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Allopatric populations of the invasive larch casebearer differ in cold tolerance and phenology

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Abstract. 1. Traits of non-native insect herbivores may vary spatially due to local genetic differences, rapid post-introduction evolution, and/or novel host plant associations.

2. Populations of larch casebearer, *Coleophora laricella* Hübner, originally from Europe have likely been isolated for > 60 years in North America on eastern larch, *Larix laricina* (Du Roi) K. Koch, and western larch, *Larix occidentalis* Nutt.

3. This study investigated cold tolerance and phenology of larvae collected from eastern larch in Minnesota, and western larch in Oregon, Idaho, and Montana, U.S.A.

4. Mean supercooling points of larvae from Minnesota were up to 10 °C lower than supercooling points of larvae from Oregon, Idaho, and Montana.

5. At ambient environmental conditions in spring, overwintering larvae from Minnesota required a mean (± SE) of 172 ± 19 degree-days above 5 °C to break winter quiescence and actively wander, significantly more than required by larvae from Oregon (66 ± 4), Idaho (64 ± 1), and Montana (60 ± 2).

6. Across all assays and despite substantial latitudinal and elevational variation among western larch sites, no significant differences in any traits were detected among larvae collected from western larch.

7. Spatial variation in cold tolerance and phenological traits of larch casebearer may be attributable to insect genetic differences and/or host plant effects, but exact mechanisms remain unknown. Differences in thermal biology between regions may result in disparate effects of climate change on insect populations and should be accounted for when forecasting insect dynamics across large spatial scales.

Key words. Degree-days, diapause, host effects, lower lethal temperature, supercooling point, trait variation.

Introduction

Establishing in novel habitats with few conspecifics can significantly influence biological variation within introduced populations (Sakai *et al.*, 2001). Adventive populations are often characterised as having reduced genetic variation relative to those in native or historical ranges (Dlugosch & Parker, 2008; Carter *et al.*, 2009, 2010; Meng *et al.*, 2015). When individuals from an adventive population establish in a novel location, genetic diversity may be further reduced (Grapputo *et al.*, 2005). If sufficient genetic variation exists on which to act, post-establishment evolution can result in trait differences between non-native and native populations (Moran & Alexander, 2014). Indeed, novel sensitivities to environmental cues such as temperature and photoperiod have evolved across short timescales in populations of introduced insects (Lounibos *et al.*, 2003; Moran & Alexander, 2014). The subspecies or population from which an invader originates can also influence invasion dynamics (Wu *et al.*, 2015; Chen *et al.*, 2016). For example, the Asian gypsy moth, *Lymantria dispar asiatica* (Vnukovskij), differs from the European gypsy moth, *Lymantria dispar dispar* (L.), in that the former has females capable of flight and a much broader host range; these traits are likely to increase spread

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rates and associated impacts (Reineke & Zebitz, 1998; Keena *et al.*, 2008; Hajek & Tobin, 2009).

Within-species variation among native and adventive populations may also be attributable to habitat differences. Introduced insect herbivores may encounter and feed on novel hosts, a process that can mediate several aspects of insect fitness (Awmack & Leather, 2002; Bertheau *et al.*, 2010). Host plants can alter insect developmental rates (Röder *et al.*, 2008), diapause incidence (Du Merle, 1999; Dambroski & Feder, 2007), voltinism (Hunter & McNeil, 1997), and cold tolerance (Morey *et al.*, 2016; Rosenberger *et al.*, 2017), among other factors. Distinct climatic regimes between habitats may also drive differences in insect phenology (Bale *et al.*, 2002; Van Asch & Visser, 2007) and cold tolerance due to acclimatisation (Régnière & Bentz, 2007; Teets & Hahn, 2018). Quantifying variation in the thermal biology of allopatric invasive populations may provide insights into how the invasion process (e.g. founder effects, novel host–plant associations) influences invader traits.

The larch casebearer, *Coleophora laricella* Hübner (Lepidoptera: Coleophoridae), is a small moth native to mountainous regions of Europe where it develops on European larch, *Larix decidua* Mill. This insect was first detected in the range of eastern larch, *Larix laricina* (Du Roi) K. Koch, in 1886 near Northampton, Massachusetts, U.S.A. (Hagen, 1886; Ryan *et al.*, 1987). A separate detection of larch casebearer occurred on western larch, *Larix occidentalis* Nutt., which is allopatric with eastern larch (Fig. 1), in the late 1950s in northern Idaho, U.S.A. (Denton, 1979; Tunnock & Ryan, 1985). Larch casebearer has not established in forests of the third larch species native to North America, alpine larch (*Larix lyallii* Parl.; Fig. 1), potentially owing to cold temperatures at the high-elevation sites where this tree species occurs (Tunnock & Ryan, 1985).

Barring human-aided movement of insects, larch casebearers residing on eastern and western larch have likely been isolated for over a half century. Recent outbreaks have been documented in both forest types in North America, despite ongoing parasitism from introduced and native natural enemies (Miller-Pierce *et al.*, 2015; Ward & Aukema, 2019b). Source populations for insects in each region remain unknown, although general life histories appear similar between insects developing on eastern and western larch. In brief, early-instar larvae mine within needles and then bear hollowed out needles as cases during late summer. Larvae overwinter as third instars within cases attached to host larches (*Larix* spp.), which are deciduous conifers. In spring, larvae moult into fourth instars and then resume feeding following needle flush. Pupation occurs inside cases attached to hosts and the eclosing small, silvery-brown-coloured moths are active from late spring through summer. Larch casebearer is univoltine and appears to have an obligate diapause, requiring exposure to both short (LD 12:12 h) and long (LD 18:6 h) photoperiods to complete development (Ryan, 1975).

