

# Are southern pine forests becoming too warm for the southern pine beetle?

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## ABSTRACT

Climate change is altering the geographic distribution of many species, including numerous forest insect pests, with the potential for severe impacts to forest ecosystems. The southern pine beetle (*Dendroctonus frontalis*), one of the world's most persistently destructive forest pests, has extended its distribution towards the north, while impacts within its historic range in the southeastern United States have diminished, indicating that a range shift may be occurring. This pattern could be explained by the hypothesis of climatic envelopes if summers in the southern part of the range are warming about as much as winters in the northern part of their range. Here, we tested whether the southeastern United States is becoming too hot for *D. frontalis* even as the northeastern United States has become climatically permissive. We measured effects of heat on insect survival, and characterized the thermal environment of *D. frontalis*, including estimating the frequency of potentially lethal heat waves and testing whether the intensity or duration of heat waves has increased over the past 80 years. We found that temperatures warm enough to kill *D. frontalis* larvae, pupae, or callow adults have been rare or absent and that there has been no change in the duration or severity of heat waves in the southern pine forest region over the last 80 years. Therefore, alternative explanations for the reduced activity of *D. frontalis* within its historic range must be considered. The broad conclusions are not restricted to *D. frontalis* because they flow from an asymmetry in climate change: at least for now in eastern North America, the coldest winter temperatures have been becoming less extreme without summer heat becoming more extreme. This creates broad potential for northward range expansions without expectation of corresponding contractions in southern distribution limits.

## 1. Introduction

The southern pine beetle (*Dendroctonus frontalis* Zimmermann; Coleoptera: Curculionidae) is one of the most aggressive tree-killing insects in the world (Vega and Hofstetter, 2015). Within its historic distribution in the southeastern United States, losses to the forest products industry exceeded \$1 billion for 28 years ending in 2004 (Pye et al., 2011) and this, along with the loss of property value and recreation space, are only some of the effects of *D. frontalis* on forests and people (Coulson and Klepzig, 2011; Coulson and Meeker, 2011).

In most years, in most forests, *D. frontalis* is a rare and relatively benign component of the forest insect fauna that primarily harbors in weakened host trees (Thatcher and Pickard, 1964). However, *D. frontalis* populations also display regional outbreaks that can last from one to several years, kill large expanses of pine trees and transform forests (Clarke et al., 2016). One or two epidemics per decade have been

common for the region (Birt, 2011). The population dynamics of *D. frontalis* are apparently governed by a nonlinear density-dependent feedback system with two locally stable equilibria (endemic and epidemic) separated by a region of positive feedback that produces an unstable equilibrium (escape threshold) (Martinson et al., 2013). When population abundance is near the escape threshold, even modest environmental effects on beetle survival and reproduction can produce a state change (e.g., endemic to epidemic). Factors that are candidates to produce such effects with *D. frontalis* include forest structure and silvicultural practices (Nowak et al., 2015; Asaro et al., 2017; Aoki et al., 2018), predation (Reeve, 1997; Weed et al., 2017), environmental effects on tree physiology (Lorio, 1986; Reeve et al., 1995; Lombardero et al., 2000a), active suppression by forest managers (Clarke and Billings, 2003; Billings, 2011), interactions involving mites and antagonistic fungi (Hofstetter et al., 2006a), the coldest night of the winter (Ungerer et al., 1999; Tran et al., 2007), and other features of weather (Reeve,

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2018).

Over the past 25 years, impacts from this insect have been declining throughout the southern pine region, despite a simultaneous increase in pine habitat (Clarke et al., 2016; Asaro et al., 2017). A number of hypotheses have been put forth to explain this pattern, including changes to forest structure and host resistance from improved management and tree breeding programs, as well as climatological impacts from anthropogenic climate change (see Asaro et al., 2017). While a climatological explanation is plausible, there has not been a discernible link between climate and *D. frontalis* outbreaks in the South. However, most studies of climatological factors have focused on the positive influence of extreme climate events promoting outbreaks via their effect on host trees (Friedenberg et al., 2008; Asaro et al., 2017). For example, drought and/or high temperatures could weaken hosts and lead to outbreaks (McNichol et al., 2019). Alternatively, regional changes in climate could directly impact survival of *D. frontalis*, and in that manner alter the occurrence of local outbreaks (Ayres and Lombardero, 2000). Such influence of climate on population has already been seen at the northern extent of their distribution, where recent increases in minimum winter air temperatures have permitted an expansion of *D. frontalis* outbreaks into New Jersey, Long Island, and Connecticut (Lesk et al., 2017; Dodds et al., 2018), even as impacts within their historic southern range were declining. One possible explanation for the increase in outbreaks at the northern edge of their range and declining impacts in the South is that southern forests have become too warm for *D. frontalis*, even as northern forests have only recently become warm enough. This would be as expected under the hypothesis of climatic envelopes (Hijmans and Graham, 2006; Green et al., 2008), which predicts approximately symmetrical changes at the warmer and cooler distribution limits given approximately uniform climate warming. The envelope model, in various forms, underlies many forms of species distribution models (Pecchi et al., 2019), but has been difficult to test (Hao et al., 2019). One alternative hypothesis is that warmer is better for many ectotherms at both the warm and cool edges of their distributions (Frazier et al., 2006).

General circulation models predict a continuing rise in mean surface temperatures across most of the northern hemisphere (IPCC, 2013). This can result in less severe minimum winter temperatures (Easterling et al., 1997; Vose et al., 2005; Tran et al., 2007; Daly et al., 2012; Weed et al., 2013) as well as more intense and longer lasting heat waves (Easterling et al., 2000; Meehl and Tebaldi, 2004; Lyon et al., 2019). Some changes in thermal extremes can affect the distribution and abundance of biological populations (Pörtner, 2002; Haynes et al., 2014; Buckley and Huey, 2016; Lloret and Kitzberger, 2018).

