

# Temperature Extremes, Density Dependence, and Southern Pine Beetle (Coleoptera: Curculionidae) Population Dynamics in East Texas

NICHOLAS A. FRIEDENBERG,<sup>1,2</sup> SUDIPTA SARKAR,<sup>3</sup> NICHOLAS KOUCHOUKOS,<sup>3</sup>  
RONALD F. BILLINGS,<sup>4</sup> AND MATTHEW P. AYRES<sup>1</sup>

Environ. Entomol. 37(3): 650–659 (2008)

**ABSTRACT** Previous studies of the southern pine beetle, *Dendroctonus frontalis* Zimm., established that its population in east Texas responds to a delayed density-dependent process, whereas no clear role of climate has been determined. We tested two biological hypotheses for the influence of extreme temperatures on annual southern pine beetle population growth in the context of four alternative hypotheses for density-dependent population regulation. The significance of climate variables and their interaction with population regulation depended on the model of density dependence. The best model included both direct and delayed density dependence of a cubic rather than linear form. Population growth declined with the number of days exceeding 32°C, temperatures previously reported to reduce brood survival. Density dependence also changed with the number of hot days. Growth was highest in years with average minimum winter temperatures. Severely cold winters may reduce survival, whereas warm winters may reduce the efficiency of spring infestation formation. Whereas most previous studies have incorporated climate as an additive effect on growth, we found that the form of delayed density dependence changed with the number of days >32°C. The interaction between temperature and regulation, a potentially common phenomenon in ecology, may explain why southern pine beetle outbreaks do not occur at perfectly regular intervals. Factors other than climate, such as forest management and direct suppression, may have contributed significantly to the timing, severity, and eventual cessation of outbreaks since the mid-1950s.

**KEY WORDS** climate change, upper lethal temperature, outbreaks, *Dendroctonus frontalis*, *Thanasimus dubius*

Population dynamics of many insect pests are characterized by large fluctuations in abundance. Efforts to find general explanations for pest outbreaks have generally pointed either to endogenous dynamics driven by natural enemies (Nicholson 1954, Anderson and May 1981, Berryman 1996, McCann et al. 2000) and other density-dependent variables (May 1976, Royama 1992, Turchin and Taylor 1992, Perry et al. 2000) or to the influence of exogenous (density-independent) factors such as climate (Andrewartha and Birch 1954, Ungerer et al. 1999, Sillett et al. 2000, Powell and Logan 2005, Reynolds et al. 2007). Increasing recognition of climate change has encouraged an integration of endogenous and exogenous factors into population models in recent decades, especially for insects (Ito 1972, Zhou et al. 1997, Esper et al. 2007).

The southern pine beetle, *Dendroctonus frontalis* Zimm. (Coleoptera: Curculionidae), exhibits outbreaks, with large impacts on the ecology (Payne 1980) and economy (Pye et al. 2006) of pine forests in the southeastern United States. Previously, Turchin et al. (1991) found that the population dynamics of southern pine beetles in east Texas could be largely explained by delayed density-dependent feedback on population growth rate and that climatic variables did not seem to contribute to the pattern of outbreaks. Further studies (Reeve 1997, Turchin et al. 1999) suggested that the delayed feedback could be attributed to the bark beetle's main predator, *Thanasimus dubius* Fab. (Coleoptera: Cleridae).

Like all insects, the southern pine beetle has temperature-dependent developmental rates and must therefore respond in some way to annual climatic variation. More generations can be completed per year when winters are short and warm (Thatcher and Pickard 1964, White and Franklin 1976, Billings and Kibbe 1978, Ungerer et al. 1999), increasing potential population growth rate (Huey and Berrigan 2001). Temperature can also directly affect survival. Southern pine beetles have a lower lethal temperature rang-

<sup>1</sup> Department of Biological Sciences, Dartmouth College, Hanover, NH 03755.

