



# Supraoptimal temperatures influence the range dynamics of a non-native insect

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## ABSTRACT

**Aim** To examine the relationship between the range dynamics of the non-native species *Lymantria dispar* (L.) and supraoptimal temperatures during its larval and pupal period.

**Location** West Virginia and Virginia, United States, North America.

**Methods** We linked the annual frequency of supraoptimal temperatures during the larval and pupal period of *L. dispar* with annual changes in its range dynamics based upon a spatially robust 20-year dataset. Correlation analyses were used to estimate the association between exposure time above the optimal temperature for *L. dispar* larval and pupal development, and the rate of invasion spread when adjusted for spatial autocorrelation.

**Results** We documented *L. dispar* range expansion, stasis, and retraction across a fairly narrow latitudinal region. We also observed differences in the amount of exposure above the optimal temperature for *L. dispar* larval and pupal development across this region. Temperature regimes in the Coastal Plain and Piedmont regions of Virginia, where the *L. dispar* range has retracted or remained static, were warmer than those in the Appalachian Mountains of Virginia and West Virginia, where *L. dispar* has expanded its range. Our analyses at a smaller spatial scale confirmed a statistically negative association between exposure time above the optimal temperature for *L. dispar* larvae and pupae, and the rate of *L. dispar* invasion spread over the 20-year period.

**Main conclusions** The shifting, expansion and retraction of species distributional ranges holds critical implications to both invasion ecology and conservation biology. This work provides novel empirical evidence of the importance of supraoptimal temperatures on the range dynamics of a non-native invasive insect with application to both non-native and native species whose physiological processes are strongly regulated by temperature.

## Keywords

Biological invasions, climate change, gypsy moth, *Lymantria dispar*, range dynamics, supraoptimal temperature.

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## INTRODUCTION

Changes in the geographic range of a species can ultimately determine whether a species is considered to be invasive, stable or declining towards extinction. Consequently, and in part due to concerns of increases in non-native species invasions and decline in native species, there is much interest in the dynamics of distributional ranges (Keitt *et al.*, 2001; Case *et al.*, 2005; Holt & Keitt, 2005; Sexton *et al.*, 2009). Several factors are known to play important roles in shaping range boundaries, such as the availability of suitable hosts, and the

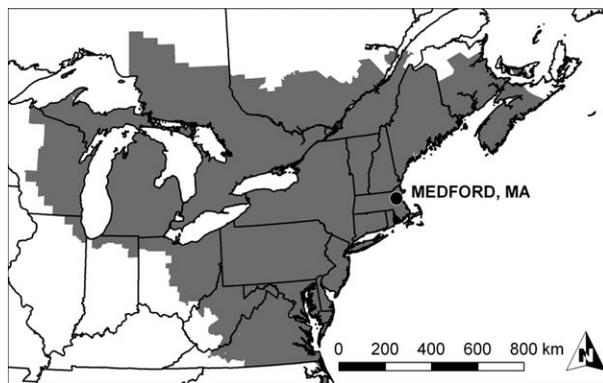
presence of competitors, mutualists and natural enemies (Case & Taper, 2000; Elkinton *et al.*, 2006; Holt *et al.*, 2011; Pigot & Tobias, 2013). In addition, climate can be a particularly important determinant of the geographic boundaries of species (Parmesan, 1996), particularly so for insects because many of their physiological processes are regulated by temperature (Gilbert & Raworth, 1996; Bryant *et al.*, 2002).

Considerable recent attention has been given to the effects of global climate change on insect dynamics (Bale *et al.*, 2002; Musolin, 2007; Deutsch *et al.*, 2008; Tobin *et al.*, 2008), resulting in a diversity of responses. For example,

some species have been shown to expand their range and abundance (Battisti *et al.*, 2005; Jepsen *et al.*, 2008; Cudmore *et al.*, 2010), while others have been detrimentally affected resulting in range retraction and decreased abundance (Thomas *et al.*, 2006; Esper *et al.*, 2007; Ims *et al.*, 2008; Johnson *et al.*, 2010; Maes *et al.*, 2010). Although insect development and survivorship generally increase with increasing temperatures, there are also species-specific upper thermal optima. At supraoptimal temperatures, developmental rate begins to decrease (Sharpe & DeMichele, 1977), and lethal and sublethal effects increase (Scriber & Slansky, 1981; Hance *et al.*, 2007; Prado *et al.*, 2010). Several prior studies have implicated increases in surface temperatures as a cause of species range expansion across broad latitudinal and altitudinal ranges (Parmesan *et al.*, 1999; Parmesan & Yohe, 2003; Hagen *et al.*, 2007; de la Giroday *et al.*, 2012). In this study, we present novel evidence that within a relatively small latitudinal gradient in North America over a 20-year period, supraoptimal temperatures during the period of larval and pupal development are associated with *Lymantria dispar* (*L.*) range retraction.

*Lymantria dispar* was introduced into North America in 1869 (Liebhold *et al.*, 1989) and has since expanded its distribution such that it now occupies a range extending from Nova Scotia to Wisconsin, and from Ontario to Virginia (Fig. 1; Tobin *et al.*, 2012). Larvae hatch from overwintering egg masses and are capable of feeding on over 300 host plant species (Elkinton & Liebhold, 1990; Liebhold *et al.*, 1995). Adults emerge in summer. Females of the European strain of *L. dispar*, which is the strain established in North America, are not capable of sustained flight. Males, which can fly, locate females by attraction to a sex pheromone. Females oviposit a single egg mass containing 250–500 eggs. There is one generation per year.

