



# Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae)

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## Abstract

The southern pine beetle, *Dendroctonus frontalis*, is among the most important agents of ecological disturbance and economic loss in forests of the south-eastern United States. We combined physiological measurements of insect temperature responses with climatic analyses to test the role of temperature in determining the northern distribution limits of *D. frontalis*. Laboratory measurements of lower lethal temperatures and published records of mortality in wild populations indicated that air temperatures of  $-16^{\circ}$  should result in almost 100% mortality of *D. frontalis*. The distribution limits for *D. frontalis* approximate the isoline corresponding to an annual probability of 0.90 of reaching  $\leq -16^{\circ}\text{C}$ . Thus, *D. frontalis* have been found about as far north as they could possibly occur given winter temperature regimes. At latitudes from  $39^{\circ}$  N (southern Ohio) to  $33^{\circ}$  N (central Alabama), winter temperatures must exert high mortality on *D. frontalis* populations in at least one year out of ten. In contrast, we reject the hypotheses that summer temperatures or the distribution of host trees constrain the northern distribution of *D. frontalis*. Because of the short generation time of *D. frontalis*, its high dispersal abilities, and the cosmopolitan distribution of suitable host trees, changes in either the mean or variance of minimum annual temperatures could have almost immediate effects on regional patterns of beetle infestations. We estimate that an increase of  $3^{\circ}\text{C}$  in minimum annual temperature could extend the northern distribution limits by 170 km. Increases or decreases in the variance of minimum annual temperatures would further relax climatic constraints on the northern distribution limits of *D. frontalis*. Results emphasize the ecological importance of spatial and temporal variability in minimum annual temperatures. The physiologically based models provide a tool for guiding land management decisions in forests and illustrate a general approach for predicting the regional effects of climatic patterns on the distribution of organisms.

## Keywords

*Dendroctonus frontalis*, lower lethal temperature, distribution, southern forest, Geographic Information System, global change, climatic variance

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## Resumen

*Dendroctonus frontalis* es considerado uno de los principales agentes responsables de alteraciones ecológicas y pérdidas económicas en los bosques del sudeste de los Estados Unidos. Nosotros combinamos medidas fisiológicas de respuesta del insecto a la temperatura con análisis climáticos con el fin de estudiar el papel que desempeña la temperatura en la determinación de los límites de distribución norte de esta especie. Medidas en el laboratorio de la temperatura letal inferior y referencias bibliográficas de alta mortalidad en poblaciones naturales del insecto indican que una temperatura del aire de  $-16^{\circ}\text{C}$  podría resultar en casi un 100% de mortalidad para *D. frontalis*. Los límites de distribución de *D. frontalis* se aproximan a la isolinéa determinada por una probabilidad anual de 0.90 de alcanzar  $\leq -16^{\circ}\text{C}$ . Por tanto *D. frontalis* se localiza todo lo norte que podría encontrarse dado el régimen de temperaturas invernales. En latitudes desde  $39^{\circ}\text{N}$  (sur de Ohio) hasta  $33^{\circ}\text{N}$  (centro de Alabama), las temperaturas invernales probablemente contribuyen a una gran

mortalidad de *D. frontalis* en al menos uno de cada diez años. En cambio rechazamos la hipótesis de que las temperaturas estivales o la distribución de sus plantas huésped limitan la distribución norte de *D. frontalis*. Debido a la corta duración su período generacional, a su gran capacidad de dispersión y la cosmopolita distribución de sus huéspedes, cambios en la media de la varianza de la temperatura anual mínima podría tener efectos casi inmediatos en los patrones regionales de brotes epidémicos. Nosotros estimamos que un incremento de 3 °C en la temperatura mínima anual podría ampliar sus límites de distribución norte del orden de unos 170 km. Un aumento o un descenso de la temperatura mínima anual podría aminorar las actuales limitaciones climáticas en la distribución norte de esta especie. Los resultados ponen de manifiesto la importancia ecológica de la variabilidad espacial y temporal de las temperaturas mínimas anuales. Los modelos con una base fisiológica proporcionan una herramienta a tener en cuenta en la toma de decisiones sobre manejo del suelo en los bosques e ilustran un enfoque general para predecir los efectos regionales de los patrones climáticos en la distribución de organismos.

## INTRODUCTION

*Dendroctonus frontalis*, the southern pine beetle, occurs in the U.S. from southern Pennsylvania to Florida and west to Texas, eastern Oklahoma and southern Missouri. It is probably the largest single cause of natural disturbance in forests of this region. The value of timber and pulpwood lost to *D. frontalis* can reach \$237 million per year (Price *et al.*, 1997). Geographic Information Systems (GIS) provide a tool for visualizing changes in the distribution and outbreak potential of pest insects (Virtanen *et al.*, 1996; Williams & Liebhold, 1997; Virtanen *et al.*, 1998) and their host trees (Sykes *et al.*, 1998).

The western distribution limits of *D. frontalis* match the limits of their host trees on the edge of the Great Plains. However, the explanation for northern distribution limits is not obvious. Here, we combine physiological measurements with response-surface modelling and GIS technology to test hypotheses explaining the contemporary geographical distribution of *D. frontalis*. We also evaluate the potential impact of global climate change on *D. frontalis*.

In principle, the high-latitude distribution limits of a forest insect can be constrained by the occurrence of host plants, by mortality from low winter temperatures (Swaine, 1925), by summer temperatures that limit development rate (Ayres & Scriber, 1994) or by spatial variation in community interactions (e.g. mutualistic fungi, natural enemies or tree resistance). It seems unlikely that the northern distribution of *D. frontalis* is limited by the occurrence of host trees. The most common hosts are *Pinus echinata* Mill., *P. taeda* L., *P. rigida* Mill., and *P. virginiana* Mill., but *P. densiflora* Sieb. and Zucc., *P. resinosa* Ait., *P. serotina* Michx., *P. pungens* Lamb., *P. strobus* L., *P. palustris* Mill., *P. glabra* Walt., *P. elliotii* Engel., *Picea rubens* Sarg., and *P. abies* (L.) Karst. are also successfully colonized (Beaker, 1972; Thatcher *et al.*, 1980). The combined geographical distribution of these tree species extends far north of *D. frontalis* into the north-eastern U.S., Canada and the

Great Lakes States. If the northern distribution limits of *D. frontalis* are restricted by winter mortality we would expect a high annual probability of reaching the lower lethal temperature for *D. frontalis* near the northern distribution limits. We tested this hypothesis by evaluating historical climate records and comparing the distribution of *D. frontalis* to isolines representing the probability of occurrence of the lower lethal temperature of *D. frontalis*. If, instead, summer temperature regime constrains the beetle distribution by limiting development in the north, then we would expect a conspicuous reduction in the annual number of generations near the northern distribution limits. We tested this hypothesis by comparing the distribution of *D. frontalis* to isolines representing the annual number of generations that can be completed given regional temperature patterns.