<sup>2</sup> Corresponding author, current address: Department of Ecology and Evolution, 650 Life Sciences Building, Stony Brook University, Stony Brook, NY 11795-5245 (e-mail: naf@life.bio.sunysb.edu).

<sup>3</sup> Lanworth, 300 Park Blvd., Ste. 425, Itasca, IL 60143.

<sup>4</sup> Texas Forest Service, 301 Tarrow, Ste 364, College Station, TX.

ing from  $-12$  to  $-18^{\circ}\text{C}$ . Accordingly, minimum winter temperature seems to determine the upper latitudinal and elevational range limits of southern pine beetles in the United States (Ungerer et al. 1999, Tran et al. 2007). Lethal low temperatures do not seem to limit southern pine beetle populations at southern latitudes (Tran et al. 2007) but have been observed to kill brood on rare occasion, particularly in thin-bark trees (Texas Forest Service 1984). In contrast, warm winters may reduce bark beetle population growth rates by affecting age structure and the timing of infestation initiation during spring dispersal (Logan et al. 1998, Friedenberget al. 2007, Tran et al. 2007), leading to the prediction that population growth rates should peak at intermediate winter temperatures. Extreme or extended periods of high temperature during the summer may also have a demographic impact. The developmental rates of most southern pine beetle life stages decrease above  $32^{\circ}\text{C}$  (Gagne et al. 1982, Wagner et al. 1984). Temperatures  $>43^{\circ}\text{C}$  are known to quickly kill brood, although such temperatures are rarely reached in the phloem of standing trees (Beal 1933). Brood survival decreases during the hottest months of the year (Thatcher and Pickard 1964, Gagne et al. 1980, Lih and Stephen 1996) and some southern pine beetle infestations have been observed to end abruptly during unusually hot summers, as indicated by a sharp boundary between killed (red-crowned) and unattacked trees at the margin of large, previously expanding infestations (R.F.B., unpublished data).

We analyzed records of the number of local southern pine beetle infestations (known as "spots") in east Texas from 1958 to 2006 to determine the relative contributions of climate and density dependence to southern pine beetle population dynamics. Whereas other studies have found varying roles of temperature and precipitation in southern pine beetle outbreaks (Kalkstein 1976, Kroll and Reeves 1978, Michaels 1984, Gumpertz et al. 2000), Turchin et al. (1991) rejected a significant role of climate in east Texas after examining the correlation between local climate records and dynamics in Hardin County, an area of frequent and well-documented southern pine beetle activity. The approach of Turchin et al. (1991) was attractive because it used a small number of biologically motivated variables and transparent analytical methods. Our study expanded the study of temperature to a larger area using a distance-weighted interpolation of many weather stations, thereby reducing noise in the climate data caused by local variation and instrument error. This approach is more likely to detect an effect of climate because it tracks temperature and population dynamics at a spatial scale over which births and deaths are more influential than immigration and emigration. Another departure from previous analyses was to entertain a wider range of models for population regulation, which were compared using information-theoretic model selection.

## Materials and Methods

**Population Data.** We analyzed the Texas Forest Service's record of southern pine beetle activity since 1958. The data consisted of southern pine beetle infestations detected in periodic aerial surveys in east Texas. Detected infestations are called "spots" because of their appearance as aggregations of 5 or more (10 or more since 1974) dead or fading trees. Only the southern half of east Texas was surveyed by plane before 1973, but ground crews reported no activity in the northern counties before that date. Beginning in 1982, the records included spots on federal land. Outbreak southern pine beetle activity ceased in east Texas and no new spots were detected after 1997. The number of trees within southern pine beetle spots ranges over three orders of magnitude, suggesting that different results might be obtained by using a population estimate that considers the total number of hosts attacked per year. Data were available for the annual volume of wood killed by southern pine beetles over the study period. However, a previous analysis found no qualitative difference in the dynamics inferred from spot counts versus volume damage estimates (Turchin et al. 1991). Our own comparisons corroborated this finding; therefore, we only report results using spot counts. We limited our analysis to infestations on nonfederal land for all of east Texas over the 39 yr from 1958 to 1997.

