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Increases in summer temperatures decrease the survival of an invasive forest insect

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Abstract Higher temperatures projected under current climate change models are generally predicted to exert an overall positive effect on the success of invasive insects through increased survivability, developmental rates and fecundity, and by facilitating geographic range expansion. However, these effects have primarily focused on the shifts in winter temperatures with limited attention to the role that summer heat may play in shaping species ranges or fitness. We examined the thermal ecology of an ecologically important invasive forest insect, the hemlock woolly adelgid (*Adelges tsugae*), by determining survival during its summer dormancy phase under increasing temperature regimens. From laboratory and field experiments, we documented a positive association between increased temperatures and duration of exposure, and *A. tsugae* mortality. *Adelges tsugae* mortality was minimal (<20%) when exposed to summer temperatures characteristic to its native range (<25 °C), but markedly increased (up to 100%) when exposed to temperatures that occur occasionally or rarely in natural settings (>30 °C). At the warmest, southernmost edge of their range, field mortality of *A. tsugae* ranged from 8.5 to 81.9% and was strongly correlated with site temperature regimens. Further, we found no significant differences in *A. tsugae* survival between populations collected from Maine and Georgia, and over a 3-year period within Georgia, indicating that *A. tsugae* may not be acclimating to heat. These results highlight the importance of including summer temperatures in studies regarding increased temperatures on insect dynamics, and may alter historical predictions of climate change impacts on invasive insects and the conservation of forest ecosystems.

Keywords *Adelges tsugae* · Aestivation · Climate change · Heat stress

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Introduction

By the end of the twenty-first century, it is predicted that average global surface temperatures may increase by more than 2 °C (IPCC 2013). One of the major taxa that are expected to directly and indirectly respond to climate change are poikilotherms, such as herbivorous insects (Bale et al. 2002). Although responses to temperatures are species-specific and variable, for most insects, higher temperatures will be favorable by increasing voltinism (Tobin et al. 2008; Stoeckli et al. 2012), decreasing winter mortality (Ayres and Lombardero 2000), and increasing distributions to higher latitudes and altitudes due to warmer winters (Musolin 2007; Cudmore et al. 2010). Conversely, climate change may have negative effects on insects due to asynchronicity with host plants (Bale et al. 2002; Uelmen et al. 2016), changes in host plant material chemistry (Ayres and Lombardero 2000), and range retraction (Tobin et al. 2014).

One adaptive strategy insects use to survive unfavorable changes in their environment, such as extreme temperatures or low food abundance/quality, is to enter a dormant physiological state (diapause) during which development is typically halted, metabolism is significantly decreased, and energy is conserved (Masaki 1980; Tauber et al. 1986; Hahn and Denlinger 2007). Although aestivation (summer diapause) is not as prevalent as winter diapause, it is a life cycle component of species within several major insect orders (e.g. Coleoptera, Diptera, Hemiptera, and Lepidoptera) and is found to occur in most parts of the world (Masaki 1980). Temperature plays a large role in the mechanics of diapause by influencing the initiation, length, and termination of dormancy (Tauber and Tauber 1976; Denlinger 2002). Although insect metabolism is reduced during periods of dormancy, it remains responsive to temperature; as temperatures increase, metabolic rates increase. Consequently, metabolic reserves in aestivating insects may be depleted during the summer, which could be exacerbated by climate change and negatively affect post-aestivation survival (Tauber and Tauber 1976; Masaki 1980; Hahn and Denlinger 2007). Studies on the effect of increased summer temperatures projected under climate change on aestivating insects are non-existent. In this paper, we show how increased summer temperatures significantly reduces post-aestivation survival of a highly invasive, non-native insect that has the potential to drastically reshape eastern North American forests.

