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Range expansion of *Lymantria dispar dispar* (L.) (Lepidoptera: Erebidae) along its north-western margin in North America despite low predicted climatic suitability

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Abstract

Aim: The European gypsy moth, *Lymantria dispar dispar* (L.), (Lepidoptera: Erebidae) is an invasive defoliator that has been expanding its range in North America following its introduction in 1869. Here, we investigate recent range expansion into a region previously predicted to be climatically unsuitable. We examine whether winter severity is correlated with summer trap captures of male moths at the landscape scale, and quantify overwintering egg survivorship along a northern boundary of the invasion edge.

Location: Northern Minnesota, USA.

Methods: Several winter severity metrics were defined using daily temperature data from 17 weather stations across the study area. These metrics were used to explore associations with male gypsy moth monitoring data (2004–2014). Laboratory-reared egg masses were deployed to field locations each fall for 2 years in a 2 × 2 factorial design (north/south aspect × below/above snow line) to reflect microclimate variation. Rates of successful egg hatch were assessed the following springs.

Results: Reductions in summer male moth captures are associated with several metrics of winter severity, such as minimum temperatures. Most egg masses suffered >95% mortality each winter. However, hatching success reached up to 80% in egg masses that had overwintered below the snow line (e.g., <30 cm from the ground).

Main Conclusions: Our findings that cold winter temperatures are associated with reduced summer trap captures of European gypsy moth, likely due to increased overwintering mortality of exposed egg masses, are consistent with previous predictions of thermal range boundaries for this species. However, high survival in egg masses deposited close to the ground are consistent with thermal escape in subnivean environs (i.e., below snow cover), and suggest that further northward range expansion will be likely in areas that receive measurable annual snowfall.

KEYWORDS
climatic envelope, climatic suitability, gypsy moth, range expansion, snow insulation, suboptimal temperatures, winter mortality

1 | INTRODUCTION

With the rise of globalization and international mobility, increased rates of introductions and establishments of nonindigenous species into naïve habitats have placed enhanced focus on species distribution models (Levine & D'Antonio, 2003; Wonham & Pachepsky, 2006). Reliable estimates of species ranges are helpful for risk assessments for potential ecosystem impacts and management priority (Leung et al., 2012; Lodge et al., 2006). There are several approaches to estimating potential biogeographical distributions of species (e.g., Kot & Schaffer, 1980; Skellam, 1951) including climatic envelope models that can predict potential ranges of invasive species as well as range shifts due to anthropogenic climate change (Jeschke & Strayer, 2008). Climate can be an important determinant of geographic boundaries of species (Parmesan, 1996), especially for insects, whose growth and development are regulated by temperature (Bale et al., 2002).

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Erebidae), is a moth found across several regions of the Northern Hemisphere (Tobin, Bai, Eggen, & Leonard, 2012; Tobin, Cremers, Hunt, & Parry, 2016). The larvae are polyphagous (Liebhold et al., 1995) and are capable of defoliating vast forest areas during periodic outbreaks (Haynes, Bjørnstad, Allstadt, & Liebhold, 2013; Haynes, Liebhold, & Johnson, 2009). The European subspecies of gypsy moth, *L. d. dispar* (L.), was accidentally introduced into eastern North America in 1869 in Medford, Massachusetts, USA (Riley & Vasey, 1870), and has been spreading westward across the USA since that time (Sharov, Roberts, Liebhold, & Ravlin, 1995; Tobin, Liebhold, Roberts, & Blackburn, 2015). Gypsy moth spread patterns are typically characterized by stratified dispersal, which integrates short-distance diffusive movement with isolated, long-distance establishments of populations (Hengeveld, 1988; Shigesada, Kawasaki, & Takeda, 1995; Tobin & Blackburn, 2008). Although adult female European gypsy moths are incapable of flight, first instars that hatch in spring from overwintered egg masses balloon short distances on silken threads (Doane & McManus, 1981). Long-distance dispersal of populations primarily occurs through the anthropogenic movement of egg masses (Liebhold, Halverson, & Elmes, 1992; Tobin & Blackburn, 2008). As isolated populations grow and coalesce, the population front can advance large distances (Liebhold & Tobin, 2008).

Because insects such as gypsy moth are poikilothermic, temperatures are often used to estimate distributional limits (Gray, 2004; Régnière, Nealis, & Porter, 2009; Sullivan & Wallace, 1972; Ungerer, Ayres, & Lombardero, 1999). Gypsy moth exhibits an obligate diapause in the egg stage, although chilling requirements for diapause completion vary regionally throughout its native range (Keena, 2015). Phenological models indicate that the potential southern margin of gypsy moth in the USA will be limited by insufficient chilling to terminate diapause (Gray, 2004). Simultaneously, exposure to extremely cold temperatures results in mortality to eggs (Madrid & Stewart, 1981; Maksimovic, 1958; Summers, 1922). As such, northern expansion of gypsy moth populations in North America has been predicted to be limited by winter temperatures, bounded by a −30°C isoline (Brown & Sheals, 1944; Sullivan & Wallace, 1972).

The current distributional range of European gypsy moth in North America extends northward to the Canadian Maritime Provinces, southward to North Carolina, and westward to Minnesota and Wisconsin (Tobin et al., 2016). Along the western expanding range front of European gypsy moth in the USA, male moths have been caught annually in north-eastern Minnesota since 2000 (Figures 1 and 2; Streifel et al., 2017), reflecting a mix of established colonies with stochastic introductions and extinctions (Tobin, 2007). Egg masses—the most definitive sign of an established, reproducing gypsy moth population—were first detected in north-eastern Minnesota in 2008. North-eastern Minnesota exhibits extensive areas of suitable forest cover, such as >20% of the basal area in preferred host genera such as *Populus* and *Betula* (Liebhold, Gottschalk, Mason, & Bush, 1997; Liebhold et al., 1995; Morin et al., 2005).

Climatically, the persistence of reproducing populations of gypsy moth in areas of the northern Great Lakes region of the USA is puzzling (Smitley, Andresen, Priest, Mech, & McCullough, 1998). The Arrowhead region of Minnesota, for example (Figure 1), is putatively climatically inhospitable to gypsy moth (Brown & Sheals, 1944) as winter temperatures frequently drop below −30°C (National Centers for Environmental Information, 2015). Moreover, phenological modelling has shown that spring and summer degree day accumulation in this region would allow few individuals to complete a life cycle each year (Gray, 2004). Delayed development due to suboptimal temperatures may also reduce exposure to chilling periods requisite for acquisition of cold hardiness, thus increasing overwintering mortality (Gray, 2004; Régnière & Nealis, 2002).