Insects die differently from heat than from cold. Many insects, including *D. frontalis*, are freeze-intolerant (Duman et al., 1991) and have a discrete lower lethal temperature that corresponds to their supercooling point (the temperature at which fluids crystallize and cell membranes rupture). In *D. frontalis*, brief exposure to temperatures below the supercooling point ensure death, whereas sustained exposure to temperatures slightly above the supercooling point have little effect on survival (Lombardero et al., 2000b). Thus, the effects of cold on overwinter survival of wild populations can be realistically modeled based on the coldest night of the winter (Tran et al., 2007); duration of exposure matters relatively little (Lombardero et al., 2000b). However, when insects die from heat, mechanisms include destabilization of membranes and proteins, increase in reactive oxygen species, as well as disruption of oxygen delivery, water budgets, and energy balance (McCue and De Los Santos, 2013). Depending on the mechanism, the duration of heat exposure required to produce mortality might vary from hours to days, and exact cause of death is likely to depend upon the intensity and duration of heat exposure (Rezende et al., 2014).

We tested the hypothesis that the historic range in the southeastern United States is becoming too hot for *D. frontalis* by (1) experimentally measuring effects of heat exposure on insect survival, (2) characterizing the thermal environment of *D. frontalis* within the inner bark of host trees, (3) estimating the historical frequency of potentially lethal heat

waves in the historic range of *D. frontalis*, and (4) testing whether the intensity or duration of heat waves has been increasing during recent decades.

## 2. Materials and methods

### 2.1. Acute high temperature exposure

Tests of mortality from high temperature exposure required exposing larvae to bouts of high temperature *in situ*. This is not easily accomplished in the field because southern pine beetle larvae inhabit the inner bark (phloem) of trees. However, it was possible to conduct laboratory experiments with beetle-infested bark from trees, and with sections of infested bole from felled trees. In July 2011, we removed portions of bark from 12 infested pitch pine trees within a southern pine beetle infestation in Hamilton, New Jersey (Table 1). The infested stand was mostly even-aged, with trees of about 25 cm diameter at breast height (dbh; 1.37 m). We collected two samples of phloem and outer bark from each of the 12 trees. These samples were approximately 30 cm × 30 cm in size and were cut at slightly above breast height from trees containing a high density of 2nd – 3rd instar beetles (estimated by head capsule width). The samples were placed into polyethylene bags with a moist paper towel added to prevent desiccation and transported back to the lab. The samples were acclimated to room temperature (25 °C) for four days prior to initiating the treatments. Once acclimated each sample was cut into two paired samples, each with approximately the same amount of southern pine beetle feeding gallery (gallery passing through tissue discolored by growth of blue stain fungi, *Ophiostoma* spp. was not considered because larvae rarely survive there; Lombardero et al., 2003). One of the paired samples was randomly assigned to one of two high temperature treatments (37 or 42 °C) and the other served as a control that was maintained at a constant 25 °C.

The treatment consisted of gradually increasing the temperature over two hours from 25 °C to the maximum high temperature (either 37 °C or 42 °C), holding maximum temperature for two hours, then gradually ramping back down to 25 °C during the final two hours. Humidity during these experiments was maintained at ≈90% RH. Following the treatments, all samples were transferred to emergence containers and maintained at a constant 25 °C, with moisture added to prevent desiccation. Emergence of brood adult beetles was monitored until it ended (approximately 4 weeks). We used a paired one-sided *t*-test to test for reduced adult emergence in experimental vs. control samples.

This experiment was replicated in July 2013 using trees from a beetle infestation in southern New Jersey (Table 1). In this instance we collected 21 bark samples (30 × 30 cm) from four infested trees. Again, the samples were acclimated, cut into pairs and the treatment halves were subjected to high temperature exposure using the same protocol as in 2011 except that we used only a single high temperature treatment (42 °C).

**Table 1**

The emergence of *D. frontalis* adults from pine phloem was not affected by exposure of developing larvae to one day when the maximum temperature reached either 37 or 42 °C compared to a control temperature of 25 °C (2011:  $t = 1.92$ ,  $p = 0.95$  and  $t = 0.41$ ,  $p = 0.65$  for 37 °C and 42 °C respectively; 2013:  $t = 0.28$ ,  $p = 0.39$ ).

Year	Treatment	Number of bark samples	Total emerging beetles	Emerging beetles per sample (mean ± SE)
2011	Control	12	481	40 ± 12
	37 °C	12	661	55 ± 14
	Control	12	418	35 ± 8
2013	42 °C	12	459	38 ± 13
	Control	21	1353	64 ± 8
	42 °C	21	1305	62 ± 8

## 2.2. Chronic high temperature exposure

To test the effect of chronic high temperature exposure on adult emergence of southern pine beetle we collected bolts in summer 2013 from infested pine trees in New Jersey (at the expanding northern edge of the distribution of *D. frontalis*), and in the Homochitto National Forest in Mississippi (within historical range of *D. frontalis*). Diverse molecular evidence indicates that *D. frontalis* populations from New Jersey and Mississippi are both within the eastern *D. frontalis* group, where there is no genetic pattern of isolation by distance and only slight differentiation among populations (Havill et al., 2019). At each location, we selected four trees of about 25 cm dbh containing a high density of 2nd–3rd instar larvae of *D. frontalis*. The trees were felled and four bolts (30–40 cm long) were cut from the central bole of each tree. The cut ends were sealed with parafilm to prevent desiccation.

The bolts were subjected to one of four chronic high temperature treatments where we varied the number of days they were exposed to a maximum temperature of 37 °C. This was designed to approximate heat waves of varying duration. The purpose of the experiment was to determine the number of consecutive exposures to high temperature necessary to impart significant mortality in the population (e.g., lethal duration 50 (LD<sub>50</sub>), the point at which 50% mortality is reached). The treatment schedule consisted of gradually raising the air temperature from 25 to 37 °C during two hours, holding at the maximum temperature for eight hours, then gradually returning to 25 °C during the next two hours, and maintaining that temperature for 12 h. This entire 24 h process constituted a single cycle of high temperature exposure. We tested exposure to 0 (control), 2, 4, and 7 days of consecutive treatment cycles. Following treatment, the bolts were placed into emergence containers and maintained at 25 °C. Emergence was monitored until completion (4–6 weeks).