The hemlock woolly adelgid (*Adelges tsugae* Annand) (Hemiptera: Adelgidae) is a small, sessile, sap-sucking insect native to Asia and western North America that is causing widespread mortality of eastern hemlock (*Tsuga canadensis*), a foundation species in eastern North American forests. (McClure et al. 2003; Ellison et al. 2005; Havill et al. 2006; Havill and Foottit 2007). In its introduced range, *A. tsugae* reproduces asexually and has two successful generations per year (sistens and progrediens) as well as the occasional unsuccessful sexuparae generation (McClure 1991; Havill and Foottit 2007). The sistens generation enters aestivation shortly after emerging in late spring/early summer and terminates aestivation typically in October when temperatures have cooled. During aestivation and maturation, sistens will remain immobile with their stylet bundle inserted at the abscission layer of a needle, preferring to colonize the youngest available twigs (McClure 1991; Young et al. 1995; McClure et al. 2003). Following aestivation, the sistens begin to produce a protective, waxy, wool-like flocculence that will cover the adults and eggs, making the minute insects (0.5–1.3 mm) easier to detect (Havill and Foottit 2007). Currently, plant defensive responses by *T. canadensis* appear to have limited effect against *A. tsugae*; tree mortality has been reported to occur in as little as 3–4 years following *A. tsugae* colonization, and occurs regardless of tree size, age, or location (McClure 1991; Orwig and Foster 1998; McClure et al. 2003; Faulkenberry et al. 2009).

Understanding the effects of multiple aspects of climate change on invasive species will allow us to better understand their biology and assist in the overall conservation of natural ecosystems threatened by them. The *A. tsugae*/*T. canadensis* system is ideal to test the effects of heat stress on an aestivating invasive insect because *A. tsugae* settles on the host tree for the duration of aestivation without their protective wool, and, as a sessile organism, is unable to escape temperature extremes. Also, the range of *A. tsugae* and *T. canadensis* encompasses a multitude of climate zones. At the northeastern edge in Maine, the average annual minimum winter temperature ranges from −26 to −29 °C, whereas, at the southern-most edge of the Southern Appalachian Mountains in northern Georgia, the average minimum temperatures range from −9 to −12 °C (USDA Agricultural Research Service 2012).

We sought to quantify the effects of supraoptimal temperatures on the survival of an aestivating insect, and determine if *A. tsugae* is acclimating in response to heat exposure.

Materials and methods

Laboratory experiment and survival assessment

Tsuga canadensis twigs were collected from a single site, Raper Creek (34.75042°N, 83.57915°W), in the Chattahoochee National Forest, Habersham County, Georgia. All *A. tsugae* were collected from a single location to avoid factors that could potentially affect insect fitness or heat tolerance, such as stand dynamics, time since infestation, or tree health. A total of 240 twigs were collected from seven trees in July and August 2011 when *A. tsugae* were aestivating. Twigs that were selected had multiple offshoots with 2–4 cm of new growth to ensure preferred conditions for *A. tsugae* sistens. Aestivating *A. tsugae* on the new growth of each twig were evaluated and the needles with those deemed to be alive at the node were marked (17.6 ± 0.3 SE *A. tsugae* twig^{-1}). Vitality was determined by the convexity of the body and the bright white coloration of the dorsal wool. Needle nodes where more than two *A. tsugae* settled were not included in the experiment as intraspecific competition could be a confounding factor.

Marked twigs were placed in 55.5 ml vials with wet florist block to prevent desiccation and then randomly assigned both a temperature and a duration treatment. Since *T. canadensis* in the southeastern U.S. are typically found in cool, high elevation areas, summer temperatures were selected that encompassed typical (20 and 25 °C), occasional (30 °C), and rare (35 and 40 °C) conditions in *T. canadensis* stands. July samples were tested at 20, 30, and 40 °C and August samples were tested at 25, 30, and 35 °C. In addition, four exposure durations (48, 96, 144, and 192 h) were tested to determine the interaction between temperature and exposure time on *A. tsugae* heat tolerance and mortality rates. Ten twigs per temperature–time treatment were placed in growth chambers ($n = 3$ chambers month^{-1}) (Model GC36, Environmental Growth Chambers, Chagrin Falls, Ohio) with 55% humidity and a daily 14 light: 10 h dark period. A decrease of 5 °C was implemented in all treatments during the dark phase to mimic cooling temperatures after sunset. The 4215 marked *A. tsugae* were examined immediately following their temperature–time treatment to evaluate their condition. Survival was assessed by using up to three steps: (1) *A. tsugae* were gently pulled out from the plant tissue about half the length of their stylet bundle and observed for body movement caused by attempted stylet reinsertion; (2) if no body movement was observed, *A. tsugae* were fully removed from the plant tissue and examined for approximately 15 s for stylet movement; and (3) if no stylet movement was observed, *A. tsugae* were crushed to see if appropriate viscosity and color of the hemolymph were present (i.e. deep red–purplish). *Adelges tsugae* that were concave, desiccated, and had no movement were considered dead. The proportion of dead *A. tsugae* from the total number marked was calculated for each twig and used in analyses. This survival method was also used on an extra 20 twigs to test the accuracy of initial *A. tsugae* vitality assessment (using convexity and dorsal wool coloration); evaluations were 97.3% accurate.