## METHODS

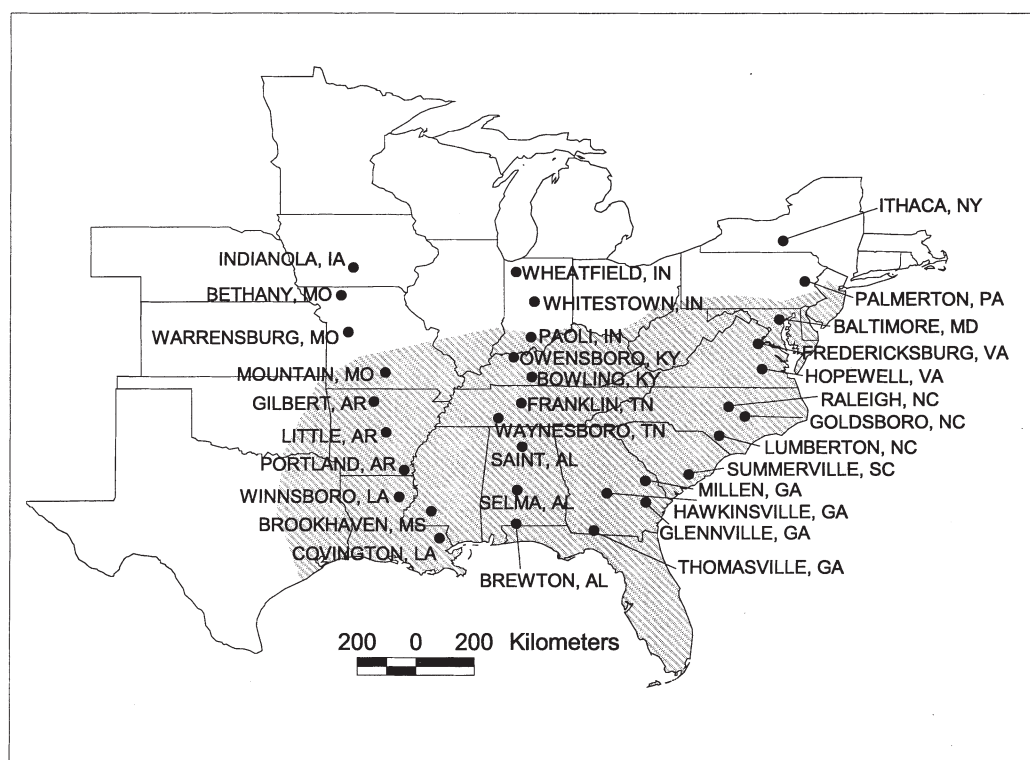
### Site selection

We selected thirty-three sites, aligned as three north–south transects through the eastern U.S. (Fig. 1), with daily climate records that exceeded 60 years (NOAA, 1995). For a site to be included in the study, daily maximum and minimum temperature records had to be complete for the winter months (Nov.–Feb.) of at least 52 years (with no more than five consecutive years with missing temperature data). For simplicity in the climate modelling, we excluded sites in the Appalachian mountains that were above 500 m in elevation; see the discussion for an evaluation of this simplification.

### Determination of lower lethal temperature

Most insects, including *D. frontalis*, are freeze-intolerant (Sømme, 1982; Lee *et al.*, 1996). The lower lethal temperature for freeze-intolerant animals is typically very discrete. It is the temperature at which the haemolymph and other body fluids crystallize when an animal is gradually cooled. Typically, exposure for even a few minutes to temperatures below the

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**Figure 1** Climate stations used in the study.

crystallization temperature causes irreparable tissue damage and death. Thus, mortality is expected in winters when temperatures drop below the lower lethal temperature at least once. Historical climate records can be used to estimate the proportion of winters when mortality occurs.

Winter mortality has been reported in natural populations of *D. frontalis* that experienced minimum air temperatures of  $-12^{\circ}$  to  $-18^{\circ}$  C (Beal, 1933; Knull, 1934; Fronk, 1947; Flavell *et al.*, 1970; McClelland & Hain, 1979; Ragenovich, 1980). This suggests a lower lethal temperature for *D. frontalis* of about  $-12^{\circ}$  C. We corroborated this with laboratory measurements using standard techniques from cryobiology (Bale, 1987). Using a programmable, low-temperature water bath, we cooled individual larvae, pupae, and adults of *D. frontalis* at  $0.2^{\circ}$  C/min and recorded the temperature at which crystallization occurred (supercooling point or SCP). The supercooling point for each individual animal was evident as a conspicuous exotherm, which was detected with a rapid-response copper-constantan thermocouple (PT-6 sensor, 0.01 s time constant, Physitemp Instruments, Clifton, NJ) interfaced with a virtual chart recorder (PowerLab Chart Recorder, AD Instruments, Dunedin, New Zealand). In November 1997 and March and June 1998, we measured eighty-seven adults, eighty-three larvae, and seventy-four pupae collected from wild populations in the Kisatchie National Forest in Louisiana. Adults were the most cold-tolerant stage: mean  $SCP \pm SD = -11.9 \pm 2.9^{\circ}$  C (larvae and pupae were  $-10.5 \pm 2.91$  and

$-8.8 \pm 2.6^{\circ}$  C, respectively), which approximates the warmest temperatures at which mortality has been reported in wild populations (see references above). There was some variability in the cold tolerance of *D. frontalis* adults, but 90% of our study population froze and died before reaching  $-15^{\circ}$  C. The outer bark of pine trees can influence the microhabitat temperatures experienced by *D. frontalis* living within the phloem, but the buffering effects on minimum night-time phloem temperatures are modest, ranging from  $0$  to  $2^{\circ}$  C (Bolstad *et al.*, 1997). If we allow for intrapopulation variability, and add  $1^{\circ}$  C to account for insulating effects of the outer bark, our physiological measurements suggest that an air temperature of  $-16^{\circ}$  C should result in mortality of  $>90\%$  of *D. frontalis* adults and virtually all of the larvae and pupae. This matches reports of cold mortality in natural populations. Therefore, our climate modelling used  $-16^{\circ}$  C as the lower lethal air temperature for *D. frontalis*.