We tested for treatment effects on adult emergence with separate randomized complete block analysis of variance tests (ANOVA), with tree as the blocking factor in R Version 3.6.2 (R Core Team, 2019). One test used data from the New Jersey population, the other from Mississippi.

## 2.3. Field temperature measurements

During the summers of 2013–2015, we studied air and phloem temperatures within nine, medium-density stands of ~30 cm diameter trees within two National Forests (Kisatchie National Forest, Louisiana, and Homochitto National Forest, Mississippi). Such stands are frequent habitat for southern pine beetles. All the study stands were predominately loblolly pine (*Pinus taeda* L.), with occasional oaks (*Quercus* spp.) and sweetgum (*Liquidambar styraciflua* L.). Stands within each location were separated by at least 1.5 km. Within each stand, we selected two adjacent, apparently healthy loblolly pine trees that were at least 50 m from a forest edge. For each tree, we recorded the diameter at breast height (DBH) and attached a K-type thermocouple inside the outer bark and within the phloem of the inner bark (without entering the sapwood) at 1.5 m above the ground. Thermocouples were inserted into the south-facing side of the tree to capture maximum possible effects from solar radiation. A second data logger recorded the shaded air temperature on the North side of an adjacent tree. Thermocouples were connected to data loggers (Onset corp., Bourne, MA, USA) that simultaneously recorded air and phloem temperatures at 15 min intervals. There was some variation in the dates of deployment of the data recorders within and among years, but in all cases the measurements captured the peak of summer temperatures.

To quantify thermal buffering in the microhabitats of bark beetles, we fit measurements of air and phloem temperatures to a model of heat conduction (Fourier's Law, see Eq. (1), Tran et al., 2007):

$$PhloemTemp_t = PhloemTemp_{t-\Delta t} + (AirTemp_t - PhloemTemp_{t-\Delta t}) \cdot K \cdot \Delta t \quad (1)$$

where  $PhloemTemp_t$  = current phloem temperature,  $PhloemTemp_{t-\Delta t}$  = previous phloem temperature,  $AirTemp_t$  = current air temperature,  $K$  = thermal conductance (estimated for each tree as the value of  $K$  that minimized the sum of squared error (SSE) using generalized reduced gradient (GRG) nonlinear solving method in Microsoft Excel 2016), and  $\Delta t$  = the thermocouple sampling interval = 0.25 h. If phloem temperatures were only a function of heat transfer (as described by Eq. (1)), the fit of Eq. (1) should closely match the flux of air temperature, and the maximum daily phloem temperatures would always be less than maximum daily air temperatures (by an amount inversely related to  $K$ ). The most likely deviation from this model would be the warming of trees from solar radiation. In this case, phloem temperatures could exceed air temperatures on sunny days, and bark beetles might experience lethally warm temperatures even when air temperatures are sublethal (Bolstad et al., 1997).

We evaluated the extent to which air temperatures in southern pine forests can be predicted from nearby NOAA weather stations. Weather data were obtained from the National Climate Data Center ([www.ncdc.noaa.gov/cdo-web/](http://www.ncdc.noaa.gov/cdo-web/)). For the Kisatchie National Forest, we used data from stations in Alexandria, Calhoun, Leesville, Ruston, and Winnsboro. For the Homochitto National Forest, we used data from stations in Brookhaven, Natchez, Port Gibson, and St. Joseph. We used linear regression to compare the average daily maximum temperature from the NOAA data with the average daily maximum temperatures recorded by our data loggers in each forest. For each tree in each stand, we evaluated the coefficient of determination ( $r^2$ ), root mean square error (RMSE), and bias (JMP® Pro 15.0, SAS Institute 2019).

## 2.4. Climate data

To evaluate long-term trends in the occurrence of heat waves in southern forests, we analyzed 80 years of daily maximum temperature records from a total of 54 weather stations in the vicinity of 14 national forests in the southeastern United States (Fig. 1, Table S-2). We used daily summaries from NOAA's National Climate Data Center ([www.ncdc.noaa.gov/cdo-web/](http://www.ncdc.noaa.gov/cdo-web/)). For each forest, we identified 3–5 weather stations within an 80-km radius of the forest center that had continuous daily records for 1940–2019. Stations with missing years, or frequent missing data for summer months were not considered. For analysis, we grouped forests (and their associated weather stations) into three regions (Gulf, Atlantic, and Intermountain) based on proximity, physiography, and climatic norms (Fig. 1, Table S-2).

For each weather station, for the 80-year record, we calculated the frequencies of heat waves. For our purposes, we defined a heat wave as one or more consecutive days with maximum temperature at or above 32 °C, to capture all possible combinations of duration and severity that could be consequential for the survival of *D. frontalis*. For each station, we calculated the proportion of years with a heat wave of 1, 2, 3, ... 15 days that exceeded at least 32, 33, 34, ... 42 °C (176 different combinations of duration × temperature).

## 2.5. Analysis of heat waves

We estimated the frequency of heat waves of different duration with a model (Eq. (2)) of the proportion of years ( $p$ ) of a heat spell of at least duration  $D$  that each day reached at least temperature  $T$ .

$$\text{logit}(p) = \beta_0 + \beta_1 T + \beta_2 D + \beta_3 T \cdot D + \beta_4 T^2 + \beta_5 D^2 \quad (2)$$

where  $T$  is the temperature that must be reached (32–42 °C),  $D$  is the duration of consecutive days (1–16) reaching or exceeding that temperature, and  $\beta_0$  to  $\beta_5$  are coefficients estimated from the data with a binomial model and a logit link function (model also included forest). The data used to fit the model were ≈760,000 observations (each a 0 or 1; up to 80 years × 54 climate stations × 176 combinations of heat wave intensity and duration). Our analyzes considered values of  $T$  (heat wave