All analyses were conducted using R statistical software (R Core Team 2015). A generalized linear mixed model was fit to the combined results of the growth chamber experiments to examine the relationship between *A. tsugae* mortality proportion at the twig level and the fixed effects of temperature, duration of exposure (hours), and temperature × hours (lme4 package; Bates et al. 2015). The model used a binomial distribution and the results were fit via Laplace approximation. To reduce multicollinearity, all predictor variables were centered. The collection tree was included as a random effect to reduce potential variability and to focus on the main parameter effects. All of the data were examined to ensure that the assumptions of a logistic model were met.

Adelges tsugae heat mortality index

Since there is currently no known physiological connection between degree days and *A. tsugae* mortality, an approximation of heat accumulation (heat mortality index; HMI) was required for forest stands to evaluate the potential correlation with field *A. tsugae* mortality (Online Resource 1). The mortality rate from each of the five growth chamber temperature linear regression models (i.e. the slopes) (R Core Team

2015) represented the weight for the average temperature reached in that chamber (17.9–37.9 °C). Because all *A. tsugae* were deemed to be alive prior to being placed in growth chambers, all linear regression models had a zero y-intercept ($\beta_0 = 0$). Post hoc pairwise comparisons to determine if *A. tsugae* mortality rates differed between the temperatures tested was done by creating a dummy variable for the temperature tested and examining the dummy × hours interaction term in a linear regression model ($\beta_0 = 0$) as a significance test for the difference between the mortality rates. An exponential model was fitted to the estimated mortality rates based on observed patterns and the inference that rates would increase rapidly as temperatures approach the critical threshold. We then extrapolated weighted mortality rates (W_j) for all degree classes above 15 °C. This cutoff temperature was selected based on the assumption that aestivating *A. tsugae* are not sensitive to heat exposure below this temperature. The HMI for a *T. canadensis* stand can then be calculated according to,

$$\mathrm{HMI}_i = \sum W_j(H_j), \quad j = 15, 16, \ldots, n \tag{1}$$

where $W_j =$ the weighted mortality rate for the *j*th degree class, and $H_j =$ the number of hours recorded at the *j*th degree class.

Field experiment

Adelges tsugae mortality from multiple field sites were examined and correlated to the corresponding site HMI to test if the effect of temperature stress observed in the growth chambers was comparable to those found in forested stands. Temperature data loggers (HOBO UA-001-64, Onset Computer Corporation, Bourne, Massachusetts) were placed in 18 *T. canadensis* stands in the Chattahoochee National Forest, Georgia to record hourly temperatures during 2011–2014. A total of 15 sites were sampled—nine in 2012 and six in 2014 (Table 1). These sites ranged in elevation from 229 to 972 m and across 76 km of the Chattahoochee National Forest. At each site, four trees within 30 m of the temperature logger were randomly selected and four twigs per tree were collected. To assess if variations in microclimate caused by aspect may play a role in *A. tsugae* mortality, half of the collected twigs were north-facing and half were south-facing. Only *A. tsugae* present on the twig's new growth were examined ($\bar{x} = 52.7 \pm 1.4$ SE *A. tsugae* twig^{-1}) to ensure that the progrediens generation was not included in counts. The sixteen twigs collected per site were examined within 24 h, and the number of live and dead *A. tsugae* were recorded. *Adelges tsugae* were deemed alive using the methods described previously and/or if they molted and initiated wool production. Again, only needle nodes with ≤2 *A. tsugae* present were included in the counts to avoid potential intraspecific competition. Overall, 2580 *A. tsugae* from 240 *T. canadensis* twigs were examined.