Similarities in the thermal biology of larch casebearer on eastern larch versus western larch have not been formally investigated. In eastern larch forests of Minnesota, larch casebearer appears to be chill-susceptible: 50% of the population survived acute exposure to temperatures as low as −29, −41, and −28 °C in autumn, mid-winter, and spring, respectively, whereas mean

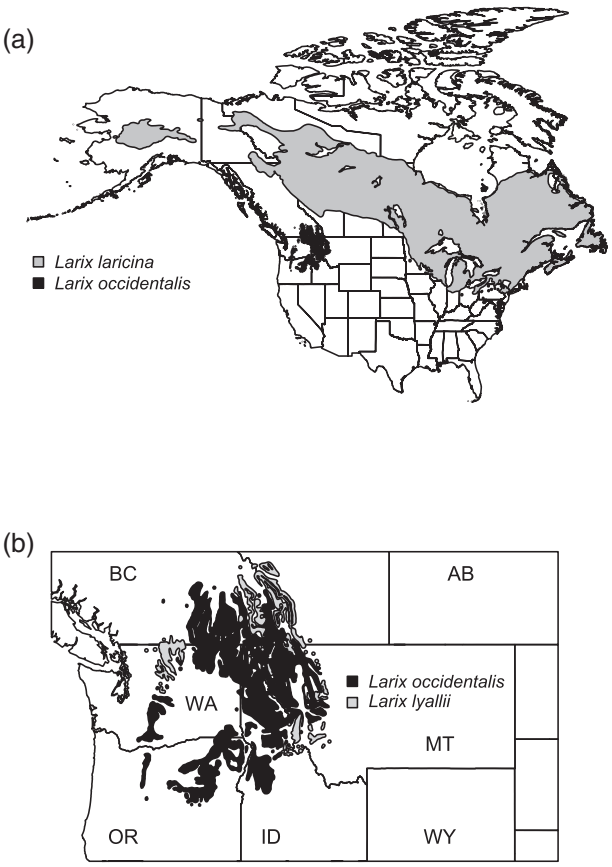

Fig. 1. Distributions of eastern larch *Larix laricina* (a; shown in grey), western larch *Larix occidentalis* (a, b; in black) and alpine larch *Larix lyallii* (b; in grey) in North America (Little, 1971; Prasad & Iverson, 2003). Western larch and alpine larch occur in the same region but are typically separated by 150–300 m of elevation (Arno & Habeck, 1972). Abbreviations for provinces or states: BC-British Columbia, Canada; AB–Alberta, Canada; WA–Washington, U.S.A.; OR–Oregon, U.S.A.; ID–Idaho, U.S.A.; MT–Montana, U.S.A.; WY–Wyoming, U.S.A.

supercooling points (SCPs; temperatures at which ice crystallisation begins in insects' bodies) in autumn, mid-winter, and spring were −37, −44, and −30 °C, respectively (Ward *et al.*, 2019c). Spring activation by larch casebearer – the transition from being attached to a twig via a silken plug to actively wandering in search of foliage – is timed such that larvae consistently activate several weeks after eastern larch has flushed new foliage (Ward *et al.*, 2019a). Larvae on eastern larch are also robust to starvation and can complete development on foliage from a variety of age classes (Ward *et al.*, 2019a). Nonetheless, the timing of spring phenology appears important for larch casebearer population dynamics on eastern larch, as it determines the onset of the growing season and, thus, may mediate the proportion of larvae that reach the overwintering stage in autumn (Ward *et al.*, 2019b). Indeed, recent outbreaks of larch casebearer on eastern larch appear to be facilitated, in part, by warmer growing seasons (Ward & Aukema, 2019a).

Spatiotemporal variation in thermal biology among invasive populations of larch casebearer (i.e. on western larch versus

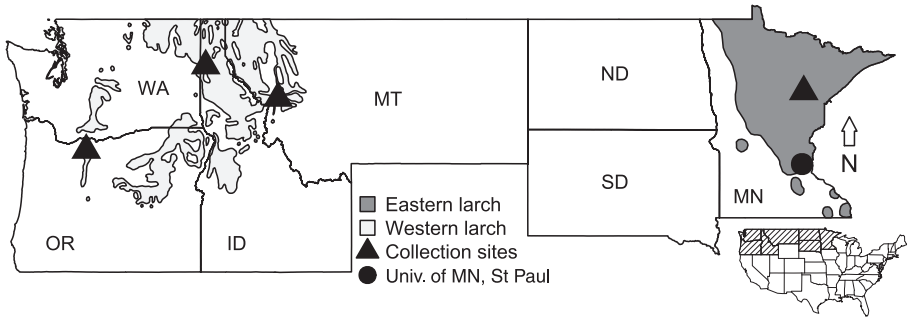

Fig. 2. Distributions of eastern larch, *Larix laricina*, in Minnesota, U.S.A., and western larch, *Larix occidentalis*, in the northwestern U.S.A., and sites from which overwintering larch casebearer larvae were collected in November/December 2017 and January 2018. Larvae were shipped to the University of Minnesota, Saint Paul, U.S.A., where all cold tolerance and phenology assays were conducted. Abbreviations for US states: WA–Washington; OR–Oregon; ID–Idaho; MT–Montana; ND–North Dakota; SD–South Dakota; MN–Minnesota.

eastern larch) have not been investigated. Differences in thermal biology could have important implications for how larch casebearer populations will respond to climate change and provide insights into how the invasion process, including novel plant–insect interactions, may drive trait differences among allopatric insect populations. Our overarching goal was to quantify if insect thermal biology varied among sites and/or host tree species and if any observed differences were dependent on time of year. We compared metrics of cold tolerance and phenology between larch casebearer larvae from a representative site in Minnesota (i.e. larvae on eastern larch trees) and one site in each of Oregon, Idaho, and Montana (i.e. larvae on western larch trees) at two time points during winter. Our objectives were to determine if the following varied among sites through winter: (i) lower lethal temperatures and SCPs of larvae; (ii) activation incidence (presence/absence) and degree-days required for activation of larvae; and (iii) morphology (larval head capsule widths, case length). We hope this work helps with forecasting larch casebearer responses to climate across broad geographical areas.

