to cold exposure (Danks, 1978). Thus, the model incorporating supercooling points of larvae is likely most useful in estimating mortality as a result of cold exposure and its use in forecasting will provide conservative estimates of overwintering mortality. Moreover, larval supercooling points did not vary among three sites investigated because supercooling points were most similar between McGregor and Jacobson (versus Floodwood), despite Jacobson being approximately 30 km farther away from McGregor than Floodwood. These sites were

Table 2 Parameter estimates for statistical models characterizing the cold hardiness of larch casebearer larvae from Minnesota, U.S.A.

Figure	Month	Number of larvae	Response	Predictor	Estimate	SE	|test statistic|	*P*
3A[a]	April/May 2016	216	Survival	Intercept	3.583	0.547	$Z = 6.56$	< 0.0001
				Temperature	0.171	0.026	$Z = 6.52$	< 0.0001
				Starved	−0.081	0.559	$Z = 0.15$	0.88
				Overwintering	1.300	0.521	$Z = 2.50$	0.0126
3B[b]	September 2016	63	Survival	Intercept	5.010	1.384	$Z = 3.62$	0.0003
				Temperature	0.288	0.075	$Z = 3.83$	0.0001
				Overwintering	3.238	1.091	$Z = 2.97$	0.0030
3C[c]	April 2017	26	SCP	Intercept	−20.876	1.068	$t = 19.55$	< 0.0001
				Overwintering	−9.474	1.510	$t = 6.27$	< 0.0001
4[d]	January 2017	68	SCP	Intercept	−42.649	0.721	$t = 59.18$	< 0.0001
				Outside × log(days)	−0.616	0.394	$t = 1.56$	0.12
				Greenhouse × log(days)	4.299	0.411	$t = 10.46$	< 0.0001

Data and models are presented in Fig. 3 and Fig. 4.

[a]Logistic regression model to describe the proportion of larvae that survived as a function of coldest, acute exposure temperature (0 to −60 °C) in the laboratory and 'status' at the time of testing [status is a single variable with levels = fed (model reference level), starved and overwintering]. The status × temperature interaction was not statistically significant ($P > 0.05$). Accordingly, the model for overwintering larvae in April/May 2016 follows the form: $P(\text{Survival}) = 1/(1 + \exp[-(3.58 + 0.17 \times T - 0.081 \times 0 + 1.3 \times 1)])$, where T is the lowest temperature (°C) to which a larva was exposed.

[b]Logistic regression model to describe the proportion of larvae that survived as a function of coldest, acute exposure temperature (0 to −60 °C) in the laboratory and status (0 if larvae were active/fed; 1 if larvae were overwintering). The status × temperature interaction was not statistically significant ($P > 0.05$). Here, the model for active/fed larvae in September 2016 follows the form: $P(\text{Survival}) = 1/(1 + \exp[-(5.01 + 0.29 \times T + 3.24 \times 0)])$, where T is the lowest temperature (°C) to which a larva was exposed.

[c]Linear regression model to describe the mean supercooling point (SCP) of larvae as a function of status (0 if larvae were active/starved; 1 if larvae were overwintering). Overall model statistics: $F_{1,24} = 39.38$, $P < 0.0001$, adjusted $r^2 = 0.61$.

[d]Linear regression model to describe the supercooling point as a function of the interaction between $\log_e$-transformed days and larval storage condition (0 if outside; 1 if in a greenhouse). Overall model statistics: $F_{2,65} = 95.77$, $P < 0.0001$, adjusted $R^2 = 0.74$.

close together relative to the geographical range of larch casebearer, and so the utility of these observations to forecast mortality in more distant sites remains to be determined. These findings suggest that our supercooling model may be useful for generating coarse estimates of mortality of larch casebearer in response to minimum temperatures across northern Minnesota. Accordingly, predicted overwintering survival increased across our study period of 1964–2016, suggesting that less extreme winters (i.e. those with higher minimum temperatures) may have contributed to the resurgence of larch casebearer around Grand Rapids, Minnesota (Fig. 5).

The lower lethal temperatures and supercooling points of larch casebearer are lowest during the months of December and January and higher in autumn and spring. These changes appear to be concomitant with transitions from the overwintering to active stage and vice versa, regardless of feeding status (Fig. 3). Thus, acquisition and loss of cold tolerance appear to be related to the onset or termination of overwintering behaviour (i.e. diapause), respectively, and not the ingestion of plant material. Model predictions using climate data did not account for larvae that may have been active during October and April and may be conservative estimates of population mortality. Linking phenology of larvae to cold tolerance may improve model predictions by enabling estimation of percentage mortality of both overwintering and actively feeding larvae.

Other mortality factors associated with cold exposure may be important for overwintering survival. For example, the duration of cold exposures (i.e. lower lethal time) may interact with the intensity of cold exposure to moderate survival (Salt, 1961; Nedvěd *et al.*, 1998). Our lower lethal time study suggested that exposure to −27 °C did not kill significantly more larvae than exposure to 2 °C. However, the lowest survival was observed at −27 °C and further investigation into lower exposure temperatures may provide insight on the role of exposure time × temperature interactions on survival of larch casebearer. The frequency of cold exposures may also be important (Marshall & Sinclair, 2015), such that locations with greater variance in temperature may result in different patterns of mortality compared with sites with similar mean temperatures but reduced variance. When held at high temperatures above 10 °C, for example, larvae of larch casebearer began to deacclimate within 1 week (Fig. 4), although such greenhouse temperatures are not ecologically relevant for January temperatures in Minnesota. Our supercooling point model did not account for the potential for short exposure to warmer temperatures during the overwintering stage to temporarily reduce cold hardiness as observed for mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae) (Régnière & Bentz, 2007). However, deacclimation by mountain pine beetle in response to warming appears to be much more rapid than for larch casebearer (Régnière & Bentz, 2007), which may be the result of a greater incidence and/or depth of diapause in larch casebearer populations. Nonetheless, because of the potential importance of variance in winter temperatures (e.g. heat waves followed by cold snaps) and duration of exposures for survival of larch casebearer, our supercooling point model provides conservative estimates for overwintering mortality.