The phenology of *L. dispar* has been thoroughly studied and consequently, the effect of temperature on egg, larval



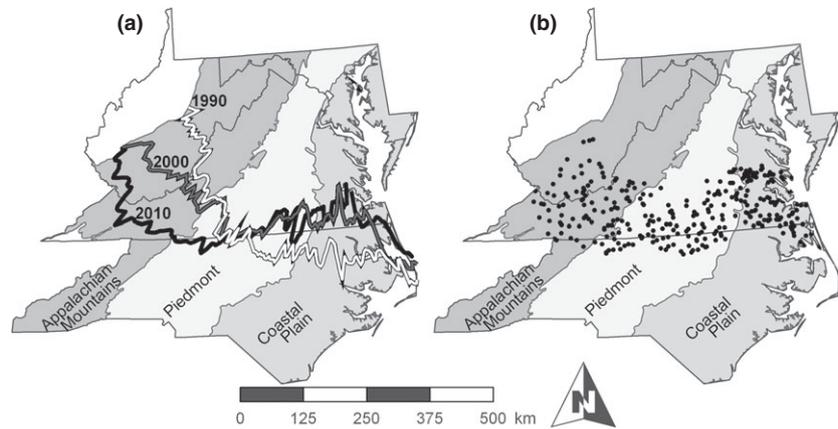
**Figure 1** Current range of *Lymantria dispar* based upon county or district quarantine records in the USA and Canada, 2012 (U.S. Code of Federal Regulations, Title 7, Chapter III, Section 301.45-3 and Canadian Food Inspection Agency, Plant Health Division, Policy Directive D-98-09). The initial site of *L. dispar* introduction was Medford, Massachusetts, in 1869. Map projection: Albers, WGS1984.

and pupal development is well understood (e.g. Johnson *et al.*, 1983; Casagrande *et al.*, 1987; Logan *et al.*, 1991; Sheehan, 1992; Sawyer *et al.*, 1993; Gray *et al.*, 1995, 2001; Gray, 2009). Considerable attention has also been given to predicting *L. dispar* establishment success based upon climatic suitability (e.g. Régnière & Nealis, 2002; Gray, 2004; Logan *et al.*, 2007; Pitt *et al.*, 2007; Régnière *et al.*, 2009). Generally, climate is thought to restrict the distributional range of *L. dispar* in three primary ways. First, overwintering eggs are adversely affected by cold temperatures; for diapausing eggs, mortality begins at  $\approx -18$  °C with a supercooling point of  $\approx -28$  °C (Summers, 1922; Sullivan & Wallace, 1972; Campbell, 1973). Thus, there are climatic barriers to successful *L. dispar* colonization at higher latitudes and elevations where these temperature regimes are consistently common (Nealis *et al.*, 1999; Andresen *et al.*, 2001). Second, as with most insects that undergo an obligatory diapause, such as *L. dispar*, an environmental cue is needed to terminate diapause (Tauber & Tauber, 1976); in the case of *L. dispar*, that cue is primarily exposure to cold temperatures (Tauber *et al.*, 1990; Gray *et al.*, 2001). Consequently, there is also a climatic barrier in regions where there is not a sufficient chilling period to terminate diapause in overwintering eggs (Gray, 2004). Third, suboptimal temperatures during post-diapause development will delay egg hatch, and suboptimal temperatures will decrease larval and pupal development; collectively, this will delay oviposition, thereby preventing eggs from reaching the cold-hardy diapause phase before the onset of freezing temperatures (Régnière & Nealis, 2002; Gray, 2004). In this study, we use a 20-year dataset to present to our knowledge the first attempt linking supraoptimal temperatures during the period of larvae and pupae with *L. dispar* range retraction.

## METHODS

We quantified the range dynamics of *L. dispar* by estimating the location of the range boundary corresponding to male moth population abundance thresholds each year, 1989–2010, and then estimating the annual displacement of the boundary (Sharov *et al.*, 1995; Tobin *et al.*, 2007a). As part of management programmes aimed at restricting *L. dispar* range expansion, grids of georeferenced pheromone-baited traps, which attract male moths, were deployed along the population front under the Appalachian Integrated Pest Management programme (1989–1992), the Slow-the-Spread pilot project (1993–1999) and currently under the Slow-the-Spread programme (2000–2013) (Reardon, 1991; Sharov *et al.*, 2002; Tobin & Blackburn, 2007). In these programmes, traps were deployed solely for the purpose of survey and do not provide population suppression. Traps were generally set 0.5–2 km apart in most areas, while in areas with higher expected population densities, traps were set 3–8 km apart. Trap catch data (average of 34,262 traps deployed annually) from the three distinct regions of Virginia and West Virginia (the Virginia Coastal Plain, the Virginia Piedmont, and the

**Figure 2** (a) Estimated *Lymantria dispar* range boundaries in 1990, 2000 and 2010 in the Appalachian Mountains of Virginia and West Virginia, the Virginia Piedmont and Virginia Coastal Plain. (b) Randomly selected locations (100 per region) used in our analyses. Map projection: Albers, WGS1984.