Materials and methods

Collections of larch casebearers

Third instar larch casebearers were collected from eastern larch and western larch in two time periods: late November/early December 2017 and late January 2018. Larvae from eastern larch were collected near Jacobson, Minnesota, U.S.A. (46.9982°N, 93.1073°W, elevation: 292 m), and larvae from western larch were collected near Mount Hood, Oregon, U.S.A. (45.2761°N, 121.6812°W, 1,204 m), Coeur d'Alene, Idaho, U.S.A. (47.7120°N, 116.8284°W, 692 m), and Missoula, Montana, USA (46.8145°N, 113.9544°W, 1,286 m) (Fig. 2). During each time period, larvae from Minnesota, Idaho, and Montana were collected within 3 days of each other, whereas larvae from Oregon were collected within *c*. 2 weeks of the others. In previous studies of larch casebearer larvae, mean SCPs and degree-days above 5 °C (DD) required for activation were lower by *c*. 4.5 °C (Ward *et al.*, 2019c) and *c*. 220 DD (Ryan, 1974b), respectively, in late January compared with early December. Thus, our design enabled us to study larch casebearer at times when larvae have different levels of cold hardiness and phenology.

For each collection period, larvae were sampled from branches within 2 m of the ground from *c*. 30 trees per site. Two or three twigs (*c*. 10 cm in length) with larvae were removed from each tree and larvae were left attached to twigs until immediately before use in cold tolerance and phenology assays. All twigs with insects from Minnesota were placed into a well-ventilated plastic box (46 × 31.1 × 17.8 cm; all plastic boxes were of this model) and set into a wooden cold frame outdoors (i.e. ambient temperatures and photoperiods) at the University of Minnesota (44.9886°N, 93.1802°W) on the same day they were collected. For collections from western larch sites, twigs with larvae were wrapped in paper towels, placed into insulated coolers (with volumes of 8.5 or 7.6 litres, depending on shipment) with ice packs, and shipped overnight to the University of Minnesota. Twigs from Oregon were stored in a refrigerator (*c*. 4 °C) for up to 2 weeks prior to shipment, whereas collections from Idaho and Montana were shipped the same day as collection. The arrival of the first collection from Oregon was delayed 5 days due to mishandling by the postal service; otherwise, shipments arrived within 24–48 h.

Upon arrival of a shipment, twigs with larvae were placed into plastic boxes in the cold frame. Thus, there were eight separate plastic boxes, one for each site (Minnesota, Oregon, Indiana, Montana) × collection period (November/December 2017 and January 2018) combination. Environmental conditions in storage boxes and all experimental locations for phenology assays (see later) were confirmed using HOBO Data Loggers (Onset Computer Corporation, Bourne, Massachusetts). Larvae were acclimatised in the cold frame for 4–8 weeks before assays. Thus, larvae collected in November/December 2017 and January 2018 were assayed in January and March 2018, respectively. Due to acclimatisation, we believe our data more accurately reflect larch casebearer biology at the time of assays rather than collection, i.e. larvae become less cold hardy between January and March (Ward *et al.*, 2019c) and require fewer degree-days for activation (Ryan, 1974b; Ward *et al.*, 2019a). Henceforth, 'month of transfer' refers to the time point at which

insects were assayed (i.e. January and March) rather than month of collection (i.e. November/December and January).

All assayed larvae were inactive, overwintering third instars. We were not able to determine if larvae were in diapause immediately before assays, as larvae that break diapause but remain quiescent are visually indistinguishable from those still in diapause. Thus, throughout, we use activation, indicative of the termination of winter quiescence and the onset of spring foraging, rather than diapause termination, which likeley occurred earlier in winter, to quantify survivorship and activity during cold tolerance assays and phenology, respectively.

Cold tolerance: supercooling

Cold tolerance assays used the same protocol as Ward *et al.* (2019c). Briefly, cases with larvae from each site were removed from twigs with forceps, placed individually into microcentrifuge tubes, and sealed inside with plastic dowels housing thermocouples (henceforth 'cold assay apparatus'). Each cold assay apparatus was sealed in a 20-cm polystyrene cube with a rubber stopper and the cube was then placed into a −80 °C freezer and cooled at a rate of approximately 1 °C min^{-1} (Carrillo *et al.*, 2004; Stephens *et al.*, 2015). Thermocouples were connected to USB data loggers and temperatures were recorded once per second with TRACERDAQ PRO software (Measurement Computing, Bourne, Massachusetts) and displayed in real time.

Supercooling points were measured between 16–18 January 2018 and 5–8 March 2018. In January and March, nine to 17 and five to six larvae were assayed per site, respectively ($n = 73$ across both months, 14–23 per site in total). Larvae were cooled until an exotherm, indicative of the release of heat due to a phase change from liquid to solid (Lee, 2010), was observed (i.e. when larvae began to freeze). The lowest temperature immediately before the exotherm occurred was recorded as the SCP. Larvae were often cooled to temperatures significantly below their SCPs, which was recorded as the lowest exposure temperature. Upon removal from the −80 °C freezer, larvae were transferred into 1.5-ml microcentrifuge tubes with four to six holes poked in the lids and placed in a growth chamber at environmental conditions promoting activation (20 °C, LD 18:6 h, 75% RH) (Ward *et al.*, 2019a). Throughout all cold tolerance and phenology assays (see the following sections), larvae were monitored for activation every 2–3 days until 2 months after activation ceased. For cold tolerance assays, larvae that did not activate across the observation window were recorded as dead. The effects of collection site, month of transfer (January or March), and their interaction on SCPs were modelled using multiple linear regression.

Control larvae, treated equivalently to those assayed but not placed in the freezer, were transferred to 1.5-ml microcentrifuge tubes and into the same growth chamber as described earlier on 2–5 January 2018 ($n = 24$ larvae per site), 16–18 January 2018 ($n = 24$ larvae per site), and 5 March 2018 ($n = 30$ larvae per site). The controls in January originated from the first collection period, whereas the controls in March originated from the second collection period. Controls were not analysed formally, but were monitored for activation to confirm that cold tolerance assays were conducted on living insects.