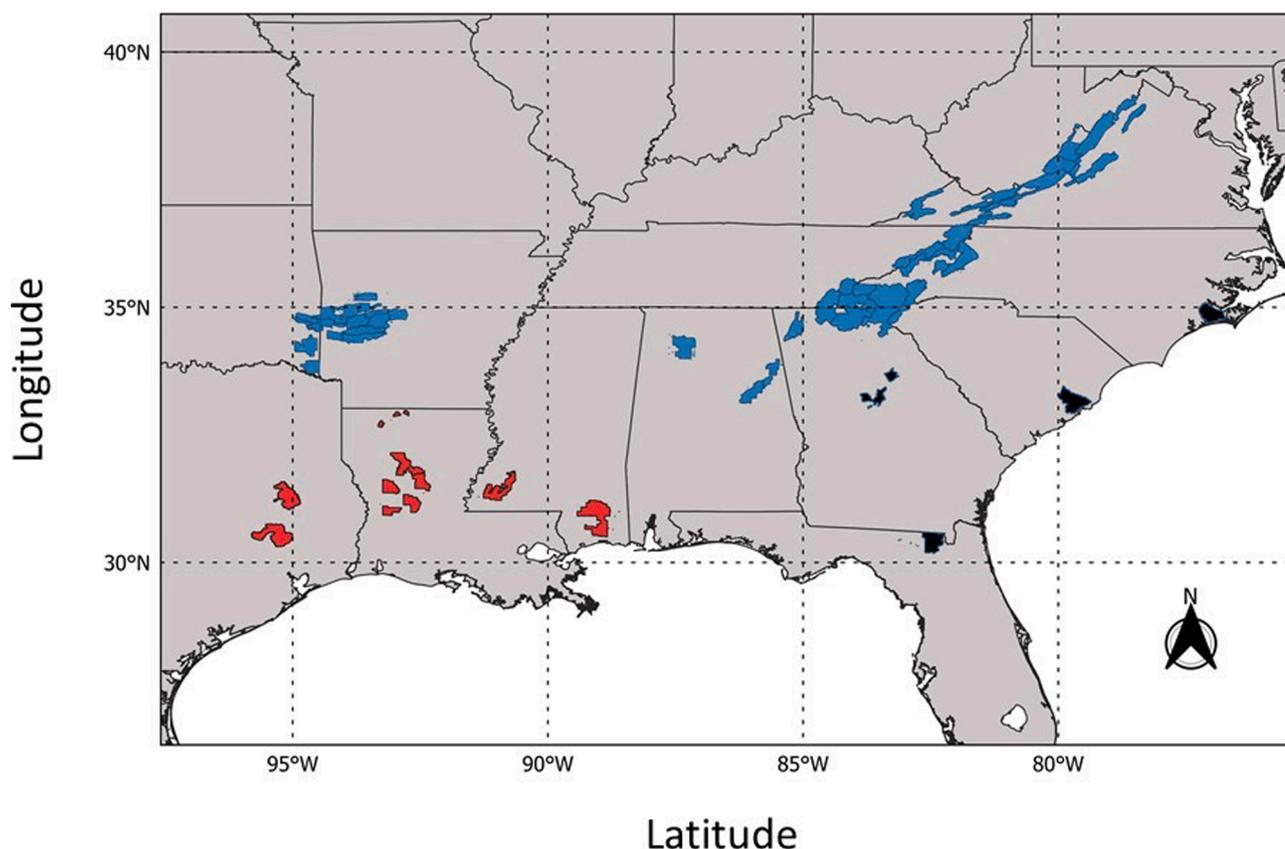


Fig. 1. The locations of 14 National Forests within the historical range of *D. frontalis* outbreaks in the southeastern United States. Color indicates region (Gulf = red, Atlantic = black, Intermountain = blue) (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.).

intensity) up to 42 °C because our experiments constrained upper lethal temperatures to >40 °C. This resulted in some  $T \times D$  combinations where the observed frequencies in historical data were 0: 32, 18, and 14% for Atlantic, Gulf, and Intermountain regions, respectively. Our analyzes emphasized the fit and form of models. We discounted p-values because there was non-independence among combinations of intensity and duration within years and stations. Using Eq. (2) fit to the data, we constructed a 3-dimensional response surface of heat waves for each of the 14 National Forests, as well as for each of the three forest regions. We constructed 2-dimensional scatter plots of observed vs. predicted to allow visual assessment of goodness of fit within the range where observed probabilities were >0 and <1.

To test for time trends in the frequency or severity of heat waves from 1940–2019, we also evaluated Eq. (3), which expands Eq. (2) by adding a term for year.

$$\text{logit}(p) = \beta_0 + \beta_1 D + \beta_2 T + \beta_3 Y + \beta_4 D \cdot T + \beta_5 D^2 + \beta_6 T^2 \quad (3)$$

where  $p$  is the proportion of years with a heat wave that reached temperature  $T$  for a duration of  $D$  consecutive days, and  $Y$  is year.  $\beta_0$  to  $\beta_5$  represent coefficients estimated from the data with a binomial model and logit link function.  $\beta_0$  (the intercept) was adjusted to represent the average forest in the region by adding to it the average of model estimates for forests.

It was possible to rearrange Eqs. (2) and 3 to solve for the combinations (isolines) of heat wave severity and duration that corresponded to a specified probability. Supplemental Eqs. (S-1), (S-2) and (S-3) are the real solutions for isolines from Eq. (2) corresponding to probabilities of  $p = 0.1$ ,  $p = 0.5$ , and  $p = 0.9$  respectively. Similarly, supplemental Eqs. (S-4), (S-5) and (S-6) correspond to the heat wave isolines of Eq. (3) for  $p = 0.1, 0.5, 0.9$  respectively. These allowed us to compare the heat wave isolines at the beginning and end of the weather records (1940 and

2019). Eqs. (2) and (3) were fit with *glm* within the *stats* package in R Version 3.6.2 (Team 2017). Isolines were solved from parameter estimates using base R.