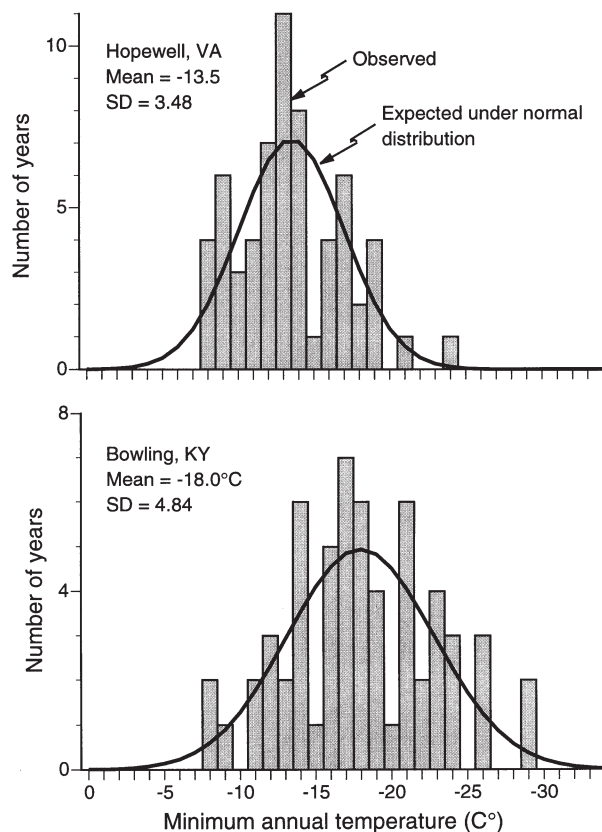
#### Modelling spatial patterns in the probability of lower lethal temperatures

We used response-surface modelling to predict the average minimum annual temperature (AMAT) and the standard deviation of minimum annual temperatures (SDMAT), as a function of latitude and longitude, using data from the thirty-three transect sites. The full regression model was  $Y =$

$\chi_0 + \beta_1 X + \beta_2 Z + \beta_3 X^2 + \beta_4 Z^2 + \beta_5 XZ + \varepsilon$  where  $Y$  = the dependent variable (AMAT or SDMAT),  $X$  = latitude,  $Z$  = longitude,  $\beta_0 - \beta_5$  were coefficients estimated by least squares regression, and  $\varepsilon$  = residual errors. We used stepwise regression techniques to develop each model. Initially, we entered terms representing the main linear effects of latitude and longitude ( $X$  and  $Z$ ); the coefficients for these main effects were always significantly different from 0 at  $P < 0.05$  so the terms were retained in the models. We then sequentially entered additional terms (beginning with those that had the largest explanatory power) until the coefficient of the next term would not be significantly different from 0 or until all five terms had been included in the model. All terms retained in the final model were significant at  $P < 0.05$ . Dependent variables met the assumption of normality. Examination of residuals revealed no systematic errors with respect to latitude or longitude.

The frequency distributions of minimum annual temperatures closely approximated a normal distribution: average skewness at thirty-three sites =  $-0.37$  (range =  $-1.07$  to  $0.31$ ) and average kurtosis =  $-0.06$  (range =  $-0.73$  to  $1.48$ ). This allowed us to use the normal distribution function, in combination with regression estimates of AMAT and SDMAT, to calculate the annual probability of reaching lower lethal temperatures for *D. frontalis* (PLLT) at any specified latitude and longitude within our study area. This approach was better than the alternative of developing a multiple regression response surface directly for PLLT, because PLLT follows a binomial distribution, so it is intrinsically nonlinear with respect to latitude and not well suited to linear regression. For validation, we compared our predictions of PLLT (derived from the normal distribution function and regression estimates of AMAT and SDMAT) with the actual proportion of years in which winter air temperatures dropped to  $-16^\circ$  or below at the thirty-three climate stations. Figure 2 shows the results of this validation for two sites. At Hopewell, Virginia, temperatures reached  $-16^\circ$  or colder in 15 of 58 years (26%); this corresponds almost exactly to the 26.2% that was predicted based upon a normal distribution with the mean and standard deviation ( $-13.9 \pm 3.26^\circ\text{C}$ ) estimated for that location by regression models for AMAT and SDMAT (compare to  $-13.5 \pm 3.48^\circ\text{C}$  calculated from the Hopewell data by itself). At Bowling Green, KY, the average minimum annual temperature was lower than at Hopewell and the interannual variance was greater. In this case, temperatures reached  $-16^\circ$  or colder in 41 of 60 years (68%), which was accurately approximated as 72.1% based upon a normal distribution with the mean and standard deviation ( $-18.6 \pm 4.49^\circ\text{C}$ ) estimated for that location by regression models for AMAT and SDMAT (compare to  $-18.0 \pm 4.84^\circ\text{C}$  calculated from the Bowling data by itself).

Using the two response surface models and the normal distribution function, we created three grid surfaces ( $1.0^\circ$  latitude  $\times$   $1.0^\circ$  longitude) spanning the eastern U.S. with values for AMAT, SDMAT, and PLLT. We then interpolated using the inverse distance weighted function of ArcView 3.0a (with spatial analyst) to create isolines for each grid surface. Each isoline coverage was overlaid with a map of the maximum reported distribution of *D. frontalis* within the eastern U.S. (after Dixon & Osgood, 1961; Payne, 1980).



**Figure 2** Frequency distribution of minimum annual temperatures in Hopewell, VA and Bowling Green, KY. Solid lines show the predicted distributions assuming a normal distribution with the corresponding mean and standard deviation.

### Modelling spatial patterns in the number of *D. frontalis* generations per year

We estimated the annual number of generations that could be completed by *D. frontalis* at the thirty-three sites using a general biophysical model of poikilotherm development (Sharpe & DeMichele, 1977; Schoolfield *et al.*, 1981) parameterized for *D. frontalis* (Wagner *et al.*, 1984; Gagne *et al.*, 1982). The biophysical model is

$$RH25 \cdot \frac{T+K}{K+25} \cdot e^{\left[ \frac{HA}{R} \cdot \left( \frac{1}{K+25} - \frac{1}{T+K} \right) \right]}$$

$$RATE(T) = \frac{1}{1 + e^{\left[ \frac{HL}{R} \cdot \left( \frac{1}{TL} - \frac{1}{T+K} \right) \right]} + e^{\left[ \frac{HH}{R} \cdot \left( \frac{1}{TH} - \frac{1}{T+K} \right) \right]}}$$

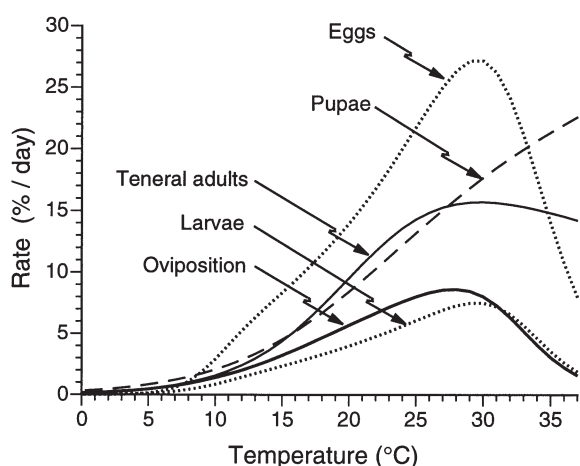
Where  $RATE(T)$  = development rate (proportion of development per day) at temperature  $T$  ( $^\circ\text{C}$ ),  $R$  is the universal gas constant ( $1.987 \text{ cal} \cdot \text{degree}^{-1} \cdot \text{mole}^{-1}$ ),  $K$  converts from  $^\circ\text{C}$  to  $^\circ\text{K}$  ( $K = 273$ ), and 25 adjusts to a standard environmental temperature. The remaining six variables have been estimated for each developmental process (oviposition, egg hatch, larval development, pupation, and adult emergence) by fitting the function to empirical data using nonlinear modelling (Table 1).