Cold tolerance: lower lethal temperatures

Larvae were assayed for lower lethal temperatures from 2–5 January 2018 and 5–8 March 2018 using the same protocol as SCP assays. Larvae were randomly assigned to a predetermined target exposure temperature between −20 and −70 °C before the assay and removed from the freezer upon reaching it. Sixteen larvae, four from each site, were assayed at a time until 19–32 larvae were assayed per site in each of January and March ($n = 208$ larvae across both months, 51–53 larvae per site in total).

Cold exposure was acute, as each larva was removed from the freezer and brought to room temperature immediately after reaching the exposure temperature. Larvae were placed in the same growth chamber as those assayed for SCPs and monitored for survival. The effects of exposure temperature, collection site, month of transfer, and all two- and three-way interactions on larval survival (presence/absence) were evaluated using logistic regression. Larvae from SCP assays were also included in analyses of lower lethal temperatures, given that we measured the lowest exposure temperatures and whether larvae survived.

Phenological comparisons: growth chambers

On 2 January and 5 March 2018, 50 larvae from each site were carefully removed from twigs using forceps ($n = 400$ larvae across both months; 100 per site in total). On each date, equal numbers of larvae were placed in growth chambers held at LD 12:12 h and LD 18:6 h (20 °C, 75% RH). Larvae were kept separated by site and in 9 × 50-mm polystyrene Petri dishes (Falcon Labware, Oxnard, California; all Petri dishes were of this model) in groups of four to six (i.e. each dish only contained larvae from a single site). Dishes were then randomly assigned to one of the two photoperiod treatments and larvae were monitored every 2–3 days for activation. These photoperiods were selected because larch casebearer larvae on eastern larch have a higher probability of activating and require fewer DD for activation at LD 18:6 h vs LD 12:12 h (Ward *et al.*, 2019a) and we were interested in determining the presence of similar responses by larch casebearer from western larch.

For phenological comparisons (see the following section as well), DD per day were calculated as $(T_{max} + T_{min})/2 - 5$ °C and DD accumulated at activation were recorded for each larva. The lower developmental threshold of 5 °C was based on laboratory studies of larch casebearer from eastern larch (Ward *et al.*, 2019a). For this study, DD accumulated after transfer to growth chambers were quantified. If larvae did not activate, they were assumed to be in a terminal diapause, perhaps due to a short-day photoperiod that maintained diapause (Ryan, 1975), and/or to have desiccated before they could activate. Larvae that activated were removed from each dish upon their discovery.

We quantified the effects of collection site, month of transfer, photoperiod and all two- and three-way interactions on larval activation across the study period and mean DD until activation. For each phenological comparison study (see later), we analysed data using mixed-effects models fitted via the LME4 package in R (Bates *et al.*, 2015), and each model included a term for Petri dish as a random intercept. Binary responses (e.g. presence/absence of activation) were analysed using generalised

linear mixed-effects models with binomial error structures and logit link functions. Continuous responses were analysed using linear mixed-effects models and *P*-values were calculated using Satterthwaite's approximation for the d.f. (Kuznetsova *et al.*, 2017).

Phenological comparisons: ambient conditions

On 5 March 2018, 40 larvae from the January collection at each site were placed into Petri dishes in groups of eight, moved into an adjacent plastic box in the cold frame, and monitored for activation. For these larvae, DD above 5 °C accumulated in the cold frame from 20 February, when most third-instar larch casebearers appear to have broken diapause (Ward *et al.*, 2019a), until activation were quantified. We investigated the effects of site on larval activation (presence/absence), mean DD until activation, and days until activation by using mixed-effects models as described in the preceding section.

Morphology

Larval head capsule widths and lengths of needle cases were measured to the nearest 0.01 mm using a Leica MZ6 microscope (Wetzlar, Germany) with real-time camera and digital micrometer ($n = 154$ larvae, 24–44 larvae per site). Head capsule widths and case lengths were measured at the widest and longest points, respectively, and compared among collection sites using ANOVA.

Statistical analyses

All analyses were conducted using R statistical software v.3.5.0 (R Core Team, 2018). A backwards selection approach was used to develop final models, in which all main effects and interactions were first fitted. Non-significant interaction terms were removed first, then main effects, until only significant variables remained in the final model ($\alpha = 0.05$). All main effects remained in models when involved in a significant interaction, regardless of *P*-value. Only final models are reported. Pairwise comparisons between combinations of collection site, month of transfer, and/or treatment (e.g. site × month of transfer × photoperiod, dependent on which models had significant interaction terms) were conducted using Tukey's honestly significant difference (Tukey HSD) tests in the EMMEANS package in R (Lenth, 2018). For general linear models, graphical inspections of residuals confirmed that assumptions of normality and homoscedasticity were met. Unless noted otherwise, point estimates are reported as means ± SEs. Data for each study are available on the Data Repository for University of Minnesota (DRUM) (http://hdl.handle.net/11299/202850).