Appalachian Mountains of Virginia and West Virginia, Fig. 2) were used to generate a continuous surface at a  $1 \times 1$  km resolution for each year (1989–2010) using median indicator kriging (Isaaks & Srivastava, 1989) in GSLIB (Deutsch & Journel, 1992). We chose these three regions for several reasons. First, the trapping histories in the Virginia Coastal Plain, the Virginia Piedmont, and the Appalachian Mountains of Virginia and West Virginia are the longest of any regions currently monitored under the Slow-the-Spread programme and its precursors. The earliest trapping data from these three regions are from 1989, which is at least 7 years earlier than any other region. Second, gypsy moth spread dynamics in these three regions have been the most unique among all the regions, from Wisconsin to Virginia (Fig. 1), in which spread has been measured. In other regions, the gypsy moth range has been expanding at variable rates, generally from 6 to 18 km year<sup>-1</sup> (Tobin *et al.*, 2007a); in contrast, we have observed range stasis and retraction in the Virginia Coastal Plain and Piedmont. Last, and most importantly, the three regions represent the most southern extent of the current gypsy moth population front (Fig. 1). Thus, gypsy moth populations in these regions are the most likely to be affected by supraoptimal temperatures and are unlikely to be affected by the confounding effect of mortality due to overwintering temperatures, which was observed to reduce gypsy moth spread rates in New England (Liebhold *et al.*, 1992) and Michigan (Sharov *et al.*, 1999).

From the interpolated grids, we estimated two annual population density boundaries (0.1 and 0.5 moth per trap) using an optimization algorithm (Sharov *et al.*, 1995). We then measured the annual displacement of both population density boundaries along 720 transects that radiated at  $0.5^\circ$  intervals from a fixed point ( $39.4285^\circ\text{N}$ ,  $-76.8264^\circ\text{W}$ ) located in Baltimore County, Maryland (Tobin *et al.*, 2007a; Fig. S1). The fixed point was chosen for our dataset so that a maximum number of the 720 transects that radiated from the point intersected the population density boundaries at an angle as close to  $90^\circ$  as possible (Fig. S1; Tobin *et al.*, 2007a). By retaining the same fixed point through time, we were thus able to estimate the annual displacement in population density boundaries, whose spatial locations can change

from year to year, as measured from this fixed point. Displacements at each transect were averaged between both population density boundaries in each year and then averaged for each of the three regions to estimate the annual rate of *L. dispar* spread (Sharov *et al.*, 1995, 1997; Tobin *et al.*, 2007a).

Weather stations tend to be preferentially located in or near settlements, especially in the Appalachian Mountain region; therefore, they do not comprise a representative spatial sampling of temperature regimes in the forested habitats of *L. dispar* (Russo *et al.*, 1993; Schaub *et al.*, 1995). Therefore, we randomly selected 100 locations within each of the three regions (Fig. 2b). We specifically selected locations that corresponded to the geographic range of *L. dispar* within our three regions. We did this by selecting locations that were within 50 km, north and south, of the 0.5 population density boundary in 2000 (the midyear of our 20-year dataset, Fig. 2b). At each randomly selected location, we estimated daily minimum and maximum temperatures for 1990–2010 using the temperature generator BioSIM v10.2.2.3 (Régnière, 1996; Régnière & St-Amant, 2007). In BioSIM, the daily minimum and maximum temperatures from up to eight weather stations (National Climatic Data Center, 2013) nearest to each of our 300 locations were used to estimate daily minimum and maximum temperatures at each location through distance-weighted interpolation. If daily temperature records were missing from a weather station, we used BioSIM to estimate them using the 1981–2010 climate normals from the station (Régnière & St-Amant, 2007). A total of 973 unique weather stations from the three regions were used in this analysis.

We used the gypsy moth life stage (GLS) model (Gray, 2004) and our daily minimum and maximum temperatures to simulate gypsy moth phenology starting with oviposition in 1988 and ending with oviposition in 2010. GLS is a multi-generational model in which population variability in developmental stages is maintained by the creation of individual cohorts corresponding to simulated daily oviposition during each generation. Phenological development is estimated by GLS in 1-hour time steps using the temperatures estimated by a sine wave interpolation of the daily minimum and

maximum temperatures (Allen, 1976). We used the dates on which *GLS* simulated 50% and 95% cumulative emergence to first instar (L1), pupae and adult stages each year in each location to estimate region-specific larval and pupal developmental times of a median individual and of the slowest 50% of the population. We used the dates on which *GLS* simulated 5% and 95% cumulative emergence to L1 and pupal stages, an optimal developmental temperature of 28 °C (Casagrande *et al.*, 1987; Logan *et al.*, 1991), and the 24-hourly sine wave-interpolated temperatures of each day of L1–pupal development to estimate the number of hours per year in which the temperature exceeded the optimum for *L. dispar* larval and pupal development in each location. The amount of exposure above the optimal temperature, across all years, was examined across the longitudinal gradient of the three regions (i.e. from the eastern Coastal Plain to the western Appalachian Mountains of Virginia and West Virginia, Fig. 2).

Because habitat quality could also affect *L. dispar* range dynamics (Sharov *et al.*, 1999), we also extracted the density of *L. dispar* preferred host species at each of the 300 randomly selected locations. These estimates were derived from interpolation of forest inventory plots and adjustment for forest density using remotely sensed data (Liebhold *et al.*, 1995; Morin *et al.*, 2005). The density of preferred host species ( $\text{m}^2 \text{ha}^{-1}$ ) was transformed using  $\log_{10}(z+1)$  to conform to the assumptions of normality. We tested for differences in host density among the three regions using analysis of variance and conducted post hoc tests using Tukey's HSD at  $\alpha = 0.05$  (R Development Core Team, 2013).