Parameter estimates	RH025	HA	TL	HL	TH	HH
Oviposition <sup>1</sup>	0.0943	6295	288	-33293	305	83846
Egg hatching <sup>2</sup>	0.2266	15655	283	-102639	306	84890
Larval development <sup>2</sup>	0.0627	14115	283	-68072	306	91990
Pupation rate <sup>2</sup>	0.7470	30000	—	—	290	27880
Emergence of adults <sup>2</sup>	0.9450	36601	—	—	292	42609

<sup>1</sup> After Gagne *et al.* (1982). Assumes that oviposition as a function of temperature matches re-emergence as a function of temperature (i.e., females at a constant temperature are assumed to oviposit at a constant rate until they re-emerge and females are assumed to lay an equal number of eggs at all temperatures until they re-emerge). Rate = proportion of total eggs/day; NGEN model was scaled to describe development of the median egg.

<sup>2</sup> After Wagner *et al.*, 1984



**Figure 3** Development rate of *D. frontalis* as a function of temperature. Functions are described by a biophysical model (see equation in text) parameterized for *D. frontalis* (Table 1).

They are interpretable as follows: RH25 = the development rate at 25° assuming no denaturation, HA = the enthalpy of activation of rate limiting enzyme, TL = the temperature at which rate controlling enzyme is 50% inactive due to low temperature inhibition, TH = the temperature at which rate controlling enzyme is 50% inactive due to high temperature inhibition, HL = the change of enthalpy associated with low temperature activation, and HH = the change of enthalpy associated with high temperature activation.

This model was incorporated into an algorithm that input daily minimum and maximum temperatures and calculated the number of *D. frontalis* generations able to complete development in each year of the climate records at each site. The model included separate temperature-driven functions for each of the five physiologically distinct developmental processes: oviposition of attacking adults, egg hatch, larval development, pupation and the emergence of adults (Fig. 3, Table 1). A sin function was used to estimate temperatures at 3-h intervals from daily minimum and maximum temperatures and development was incremented at 3-h intervals based upon prevailing temperatures. For each site, we calculated the average number of generations that could be completed per year

**Table 1** Parameter estimates for the biophysical model (equation in text) fitted to *D. frontalis* development rates. Functions shown in Fig. 3.

(NGEN) based upon the 39–59 years for which temperature data were complete. Then we developed a response surface model as before to predict NGEN as a function of latitude and longitude. Also as before, a grid surface based on the model was interpolated to create isolines that were overlaid with the *D. frontalis* distribution and eastern U.S. maps.

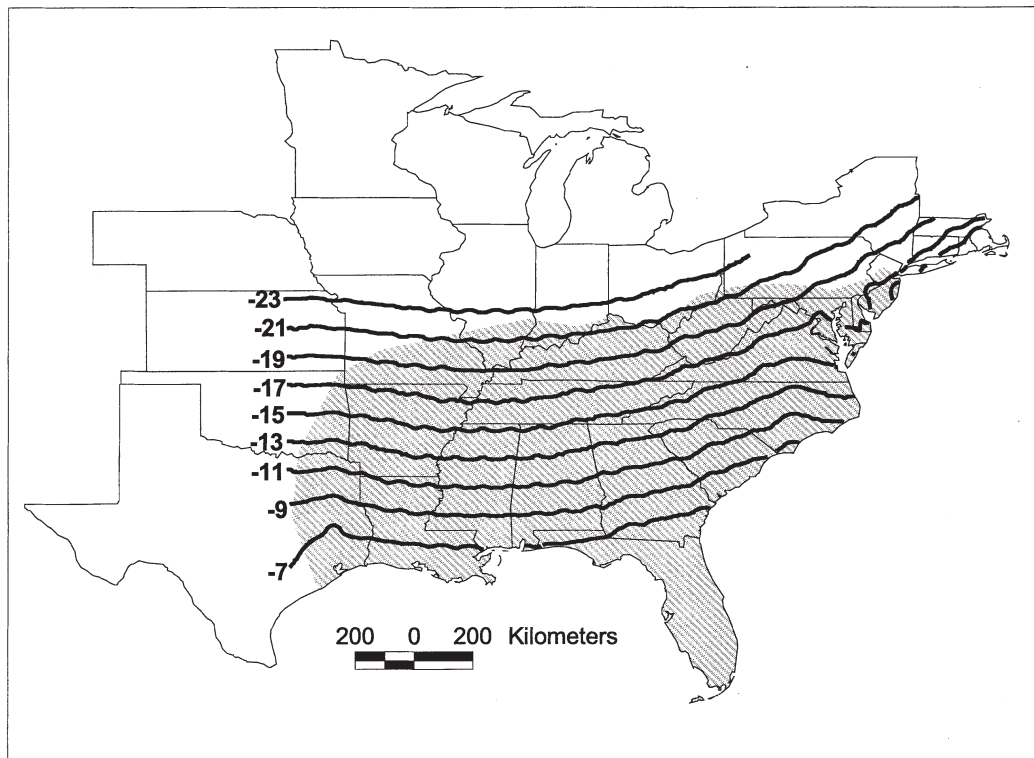
### Climate change scenarios

General Circulation Models predict an increase of  $\approx 3$  °C in average surface air temperatures in our study region, with surface warming at higher latitudes greater than the global average during winter (Cooter, 1997). We evaluated the potential change in PLLT under each of the following climate scenarios: (1) increasing the average minimum annual temperature by 3 °C; (2) increasing the standard deviation of minimum annual temperatures by 3 °C; (3) decreasing the standard deviation of minimum annual temperatures by 3 °C; (4) increasing the mean and the standard deviation by 3 °C; and (5) increasing the mean and decreasing the standard deviation by 3 °C. For each scenario, we adjusted the AMAT and SDMAT response surface models and then used the normal distribution function to calculate the change in PLLT. Similarly, we evaluated the change in NGEN associated with an increase of 3 °C in the mean daily minimum and maximum air temperatures (by re-running the development models for each of the thirty-three sites and fitting the response surface for expected number of generations per year under a warmed climate).

## RESULTS

### Spatial patterns in the probability of lower lethal temperatures

The average minimum annual temperature (AMAT) decreased almost linearly from about -7 °C in the southern gulf states to -23 °C in southcentral Illinois, Indiana, and Ohio (Fig. 4, Table 2). The isolines were deflected northward in the eastern states, presumably due to maritime effects of the Atlantic Ocean. The response surface model provided an excellent fit to the thirty-three sites ( $r^2 = 0.94$ ): observed values were within 2 °C for all but four sites, and within 3° for all sites except



**Figure 4** Average minimum annual temperature (AMAT). Shaded area shows the maximum reported distribution of *D. frontalis* within the eastern U.S. (Dixon & Osgood, 1961; Payne, 1980). Note that the altitudinal effects of the Appalachian Mountains have been excluded from this response surface and those shown in Figs 5, 6, and 8.