### 3. Results

There were no effects on survival of *D. frontalis* from acute exposure (one day) to a maximum daily temperature of either 37 °C or 42 °C (Table 1). By comparison, Beal (1933), who studied sun-warmed logs, reported some mortality of *D. frontalis* with phloem temperatures of 38 °C and high mortality at 43 °C. Thus, the upper lethal temperature for 50% mortality of *D. frontalis* from a one-day exposure is no less than 38 °C and is probably >40 °C. We found no effects of chronic high temperature exposure on survival of *D. frontalis* even when maximum daily temperature reached 37 °C for up to seven consecutive days (Table 2).

Table 2

The emergence of *D. frontalis* adults from pine phloem was not affected by exposure of developing larvae to 2–7 consecutive days when the maximum temperature reached 37 °C (Mississippi:  $F = 0.12$ ,  $p = 0.94$ ; New Jersey:  $F = 2.71$ ,  $p = 0.11$ ).

Source population	Days of exposure to 37 °C	Number of pine bolts	Total emerging beetles	Emerging beetles per sample (mean ± SE)
Mississippi	Control	4	818	205 ± 49
	2	4	739	185 ± 54
	4	4	731	183 ± 56
	7	4	853	213 ± 56
New Jersey	Control	4	1022	256 ± 90
	2	4	684	171 ± 86
	4	4	767	192 ± 63
	7	4	680	170 ± 58

Temperatures within the inner bark (phloem) of pine trees, where *D. frontalis* spend all but a few days of their life cycle, closely tracked local air temperatures, but tended to be buffered on the warmest days by 3–4 °C (Fig. S-1). The heat transfer model (Eq. (1)) provided reasonable predictions of phloem temperature as a function of air temperature ( $r^2 = 0.77$  to  $0.96$ ; Table S-1). Estimates of  $K$  (thermal conductance) ranged from 0.112 to 0.436 (mean  $\pm$  SD =  $0.24 \pm 0.09$  °C • °C<sup>-1</sup> • 0.25 h<sup>-1</sup>) for pine trees of sizes typically attacked by *D. frontalis* (20–30 cm diameter), within pine stands typical of where *D. frontalis* infestations occur (approximately even-aged pines with basal area >22 m<sup>2</sup>/ha) (Table S-1). We found evidence of solar input to the thermal budgets of tree boles in that phloem temperatures usually increased slightly earlier in the day and cooled off sooner than predicted by the simple conductivity model (Fig. S-2). However, these effects were minor with respect to the physiology of beetle heat tolerance; maximum phloem temperatures were generally well predicted by the simple heat conduction model ( $r^2$  usually > 0.90, root mean square error of ~1 °C, and average bias of < |0.6 °C|; Table S-1). Phloem temperatures exceeded the air temperature in only 9% of our measurements, and never by more than 4 °C (Fig. S-1).

Maximum daily air temperatures within pine stands that are habitat for *D. frontalis* were usually predicted to within 3 °C by the maximum daily air temperatures from nearby NOAA weather stations (Fig. S-3). The warmest temperatures that we recorded in pine forests were on the same days as the warmest temperatures from NOAA data and reached about the same level: maxima of 37.8 vs. 35.6 °C and 40.6 vs. 37.9 °C in forest vs. station for Homochitto and Kisatchie National forests,

respectively (Fig. S-3).

Analysis of summer temperatures using 80 years of daily measurements at 54 climate stations associated with 14 National Forests spread across three regions of the southeastern United States indicated that mortality from acute heat exposure has been rare within the zone of historically high impacts from *D. frontalis*. From 1940 to 2019, maximum daily temperatures have seldom reached even 42 °C (Fig. 2, Table S-2), which we now know to be lower than the threshold for acute mortality in the beetles (Tables 1 and 2). Over the 80-year study period, for 14 National Forests, the average of the maximum annual air temperature ranged from 37.0 to 40.5 °C. As expected, long term patterns in yearly maximum temperature varied among the regions, and the percentage of years with a maximum temperature that exceeded 42.0 °C ranged from 7.5% in the Atlantic, to 2.2% in the Intermountain region (Fig. 4). The mean ( $\pm$  SD) maximum yearly temperature for all years in the Gulf, Atlantic, and Intermountain regions were similar ( $39.9 \pm 1.9$ ,  $39.2 \pm 1.7$ , and  $40.6 \pm 2.1$  °C, respectively). There was no evidence for recent increases in the probability of mortality from acute exposure to heat: i.e., no forest or region showed an upward trend across years in the annual maximum of maximum daily temperatures (Fig. 2, Table S-2). Similarly, time series of the warmest 4-days per summer also showed no trends in the intensity of heat waves (Fig. S-4).

The empirical probabilities of heat waves of specified intensities and durations were well fit with the response surface model (Eq. (2), Fig. 3, Fig. S-5,  $r^2 > 0.99$  for all three regions). The estimated coefficients (Table S-3) permitted comparisons across regions of the historical