To statistically determine the relationship between supraoptimal temperatures and range dynamics across the three regions (the Virginia Coastal Plain, the Virginia Piedmont, and the Appalachian Mountains of Virginia and West Virginia), we measured the correlation between the spatially explicit estimates of annual spread rate (i.e. individual estimates of boundary displacement between year  $t-1$  and year  $t$ , where  $t = 1990-2010$ ) and the estimated number of hours per year during L1–pupal development above the optimal developmental temperature (28 °C; Logan *et al.*, 1991) in year  $t$  at the location (where we estimated temperatures) closest to the displacement (Fig. S1). We considered five supraoptimal temperature groups: optimum plus 1, 2, 3, 4 and  $\geq 5$  °C. Past work has shown spatial autocorrelation in *L. dispar* trap catch data from our study region (Sharov *et al.*, 1996, 1997), and we observed spatial autocorrelation in supraoptimal temperatures (Fig. S2). Because spatially autocorrelated data violate the assumption of independence among samples and induce bias in the variance of the correlation coefficient (Clifford *et al.*, 1989; Dutilleul, 1993), we used a modified *F*-test for assessing significance (Dutilleul *et al.*, 2008) using the 'SpatialPack' package (Osorio *et al.*, 2012) in R (R Development Core Team, 2013). We also measured the correlation between the local estimates of annual spread rate (from year  $t-1$  to year  $t$ , where  $t = 1990-2010$ ) and the density of preferred host species (Morin *et al.*,

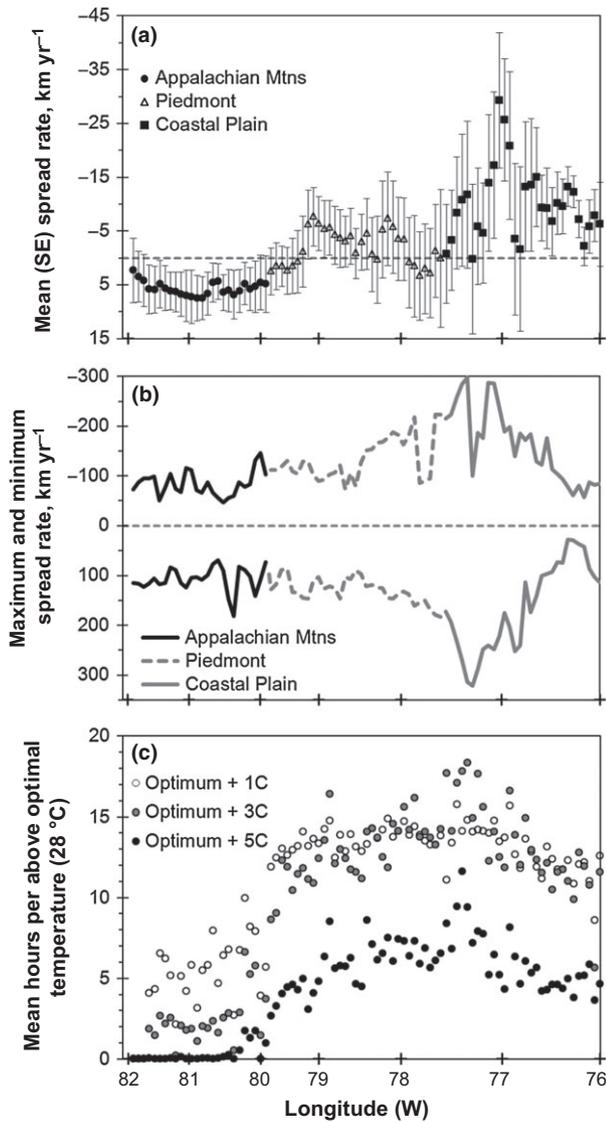
2005) corresponding to the location of population boundary displacement. Due to spatial autocorrelation in host density (Morin *et al.*, 2005), we used the modified *F*-test for assessing significance (Dutilleul *et al.*, 2008; Osorio *et al.*, 2012; R Development Core Team, 2013).

## RESULTS

We observed considerable differences in range dynamics of *L. dispar* in the Appalachian Mountains, the Virginia Piedmont and the Virginia Coastal Plain over a 20-year period (1990–2010). We detected range expansion in the Appalachian Mountains with an overall mean rate (95% CI) of  $5.7 \text{ km year}^{-1}$  (4.1, 7.4) and range retraction in the Coastal Plain with an overall mean rate of  $-9.6 \text{ km year}^{-1}$  (-13.0, -6.2). Spread in the Piedmont was the most variable, with range expansion in the western portion (bordering the Mountains), range stasis in the middle and range retraction in the eastern portion (bordering the Coastal Plain) (Fig. 2); the overall mean (95% CI) spread rate in the Piedmont was  $-1.8$  (-4.0, 0.4). Another interesting aspect of the differing range dynamics among these three regions is the variability in annual spread rate. Variation in annual spread rate increased along a longitudinal gradient, from low levels in the Appalachian Mountains to high levels in the Coastal Plain (Fig. 3a). Moreover, both the maximum 1-year range expansion and maximum 1-year range retraction were largest in the Coastal Plain (Fig. 3b). Indeed, we observed the largest 1-year range expansion in the Coastal Plain even though there was net range retraction over the 20-year period.