Results

Cold tolerance: supercooling points

Survival rates among control larvae in cold tolerance trials were similar among our four sites: 84 ± 5%, 76 ± 6%, 87 ± 4%, and 85 ± 5% in January and 83 ± 7%, 93 ± 5%, 100 ± 0%, and 100 ± 0% in March for larvae from Minnesota, Oregon, Idaho, and Montana, respectively. Supercooling points were influenced by site ($F_{3,65} = 38.38$, $P < 0.0001$), month of transfer ($F_{1,65} = 82.32$, $P < 0.0001$), and their interaction ($F_{3,65} = 5.80$, $P = 0.0014$; Fig. 3). Supercooling points of larvae from Minnesota were lower than those of larvae from western larch sites within both months of transfer (Tukey HSD, all $t_{64} > 4.57$, $P < 0.001$). In January, larvae from Minnesota had a mean SCP of −43.7 ± 0.6 °C, as compared with −37.0 ± 0.7, −37.9 ± 0.9, and − 39.4 ± 0.6 °C for larvae from Oregon, Idaho, and Montana, respectively. In March, the mean SCP of larvae from Minnesota was −41.5 ± 0.7 °C, compared with −30.5 ± 2.4, −31.2 ± 0.6, and − 29.6 ± 0.5 °C for larvae from Oregon, Idaho, and Montana, respectively. Thus, between January and March, SCPs for third instars from Minnesota increased by 2.2 °C on average, but this change was not significant (Tukey HSD, $t_{65} = 1.78$, $P = 0.64$). SCPs increased significantly by 6.5, 6.7, and 9.8 °C from January to March for third instars collected from Oregon, Idaho, and Montana, respectively (Tukey HSD, all $t_{64} > 4.41$, $P < 0.01$). Within each month of transfer, SCPs did not differ among larvae from western larch sites (Tukey HSD, all $t_{64} < 2.18$, $P > 0.37$).

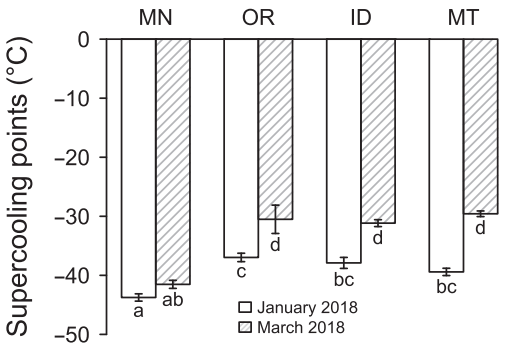

Fig. 3. Mean (± SE) supercooling points of overwintering larch casebearer larvae by site and month of transfer (site × month interaction, $F_{3,65} = 5.80$, $P = 0.0014$). Larvae were collected from eastern larch in Minnesota (MN) or western larch in Oregon (OR), Idaho (ID), and Montana (MT), USA. Different letters indicate significantly different groupings based on Tukey's honestly significant difference tests ($\alpha = 0.05$).

Cold tolerance: lower lethal temperatures

The main effects for lowest-exposure temperature ($\chi^2_1 = 208.15$, $P < 0.0001$), site ($\chi^2_3 = 37.46$, $P < 0.0001$), and month of transfer ($\chi^2_1 = 14.78$, $P = 0.0001$) influenced larval survival. No two-way interactions were significant (all $P > 0.30$), but the three-way interaction of lowest-exposure temperature × site × month of transfer influenced larval survival ($\chi^2_3 = 8.08$, $P = 0.0443$; Fig. 4). Overall, larvae from Minnesota were more cold hardy than those from western larch sites. For example, in January, after acute exposure to temperatures between −30 and −40 °C, 100% of larvae from Minnesota survived whereas only 27 ± 13%, 58 ± 14%, and 43 ± 13% of larvae from Oregon, Idaho, and Montana survived, respectively.

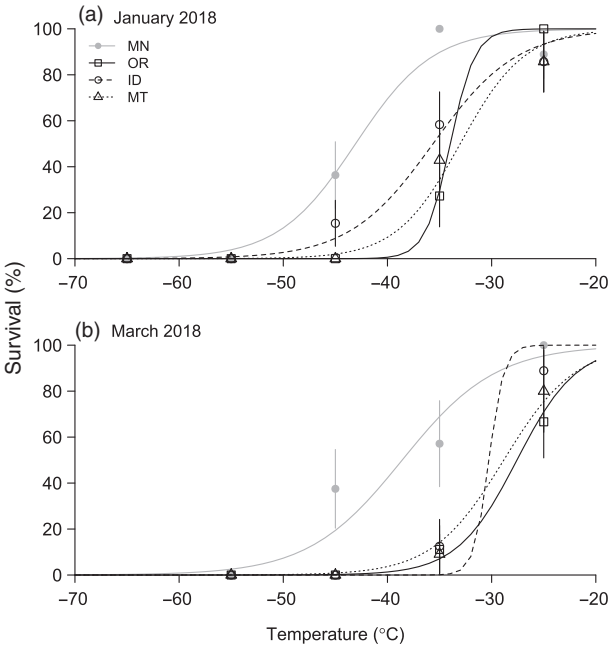

Fig. 4. Effect of minimum exposure temperature, site, and month of transfer on mean (± SE) percentage of larch casebearer larvae that survived (temperature × site × month interaction, χ^2_3 =8.08, $P = 0.0443$). Overwintering larvae were collected from eastern larch in Minnesota (MN) or western larch in Oregon (OR), Idaho (ID), and Montana (MT), U.S.A. Temperature was analysed as a continuous variable but has been discretised into 10 °C increments for graphical depiction. Fit lines on both panels are from a single generalised linear model (i.e. data from both panels were analysed in a single model). Data are split by panel to illustrate differences in the effect of temperature by groupings.

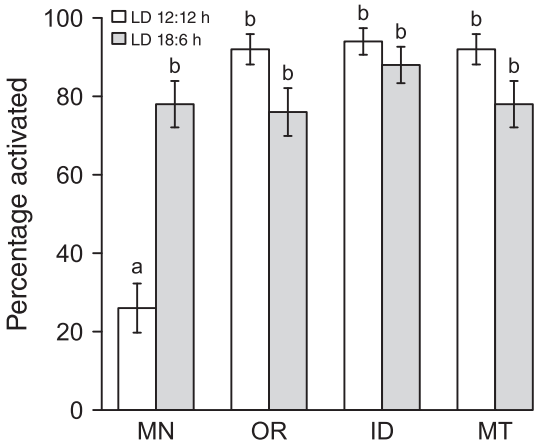

Fig. 5. Mean (± SE) percentage of overwintering larch casebearer larvae that activated by site and photoperiod (site × photoperiod interaction: $\chi^2_3 = 32.60$, $P < 0.0001$). Larvae were collected from eastern larch in Minnesota (MN) or western larch in Oregon (OR), Idaho (ID), and Montana (MT), U.S.A. Different letters indicate significantly different groupings based on Tukey's honestly significant difference tests ($\alpha = 0.05$).