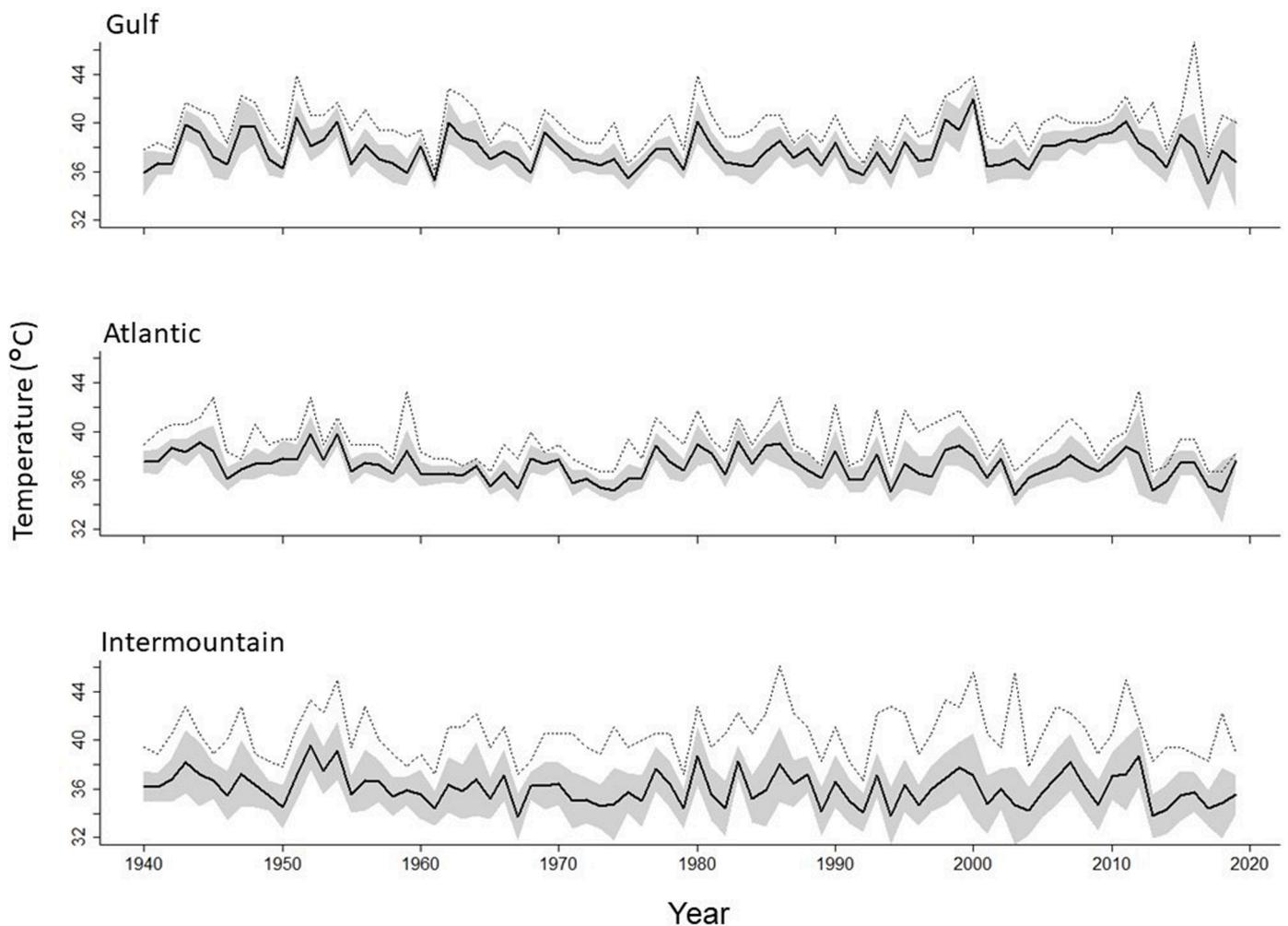
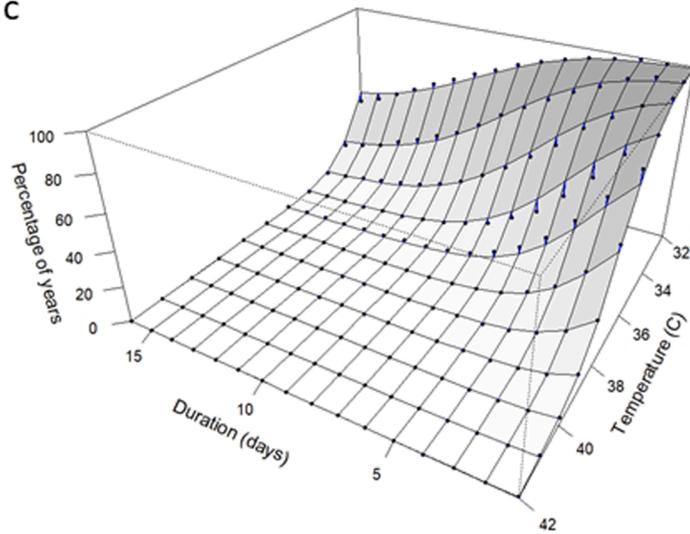
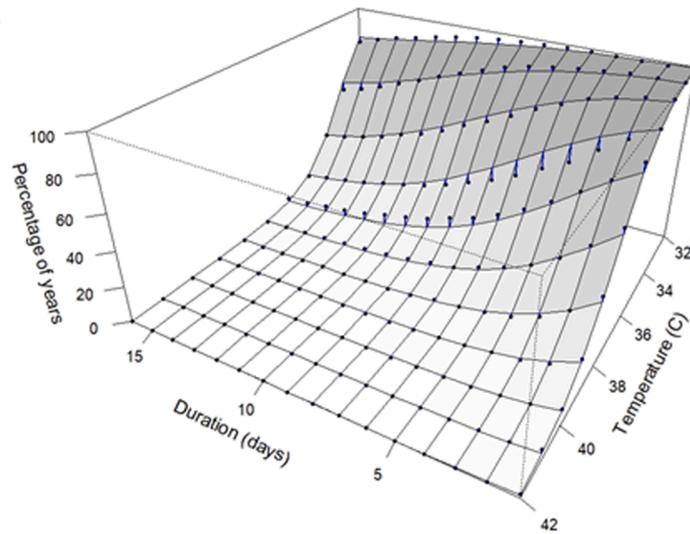


Fig. 2. Mean (solid line), standard deviation (shaded area), and maximum (dotted line) of yearly maximum temperatures from 54 weather stations associated with National Forests in three regions of the southeastern United States that represent the core range of *D. frontalis* (Fig. 1; Table S-2; [www.ncdc.noaa.gov/cdo-web/](http://www.ncdc.noaa.gov/cdo-web/)).