**Table 2** Summary of response surface models that predict spatial patterns in average minimum annual temperature (AMAT), the standard deviation in minimum annual temperature (SDMAT), and the average number of *D. frontalis* generations per year (NGEN). Models were fit to thirty-three sites throughout the southeastern United States (Fig. 1).

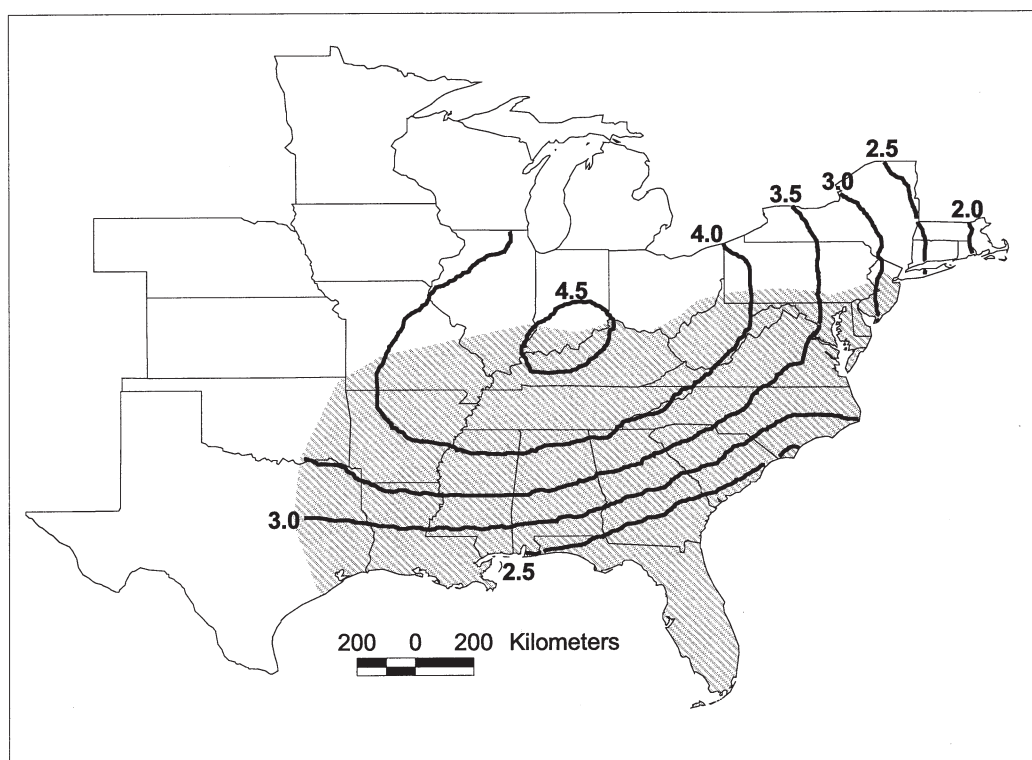
Dependent Variable	$r^2$	Coefficient <sup>a</sup> (SE)					
		Intercept	Latitude	Longitude	Latitude <sup>2</sup>	Longitude <sup>2</sup>	Latitude × Longitude
AMAT	0.94	355.89 (80.68)	-1.84 (0.09)	-6.86 (1.86)	—	0.0383 (0.0110)	—
SDMAT	0.73	-196.3 (33.5)	3.99 (0.75)	2.87 (0.62)	-0.0342 (0.0075)	-0.0131 (0.0033)	-0.0158 (0.0045)
NGEN	0.95	58.3 (15.2)	-0.69 (0.19)	-0.83 (0.31)	—	0.0038 (0.0016)	0.0048 (0.0022)

<sup>a</sup> All coefficients differed significantly from 0 at  $P < 0.05$ . See text for full regression model.

Baltimore, Maryland, which the model underestimated by 5 °C. Spatial patterns in the standard deviation around minimum annual temperatures (SDMAT) were more complex (Fig. 5, Table 2). Standard deviations ranged from a low of about 2.5 °C in southern Georgia to a maximum near 4.5 °C in southern Indiana. Standard deviations decreased in all directions from climate stations in southern Indiana. Again, the response surface model provided a good fit to the data

( $r^2 = 0.73$ ): predicted values for twenty-five of thirty-three sites were within 0.5 °C of observed values and all sites were within 0.8 °C.

The annual probabilities of reaching lower lethal temperature for *D. frontalis* (PLLT) were very low in the south (< 0.10 throughout the southern gulf states) and then increased by  $\approx 0.12/100$  km until reaching 0.9 in central Illinois, Indiana, Ohio and Pennsylvania (Fig. 6). As with the minimum annual



**Figure 5** Standard deviation of minimum annual temperature (SDMAT). Maximum reported *D. frontalis* distribution shown as shaded area.

temperatures, PLLT isolines were deflected northwards in the eastern states. Model predictions of PLLT provided a very good fit to actual historical probabilities at the thirty-three climate stations ( $r^2=0.93$ , Fig. 7). The only conspicuous outlier was Baltimore, where the estimated PLLT was 0.62 while the historical probability was only 0.08 (Fig. 7). Predicted values were within 0.20 of the historical frequency at all other sites and within 0.10 at all but three sites. The overlay of PLLT isolines with *D. frontalis* distribution indicates that the reported northern distribution limits are coincident with PLLT = 0.8–0.9 (Fig. 6). The northern limits of regular outbreaks of *D. frontalis* (Price *et al.*, 1997) are more restricted and correspond to PLLT = 0.40–0.50.

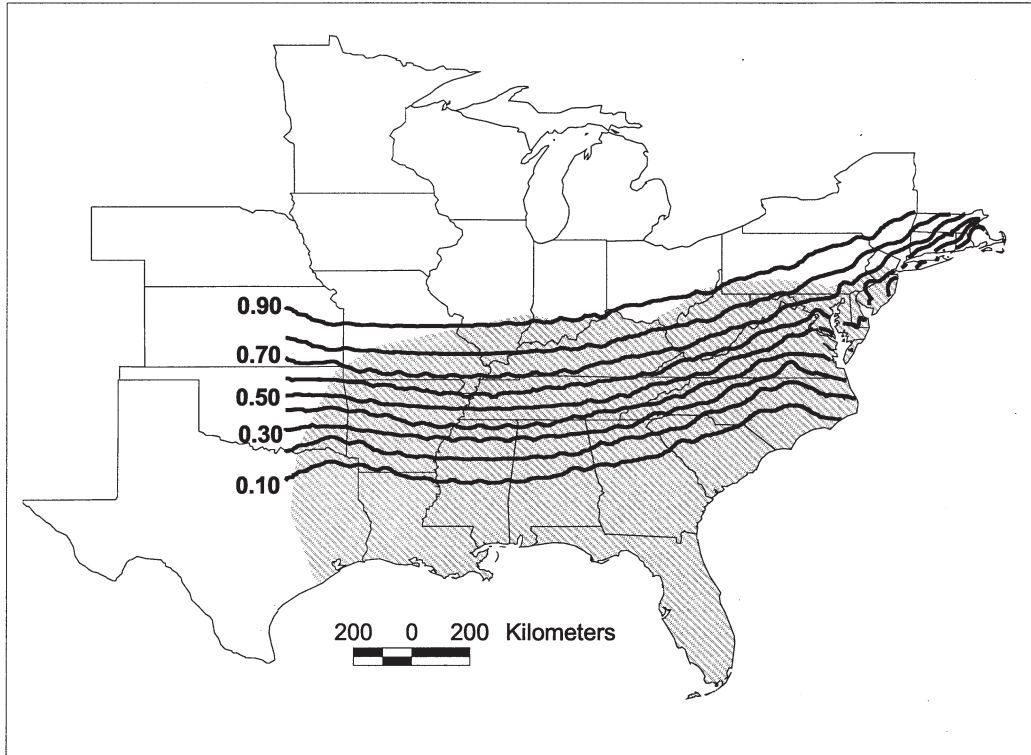
#### Spatial patterns in the number of *D. frontalis* generations per year