Patterns of cold tolerance displayed by larch casebearer are comparable with defoliators native to northern Minnesota. In their most cold hardy conditions in January, 50% of larch casebearer larvae are expected to survive temperatures down to approximately −40 °C. The mean supercooling points of

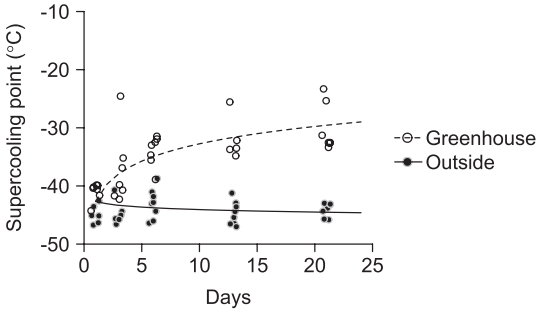

Figure 4 Change in supercooling points of larch casebearer larvae from Minnesota, U.S.A., over time. Data are jittered in the *x*-direction. Larvae in the greenhouse experienced 10.5–30.3 °C and 12–43% relative humidity and larvae outside experienced −14.2 to 3.7 °C and 54–100% relative humidity; both were exposed to natural photoperiods. Larvae were placed into treatment locations on 14 January 2017. Coefficients for the modelled line are provided in Table 2.

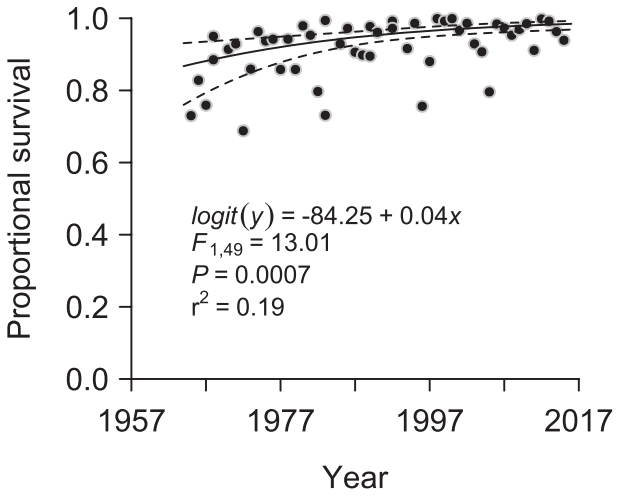

Figure 5 Estimated annual overwintering survival of larch casebearer larvae at Grand Rapids, Minnesota, U.S.A. from 1964 to 2016. Dashed lines are 95% confidence intervals.

overwintering, pharate larvae of forest tent caterpillar *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae) range from approximately −38 to −40 °C (Uelmen *et al.*, 2016), whereas larvae of spruce budworm *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae) supercool to an average of approximately −42 °C in February (Han & Bauce, 1995). These insects are sympatric with larch casebearer in large areas of its introduced range on eastern larch. Similar seasonal changes in supercooling points of larch casebearer were observed with spruce budworm because the mean supercooling points of spruce budworm were closer to −34 °C in autumn and spring (Han & Bauce, 1995). Thus, the cold tolerance of larch casebearer has likely contributed to its invasive success in this region.

Several factors, including spring phenological synchrony (Visser & Holleman, 2001; Van Asch & Visser, 2007), efficacy of natural enemies (Dwyer *et al.*, 2004), forest structure (Roland, 1993) and their interactions (Hunter & Elkinton, 2000), may contribute to outbreaks of forest lepidopterans in addition to potential changes in overwintering survival (Neuvonen *et al.*, 1999). Forecasting the impacts of climate change on insects will require understanding how intra- and interspecific interactions are moderated by changes in annual temperatures (Fleming & Volney, 1995; Volney & Fleming, 2000; Bentz *et al.*, 2010; Van der Putten *et al.*, 2010). Indeed, overwintering survival by larch casebearer larvae is just one of many factors that likely drive this insect's population dynamics. Linking landscape patterns in population dynamics to overwintering survival remains challenging. For example, for two North American *Dendroctonus* spp., predictions of population change in response to changes in overwintering survival are variable (Trân *et al.*, 2007; Sambaraju *et al.*, 2012; Weed *et al.*, 2015). Nonetheless, increased overwintering survival can facilitate shifts in the distribution and abundance of insects and, in turn, influence population growth rates. The supercooling point model developed in the present study suggests that overwintering survival has contributed to the increase in abundance of larch casebearer around Grand Rapids, Minnesota, and will aid in forecasting potential changes in the elevation and latitudinal range limits of this insect.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

File S1. Cooling rates for the −80 °C freezer and cooling bath used in cold tolerance assays.

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