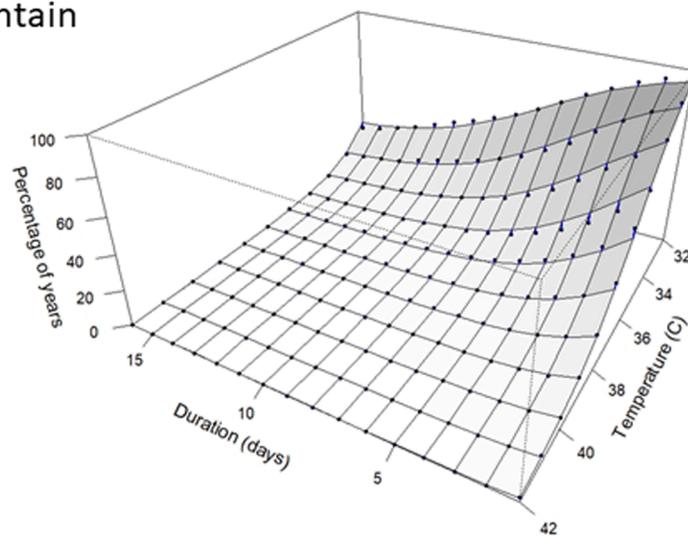
### Atlantic



### Gulf



### Intermountain



**Fig. 3.** Annual probability of heat waves of varying intensity and duration for three southern forest regions in the United States. The surface shows Eq. (2) fit to the data. The balls on sticks at each gridpoint show the observed data (actual historical frequencies during 1940 to 2019) ( $r^2 > 0.99$  for all three regions). Fig. 1 and Table S-2 describe the forests and weather stations associated with each region.

occurrence of potentially lethal summer temperatures for *D. frontalis*. The annual probability of a heat wave of at least 7 consecutive days that reached at least 36 °C was 0.22 in the Gulf Region and 0.05 in Atlantic and Intermountain regions. Our experimental data (Table 2) indicate that such a heat wave is not sufficient to kill *D. frontalis*. More severe but similarly sustained heat waves have been rare. For example, the probability of a 7-day heat wave that reached at least 38 °C was only 0.03, 0.01, and 0.01 (Gulf, Atlantic, and Intermountain, respectively) and even those temperatures may not be lethal for *D. frontalis*. In our experiments, one day of exposure to 42 °C was insufficient to produce measurable mortality. The frequency of multiple days in a row that are so warm has been very rare: the probability of even a 2-day heat wave of 42 °C was <0.015 in all regions. Thus, temperatures that exceeded the upper physiological limits of *D. frontalis* have been rare, if they have occurred at all, in 80 years of recent summer weather in the southern United States.

There has been no increase in the severity or duration of summer heat waves in the core range of *D. frontalis* (Fig. 1). We evaluated this by extending Eq. (2) to include  $+ \beta_6 \cdot \text{Year}$ , where year is a continuous variable ranging from 1940 to 2019. In this model, increases in the severity or duration of heat waves would be indicated by positive values of  $\beta_6$ . In fact, the estimates of  $\beta_6$  were slightly less than 0 for all three regions (Table S-3, Fig. 4). Neither the length nor the severity of summer heat waves has been increasing within the historic range of *D. frontalis* in the southern United States.

#### 4. Discussion

The reduced abundance of *D. frontalis* in southern forests is not due to direct mortality from an increase in the maximum summer temperatures. Rarely, if ever, have air temperatures approached lethal levels for *D. frontalis* over 80 years of daily records for our study region. Moreover, there has been no increase in yearly maximum temperatures, nor any significant change in the duration or severity of sequential warm days (heat waves). Other studies have similarly reported that maximum temperatures in the southeastern United States have not been increasing as in other regions (Pan et al., 2004; Portmann et al., 2009; Meehl et al., 2012). More surprising was the absence of even modest increases in the severity or duration of heat waves in the southeastern United States. Heat waves have been expected to increase in general (see Meehl and Tibaldi, 2004) and increases have already become apparent in some other regions of the country (Smith et al., 2013; Mazdiyasn and Agha-Kouchak, 2015).

Thus, we can reject increases in the duration or intensity of heat waves as the reason for the decrease of *D. frontalis* outbreaks within its historic southern range, which has coincided with an increase in outbreaks at the insect's northern range limit. Instead, reduced activity of *D. frontalis* within its historic range must have another explanation. This is consistent with the analyzes of climate-based hypotheses by Asaro et al. (2017). One alternative possibility is that this change is a result of steady improvements in southern pine beetle detection, suppression, and prevention methods (Nowak et al., 2015; Asaro et al., 2017). Another possibility is that the appearance of reduced abundance in southern populations is the spurious consequence of naturally episodic dynamics in *D. frontalis* populations (Turchin et al., 1991; Martinson et al., 2013). Some support for this possibility is offered by two recent severe southern pine beetle outbreaks in Mississippi (spbpredict.com, 2021). Finally, while our analysis found no change in extreme summer heat that could explain reduced beetle abundance, there are other facets of climate change that were not considered in our study and could influence *D. frontalis*. For example, warmer – but nonlethal – temperatures tend to disfavor a beneficial fungal associate of *D. frontalis* (*Entomocorticium cobbii*) relative to other fungal species with which it competes (Hofstetter et al., 2006b, 2007). Temperatures of 25 – 28 °C favor the abundance of *Tarsonemus* spp. mites, which are strong indirect antagonists of *D. frontalis* (Lombardero et al., 2003). Also, temperature can