The predicted number of *D. frontalis* generations per year ranged from six in the southern gulf states to four near the northern limits of *D. frontalis* (Fig. 8). Maritime effects on NGEN were much weaker than on AMAT, SDMAT, and PLLT (Figs 5,6,7,8; longitude effects in Table 2). This was because the coastal climates, although they had generally cooler summer temperatures, had more days per year when temperatures allowed beetle development to proceed. The response surface model provided a good fit to spatial variation in the eastern United States ( $r^2=0.95$ ): average values for all thirty-three sites were within 0.5 generations of predictions from the response

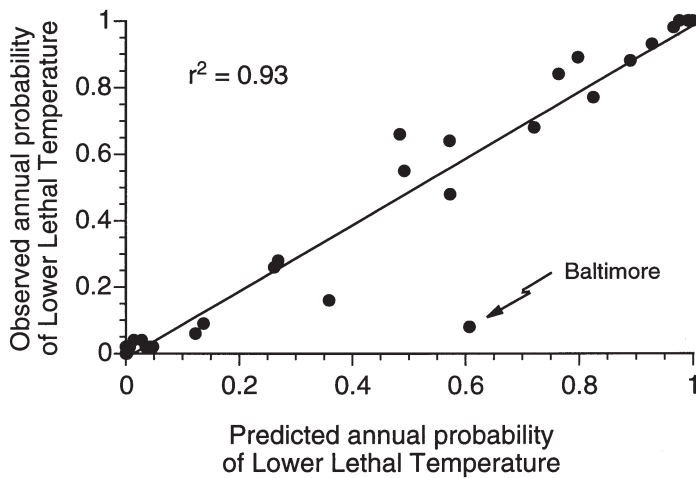
surface model. There was remarkably little year-to-year variation in the predicted number of generations: the standard deviation around NGEN averaged only 0.33 (range = 0.10 – 0.51 for the thirty-three sites). There were no discontinuities in the number of *D. frontalis* generations per year that corresponded to distribution limits (Fig. 8) and no obvious explanation for the distribution limits based upon climatic variation in beetle development rates.

#### Evaluation of climate change scenarios

All climate change scenarios suggested meaningful effects on the distribution of *D. frontalis* as a result of changes in the probability of winter mortality from exposure to lethal temperatures (Fig. 9). When the average minimum annual temperature was increased by 3 °C (Fig. 9a), the annual probability of winter mortality was decreased by up to 0.27 (greatest effects at 36.0° N), and the isocline at PLLT = 0.5, which approximates the northern limits of regular outbreaks by *D. frontalis*, moved from 35.4° N to 37.0° N. If the standard deviation among minimum annual temperatures was increased by 3 °C with the average held constant (Fig. 9b), PLLT was increased by up to 0.14 (at 32.6° N) and decreased by up to 0.12 (at 38.6° N); the isocline at PLLT = 0.5 remained largely unchanged. The changes in winter mortality due to an increase in the standard deviation occurred at a higher latitude than those resulting from an increase in the average. When the standard deviation was decreased by 3 °C (Fig. 9c), PLLT



**Figure 6** Annual probability of reaching the lower lethal temperature for *D. frontalis* (PLLT; = -16 °C air temperature). Maximum reported *D. frontalis* distribution shown as shaded area.

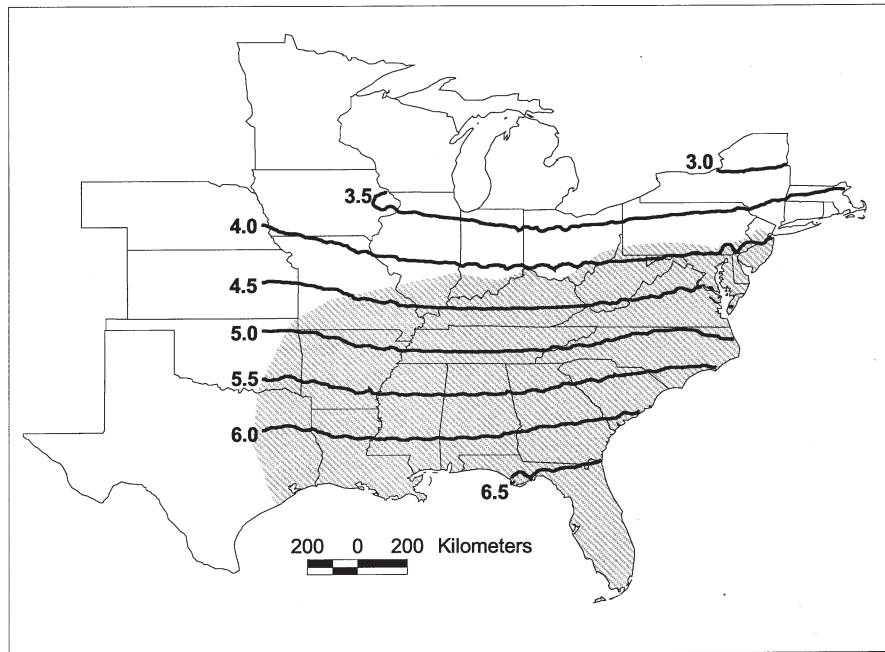


**Figure 7** Predicted probabilities vs. observed probabilities for reaching the lower lethal temperature of *D. frontalis* (= -16 °C air temperature) at thirty-three climate stations. Observed probabilities were calculated from historical data. Predicted probabilities were calculated from the response surfaces in Figs 4,5. Baltimore is labelled because it was a conspicuous outlier, presumably due to local maritime effects.