In 2012, an unseasonably warm late winter and early spring resulted in a rapid maturation of both the previous year's sistens and their progrediens offspring; progrediens hatching was witnessed in early February, 6–8 weeks earlier than normal. Hence, temperature exposure for the sistens examined in 2012 was estimated to have begun in mid-April when a large portion of the population was observed aestivating. Conversely, 2014 had an unseasonably cold winter, caused by a southward shift of the North Polar Vortex, that resulted in delayed maturation for *A. tsugae*. Temperature exposure for 2014 was therefore estimated to have begun in early June. Temperature data from loggers were categorized by cumulative hours spent at each one-degree class greater than 15 °C. The weighted mortality rates (W_j) were multiplied by the number of hours exposed to the corresponding degree class and then the products were summed for an overall heat mortality index (HMI) for each site (Eq. 1; Online Resource 1). A generalized linear mixed model (lme4 package, Bates et al. 2015) was used to examine the relationship between the average *A. tsugae* field mortality at the site level and the fixed effect of HMI; collection time was included as the random factor to account for variability across years. Again, the model used a binomial distribution and the results were fit via Laplace approximation. A post hoc Hosmer–Lemeshow test (ResourceSelection package; Lele et al. 2014) was conducted to determine the goodness of fit for the resultant field *A. tsugae* mortality model. *Adelges tsugae* mortality as a function of the spatial aspect of the collected *T. canadensis* twigs was compared using the Mann–Whitney U test due to a lack of normally distributed data (R Core Team 2015).

Table 1 Site data for all 15 samples collected in 2012 and 2014 in the Chattahoochee National Forest, Georgia

Site elevation (m)	Collection year/month	Heat mortality index (HMI)	Average *Adelges tsugae* mortality	Standard error
229	2012/11	4.5321	0.7891	0.0333
229	2014/12	2.2520	0.5925	0.0400
444	2012/11	4.0931	0.7426	0.0359
444	2014/12	2.9515	0.8190	0.0298
457	2012/07	2.8686	0.3791	0.0382
457	2012/11	4.0876	0.7153	0.0240
457	2014/12	2.9258	0.6547	0.0439
521	2014/12	2.3116	0.7009	0.0399
523	2014/12	2.5097	0.7351	0.0329
523	2014/12	2.3132	0.6437	0.0396
524	2012/07	2.2531	0.2598	0.0274
647	2012/11	2.8969	0.2543	0.0232
660	2012/11	3.4224	0.3158	0.0359
929	2012/11	2.1701	0.3313	0.0299
972	2012/07	1.5238	0.0854	0.0198

Acclimation experiment

The heat tolerance of *A. tsugae* from the latitudinal range extremes—around Soque River (34.71590°N, 83.57632°W) in Habersham County, Georgia and Cutts Island (43.089708°N, 70.673956°W) in York County, Maine—was tested to elucidate whether the southern population is exhibiting signs of temperature acclimation. We hypothesized that if *A. tsugae* were acclimating to higher summer temperatures in Georgia, then populations collected from the region should experience lower summer mortality relative to conspecifics collected from Maine. In August and September 2013, 36 twigs were collected from three trees in Georgia and Maine respectively, and live *A. tsugae* were marked (17.01 ± 0.26 SE *A. tsugae* twig^{-1}). All of the 72 twigs were exposed to the same temperature treatment (30 °C) for 48, 96, 144, or 192 h and then the 1225 aestivating *A. tsugae* were assessed for survival. To account for the different temperature regimens in Maine and Georgia in 2013 prior to the growth chamber experiment, hourly field temperatures from temperature data loggers were cataloged for the aestivating months and the calculated field HMI (Eq. 1) was added to the growth chamber HMI (Eq. 1) for standardization. Aestivation in Maine was estimated to have begun in mid-July, whereas Georgia saw aestivation occur in late May. Logistic regression (R Core Team 2015), with collection location, HMI, and a collection × HMI interaction term, was used to determine if the effect of heat differed between the range extremes of Maine and Georgia. In addition, the effect of heat stress was compared between the 2 years Georgia samples were examined in temperature experiments (2011 and 2013) to determine if mortality rates varied significantly. If *A. tsugae* is acclimating to the heat in Georgia, we would expect that 2013 mortality rates would be less than those observed in 2011. Again, the interaction term (year × HMI) in a logistic regression model was used to evaluate this relationship.