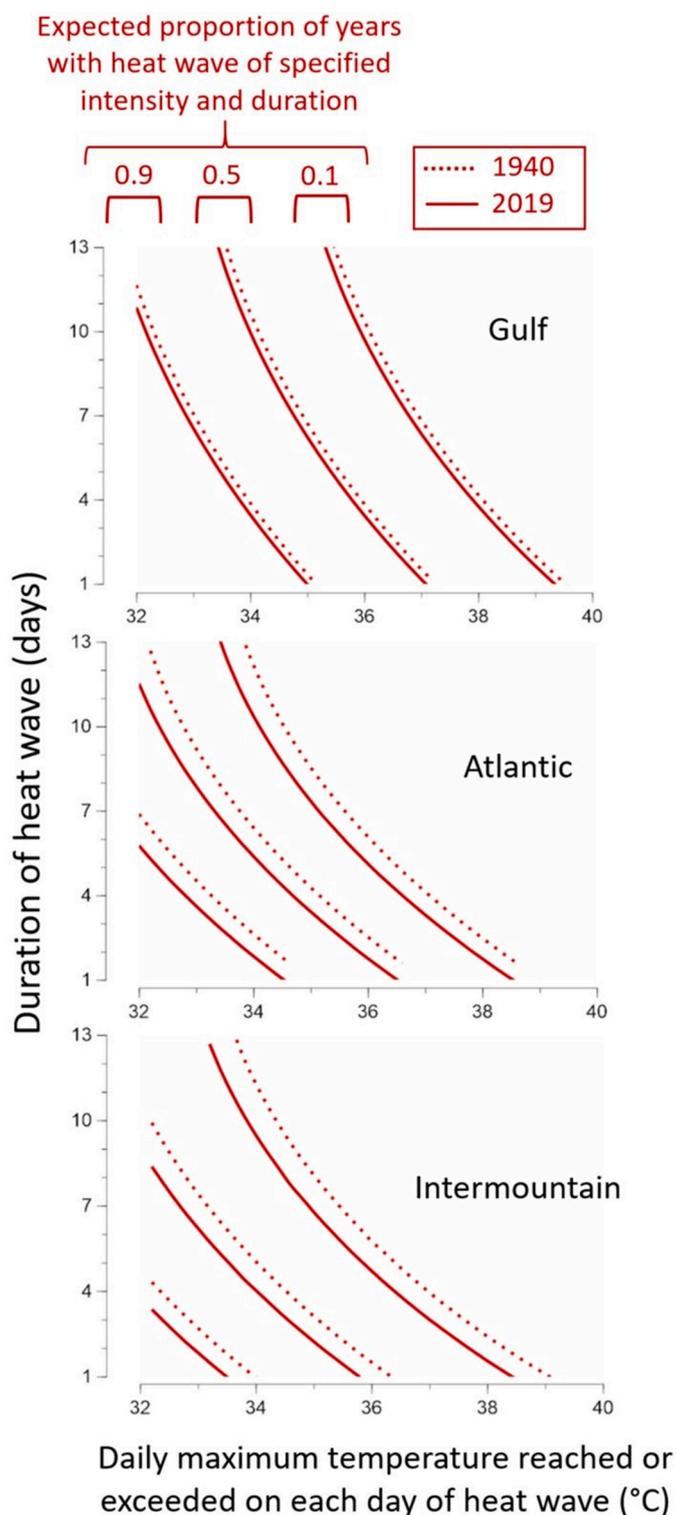


Fig. 4. Isolines indicate the intensity (temperature) and duration of heat waves that have occurred with annual probabilities of 0.90, 0.50, and 0.10 in three regions of the southeastern United States. The solid and dashed lines represent estimated probabilities at the beginning and end of the time series (2019 and 1940, respectively). Isolines were calculated from the same models as in Fig. 3 but with the addition of Year as a linear effect (Table S-3, Eqs. (4)–(9)).

influence the abundance, seasonality, and generation time of the primary predator of *D. frontalis* (*Thanasimus dubius* F.) (Reeve, 2000). Increases in winter and spring temperatures can influence the synchrony of spring emergence by *D. frontalis* and therefore their success in

aggregating for mass attacks on host trees (Lombardo et al., 2018). Further, there could be effects from various features of weather or climate that influence the structure of pheromone plumes used by *D. frontalis* for coordinating mass attacks (Thistle et al., 2011). Anticipating future patterns in the distribution and abundance of *D. frontalis* will require increased capacity to consider effects of both weather and management (Munro et al., 2021).

We do not reject the possibility that future warming will produce temperatures that exceed the upper lethal temperature for *D. frontalis*. Analyzing into this possibility would require (1) studies of mortality in *D. frontalis* at higher temperatures than we employed here, and (2) analyses of climate forecasts with respect to the duration and intensity of heat waves. It remains unknown how frequent and intense killing heat waves would need to be to produce meaningful changes in the frequency and intensity of *D. frontalis* outbreaks.

The apparent climatically enabled expansion of the northern range limit of *D. frontalis* resembles that of several other congeneric species that are also high impact forest pests (Reeve et al., 2012). For example, outbreaks of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) have caused unprecedented forest disturbance across the western United States and Canada in the last two decades (Kurz et al., 2008). Climate change has been implicated in the increased severity of these outbreaks (Mitton and Ferrenberg, 2012) as well as their occurrence in forests at increasingly higher latitudes and elevations (Aukema et al., 2008; Logan et al., 2010; Safranyik et al., 2010; Weed et al., 2015; Bentz et al., 2016). The spruce beetle (*Dendroctonus rufipennis* Kirby) has similarly expanded its impacts in the northern cooler regions of its distribution (Berg et al., 2006; Schebeck et al., 2017). However, the potentially lethal effects of high temperatures have not been studied for southern populations of *D. rufipennis* or *D. ponderosae* (but see Bentz et al., 2011, Bentz et al., 2019). It remains unknown if southern populations of *Dendroctonus* species will be similar in their response to climate change as are northern populations. It would be illuminating to study the effects of temperatures on *Dendroctonus* spp. in the center of their diversity in Mesoamerica (Armendariz-Toledano et al., 2014; Valerio-Mendoza et al., 2017; Soto-Correa et al., 2019), but historical records of temperatures and beetle abundance are presently limiting.

The absence of change in the severity or duration of heat waves in the southeastern United States indicates that, at least for now, climate change is not increasing direct mortality from heat stress for *D. frontalis* or other organisms in this region. This reveals a striking asymmetry in the ecological effects from climate warming in eastern North America. The warming of winter minima is relaxing northern distribution limits (e.g., Lesk et al., 2017), but in the southeastern United States there has been no countervailing increase in summer maxima to challenge the physiology of species at their southern limits. More information is needed to judge whether this climatic asymmetry is unique to eastern North America or globally common. Some of the methods used in this study could be generalized for other species in other regions.

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## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2022.108813](https://doi.org/10.1016/j.agrformet.2022.108813).

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