We also observed differences in the amount of time *L. dispar* larvae and pupae were exposed to supraoptimal temperatures across a longitudinal gradient from the Coastal Plain to the Appalachian Mountains (Fig. 3c). However, there seemed to be only subtle differences in the durations of larval and pupal stages (Table 1) across this gradient, despite the differences in exposure time to supraoptimal temperatures (Fig. 3c). In fact, predicted developmental times were shorter in the Coastal Plain and Piedmont relative to the Appalachian Mountains. Thus, even though insect developmental rate declines at supraoptimal temperatures (e.g. Sharpe & DeMichele, 1977), including *L. dispar* (Logan *et al.*, 1991), the slower development during the more frequent exposure to supraoptimal temperatures in the Coastal Plain and Piedmont was likely offset by the faster development during the just-less-than optimal temperatures that were also more frequent in these regions.

Across all regions and years, we did observe a significant negative correlation between the annual rate of spread and the predicted number of hours per year during L1–pupal development at each of the supraoptimal temperature groups (Table 2, Fig. 4). Moreover, the estimate of the correlation coefficient consistently decreased as the deviation from the optimal temperature increased, such that the most negative correlation was between spread rates and the number of hours above the optimal  $+ \geq 5$  °C temperature (Table 2). It



**Figure 3** (a) Mean ( $\pm$ SE) rates of *Lymantria dispar* spread across 1990–2010, (b) the maximum and minimum spread rate of *L. dispar* during the 1990–2010 period and (c) the mean hours above the optimum + 1, 3 or  $\geq 5$  °C, across the 1990–2010 period.

is also noteworthy, when regressing the rate of spread against the hours per year at supraoptimal temperatures, that it did not require much mean exposure (i.e.  $> 15$  hours at the

optimal + 2 °C group and  $> 2$  hours at the optimal +  $\geq 5$  °C group) to result in mean range retraction (Fig. 4).

We detected significant differences in the density of preferred *L. dispar* host species across the three regions ( $F_{2,297} = 28.1$ ;  $P < 0.01$ ). Host density was significantly higher in the Appalachian Mountains (mean = 6.4, SD = 3.1, range = 0.4–14.5 m<sup>2</sup> ha<sup>-1</sup>) than in the Piedmont (mean = 4.2, SD = 1.9, range = 0.4–9.2 m<sup>2</sup> ha<sup>-1</sup>), which was significantly higher than in the Coastal Plain (mean = 3.4, SD = 2.0, range = 0.0–8.7 m<sup>2</sup> ha<sup>-1</sup>). Despite these differences, however, we did not detect a significant correlation between host density and *L. dispar* spread rates ( $\rho = 0.06$ ;  $F_{1,468} = 1.96$ ;  $P = 0.16$ ; Fig. 5).

## DISCUSSION

*Lymantria dispar* range dynamics varied from expansion to stasis to retraction across Virginia and West Virginia, and this variation was significantly associated with supraoptimal temperatures during larval and pupal development (Fig. 4). Moreover, exposure to supraoptimal temperatures in *L. dispar* populations in the Coastal Plain could be driving the year-to-year variation in spread rates in this region. Even though we documented net range retraction over a 20-year period in the Coastal Plain (Fig. 3a), we also note the greater variability in this region including maximum rates of spread that are the highest over the three regions (Fig. 3b). Thus, in years in which the degree of exposure to supraoptimal temperatures is reduced, our results suggest that range expansion in the Coastal Plain could occur at potentially faster rates than in the Piedmont or Appalachian Mountain regions.

In the case of *L. dispar*, as with other insects, high temperatures could have both positive and negative effects on population growth. Our simulations indicated that average developmental rates are faster in areas experiencing higher temperatures, despite the fact that larvae are exposed to more frequent supraoptimal temperatures (Fig. 3c). Even though developmental rates decline at supraoptimal temperatures (Logan *et al.*, 1991), the overall upward shift in all temperatures causes a net acceleration in developmental rates. While faster developmental rates can have favourable impacts on generational population growth rates, exposure to supraoptimal temperatures is also likely to have adverse impacts on physiological processes that negatively impact population growth rates. Our finding of an association

**Table 1** Region-specific developmental times of *Lymantria dispar* from larvae (L) to pupae (P), and from pupae to adult (A)

Region	Mean ( $\pm$ SE) developmental time (days)			
	50% L1 – 50% P	50% L1 – 100% P	50% P – 50% A	50% P – 100% A
The Appalachian Mountains	68.2 (0.09)	78.7 (0.09)	16.8 (0.02)	25.1 (0.03)
Piedmont	66.9 (0.10)	76.7 (0.10)	15.7 (0.02)	23.1 (0.02)
Coastal Plain	64.9 (0.10)	74.9 (0.11)	15.4 (0.02)	23.0 (0.03)

**Table 2** Correlation between rates of *Lymantria dispar* spread and the hours per year above optimal temperatures, 1990–2010, across all regions ( $N = 5162$ )