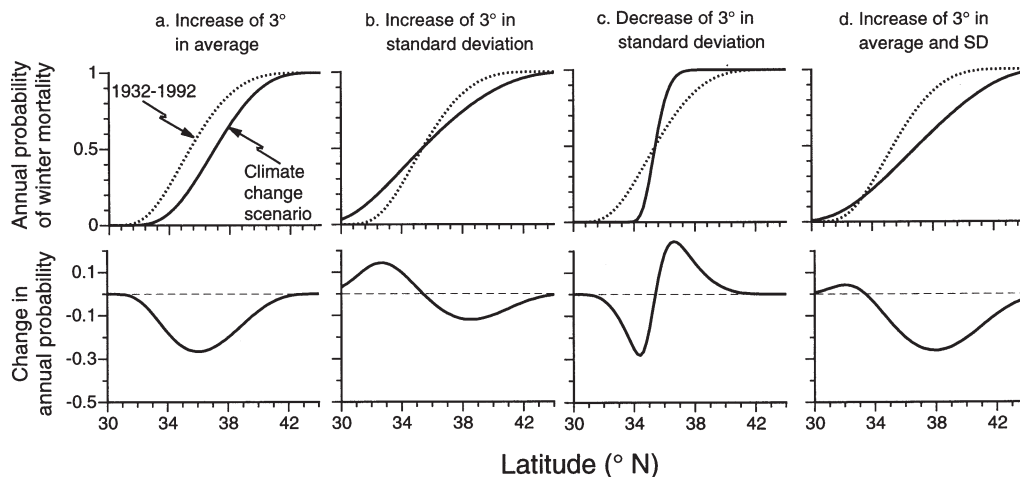
decreased by 0.28 at 34.4° N and then was increased by 0.25 at 36.6° N; again, the isocline at PLLT=0.5 remained near 35.4° N. When both the average and the standard deviation were increased by 3 °C (Fig. 9d), PLLT was decreased by up to 0.26 (at 38.0° N) and the effects occurred farther north and over a broader range of latitudes than the changes associated with an increase in the average alone (PLLT was increased by ≈0.20 over 465 km from 33.6 to 37.0° N). Under this scenario, the isocline for PLLT = 0.6 moved from 35.4 to 37.0°,

suggesting that regular outbreaks could be expected up to 170 km north of where they presently occur (to northern Missouri, Illinois, Indiana, Ohio, Pennsylvania, and New York); similarly, the isocline for PLLT=0.9 moved 310 km north, suggesting that under this climate, *D. frontalis* infestations might sometimes occur as far north as the pine forests of Minnesota, Wisconsin, Michigan and New England. The projection that produced the largest climatic amelioration for *D. frontalis* was that where the average was increased by 3 °C





**Figure 8** Predicted number of *D. frontalis* generations per year (NGEN) based upon a biophysical model of development rate (Figure 3, Table 1) and daily temperatures over 39–59 years. Maximum reported *D. frontalis* distribution shown as shaded area.



**Figure 9** Changes in the annual probability of winter mortality for *D. frontalis* under four scenarios of climate change: (a) an increase of 3 °C in average minimum; (b) an increase of 3 °C in the standard deviation of minimum annual temperatures; (c) a decrease of 3 °C in the standard deviation of minimum annual temperatures; and (d) an increase of 3 °C in the average and standard deviation of minimum annual temperature. Dashed lines in upper figures show the latitudinal pattern under historical climates (1932–92)

while the standard deviation was decreased by 3 °C; in this case, PLLT was decreased by  $\approx 0.20$  from 33.6° N to 37.0° N with a maximum decrease of 0.52 and the expected northern limits for regular outbreaks (PLLT = 0.5) moved from 35.4 to 37.1° N.

In contrast to the situation for winter mortality, an increase of 3 °C in average daily minimum and maximum temperatures produced only a modest effect on the expected number of *D.*

*frontalis* generations per year. This warmer scenario increased the development rate of *D. frontalis* by an average of only 0.80 generations per year (range = 0.4–0.9 for thirty-three sites). The limited effect of climatic warming on development rates was partly because the temperature responses of *D. frontalis* development rates are relatively flat from 25 to 30 °C, which encompasses much of the relevant temperature scale for *D. frontalis* in the United States.

## DISCUSSION

### Determination of contemporary distribution limits

Our results support the hypothesis that the northern distribution limits of *D. frontalis* are maintained by the occurrence of lethal winter temperatures. The reported distribution limits approximate the isoline corresponding to an annual probability of 0.90 of reaching temperatures below the lower lethal temperature for *D. frontalis* (Fig. 7). This suggests that *D. frontalis* have been found about as far north as they could possibly occur given winter temperature regimes (i.e. in regions where we expect winter survival in only 1 of 10 years). Presumably, the distribution limits for *D. frontalis* as indicated in Fig. 7 reflect the extreme occurrences rather than the average occurrence. (The literature contains one report of *D. frontalis* in Ohio, but all distribution maps since then have included Ohio.) The northern limits for economically meaningful infestations is  $\approx 300$  km farther south (Price *et al.*, 1997) where the annual probability of winter mortality is  $\approx 0.5$ . We predict that systematic sampling for *D. frontalis*, as can be done with pheromone traps (Billings & Bryant, 1983), would indicate that the actual northern distribution limits fluctuate by several hundred kilometers depending on the recent history of winter temperatures. In fact, *D. frontalis* outbreaks in Pennsylvania during 1932–33 followed warmer than average winter temperatures in 1930–31 and 1931–32 (Knull, 1934). Unlike the situation for tree species (Loehle & LeBlanc, 1996), the realized distribution limits for insects can respond very quickly to changes in critical environmental variables (Hippa & Koponen, 1977). In the case of *D. frontalis*, it is clear that warmer winter temperatures are a necessary condition for expansion of the northern distribution limits and it seems probable that population dynamics are influenced by winter temperatures throughout a latitudinal transect of  $\approx 500$  km (from central Georgia to southern Ohio the expected frequency of lethal winter temperatures ranges from 1 in 10 years to 9 in 10 years; Fig. 7). South of the 0.10 isoline (e.g. in east Texas and Louisiana; Fig. 7), we expect that the population dynamics of *D. frontalis* are largely driven by endogenous dynamics (Turchin *et al.*, 1991) and climatic effects on host tree physiology (Reeve *et al.*, 1995; McNulty *et al.*, 1997; Wilkens *et al.*, 1997) rather than by direct climatic effects on the beetles.

We cannot be certain that a reduced probability of lethal winter temperatures would permit range expansion of *D. frontalis*, but there are no other obvious barriers to northern range expansion. Summer temperature regimes could allow three generations per year even well north of current distribution limits (Fig. 8) and suitable host trees already occur north of the Great Lakes into Canada. *D. frontalis* can be added to the list of insect herbivores who do not occur as far north as their host plants and whose northern distribution limits appear to be due to direct temperature effects on the insect (Hippa & Koponen, 1977; MacLean, 1983; Rice, 1986; McClure, 1989; Ayres & Scriber, 1994; Virtanen *et al.*, 1996; Virtanen & Neuvonen, 1999; Virtanen *et al.*, 1998). A strength of our study is that climate analyses were derived from direct physiological measurements (of lower lethal temperatures and

development rates). We agree with Loehle & LeBlanc (1996) that this approach allows stronger inference than studies that screen for correlations between distribution limits and numerous climatic variables with unspecified physiological effects (e.g. Jeffree & Jeffree, 1994; Williams & Liebhold, 1995; Bowman & Connors, 1996; Kadmon & Heller, 1998).