In this study, we investigate how annual summer male gypsy moth densities vary with the severities of preceding winters during its invasion into the Arrowhead region of Minnesota, USA from 2004–2014. We further test a hypothesis of climatic limitation by examining hatching success rates of 705 egg masses deployed to 12 field sites in north-eastern Minnesota during the winters of 2014 and 2015. Female gypsy moths oviposit egg masses in locations close to their pupation sites (Odell & Mastro, 1980); we further examine how variation in egg mass placement in both aspect and height on trees (i.e., above/below winter snow line) may affect overwintering mortality due to microclimate variation. Overall, we attempt to gain insight into how this invasive insect's range continues to expand into this putatively climatically unsuitable region.

2 | MATERIALS AND METHODS

2.1 | Modelling links between winter temperatures and survey trap catch

2.1.1 | Data preparation

Male gypsy moth trap catch data were obtained from the Minnesota Department of Agriculture for the state of Minnesota, USA, from
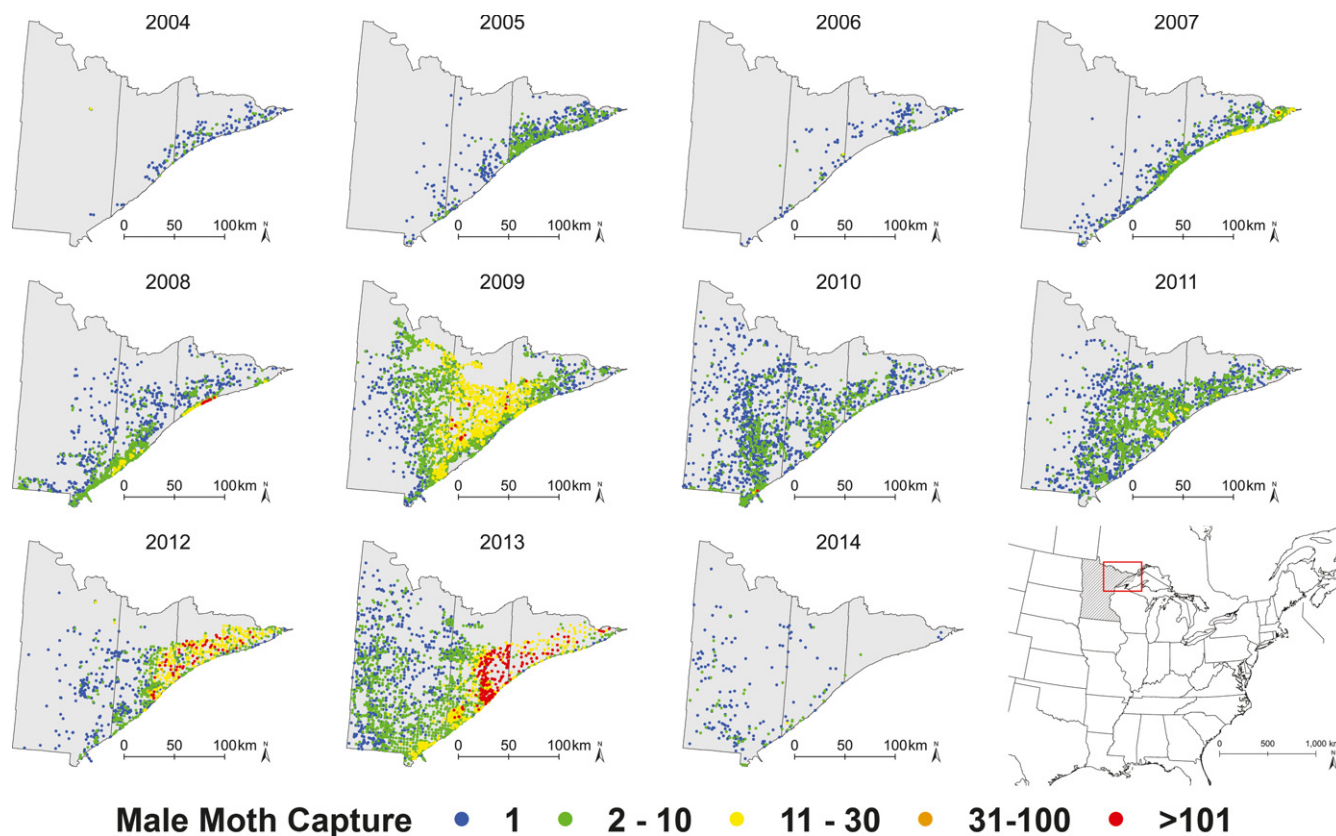
FIGURE 1 Distribution of male gypsy moth trap catches within the Arrowhead region of Minnesota, 2004–2014 [Colour figure can be viewed at wileyonlinelibrary.com]
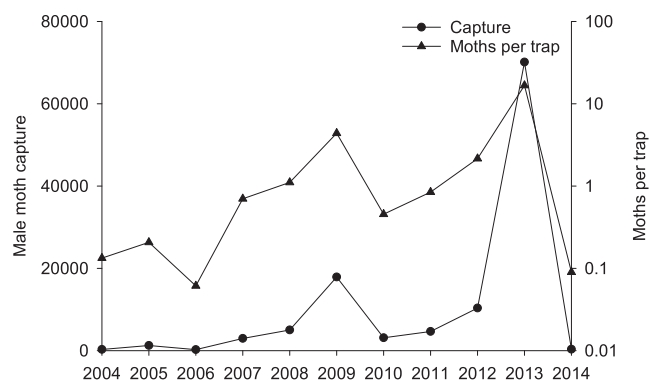

FIGURE 2 Annual summer male gypsy moth trap capture and annual number of moths per trap in the Arrowhead region of Minnesota, 2004–2014

2004–2014 (Appendix S1). A region encompassing Cook, Lake, and St. Louis counties were selected for analysis because (a) there was a minimum of 10 years of consistent trap captures of male gypsy moths, (b) this region had exhibited recoveries of non-adult life stages, indicating established and reproducing populations, and (c) this northern area exhibits robust winter conditions (see Results). Thiessen polygons were constructed around 17 weather stations located across the study area (Figure 3). Male moth capture was quantified for each Thiessen polygon through the summation of annual male gypsy moth capture from all traps deployed within polygon boundaries. The number of traps set varied annually. Areas treated with aerial application of the bacterial insecticide *Bacillus thuringiensis* var. *kurstaki* (Btk) or synthetic pheromone for mating disruption were removed from data analysis to avoid confounding effects of management activities on trap capture (Appendix S1).