Results

Growth chamber temperature (Wald $z = 11.823$, $P < 0.001$), hours of heat exposure (Wald $z = 5.547$, $P < 0.001$), and their interaction (Wald $z = 2.734$, $P = 0.006$) were all found to have a significantly negative effect on *A. tsugae* survival. We observed minimal mortality (<15%) in *A. tsugae* after exposure to temperatures typical for *T. canadensis* stands in the summer (20 and 25 °C) for 192 h, whereas relatively rare summer temperatures (35 and

40 °C) resulted in 100% *A. tsugae* mortality after 48 h of exposure (Fig. 1). Post hoc pairwise comparisons of the linear relationships of *A. tsugae* mortality over time found that the mortality rates were significantly different between all of the tested temperatures (all P values < 0.01). Weighted mortality rates (Online Resource 2) extrapolated from the exponential model (Fig. 2) were used to calculate the HMI for various *T. canadensis* stands by incorporating temperatures from the onset of aestivation (variable by year) until mid-October when the majority of *A. tsugae* came out of aestivation. Although it may appear that the extrapolated weights for the higher temperatures could be overestimated (Fig. 2), it is worth noting that upper temperatures (>30 °C) were rarely, if ever, reached at the higher elevation, cooler sites, and warmer sites only experienced about 20 h above 33 °C. This heat exposure contributes to less than 5% of the total HMI value, making significantly different interpretations unlikely.

In the Chattahoochee National Forest, it was found that *A. tsugae* summer mortality was significantly correlated to HMI; as site HMIs increased, *A. tsugae* mortality increased (Wald $z = 32.83$, $P < 0.001$, Fig. 3). Although the sampling years showed differences, the non-significant year × HMI interaction term ($P = 0.39$) indicated that both sampling periods functionally responded to HMI in the same way (i.e. same slopes) (Fig. 3). Because 2012 and 2014 represent above and below average temperature years, the combined mixed effects model represents a good estimate of predicted average mortality. The maximum temperature reached in these sites varied from 37 °C at lower elevation sites to 28 °C at higher elevations. Observed *A. tsugae* mortality at the sites sampled during 2012 and 2014 ranged from 8.5 to

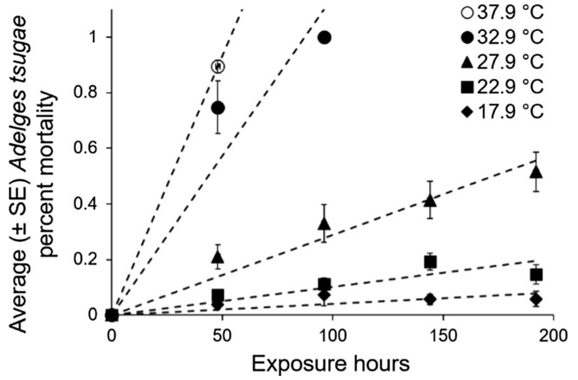

Fig. 1 Linear relationships between average *Adelges tsugae* mortality (±SE) and duration of exposure (hours) for each growth chamber mean temperature (°C). Regression model: $y = \beta x$, where y is *A. tsugae* mortality (0–1), β is the mortality rate, and x is hours. 17.9 °C: $y = 0.00040x$, $df = 39$, $p < 0.001$, $R^2 = 0.28$; 22.9 °C: $y = 0.00101x$, $df = 39$, $p < 0.001$, $R^2 = 0.69$; 27.9 °C: $y = 0.002883x$, $df = 79$, $p < 0.001$, $R^2 = 0.65$; 32.9 °C: $y = 0.011446x$, $df = 19$, $p < 0.001$, $R^2 = 0.92$; 37.9 °C: $y = 0.018731x$, $df = 9$, $p < 0.001$, $R^2 = 0.99$. Results based on the examination of 4215 *A. tsugae* collected in 2011 from the Chattahoochee National Forest, Georgia