The northern distribution limits of *D. frontalis* are clearly not due to the effects of summer temperatures on development rate (Fig. 8). Results of the NGEN model agree quite well with previous, independently derived, estimates of the number of *D. frontalis* generations per year. Thatcher & Pickard (1967) reported two to five generations per year in the more northerly areas of *D. frontalis* distribution and approximately six to seven generations from eastern Texas to Georgia. The development times from egg to adult predicted by the biophysical model of *D. frontalis* development were 29–100 d when temperatures averaged 15–35 °C, also in accord with those reported by Thatcher (1960, 1967).

### Model evaluation

Geographic response-surface models can be more accurate than adiabatic lapse models in predicting landscape-scale air temperature relationships (Bolstad *et al.*, 1997). By using standard linear regression techniques to parameterize physiologically based models, we were able to generate accurate and parsimonious response surfaces for the annual probability of lower lethal temperatures (PLLT) and the average number of generations per year (NGEN). Coefficients of correlation ( $r^2$ , Table 2) and graphical comparisons of observed *v.* predicted values (e.g. Figure 7) allowed easy evaluations of goodness-of-fit. This approach limited our reliance on the built-in interpolation methods of GIS software packages, which are generally not designed to facilitate statistical evaluations of model parsimony or goodness-of-fit. Employing linear regression for developing response surfaces should be especially valuable when analyses require long or detailed data series that are only available at limited sites, which will generally be true when the variable of interest is related to annual probabilities. The modelling approaches employed here for *D. frontalis* could be used with little modification to evaluate climatic effects on the many organisms for which relevant physiological measurements can be obtained.

The PLLT model could potentially be improved through additional physiological studies that test for seasonal and geographical variation in *D. frontalis* supercooling points. Our measurements have not yet revealed any seasonal patterns in supercooling points, which is consistent with the lack of diapause in *D. frontalis* (Thatcher *et al.*, 1980). However, seasonal changes in cold tolerance (as occurs in some related species; Miller & Werner, 1987) could be incorporated into the models through climatic analyses that compare daily minimum temperatures with a lower lethal temperature that is a function of date and/or previous temperatures. Similarly, geographical variation in lower lethal temperatures (perhaps due to genetic differentiation among populations; e.g. Kukul *et al.*, 1991) could be incorporated into the modelling framework by including one or more spatial parameters as independent variables to predict

lower lethal temperatures. For *D. frontalis*, the close agreement between measured supercooling points and numerous published accounts of natural winter mortality suggests that a single, fixed estimate of lower lethal temperature is reasonable.

Our model assumes that lower lethal temperature is equal to the supercooling point. This is reasonable because we have verified that *D. frontalis* cannot survive beyond their supercooling point and that virtually all individuals survive brief exposure to temperatures just above their supercooling point. However, some insect species suffer mortality from prolonged exposure to temperatures slightly warmer than their supercooling point (Bale, 1987; Pullin & Bale, 1989; Bale, 1991; Turnock & Bodnaryk, 1991). Further experiments would be required to learn if this occurs with *D. frontalis*. If so, appropriate modifications to the model could increase the expected overwintering mortality in regions that frequently encounter sustained (multiday) bouts of temperatures that approach, but do not drop below, the supercooling point. This modification could only increase the expected overwintering mortality, which would reinforce our conclusions regarding the ecological importance of winter temperatures.

Possible improvements to the model also include more explicit treatment of variation among individual animals within a population. Currently, the model treats winter mortality for any site and year as a binomial variable (no mortality or 100% mortality). This was reasonable because we were chiefly interested in climatic events that produce local extinctions. However, this simplification ignores microclimatic variation within a site and the variability among lifestages and individuals, so our model results are not very sensitive to climatic events that have less absolute effects on population abundance (e.g. 18% of adults, 43% of larvae and 68% of pupae are expected to die with exposure to  $-10^{\circ}\text{C}$ ). For studies that focus on temporal patterns in local population dynamics, the model could be expanded to predict proportional mortality per year based on (1) mean and variance in cold tolerance for each life stage (2) the relative abundance of different life stages, and (3) spatial variation in temperatures across microhabitats occupied by *D. frontalis*.

Finally, the response surface models for AMAT, SDMAT and NGEN are simplified in that they do not account for the effects of altitude. If the effects of altitude were included, the isolines for average minimum annual temperature, annual probability of lower lethal temperatures and number of generations per year (Figs 4, 6, 8) would all be deflected southwards in the Appalachian Mountains, but our conclusions would not be affected. Altitudinal patterns in climatic effects on insects can be accurately modelled (Tenow & Nilssen, 1990; Bolstad *et al.*, 1997; Virtanen *et al.*, 1998), but this is a challenging problem because of the strong effects of regional topography on local air movements and local climates. We were able to ignore this complication because there is not much altitudinal variation across our region of study.

#### Potential impacts of climate change on the *D. frontalis* distribution

Our analyses clearly indicate that interannual variance in minimum temperature is a critical determinant of overwinter

survival and the geographical distribution of *D. frontalis* (Fig. 6, Fig. 9a,b,c,d). For the same reasons that it is important to *D. frontalis*, interannual variance in minimum temperature is likely to be important to many other plant and animal species. To our knowledge, none of the general circulation models have been adapted to estimate interannual variance in minimum temperature under future climates. Indeed, the literature contains few specific predictions about the future variability of any climatic parameters. Several authors have suggested that climate change could exert some of its most important effects by changing climatic variability (e.g. frequency of severe storms, heat waves and extreme temperature events; Mearns *et al.*, 1984; Wigley, 1985; Schneider, 1993; Karl *et al.*, 1995; Mearns *et al.*, 1997). It appears that many biological questions require a better understanding of climatic variability in general and interannual temperature variance in particular (Amien *et al.*, 1996; Mearns *et al.*, 1996; Riha *et al.*, 1996; Ayres & Reams, 1997).

Northerly *D. frontalis* populations are currently precluded from occupying suitable pine habitat by low winter temperatures (Fig. 7). However, *D. frontalis* has a very rapid generation time and high dispersal (Turchin & Thoeny, 1993), so populations could respond within a few years to any change in winter mortality rates. All of the climate change scenarios that we evaluated indicated the potential for relatively modest changes in climate to exert important effects on *D. frontalis* populations over  $>200$  km of latitude. One scenario (an increase of  $3^{\circ}\text{C}$  in the mean and standard deviation of minimum annual temperature) projects that *D. frontalis* infestations could become common in Ohio and southern Pennsylvania, where the beetle is now rarely found, and that occasional infestations could occur as far north as Michigan, Wisconsin, New York and Massachusetts. This information may be relevant to forest management decisions that are being made now (e.g. selection of tree species and sites to be managed for timber), which depend upon assessing future risks from forest insects.

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