2.1.2 | Weather data

Daily maximum and minimum temperatures were obtained from the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Information (http://www.ncei.noaa.gov/) and MesoWest (http://mesowest.utah.edu/), Department of Atmospheric Sciences, University of Utah for each of the 17 weather stations (Figure 3). Weather data spanned October 2003 through May 2014. Data were analysed from October of the previous year to May of the trapping year to reflect time periods when overwintering egg masses would be exposed to freezing temperatures. Less than 3% of the daily weather data contained missing observations. For a given daily temperature series, if only one observation was missing, the value was interpolated using a first-order autoregressive model. If temperature observations were missing for several consecutive days, data were obtained using the single best estimator technique, in which observations from the closest neighbouring weather station with the strongest positive correlation to the target station are used (Eischeid, Baker, Karl, & Diaz, 1995).
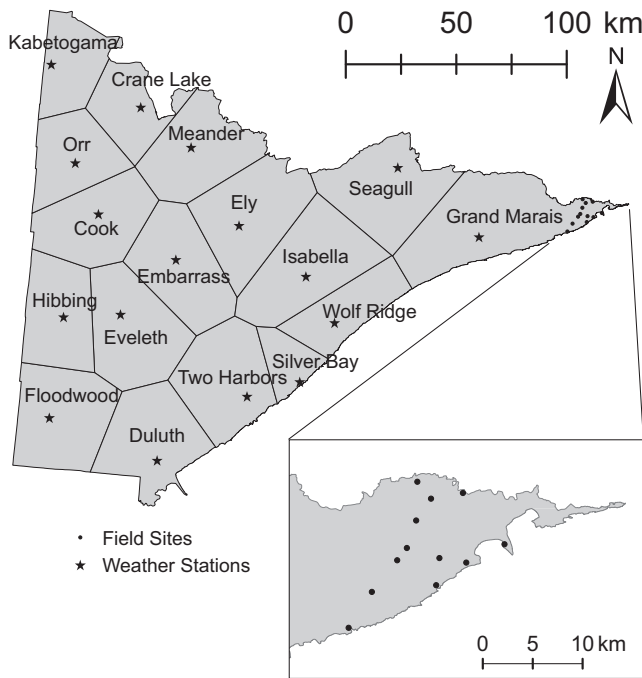
FIGURE 3 Map of the Arrowhead of Minnesota with Thiessen polygons drawn around weather stations used for modelling association between winter severity and subsequent summer moth capture. Thiessen polygons were used to assign temperature variables to trap catch data for each year, 2004–2014. Inset map shows location of field sites within Grand Portage Reservation used to experimentally monitor overwintering mortality during the winters of 2014 and 2015

Nine measures of winter severity were constructed to quantify the number of cold exposure events as well as total cold exposure. Cold exposure events were summarized as the number of days that the daily minimums dropped below thresholds of −10, −15, −20, −25, and −30°C, to reflect temperature profiles approaching and surpassing putative ecological impacts to gypsy moths (Doane & McManus, 1981; Madrid & Stewart, 1981; Waggoner, 1985). Total cold exposure was quantified as mean monthly minimum temperatures for December, January, and February as well as the absolute minimum winter temperature.

2.1.3 | Statistical analysis

Linear regressions were used to examine the relationship between a response variable of trap captures of male moths each summer and several predictor variables. These explanatory variables reflected various measures of the preceding winter's severity, as well as trap variables describing trapping dynamics within each polygon, such as the polygon area, the number of traps within each polygon for a given year, and the previous year's male moth capture. We first fit variables of interest individually to assess their effect on summer trap captures of male gypsy moths. There was a positive relationship found between male moth capture and the previous year's capture (regression slope coefficient t_{152} = 9.17, p < 0.001) as well as the number of traps deployed (regression slope coefficient t_{173} = 7.73,

p < 0.001). Hence, we included these variables a priori in multiple regression approaches so that we could isolate the effects of various measures of winter severity after accounting for variations in moth capture due to trapping effort (i.e., number of traps deployed in a polygon) and number of moths captured in the previous year. Trap capture variables were $\log_2(y + 1)$ transformed to satisfy assumptions of homogenous variances and normality of residuals. All data analyses were conducted in R (R Core Team, 2016).

The unit of replication was the Thiessen polygon (17 in the study area × 11 years). We contended with spatial autocorrelation by making the polygons of sufficient size to account for any spatial dependence, which is generally at scales of 10 km for gypsy moth (Sharov, Liebhold, & Roberts, 1996, 1997). Temporal autocorrelation can also bias inferential tests; temporal autocorrelation in model residuals was assessed by conducting a Durbin–Watson test using the "car" package in R (Fox & Weisberg, 2011). Inclusion of a $\log_2(y + 1)$ transformed lagged trap capture variable in the multiple regression models successfully eliminated the temporal autocorrelation that was initially present in the model residuals.

2.2 | Overwintering mortality within egg masses in Minnesota

2.2.1 | Field experiment design

Laboratory-reared, diapausing New Jersey Standard Strain egg masses (NJSS F69 in 2014 and F71 in 2015) on paper backing were obtained from United States Department of Agriculture Animal and Plant Health Inspection Service, Center for Plant Health Science and Technology (Otis Air National Guard Base, Buzzards Bay, MA). Egg masses were enclosed in individual mesh pouches to enhance containment and prevent field predation. In 2014, mesh pouches were constructed using 20 × 20 mesh Lumite® (Andresen et al., 2001). In 2015, pouches were constructed using 50 × 24 mesh antivirus insect screen (BioQuip Products, Rancho Dominguez, CA) due to product availability.

Egg masses were deployed to 12 field sites on the Grand Portage Reservation in north-eastern Minnesota, located along Lake Superior (Figure 3). The egg masses were deployed in November of each year over two winter field seasons, 2013–2014 and 2014–2015 (subsequently referred to as 2014 and 2015, respectively), and retrieved in April of the subsequent spring. Each field site received n = 28 experimental egg masses, with four egg masses affixed to seven trees in a 2 × 2 factorial design (north/south aspect × high/low placements). High placements were located above breast height (1.5 m). Low placements were located near ground level (~30 cm) where they would be covered by winter snow accumulation. Experimental egg masses were secured using 14 mm staples (Arrow Fastener Co., Inc., Saddle Brook, NJ) affixed above pouch seams to maintain mesh integrity and prevent thermal conductance. We selected field sites consisting of deciduous trees, which permitted snow accumulation around the boles. In 2015, 15 "control" egg masses were allowed to overwinter outdoors in Syracuse, New York, a climatically suitable location (Gray, 2004), to serve as a positive experimental control.