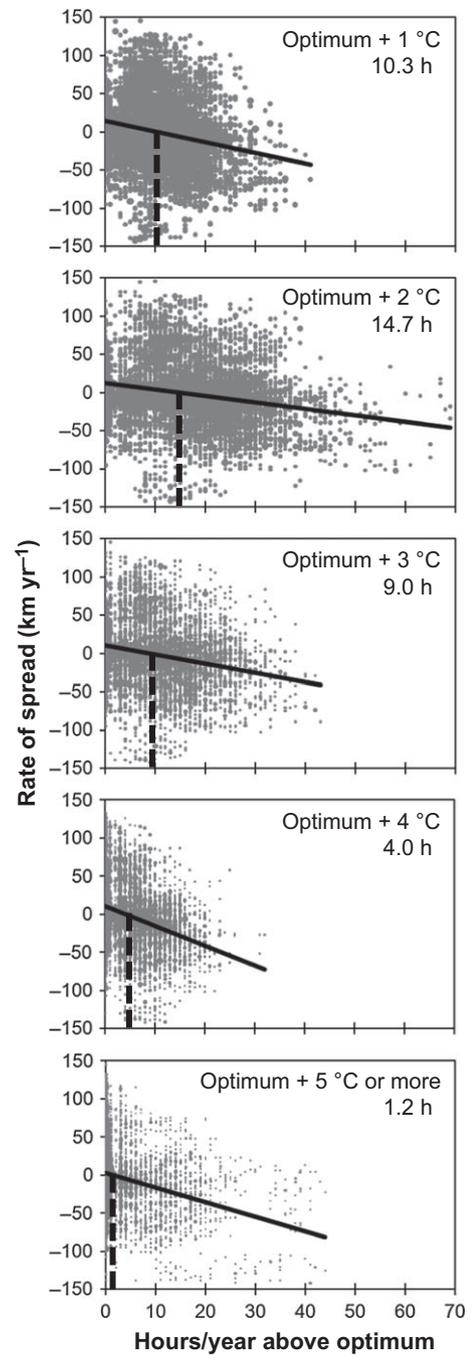
	$\rho$	$F^*$	d.f.*	$P$
Optimum + 1 °C	-0.183	11.0	1, 319.5	< 0.001
Optimum + 2 °C	-0.187	8.1	1, 224.5	< 0.001
Optimum + 3 °C	-0.191	8.1	1, 213.6	< 0.001
Optimum + 4 °C	-0.278	21.9	1, 262.9	< 0.001
Optimum + $\geq 5^\circ\text{C}$	-0.309	63.2	1, 599.0	< 0.001

\*cf. Dutilleul *et al.* (2008).

between exposure to supraoptimal temperatures, and range expansion or retraction (Table 2, Fig. 4), indicates that the adverse effects of these high temperatures could exceed the beneficial effects on population growth.

The differences in *L. dispar* range dynamics do not appear to be driven by differences in host density as measured by the basal area of preferred *L. dispar* host species (Fig. 5). Prior work suggested that host density played a role in the spread rate of *L. dispar* through the lower peninsula of Michigan; in this case, spread rates were higher in the northern areas, which also experienced less favourable overwintering conditions as measured by minimum January temperatures (Sharov *et al.*, 1999). However, another study suggested that within a broad range of host density, which included the range of host densities from our study regions, persistence of invading, low-density colonies was not affected by host density (Whitmire & Tobin, 2006). Because *L. dispar* larvae are generalists that can exploit over 300 host tree species including 79 species that are considered to be preferred hosts (Liebhold *et al.*, 1995), many of which are present throughout Virginia and West Virginia (Morin *et al.*, 2005), it is not surprising that host density failed to influence initial establishment. Populations could be able to establish where only some low level of host density is present. However, host density is strongly associated with the development and dynamics of outbreak densities (Houston & Valentine, 1977; Herrick & Gansner, 1986; Gottschalk, 1993). We also note that the density of preferred host species in the Coastal Plain is slightly higher than that in Wisconsin (Morin *et al.*, 2005; Whitmire & Tobin, 2006), a region where rates of *L. dispar* range expansion have been consistently the highest across the entire *L. dispar* invasion front (Tobin *et al.*, 2007a,b; Tobin & Blackburn, 2008).

Prior work examining the role of temperature on *L. dispar* range boundaries has generally focused on spatial variation in seasonality or climatic suitability, or specifically the degree to which a climate satisfies the life cycle requirements of the population (Régnière & Nealis, 2002; Gray, 2004; Logan *et al.*, 2007; Pitt *et al.*, 2007; Régnière *et al.*, 2009). The dominant requirement has been that the population be in the cold-tolerant diapause phase (Leonard, 1968) before the onset of freezing temperatures (Gray, 2013) and that winter temperatures satisfy diapause requirements (Gray *et al.*, 2001). Thus,



**Figure 4** Relationship (correlation coefficients listed in Table 2) between the annual rate of spread of *Lymantria dispar* and the hours per year above the optimal temperature of 28 °C across all regions. The solid line represents a linear regression fit, from which exposure thresholds (indicated by the dashed vertical lines and listed in each figure) were estimated as the hours above the optimum + 1, 2, 3, 4 or  $\geq 5^\circ\text{C}$  at which the yearly spread rate is estimated to be 0 (i.e. range stasis).

climatic suitability is lower at higher latitudes because the lower spring temperatures result in later egg hatch, lower summer temperatures result in slower larval development, and the summer is shorter; these conditions conspire to keep

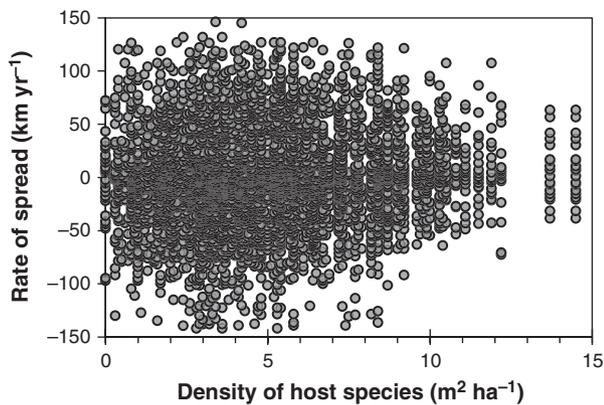


Figure 5 Relationship between annual rates of spread and the density of preferred *Lymantria dispar* host species.