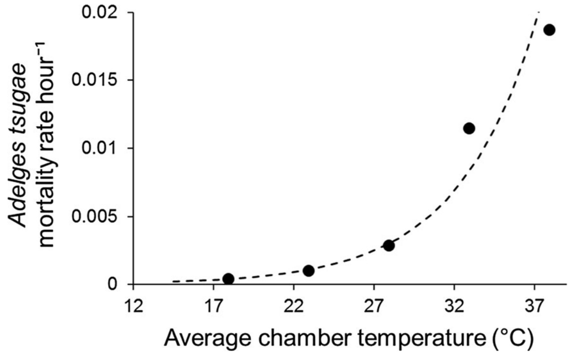

Fig. 2 Exponential model for estimating *Adelges tsugae* weighted mortality rates (W_j) based on observed coefficients (β) from five growth chamber linear regression models. Exponential model: $y = Ar^x$, where y = the estimated temperature weight (W_j), A = initial value, r = rate of increase, and x = temperature (°C); $W_j = (1.08e{-}5)(1.22)^{\mathrm{Temp}}$

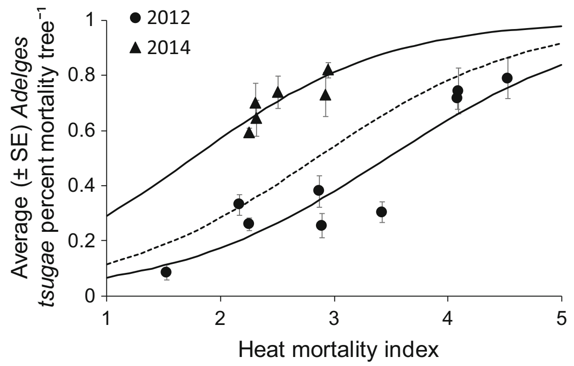

Fig. 3 Logistic relationship between average *Adelges tsugae* mortality (±SE) and heat mortality indices (HMI) of natural *Tsuga canadensis* stands. Predictive model (*dotted line*) based on 12,580 *A. tsugae* collected from 15 stands sampled in 2012 (*circles*) and 2014 (*triangles*) in the Chattahoochee National Forest, Georgia. *Solid lines* represent the fit for the individual sampled years. Logistic model: $M = 1/1 + e^{-(\beta_0+\beta_1 x)}$, where M = predicted *A. tsugae* mortality proportion (0–1), and x = site heat mortality index (HMI_i). $M = 1/\left(1 + e^{-[-3.134+1.102(\mathrm{HMI}_i)]}\right)$

81.9% (Table 1). The Hosmer–Lemeshow goodness-of-fit test resulted in a χ^2 of 1.05 that was found to be insignificant ($P = 0.99$). Thus, the predicted model of mortality (M; Eq. 2) fits well to the observed data.

$$M = \frac{e^{(-3.134+1.102(\mathrm{HMI}_i))}}{1 + e^{(-3.134+1.102(\mathrm{HMI}_i))}}, \quad i = 1, 2, \ldots, n \qquad (2)$$

where −3.134 and 1.102 are the parameter estimates for the y-intercept and the slope respectively, and HMI_i = the heat mortality index for the ith site. The direction the twigs faced, and potential differences in microclimate, did not have a significant effect on *A. tsugae* mortality ($W = 6826$, $P = 0.92$). Comparisons between Georgia and Maine found that the two latitudinal extremes showed no significant difference in the effects of heat stress on mortality ($z = -1.20$, $P = 0.23$, Fig. 4). In addition, there was no significant difference in temperature effects over time (2011 vs. 2013) in Georgia ($z = -1.12$, $P = 0.26$). These results within and among states indicate that *A. tsugae* may not be acclimating to the warmer summers in Georgia.

Discussion

Using experimental and observational data, we demonstrate that increasing heat stress significantly decreases the survival of an aestivating invasive forest insect. This is likely a direct effect of temperature since *A. tsugae* had not begun feeding and were therefore, unlikely to be influenced by host health or defenses. Also, aestivating sistens had not produced their protective wool, leaving them directly exposed to summer temperatures on the branches of the tree. Other studies on aestivating *A. tsugae* have reported that mortality increased substantially (up to 100%) when trees were exposed to direct sunlight (Sussky and Elkinton 2015). This suggests that soft-bodied *A. tsugae* may be sensitive to heat-induced desiccation or ultraviolet radiation. In addition, increasing temperatures may have elevated insect metabolic rates (Neven 2000), which could have depleted *A. tsugae* reserves. Research has also indicated that heat stress can have an indirect effect on insect fitness by negatively influencing bacterial endosymbionts that may be sensitive to heat shock (Dunbar et al. 2007; Burke et al. 2010).