HOBO Pro V2 temperature data loggers (Onset Computer Corporation, Bourne, MA) recording at 30-min intervals were placed within solar radiation shields and deployed at each field site to monitor ambient air temperatures at each of the four treatment positions. The radiation shields were constructed using 10.2 cm diameter polyethylene triplewall drain pipes (Advanced Drainage Systems, Buffalo, MN) cut into 30.5 cm sections with 10.2 cm plastic drain grates (NDS, Woodland Hills, CA) affixed at each end to allow free airflow. The temperature data loggers were suspended centrally within each radiation shield with a tension wire mechanism utilizing 24-gauge galvanized steel wire. The data loggers were placed on a central tree within each field site, and always affixed below deployed egg masses to prevent shading.

Egg masses were retrieved each April before eclosion and returned to the laboratory, where they were removed from their mesh pouches, placed within 29.6 ml portion cups (Dixie®, Atlanta, GA), and maintained at room temperature (~21°C). The cups were maintained for 30 days following initiation of emergence, which should have permitted complete emergence. Egg masses were then gently homogenized to separate individual eggs, vacuumed with a custom mesh attachment to remove hairs and scales, and assessed for eclosion. We counted the number of emerged larvae, fertilized unemerged eggs, and unfertilized eggs in each egg mass. Fertilized eggs are spherical and grey in colour, whereas unfertilized eggs are white and may be sunken in appearance. Overwintering mortality was quantified by dividing the number of unemerged fertilized eggs by the total number of viable eggs.

2.2.2 | Temperature data analysis

From the temperature data loggers, we quantified the number of days that minimum temperatures were less than or equal to thresholds of −25, −27, and −30°C; i.e., around the supercooling point of eggs (Doane & McManus, 1981). The duration of cold exposure, in hours, was quantified by dividing the number of 30-min observations at which temperatures were less than or equal to the given thresholds by two. In 2014, one data logger experienced short duration logging failures over the study period. In this case, missing data (0.75% of observations) were interpolated using first- or second-order autoregressive techniques. In 2015, one data logger experienced extensive recording failure, such that interpolation of missing data was not feasible. Hence, we discarded temperature observations for egg masses placed on the southern aspect of a tree at one site.

2.2.3 | Statistical analysis

Overwintering mortality was expressed as a binomial presence/absence response of the number of fertilized, unemerged eggs relative to the number emerged larvae. This binomial response variable accounted for differences in the number of eggs between egg masses. To estimate the annual mean mortality rate, the mortality binomial response variable was fit to a constant intercept model, that was then back transformed with the logit link function (i.e. p (Mortality) = $\frac{\exp^{\%_0}}{1+\exp^{\%_0}}$). We explored the effects of egg mass placement (height/aspect), various measures of winter severity, and their interactions on overwintering mortality as a binomial response variable using a generalized linear mixed effects model with field site incorporated as a random intercept. The best models describing overwintering mortality exhibited the lowest AIC values. Both years of field data were analysed independently using the "lme4" package (Bates, Maechler, Bolker, & Walker, 2015) in R.

3 | RESULTS

Gypsy moth population levels within the Arrowhead region of Minnesota have exhibited large fluctuations among years since 2004, with numbers generally increasing (Figures 1 and 2). Male moth capture peaked in 2013, when 70,133 moths were captured. Captures of males can be quite high despite relatively few traps being set. Trap catch in 2009 increased 257% over 2008, for example, despite 9.9% fewer traps being set in 2009.

3.1 | Winter temperatures

Winter severity within the Arrowhead region of Minnesota was highly variable from year-to-year, although the winter of 2013–14 (October 2013–May 2014; winter 2014 hereafter) was the coldest according to most measures of winter severity (Figure 4). The mean minimum monthly temperature in 2014 was on average 7°C colder than the mean for the previous decade (December: −23.31°C in 2014 vs. −14.63°C mean 2004–2013, Figure 4a; January: −25.41°C vs −18.60°C mean 2004–2013, Figure 4b; February: −23.32°C vs −17.25°C mean 2004–2013, Figure 4c). Winter 2014 exhibited the most days that minimum temperatures reached temperature thresholds of −10, −15, −20, −25, and −30°C (Figure 4d–h). In fact, temperatures dropped below −20°C a mean total of 79 times across the 17 weather stations in 2014 compared to a mean total of 38 times in the previous decade (Figure 4f). Surprisingly, 2014 did not exhibit the coldest temperature recorded during the study period, which was −47.8°C in Embarrass, Minnesota.

Despite the consistency by which our measures of winter severity described 2014 as the most "severe" winter (i.e., eight of the nine metrics in Figure 4), the year with the "mildest" winter temperatures varied depending on the metric used. For example, 2007 had the highest mean minimum December temperature (Figure 4a), whereas 2006 observed the highest mean minimum January temperature (Figure 4b). Overall, 2012 was the mildest winter as described by seven of the nine metrics, such as minimum February temperature (Figure 4c). Despite 2012 being among the milder winters, temperatures putatively lethal to gypsy moth egg masses were still observed (i.e., <−27°C; Leonard, 1972; Sullivan & Wallace, 1972; Madrid & Stewart, 1981; Waggoner, 1985).