more of the population from reaching diapause before the onset of freezing conditions. Climatic suitability is lower at lower latitudes because winter temperatures are too high to satisfy diapause requirements (Gray, 2004). However, higher temperatures may not result in a lower estimate of climatic suitability because the slower developmental rate during the increased time spent at supraoptimal temperatures may be offset by the higher developmental rate from the higher, but still suboptimum, temperatures during the remainder of each day (e.g. Table 2). Although it is well understood that supraoptimal temperatures will slow developmental rate (Casagrande *et al.*, 1987; Logan *et al.*, 1991), other possible negative effects on fitness have not been adequately quantified and are not included in estimates of climatic suitability. Past work has indicated that *L. dispar* rate of spread was reduced, although still positive, in areas with a mean minimum January temperature  $< 7^{\circ}\text{C}$  (Liebhold *et al.*, 1992). We believe this study to be the first that examines the role that supraoptimal temperatures could play in not only restricting the rate of range expansion but also resulting in range retraction.

## CONCLUSIONS

The effect of climate warming on species' ranges is an important ecological question. Between 30 and 75% of butterfly species have exhibited a northern expansion, and  $< 20\%$  have exhibited a southern retraction in Europe (Parmesan, 2006). Range limits have also moved northward an average of 6 km per decade in the direction predicted by climate change (Parmesan & Yohe, 2003). For example, the northern range limit of non-diapausing butterfly species has shifted northward from California to Washington (Crozier, 2004). Although many insect species have undoubtedly benefited from warmer temperatures, some have not; for example, cool adapted butterfly species in southern France have shown a range retraction at low elevations (Descimon *et al.*, 2005). Many studies have suggested positive effects of climate change on insect dynamics in temperate climatic zones, such as increases in voltinism and abundance owing to

temperature-dependent developmental rates and decreases in overwintering mortality (Porter *et al.*, 1991; Yamamura & Kiritani, 1998; Logan *et al.*, 2003; Tobin *et al.*, 2008). However, the response of insects to climate change can be considerably more complex (Cannon, 1998; Bale *et al.*, 2002; Ims *et al.*, 2008; Couture & Lindroth, 2012). Furthermore, the increased frequency of introductions of non-native species, due to increases in global trade (Aukema *et al.*, 2010; Liebhold *et al.*, 2012), adds to the importance of understanding the interplay between climate change and biological invasions (Hellmann *et al.*, 2008; Walther *et al.*, 2009; Engel *et al.*, 2011). As we highlight in this study, these responses can also differ greatly within a species depending on the degree of exposure to supraoptimal temperatures. This work also underscores the importance of climate and changes in climate in causing range shifts as opposed to expansion along all directions. Greater attention should be given to the role of supraoptimal temperatures in inducing lethal and sublethal effects, with direct and indirect consequences to fitness, population persistence and population growth rates.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Linking supraoptimal temperatures with *Lymantria dispar* range dynamics.

**Figure S2.** Spatial autocorrelation in supraoptimal temperatures.

## BIOSKETCHES

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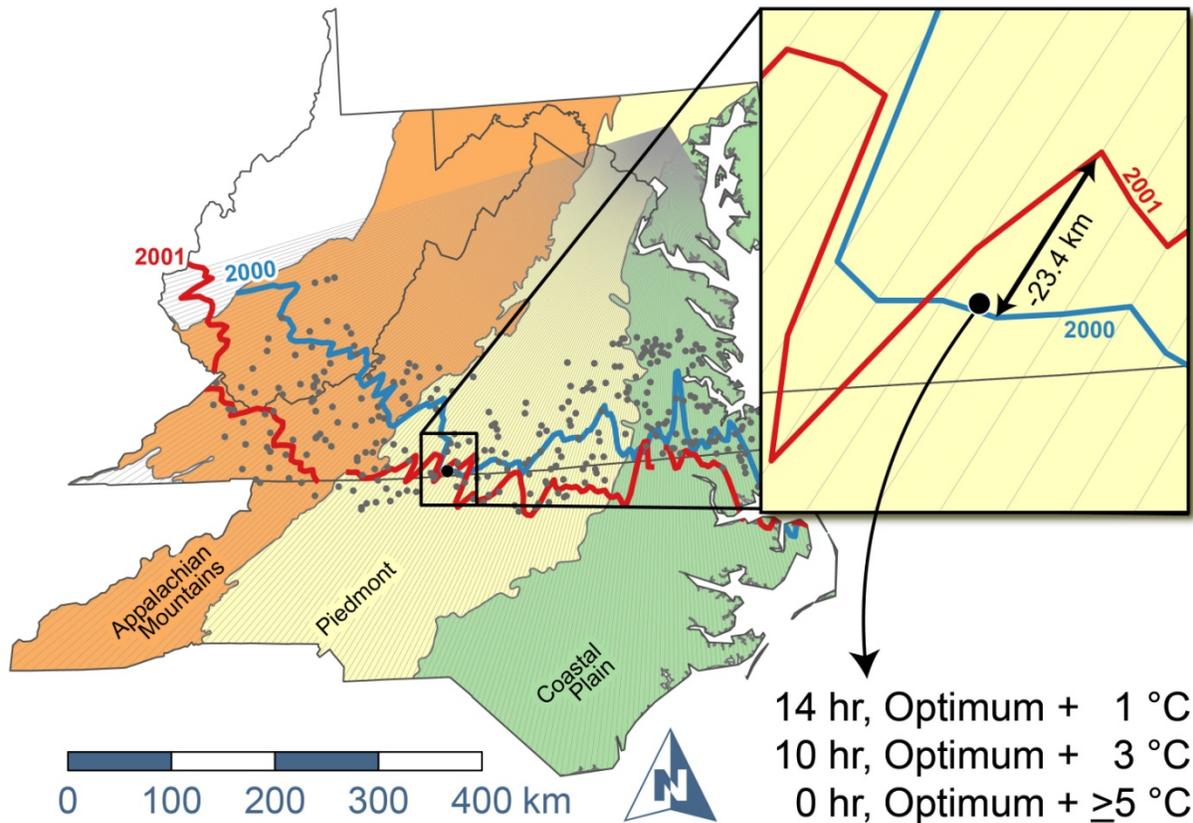
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Author contributions: P.C.T. and A.M.L. developed the concept of the study. D.R.G. conducted the phenological modelling, and P.C.T. estimated range dynamics. P.C.T. led the data analysis with input from D.R.G. and A.M.L. All authors contributed to manuscript writing.