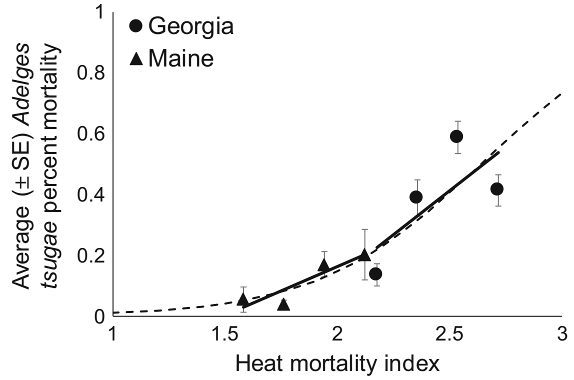

Fig. 4 Comparison of average *Adelges tsugae* mortality (±SE) between two latitudinal extremes, Georgia (*circles*) and Maine (*triangles*), following 48, 96, 144, and 192 h exposure to 30 °C. Individual state trends (*solid lines*) did not differ significantly from the combined model (*dotted line*). Model calculations were based on the examination of 580 *A. tsugae* collected from Georgia and 645 *A. tsugae* collected from Maine

Another explanation for the effect of supraoptimal temperatures on the mortality of *A. tsugae* is that temperatures in Georgia may be higher than those in its native range of Japan. Historical weather data for Takatsuki, Japan (34.84518°N, 135.614141°E) and Dahlonega, Georgia (34.7636°N, −84.1156°W) were compared for 2010–2014 to test this explanation. The maximum daily temperatures were examined for the main aestivating months (July–September) for the 5 years (n = 15 months) and compared between the two locations. Surprisingly, Takatsuki, Japan had warmer days than Dahlonega, Georgia for 93% of the summer months (University of Georgia 2011; The Weather Channel 2014). While the level of *A. tsugae* summer mortality in Japan is unknown, this could mean that *A. tsugae* is more sensitive to temperatures in a non-native range or on a non-native host. This is supported by other research that examined winter cold hardiness of *A. tsugae* and found that field and laboratory populations in the eastern United States suffer greater mortality than native populations in Japan (Parker et al. 1998, 1999).

Summer mortality of *A. tsugae* may also be due to maternal effects on the aestivating generation. For many insects, the temperatures experienced by the parental generation significantly influence the fitness/quality of the diapause stage (Mousseau and Dingle 1991; Denlinger 2002). This is evident in *A. tsugae*'s life history as progrediens preconditioned at different temperatures resulted in different aestivation regimens for the sistens generation (Salom et al. 2001). When comparing the maximum daily temperatures during progrediens maturation (March–May) for 2010–2014, Dahlonega, Georgia was warmer than Takatsuki, Japan for 87% of the months and reached a maximum of 33 °C during that time (University of Georgia 2011; The Weather Channel 2014). It is possible that the progrediens' exposure to higher spring temperatures in Georgia may be limiting the ability for the sistens generation to respond appropriately to summer temperatures. Comparing controlled temperature effects for aestivating *A. tsugae* collected from multiple locations that vary in spring temperatures may help evaluate this potential maternal effect.

Increasing temperatures can also indirectly benefit *T. canadensis* trees by reducing the feeding time of *A. tsugae*. In the southern portion of *T. canadensis*'s range, warmer year-round temperatures have been associated with an accelerated maturation of *A. tsugae*, resulting in the spring generation hatching months earlier in early winter (Leppanen and Simberloff 2017). In turn, sistens in warmer regions have been found to hatch, and subsequently enter aestivation, months earlier. For example, our research found that *A. tsugae* in Georgia were aestivating as early as April whereas *A. tsugae* in Connecticut typically enter aestivation in July (McClure et al. 2003). In addition, regular visits to the Chattahoochee National Forest found that, although they entered aestivation earlier, *A. tsugae* wool production (i.e. the post-aestivation phase) began at the expected time (October/November). Since *A. tsugae* is not actively feeding while aestivating, this indicates that trees in Georgia may be experiencing 33% less feeding than trees in the northern, cooler regions. It is currently unknown whether this prolonged aestivation time has any negative effects on *A. tsugae* fitness.