In Table 1, we present analyses exploring whether various variables describing winter severity can describe variation in male moth
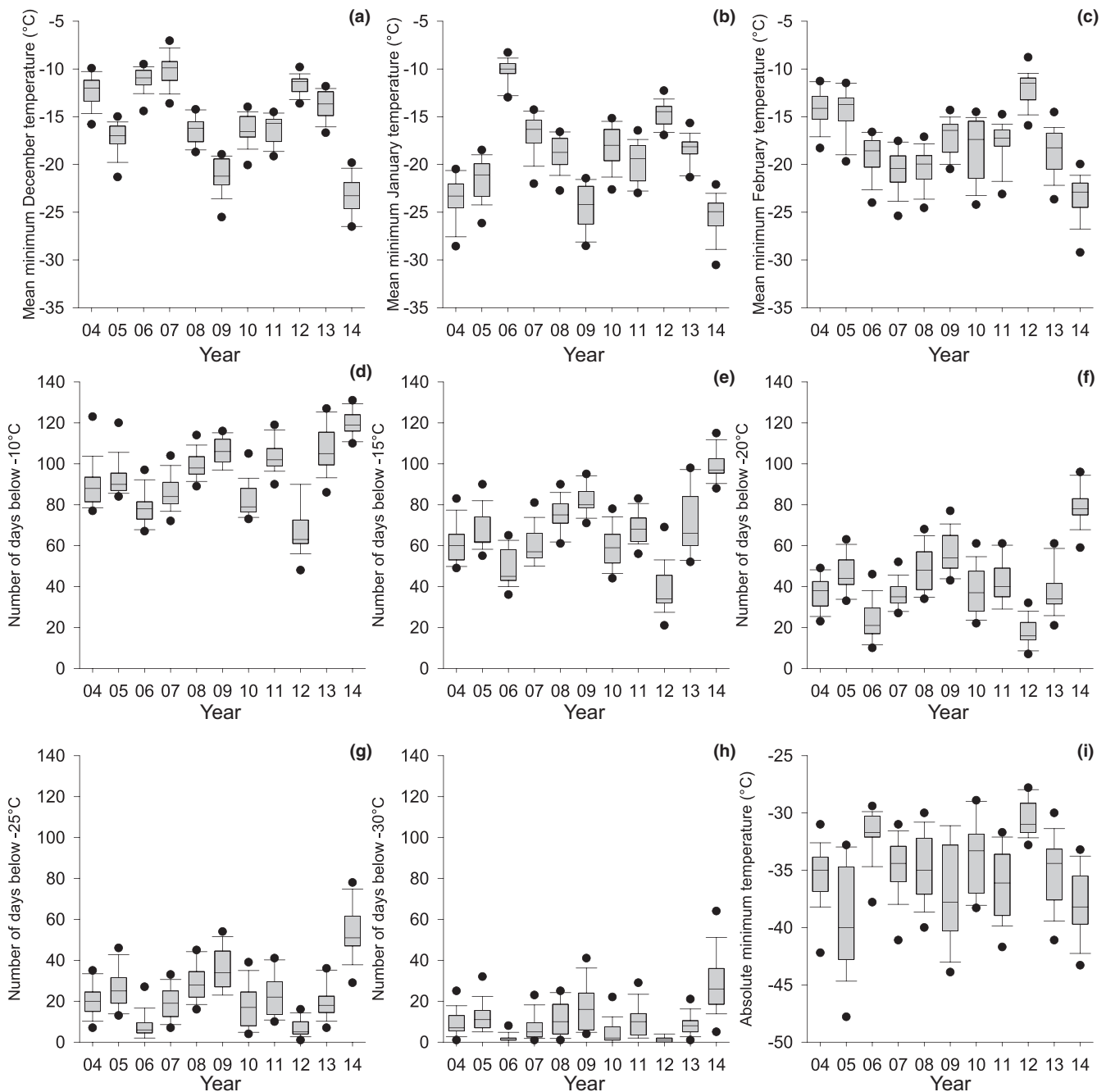
FIGURE 4 Box and whisker graphs for various temperature variables characterizing overwintering conditions in the Arrowhead region of Minnesota, 2004–2014: (a) mean December minimum temperature, (b) mean January minimum temperature, (c) mean February minimum temperature, (d) number of days below −10°C, (e) number of days below −15°C, (f) number of days below −20°C, (g) number of days below −25°C, (h) number of days below −30°C, and (i) absolute minimum temperature. Box boundaries indicate 25th and 75th percentiles; line is median. Whiskers indicate 10th and 90th percentiles and dots represent outlying points

capture after accounting for trapping effort and the previous year's catch. The number of cold exposure events did not affect summer male gypsy moth trap capture at thresholds of −10 or −15°C ($t_{150} = 0.42$, $p = 0.66$, and $t_{150} = -0.76$, $p = 0.45$, respectively). However, the number of cold exposure events were associated with reduced male moth capture beginning at a threshold of −20°C ($t_{150} = -2.143$, $p = 0.0338$). This pattern remained—and, in fact, became more significant—when examining threshold temperatures

of −25 and −30°C as well ($t_{150} = -2.379$, $p = 0.0186$ and $t_{150} = -2.634$, $p = 0.00932$).

After accounting for the previous year's capture and the number of traps set, the number of male gypsy moths captured in the subsequent summer were reduced by 50% for every 18 days with minimum temperatures below −30°C (i.e., 1 divided by the slope estimate of −0.057 in Table 1 = 18). Such temperatures or durations are not unusual for this area (Figure 4h). Measures of winter severity

TABLE 1 Summary of multiple regression models constructed to explain the relationship between the total annual summer trap catch of male gypsy moths and winter severity while accounting for the previous year's catch and the number of traps set in the Arrowhead region of Minnesota, 2004–2014. Models with significant winter severity variables are listed in bold type