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**Figure S1. Linking supraoptimal temperatures with *Lymantria dispar* range dynamics**

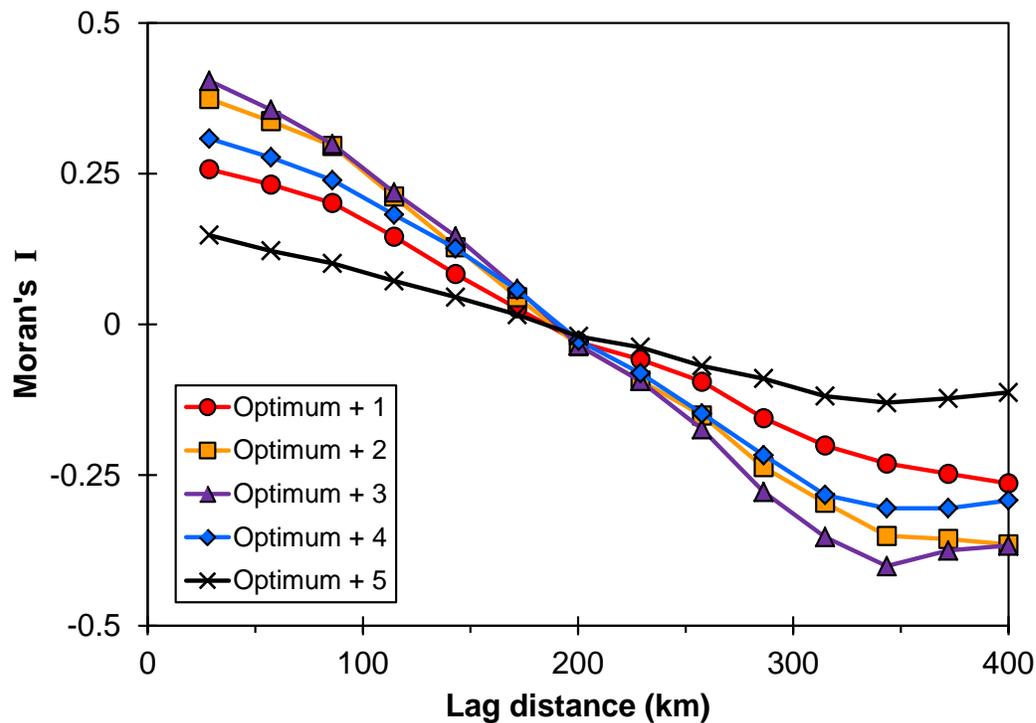


Local estimates of annual spread rate were based on population boundary displacement between year  $t-1$  and year  $t$ ; the example above shows the locations of the 0.5 moths per trap boundary in 2000 and 2001. Displacements at 720 transects radiating at  $0.5^\circ$  intervals from a fixed point ( $39.4285^\circ\text{N}$ ,  $-76.8264^\circ\text{W}$ ) were used to estimate yearly local spread rates (Sharov *et al.*, 1995, Tobin *et al.*, 2007). We then matched the closest transect to each of the 300 randomly-selected locations at which we estimated temperature. In the insert graph, we depict a representative location of one of the 300 locations, at which we estimated, for example, 14, 10, and 0 hours above the optimum temperature + 1, 3, and  $\geq 5^\circ\text{C}$ , respectively, in 2001. The spread rate from 2000 to 2001 for the transect closest to this location was estimated at  $-23.4$  km. After matching

all of the randomly-selected locations (where temperatures were estimated) with the closest transect (where spread rates were estimated), we then correlated rates of *L. dispar* spread with supraoptimal temperatures after adjusting for spatial autocorrelation in both (Dutilleul, 1993; Dutilleul *et al.*, 2008). In some cases, we could not link a location with a transect; for example, in some years, we could not accurately estimate population density boundaries everywhere throughout the three regions. However, out of 6,000 possible pairings (300 locations  $\times$  20 years), we were able to link a location with a transect in 5,162 cases. Map projection: Albers, WGS1984.

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**Figure S2. Spatial autocorrelation in supraoptimal temperatures**

Estimates of Moran's I of the spatial distribution of the hours above the optimum temperature + 1, 2, 3, 4, or  $\geq 5^{\circ}\text{C}$  estimated at 300 randomly selected locations (100 in each region: the Appalachian Mountains of Virginia and West Virginia, the Virginia Piedmont, and Virginia Coastal Plain, revealing the presence of spatial autocorrelation. Estimates of Moran's I were calculated using the 'SpatialPack' package (Osorio et al. 2012) in R (R Development Core Team 2013).

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