In March, after acute exposure to temperatures between −30 to −40 °C, 57 ± 19% of larvae from Minnesota survived whereas only 11 ± 10.5%, 12 ± 11.7%, and 9 ± 8.7% of larvae from Oregon, Idaho, and Montana survived, respectively.

Phenological comparisons: growth chambers

Larval activation was significantly influenced by the main effect of site ($\chi^2_3 = 33.43$, $P < 0.0001$) and the interaction of site × photoperiod ($\chi^2_3 = 32.60$, $P < 0.0001$; Fig. 5). The main effect of photoperiod was not significant ($\chi^2_1 = 0.62$, $P = 0.43$). Activation rates did not change significantly with month of transfer ($P > 0.05$). When held at LD 12:12 h, only 26 ± 6% of larvae from Minnesota activated compared with 92 ± 4%, 94 ± 3%, and 92 ± 4% of larvae from Oregon, Idaho, and Montana, respectively. When held at LD 18:6 h, 78 ± 6% of larvae from Minnesota activated compared with 76 ± 6%, 88 ± 5%, and 78 ± 6% of larvae from Oregon, Idaho, and Montana, respectively. That is, *c*. 50% more larvae from Minnesota activated at LD 18:6 h compared with LD 12:12 h across both months of transfer (Tukey HSD, $Z = 4.92$, $P < 0.0001$). Among larvae from western larch sites, a non-significant decrease in larval activation was observed at LD 18:6 h compared with LD 12:12 h (Tukey HSD, all $Z < 2.08$, $P > 0.42$). Activation was statistically similar for larvae from all western larch sites at both photoperiods (Tukey HSD, all $Z < 1.54$, $P > 0.78$).

The mean DD until larval activation was influenced by main effects of site ($F_{3,293} = 72.02$, $P < 0.0001$), month of transfer ($F_{1,293} = 341.28$, $P < 0.0001$), photoperiod ($F_{1,294} = 97.94$, $P < 0.0001$) as well as the two-way interaction between month of transfer × photoperiod ($F_{1,293} = 63.41$, $P < 0.0001$) and the site × month of transfer × photoperiod interaction ($F_{3,293} = 4.86$, $P = 0.0026$; Fig. 6). The two-way interactions of site × month of transfer ($F_{3,293} = 2.33$, $P = 0.0746$) and site × photoperiod ($F_{3,293} = 2.57$, $P = 0.0543$) were not significant. In both January and March, activation of larvae from Minnesota was significantly delayed across both photoperiods compared with larvae from Oregon, Idaho, and Montana. There were no differences among larvae from western larch sites within any month of transfer × photoperiod combination (Tukey HSD, all $t < 3.15$, d.f. > 292, $P > 0.12$). At LD 12:12 h in January, activation of larvae from Minnesota averaged 902 ± 109.5 DD compared with significantly lower averages of 505 ± 24, 606 ± 35, and 527 ± 24 DD for larvae from Oregon, Idaho, and Montana, respectively (Tukey HSD, all $t > 6.60$, d.f. > 292, $P < 0.0001$). At LD 18:6D in January, DD until activation of larvae from Minnesota averaged 499 ± 39 DD compared with significantly lower averages of 355 ± 17, 354 ± 13 and 365 ± 34 DD for larvae from Oregon, Idaho, and Montana, respectively (Tukey HSD, all $t > 3.77$, d.f. > 292, $P < 0.05$). In March, there were no significant differences in DD until activation between LD 12:12 h and LD 18:6 h within sites (Tukey HSD, all $t < 1.18$, d.f. > 292, $P > 0.99$). Across both photoperiods in March, DD until activation of larvae from Minnesota averaged 494 ± 26 DD, significantly more than the 195 ± 19, 178 ± 27, and 191 ± 24 DD required for activation of larvae from Oregon, Idaho, and Montana, respectively (Tukey HSD, all $t > 9.40$, d.f. > 292, $P < 0.0001$).

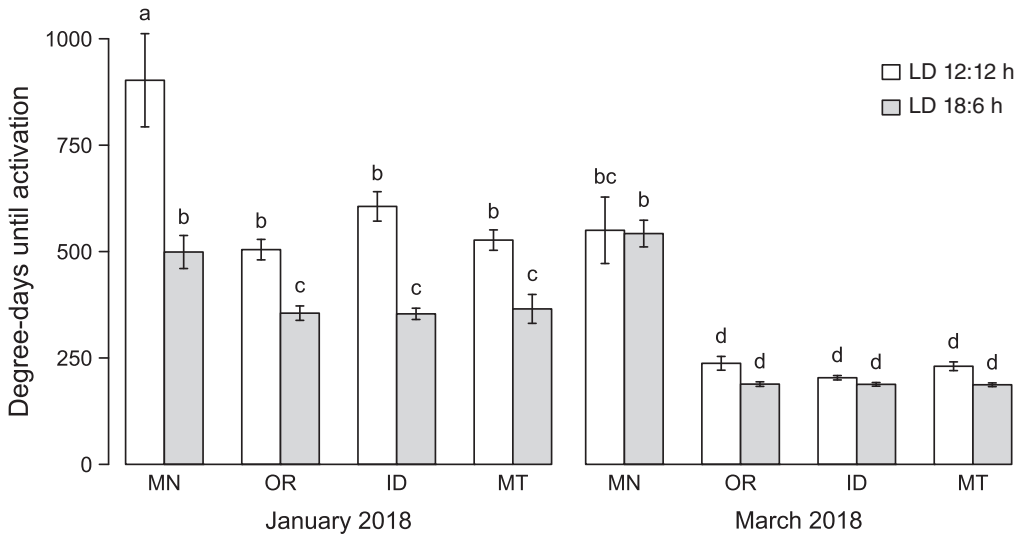

Fig. 6. Mean (±SE) degree-days above 5 °C until activation of overwintering larch casebearer larvae by collection site, month of transfer, and photoperiod (site × month × photoperiod interaction, $F_{3,293} = 4.86$, $P = 0.0026$). Larvae were collected from eastern larch in Minnesota (MN) or western larch in Oregon (OR), Idaho (ID), and Montana (MT), U.S.A. Different letters indicate significantly different groupings based on Tukey's honestly significant difference tests ($\alpha = 0.05$).