Measure of winter severity	Intercept		$\log_2(\text{Catch}_{(t-1)}+1)$			Traps			Winter severity			Model R^2
	Est (SE)	$t_{(150)}$ (p-value)	Est (SE)	$t_{(150)}$ (p-value)	Partial R^2	Est (SE)	$t_{(150)}$ (p-value)	Partial R^2	Est (SE)	$t_{(150)}$ (p-value)	Partial R^2	
Days below −10°C	0.936 (1.35)	0.69 (0.49)	0.469 (0.0677)	6.92 (<0.0001)	0.307	0.0045 (0.0010)	4.40 (<0.0001)	0.114	0.0060 (0.014)	0.42 (0.66)	0.001	0.431
Days below −15°C	2.159 (0.964)	2.24 (0.027)	0.484 (0.0672)	7.19 (<0.0001)	0.332	0.0042 (0.0010)	4.10 (<0.0001)	0.101	−0.00975 (0.0128)	−0.76 (0.45)	0.004	0.432
Days below −20°C	**2.690 (0.698)**	**3.85 (0.0002)**	**0.497 (0.0662)**	**7.51 (<0.0001)**	**0.340**	**0.0038 (0.0010)**	**3.71 (0.0003)**	**0.084**	**−0.027 (0.0126)**	**−2.143 (0.0338)**	**0.030**	**0.447**
Days below −25°C	**2.413 (0.571)**	**4.23 (<0.0001)**	**0.496 (0.0657)**	**7.54 (<0.0001)**	**0.343**	**0.0037 (0.0010)**	**3.64 (0.0004)**	**0.081**	**−0.035 (0.0149)**	**−2.379 (0.0186)**	**0.036**	**0.450**
Days below −30°C	**2.192 (0.496)**	**4.42 (<0.0001)**	**0.485 (0.0650)**	**7.46 (<0.0001)**	**0.341**	**0.0037 (0.0010)**	**3.79 (0.0002)**	**0.087**	**−0.057 (0.0215)**	**−2.634 (0.0093)**	**0.044**	**0.455**
Mean Dec minimum	2.758 (0.941)	2.93 (0.0039)	0.504 (0.0688)	7.33 (<0.0001)	0.327	0.0040 (0.0010)	4.01 (<0.0001)	0.097	0.084 (0.0562)	1.49 (0.14)	0.015	0.439
Mean Jan minimum	1.473 (1.047)	1.41 (0.16)	0.474 (0.0676)	7.02 (<0.0001)	0.320	0.0044 (0.0010)	4.34 (<0.0001)	0.112	−0.0016 (0.0520)	−0.031 (0.98)	0.000	0.430
Mean Feb minimum	**5.123 (1.263)**	**4.06 (<0.0001)**	**0.479 (0.0644)**	**7.44 (<0.0001)**	**0.354**	**0.0036 (0.00099)**	**3.64 (<0.0001)**	**0.081**	**0.189 (0.0624)**	**3.039 (0.0028)**	**0.058**	**0.463**
Absolute minimum	4.710 (2.359)	2.00 (0.0477)	0.458 (0.0671)	6.83 (<0.0001)	0.303	0.0041 (0.001)	4.10 (<0.0001)	0.101	0.0872 (0.0631)	1.38 (0.17)	0.013	0.437

quantifying total cold exposure, such as absolute minimum temperature and mean minimum January temperature, were not correlated with reduced male moth captures (t_{150} = 1.49, p = 0.17 and t_{150} = −0.031, p = 0.98, respectively). However, warmer February temperatures were associated with increased male gypsy moth capture (t_{150} = 3.039, p = 0.0028).

3.2 | Overwintering mortality of egg masses

There were marked differences in ambient air temperatures recorded by HOBO data loggers, and thus egg masses, placed high or low on the tree (Figure 5). In general, egg masses placed at 1.5 m experienced between 2–4 × the number of cold days with temperatures ≤−25°C as those placed within 30 cm of ground level. The winter of 2014 was colder than the winter of 2015, but we did not observe any differences in temperature between north/south aspects of a tree. Egg masses generally experienced warmer winter temperatures with increasing distance from Lake Superior in both 2014 and 2015 (results not shown).

In 2014, 355 egg masses were deployed to the field. Overwintering mortality was high, with only 111 egg masses exhibiting any emergence. The mean mortality rate in 2014 was 96.78% (95% CI: 96.72%, 96.85%). One hundred and eighty egg masses were deployed at a height of 1.5 m, and these egg masses experienced near complete mortality (mean mortality of 99.95% [95% CI: 99.94%, 99.96%]). Egg masses located within 30 cm of the ground exhibited a mean mortality of 93.52% (95% CI: 93.39%, 93.65%), an overall increase in survival of 6.43%. The maximum eclosion rate was 82%, which occurred in an egg mass placed that was located within 30 cm of the ground, in a site 4.8 km from Lake Superior. This egg mass did not yield the highest number of first instars; 638 (vs. 195) larvae emerged from an egg mass with a higher number of eggs but lower rate of eclosion (40%). This egg mass was also the one that had been placed 30 cm from ground level. Across all 355 egg masses, 8,997 of 297,683 eggs hatched (3.0%).

In 2015, 366 egg masses were deployed in north-eastern Minnesota. Similar to 2014, overwintering mortality was high. Only 55 egg masses exhibited any emergence, with an average mortality rate of 98.58% (95% CI: 98.54%, 98.63%). Similar to 2014, egg masses that were placed at 1.5 m experienced near total mortality, with a mean mortality rate of 99.997% (95% CI: 99.992%, 99.999%). Only one egg mass from this group exhibited any emergence, which was 5%. Egg masses located 30 cm from the ground also exhibited high rates of mortality (mean mortality rate of 97.1%; 95% CI: 97.01%, 97.19%), although the lower placement was associated with 2.9% increased survivorship. The highest eclosion rate in 2015 was 58% for an egg mass placed 30 cm from the ground, in a site 4.8 km from Lake Superior. Similar to 2014, a separate egg mass, which also overwintered at 30 cm within 5 km of Lake Superior, had more first instars emerge (428 vs. 414) despite a lower rate of eclosion (36%). Across all 366 egg masses, 3,954 of 279,303 eggs hatched (1.4%). All 15 "control" egg masses that were sent to overwinter in Syracuse, New York successfully emerged, regardless of placement
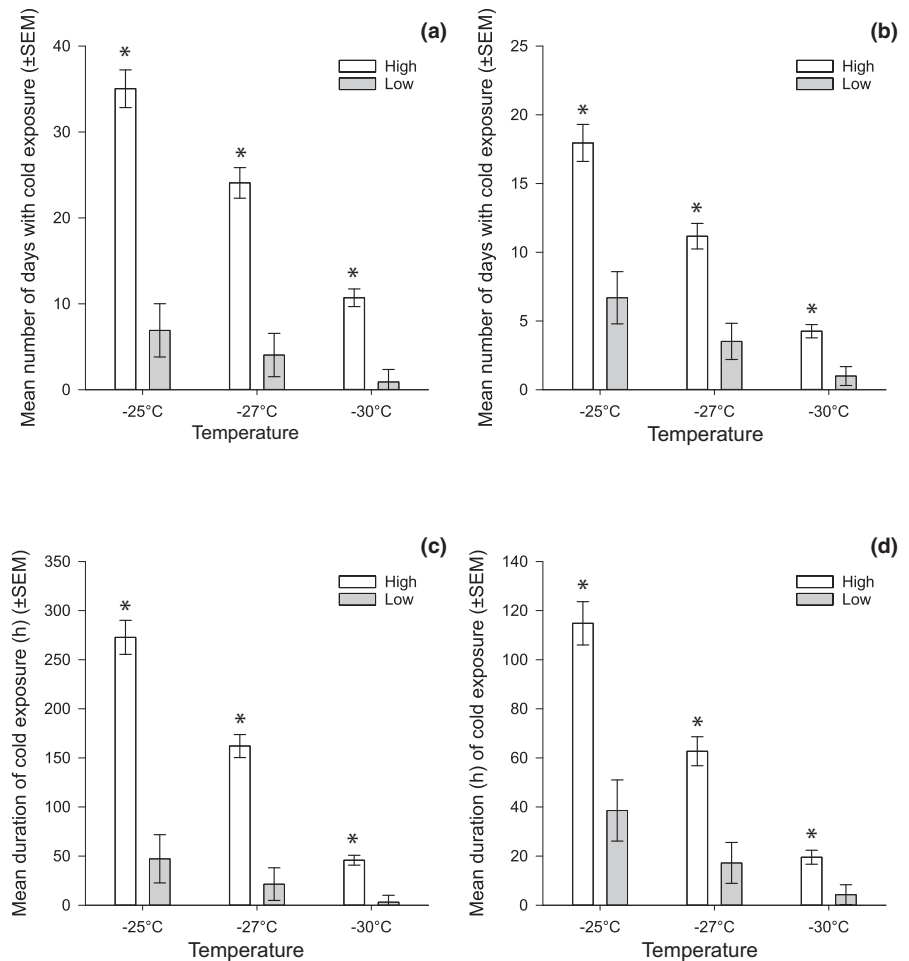
FIGURE 5 Cold exposure experienced by egg masses at high and low placements at 12 field sites on the Grand Portage Reservation, 2014–2015. Note y axes are on different scales. Number of days (±SEM) that minimum temperatures dropped below various thresholds. (a) 2014. (b) 2015. Duration, in hours (±SEM), that temperatures were less than or equal to various temperature thresholds. (c) 2014. (d) 2015. Significant differences in cold exposure between high and low placements are denoted by an asterisk