Results from this study provide evidence of the negative effects of prolonged supraoptimal temperatures on the survivability of a non-native invasive insect. Combined with climate change predictions, this has implications for the future of *T. canadensis* stands in the southeastern United States. Previously, most predictions regarding non-native insects, including *A. tsugae*, examined only the effects of warming winter temperatures. Based on climatic models, locations that reach low enough winter temperatures to cause *A. tsugae* mortality will be limited to small pockets in the northern region of *T. canadensis*' range by the year 2070 (Dukes et al. 2009). If warmer winter temperatures are solely considered, this implies that *T. canadensis* could experience a severe range retraction and be removed from the Southern Appalachian landscape. Our results indicate that increasing summer temperatures should also be taken into consideration and that *T. canadensis* may persist in pockets in the southern region under the current climate change models.

The hypothesis that southern populations of *T. canadensis* will persist is contingent upon its ability to survive low densities of *A. tsugae* as well as the increase in summer temperatures and other factors associated with climate change, such as increased drought events. In Western North America and Asia, all *Tsuga* species, including *T. canadensis* specimens in urban and arboretum settings, can survive in areas with low densities of *A. tsugae* (McClure et al. 2003; Weed et al. 2016; *personal observation*), so it seems likely that *T. canadensis* in the southeastern U.S. could as well. Although a low, stable *A. tsugae* population density has yet to be quantified, increased mortality of *A. tsugae* by heat has the potential to extend the lifespan of *T. canadensis* (due to reduced nutrient depletion) providing time for biological control methods to become effective. Since 2004, over one million predator beetles have been released in the Chattahoochee National Forest with evidence of successful establishment (Jones et al. 2014). The survival of *T. canadensis* in western North America indicates that top-down pressure from natural enemies, such as those currently being released in eastern North America, can result in lower, tolerable *A. tsugae* densities.

Within the Chattahoochee National Forest, variations in tree vigor appear to be related to temperature. For example, a warmer, low elevation site (444 msl) and a cooler, high elevation site (972 msl) have been infested with *A. tsugae* for the same length of time (10 years), but the trees at the lower elevation are experiencing, on average, less than 40% dieback with abundant regrowth, whereas trees at the higher elevation are experiencing more than 70% dieback (Mech 2015). Based on historical temperatures at these sites, the predictive model (Eq. 2) would estimate *A. tsugae* mortality at the lower elevation to be 50–80%, based on the year, compared to 20–30% at the higher elevation. In addition, although the southern extent of the native range of *T. canadensis* is the mountains of northern Georgia, trees can successfully grow in locations further south, such as Atlanta, Georgia (e.g. 33.786732°N, 84.365817°W), where temperatures can be up to 5 °C warmer (University of Georgia 2011). This indicates that *T. canadensis* may be able to handle not only low densities of *A. tsugae*, but also an increase in summer temperatures. However, *T. canadensis* is recognized as a drought-intolerant species suggesting that the predicted potential increase in drought periods associated with climate change could negatively affect its survival (Godman and Lancaster 1990; Intergovernmental Panel on Climate Change 2013).

Overall, the increasing temperatures associated with climate change may have a positive influence on the conservation of *T. canadensis*, an important foundation species in the Southern Appalachian Mountains, through its negative effects on a destructive non-native species. Our findings also underscore the necessity of examining increasing summer temperatures in attempts to understand the full effects of climate change on native and non-native invasive insects. Future research may find that the increased frequency and severity of heat waves associated with climate change may reduce insect fitness if summer temperatures go beyond the optimal temperature for the species (Huey et al. 2012). The methodology behind calculating the HMI for *A. tsugae* can also be used to calculate the HMI for other insects (Online Resource 1). These values can then be used to help ascertain which insect species may be negatively impacted by summer extremes. Whether positive or negative, the effects of increasing temperatures on invasive insects will continue to play a pivotal role in shaping conservation efforts for threatened forests.

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