Phenological comparisons: ambient conditions

Significantly fewer larvae from Minnesota (62 ± 8%) activated compared with Oregon (90 ± 5%), Idaho (95 ± 3%), and Montana (98 ± 2%) (Tukey HSD, all $Z > 2.74$, $P < 0.05$; Fig. 7a). There were no differences in activation among larvae from western larch sites (Tukey HSD, all $Z < 1.30$, $P > 0.56$). Degree-days until activation averaged 172 ± 19 DD for larvae from Minnesota, significantly more than the 66 ± 4, 64 ± 1, and 60 ± 2 DD required by larvae from Oregon, Idaho, and Montana, respectively (Tukey HSD, all $t > 9.60$, d.f. > 128, $P < 0.0001$; Fig. 7b). The >100 DD difference equated to an 8-day delay in mean activation of larvae from Minnesota compared with those from western larch sites (Tukey HSD, all $t > 9.83$, d.f. > 128, $P < 0.0001$; Fig. 7c). Moreover, larvae from Minnesota emerged across a period of 25 days compared with periods of 14, 2, and 14 days for larvae from Oregon, Idaho, and Montana, respectively.

Morphology

When comparing larval morphology, head capsule widths were equivalent across sites (Tukey HSD, all $t < 1.54$, d.f. > 146, $P > 0.41$). Larval head capsule widths for Minnesota, Oregon, Idaho, and Montana were 0.29 ± 0.006, 0.29 ± 0.008, 0.30 ± 0.007, and 0.30 ± 0.008 mm, respectively . However, larvae from Minnesota had significantly shorter needle cases than those from western larch sites (Tukey HSD, all $t_{150} > 3.13$, $P < 0.05$), with no differences detected among larvae from western larch sites (Tukey HSD, all $t_{146} < 1.05$, $P > 0.72$). Needle case lengths were 2.69 ± 0.14, 3.24 ± 0.08, 3.19 ± 0.06, and 3.12 ± 0.09 mm for larvae from Minnesota, Oregon, Idaho, and Montana, respectively.

Discussion

The phenotypes and genotypes of non-native insects can be significantly influenced by founder effects (Ross & Shoemaker, 2008), post-establishment evolution (Grapputo *et al.*, 2005; Bean *et al.*, 2012) and/or interactions with invaded communities (Sakai *et al.*, 2001). In North America, larch casebearer has invaded the range of two allopatric hosts, eastern larch and western larch. Populations residing on each tree species have likely been isolated for over 60 years, barring the possibility of multiple introductions or human-mediated movement of casebearers. Across every assay we conducted, larvae from eastern larch differed significantly in their cold hardiness and phenology from those on western larch.

Temperature and photoperiod are the main determinants of insect development and the initiation, maintenance, and termination of diapause (Tauber & Tauber, 1976; Koštál, 2006; Bale & Hayward, 2010). Larvae on western larch were sourced from sites that were 228–616 km distant from each other and located across a wide range of latitudes (45.3–47.7°N) and elevations (292–1286 m), probably experiencing disparate regimes of temperature and photoperiod. Despite these differences, larvae from western larch displayed extremely similar cold tolerance and phenology. Previous work has shown that SCPs (Ward *et al.*, 2019c) and DD required for activation (Ward *et al.*, 2019a) of third-instar larch casebearers from northern Minnesota do not vary across sites separated by 10–38 km and latitudes in the range of 46.6–46.9°N. Although some of the thermal biology metrics we investigated could have been influenced by ambient environmental cues (Kim & Song, 2000; Colinet *et al.*, 2015), it appears more likely that genetic differences between insect populations or host plant effects, rather than region-specific climatic or photoperiod regimes, drove observed differences in larch casebearer biology between eastern and western larch.