height, with an average eclosion rate of 94.7% (95% CI: 95.08%, 94.29%).

The rates of successful spring eclosion decreased with cold temperatures (Table 2). In 2014, the positive relationship between mortality and the number of days that temperatures reached −25, −27, or −30°C became more accentuated at cold temperature thresholds, as evidenced by decreasing AIC values moving through regressions from −25 to −30°C (Table 2a). In 2015, the strongest relationship between cold temperatures, or their duration, and overwintering mortality was apparent when temperatures reached −27°C (Table 2 b). A negative relationship between survival and cold was noted at all temperature thresholds tested for both years.

4 | DISCUSSION

Our findings that cold winter temperatures are associated with reduced numbers of male gypsy moths captured in the subsequent summer are consistent with high rates of overwintering mortality in exposed, overwintering egg masses. For this reason, it has been predicted that the Arrowhead region of Minnesota along the expanding range front would be climatically unsuitable (Gray, 2004; Régnière & Nealis, 2002). In contrast, generally increasing numbers of moths per trap (Figure 2) and repeated observations of egg masses in the field

suggest that reproducing populations are present and northward range expansion continues to occur (Smitley et al., 1998; Tobin et al., 2016). While many range studies of gypsy moth use climatic envelopes based on temperature (Gray, 2004; Régnière & Nealis, 2002; Sullivan & Wallace, 1972), our results support a hypothesis that thermal insulation provided by snow cover provides protection to egg masses oviposited close to ground level (Andresen et al., 2001; Brown & Sheals, 1944; Leonard, 1972; Madrid & Stewart, 1981; Nealis, Roden, & Ortiz, 1999; Smitley et al., 1998; Sullivan & Wallace, 1972). That is, even in regions where more than 99.5% mortality may occur due to freezing, a sufficient number of insects may hatch to sustain the population. In our study, a total of 12,951 eggs eclosed over both years (excluding control egg masses). Assuming an unbiased sex ratio (Doane & McManus, 1981) and a mortality rate of 90% from early instar to adulthood, a cohort of 647 females may have developed. In theory, reducing overwintering mortality rates to 97% (observed for egg masses placed within 30 cm of the ground) and maintaining 10% survival between early instar and adults would still result in a net increase in the population from generation to generation if egg masses averaged between 650–700 individuals.

Enhanced survival of pharate larvae under natural conditions, especially in subnivean environments, could facilitate further range expansion in northern areas (Brown & Sheals, 1944; Smitley et al., 1998), especially where certain demographic regulatory processes

TABLE 2 The effects of observed air temperature on overwintering mortality of experimental gypsy moth egg masses, Grand Portage Reservation, MN, USA, 2014–2015. The probability of mortality can be evaluated $p(\text{Mortality}) = 1 - \frac{\exp^{\beta_0 + \beta_1 x}}{1 + \exp^{\beta_0 + \beta_1 x}}$ for various measures of winter severity; that is, either the number of days that temperatures drop below a given threshold or the duration in hours that temperatures are below the listed threshold

Temperature threshold	Days below					Duration (h)				
	Intercept (β₀)		Variable (β₁)			Intercept (β₀)		Variable (β₁)		
	Est (SE)	Z (p-value)	Est (SE)	Z (p-value)	AIC (ΔAIC)	Est (SE)	Z (p-value)	Est (SE)	Z (p-value)	AIC (ΔAIC)
(a) 2014										
	−4.75 (0.62)	−7.61 (<0.001)	(–)	(–)(–)	33,355.6 (–)	−4.75 (0.62)	−7.61 (<0.001)	(–)(–)	(–)(–)	33,355.6 (–)
−25°C	−3.38 (0.58)	−5.83 (5.61e-9)	−0.12 (0.0017)	−68.81 (<0.001)	22,021.5 (11,334.1)	−3.41 (0.61)	−5.57 (2.51e-8)	−0.016 (0.00023)	−68.94 (<0.001)	21,859.3 (11,496.3)
−27°C	−3.41 (0.61)	−5.6 (2.28e-8)	−0.19 (0.0027)	−68.15 (<0.001)	21,947.7 (11,407.9)	−3.49 (0.64)	−5.49 (3.93e-8)	−0.031 (0.0005)	−62.41 (<0.001)	21,666.2 (11,689.4)
−30°C	−3.64 (0.65)	−5.59 (2.32e-8)	−0.68 (0.013)	−51.43 (<0.001)	21,142.4 (12,113.2)	−3.76 (0.63)	−5.95 (2.63e-9)	−0.18 (0.0036)	−49.78 (<0.001)	21,921.3 (11,434.3)
(b) 2015										
	−5.96 (0.89)	−6.7 (<0.001)	(–)	(–)(–)	17,711.5 (–)	−5.96 (0.89)	−6.7 (<0.001)	(–)(–)	(–)(–)	17,711.5 (–)
−25°C	−4.47 (0.81)	−5.54 (3.03e-8)	−0.15 (0.0038)	−40.55 (<0.001)	13,626.3 (4,085.2)	−4.49 (0.86)	−5.20 (2.01e-7)	−0.026 (0.00063)	−41.18 (<0.001)	13,267.2 (4,444.3)
−27°C	−4.37 (0.87)	−5.03 (4.88e-7)	−0.31 (0.0079)	−39.30 (<0.001)	12,863.0 (4,848.5)	−4.65 (0.93)	−5.02 (5.23e-7)	−0.049 (0.0012)	−39.50 (<0.001)	13,051.3 (4,660.2)
−30°C	−4.70 (0.86)	−5.476 (4.36e-8)	−0.87 (0.024)	−35.74 (<0.001)	13,093.9 (4,617.6)	−4.57 (0.80)	−5.74 (9.42e-9)	−0.25 (0.0072)	−34.75 (<0.001)	12,847.4 (4,864.1)

The first line under each year represents the constant intercept or null model without covariate, to which all other models' AIC values are compared.

are relaxed. For example, extreme winter temperatures may reduce population densities below critical thresholds that induce Allee effects, which are manifested through mechanisms of mate-finding failure and unsuccessful reproduction (Johnson, Liebhold, Tobin, & Bjørnstad, 2006; Liebhold & Bascompte, 2003; Sharov, Liebhold, & Ravlin, 1995; Tobin et al., 2009). Gypsy moth Allee thresholds vary regionally, however, with lower thresholds observed in northern regions (Tobin, Whitmire, Johnson, Bjørnstad, & Liebhold, 2007; Whitmire & Tobin, 2006). As such, smaller densities of gypsy moth populations in northern regions, which are more likely to be negatively affected by cold winters than southern regions (e.g., 35° N), may persist due to lower Allee thresholds.

Nonetheless, generational survival along the northern invasion front is difficult to predict. Studies to elucidate localized density-dependent mortality factors, and how they might scale across the expanding range front, are key areas of future research (Grayson & Johnson, 2018). Likewise, ovipositional behaviour within moth populations is under selective pressure with several potential trade-offs (Higashiura, 1989). Ovipositional site selection varies among species and subspecies of *Lymantria*, including *L. dispar* (Higashiura, 1989; Pogue & Shafer, 2007; Sasaki, Jikumaru, Azuma, Kuroda, & Ishii, 2016). Eggs laid high in a tree canopy facilitate dispersal of ballooning of first instar larvae to proximate food sources, but increase the risk of avian predation (Higashiura, 1989). In contrast, eggs laid close to the ground offer winter protection from avian foraging (Higashiura, 1989) and thermal insulation from cold temperatures where snowpacks exist (Figure 5; Leonard, 1972; Smitley et al., 1998).

Our study further illustrates that gypsy moth egg mass mortality can also occur with prolonged exposure to freezing temperatures above the supercooling point, which is the minimum temperature above which pharate larvae may be expected to survive (Fält-Nardmann, Ruohomäki, Tikkanen, & Neuvonen, 2018; Madrid & Stewart, 1981; Sullivan & Wallace, 1972). Winter severity metrics quantifying the duration of cold exposure became statistically significant predictors of male moth trap capture beginning at a threshold of −20°C (Table 1), which is warmer than the c. −27°C supercooling point of gypsy moth eggs (Doane & McManus, 1981). Varying rates of mortality have been observed in laboratory and field studies due to the degree of acquired cold hardiness and duration of exposure time (Denlinger, Lee, Yocum, & Kukal, 1992; Madrid & Stewart, 1981). Cold hardiness increases with prior chilling; eggs that have not been chilled have a mean supercooling point of −28 vs. −30°C for those that have been cold hardened through chilling (Madrid & Stewart, 1981; Sullivan & Wallace, 1972).

We note two limitations of our approach that could have resulted in conservative estimates of survival, such that more moths may be expected to survive in natural situations than we observed. First, we used egg masses from a population of insects reared under laboratory conditions since 1967 (NJSS) because moth numbers were too low to find and collect egg masses from the field. Notable phenotypic differences in NJSS individuals compared to wild strains

include more rapid and synchronous hatching rates (Keena & Odell, 1994) and lower chilling requirements to complete diapause (Keena, 2015). Because cold hardiness is a trait that can be under selective pressure, future research on overwintering mortality should seek to use wild collected strains reared in the laboratory for one generation to reduce maternal effects, while maintaining a wild genotype. Second, fulfilment of chilling requirements for diapause completion in all egg masses received and deployed could have enhanced mortality. Under laboratory rearing protocols, egg masses are allowed to embryonate for 60 days after oviposition, chilled at 12.8°C for 10–15 days, and then transferred to refrigerators set at 4.4°C for 150 days to satisfy diapause requirements. Since diapause chilling requirements were already met, postdiapause development could have resumed during the experimental period, resulting in less cold hardiness and/or depleting energetic reserves before unfavourable (i.e., winter) conditions passed.

While temperature is the primary climatic variable given attention in many studies of insect range boundaries (Bale, 2002; Bryant, Thomas, & Bale, 2002; Tobin, Gray, & Liebhold, 2014), our research provides empirical evidence that other variables such as winter precipitation in the form of snowfall can be an important mediator of northern range boundaries by providing thermal refuge for egg masses of this insect (Leonard, 1972; Madrid & Stewart, 1981; Nealis et al., 1999; Smitley et al., 1998). Climate change is likely to have multiple and interacting effects on species ranges, and may result in range shifts rather than range expansions for European gypsy moth in North America (Brown & Sheals, 1944). The potential southern range of gypsy moth in the United States is limited by insufficient chilling periods required to terminate diapause (Gray, 2004) as well as larval and pupal exposure to supraoptimal temperatures (Thompson et al., 2017; Tobin et al., 2014). As such, adverse effects of high temperatures could exceed the beneficial effects on population growth in those regions as this invasive herbivore's range shifts northward.

DATA ACCESSIBILITY

Data available from the Data Repository for University of Minnesota (DRUM) https://doi.org/10.13020/d6gd7j (Aukema 2018).

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SUPPORTING INFORMATION

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