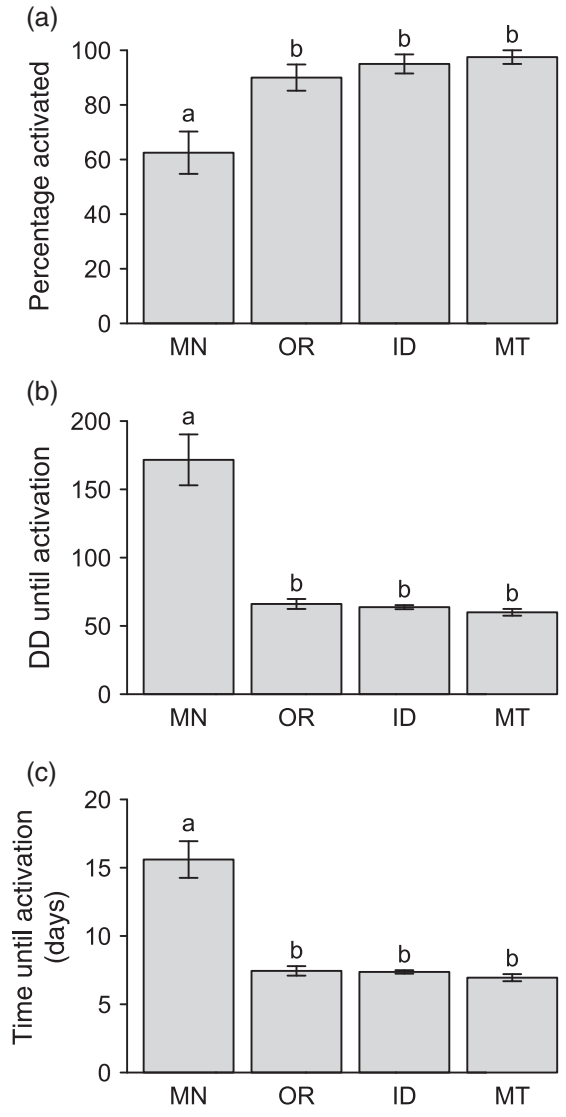

Fig. 7. The effect of site on mean (±SE) percentage of larvae that activated (a; model statistics, $\chi^2_3 = 19.11$, $P = 0.0003$), degree-days above 5 °C until activation (b; $F_{3,129} = 45.46$, $P < 0.0001$), and time after 25 April (days) until activation (c; $F_{3,128} = 47.33$, $P < 0.0001$) for overwintering larch casebearer larvae stored outside in ambient environmental conditions in Saint Paul, Minnesota. Larvae were collected from eastern larch in Minnesota (MN) or western larch in Oregon (OR), Idaho (ID), and Montana (MT), U.S.A. Letters indicate significantly different groupings based on Tukey's honestly significant difference tests ($\alpha = 0.05$).

The invasion process can result in significant reductions in genotypic and phenotypic variation (Tsutsui *et al.*, 2000; Sakai *et al.*, 2001; Cai *et al.*, 2008). Insect traits can also be influenced by the subpopulation from which an invader arrives and extreme trait differences can exist between insect congeners and/or subspecies (Keena *et al.*, 2008; Chen *et al.*, 2016). We cannot rule out the possibility that the population of larch casebearers on western larch was introduced from Russia or eastern Asia, where several congeners of *Coleophora laricella* exist: *Coleophora sibiricella* Falkovitsh, *Coleophora obducta* Meyrick, and *Coleophora sinensis* Yang. Indeed, others have speculated that larch casebearers on western larch may have become established from a source other than invasive populations on eastern larch (Shepherd & Ross, 1973). Our morphological comparisons suggested that larval size was equivalent across sites, but larvae from western larch constructed longer cases. Equivalent larval size is not sufficient confirmation of identical *Coleophora* species and variation in case length may be due to differences in host tree size or health, which could affect needle length, rather than behavioural differences. We also cannot rule out the possibility that evolution across the *c*. 60 years of separation between these two populations – if identical species – has resulted in differences in thermal biology.

Host tree species can also have substantial effects on insect traits (Jaenike, 1990; Awmack & Leather, 2002), including impacts on overwintering physiology (Liu *et al.*, 2009) and larval development (Röder *et al.*, 2008). For example, SCPs of light brown apple moth, *Epiphyas postvittana* (Walker), differed by > 3 °C when feeding on different host plant species (Morey *et al.*, 2016). The SCPs and LT_{50} of mountain pine beetle, *Dendroctonus ponderosae* (Hopkins), varied from −28.2 to −33.2 °C and −29.4 to −33.3 °C, respectively, with host pine species (Rosenberger *et al.*, 2017). At equivalent environmental conditions but on different host species, egg–adult development time of the sweetpotato whitefly, *Bemisia tabaci* (Gennadius), ranged from 19 to 30 days (Coudriet *et al.*, 1985). Diapause initiation and maintenance can also be influenced by host plant species (Hunter & McNeil, 1997) and/or quality (Goehring & Oberhauser, 2002). Thus, physiological differences between larvae from eastern and western larch may be attributable to host effects; however, further investigations are required to disentangle the relative contributions of host plants and genetics to variation in larch casebearer thermal biology.

Physiological patterns may also be facilitated by differences in larval diapause intensity, defined as the relative length of developmental arrest when exposed to diapause-terminating environmental cues (Koštál, 2006), between regions. Cold hardiness may be directly or indirectly linked with diapause intensity, as similar environmental cues may drive diapause development and the production or reduction of cryoprotectants (Denlinger, 1991; Atapour & Moharramipour, 2009). A more intense diapause by larvae on eastern larch that conferred greater cold tolerance and delayed activation, or earlier termination of diapause by larvae from western larch that reduced cold tolerance and accelerated activation, are both consistent with our results.

We note that our experimental protocol could have influenced findings. Larvae from one western state, Oregon, were stored for *c*. 2 weeks in darkness at 4° C prior to shipment, which was also delayed. Larvae from Minnesota, Oregon, Idaho, and Montana were moved 2.00°, 0.29°, 2.72°, and 1.83° of latitude south to the University of Minnesota, respectively. Despite these factors, no statistical differences in cold tolerance or phenology were detected among larvae from western states. Moreover, larvae on western larch appear to develop synchronously regardless of elevation (Ryan, 1974a) and larch casebearer larvae do not appear to advance their activation in response to accumulation of DD across autumn or early winter (Ward *et al.*, 2019b). Thus,

we find it unlikely that shipping, DD accumulated prior to the start of phenology assays, and/or transfer to a different ambient photoperiod altered our conclusions.

Latitudinal (Sambaraju *et al.*, 2012) and elevational (Raffa *et al.*, 2013; Bentz *et al.*, 2016) range expansions by insects can occur with global climate change and may result in novel host-plant associations (Stastny *et al.*, 2006; Cullingham *et al.*, 2011; Erbilgin *et al.*, 2014). Warming temperatures may increase suitability of currently uninhabited forests of alpine larch, a high-elevation species, for larch casebearer, which would result in a novel plant–insect association. Our results suggest that invasion success on alpine larch could be mediated by: (i) the source population of invaders (e.g. larvae from eastern versus western larch forests) and/or (ii) host-mediated changes in the thermal biology of larch casebearer. Investigations following laboratory crossings of insects from eastern larch and western larch, common garden studies, and genetic analyses are needed to elucidate drivers of geographical variation in larch casebearer thermal biology.

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Author contributions

SW conceived and directed the study and wrote the initial draft of the manuscript. All authors made substantial contributions to experimental design, data collection, and writing of subsequent drafts.

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