**Climate Variables.** Two climate variables, reflecting different aspects of seasonal temperature variations, were analyzed with *a priori* expectations of their effects on population dynamics. These daily temperature data were derived from the NCEP NCAR Climate Data Assimilation System over the Continental United States. The NCEP NCAR reanalysis was chosen as the source of daily data because of their robust real-time data assimilation scheme and rigorous quality control (Kalnay et al. 1996). All data were regridded to  $1^{\circ}$  resolution through a piecewise linear interpolation and reported for the grid-square containing all counties with common southern pine beetle activity in east Texas. Yearly temperature cycles were organized according to southern pine beetle life history, beginning and ending on Julian day 60 (spring to spring).

First, we found the number of days per year on which the maximum temperature exceeded  $32^{\circ}\text{C}$  (Fig. 1a). The number of days above this temperature threshold is positively correlated with mean and maximum annual temperature but also distinguishes years with prolonged bouts of hot weather from those with isolated heat events. Extreme heat can have acute effects on southern pine beetle brood survival (Beal 1933). However, the infrequency of lethal temperatures and the shading and thermal buffering provided by standing trees and by bark suggest chronic exposure to sublethal high temperatures may be a more important contribution to variation in population growth rate. High temperatures may also contribute to the increase of pathogens (Hofstetter et al. 2006b) and competitors such as *Monochamus* spp. or may decrease

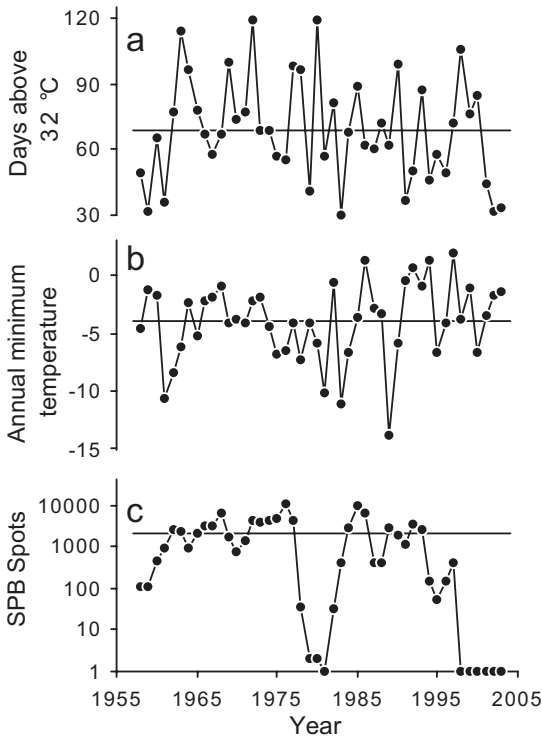


Fig. 1. Climate patterns and southern pine beetle dynamics in east Texas for 1958–2003. (a) Days per year  $>32^{\circ}\text{C}$ . (b) Annual minimum air temperature (from spring to spring). (c) The number of local infestations (spots) on state and private land counted in annual surveys that run from spring through summer. Horizontal lines are arithmetic means.

the activity of mutualistic fungi (Hofstetter et al. 2007).

The second climatic variable analyzed was minimum winter temperature, taken as the lowest daily mean temperature from spring to spring (Fig. 1b). We tested two contrasting hypotheses regarding the effect of low temperature on southern pine beetle dynamics. One expectation is that warm winters facilitate southern pine beetle outbreaks in Texas by allowing more generations per year (Thatcher and Pickard 1964, Kroll and Reeves 1978, Huey and Berrigan 2001, Frazier et al. 2006). A competing expectation is that, whereas extreme cold will significantly reduce overwinter survival (Beal 1933, Tran et al. 2007), even in east Texas (December 1983; Texas Forest Service 1984), cold winters may also foster southern pine beetle outbreaks by synchronizing brood development and increasing the efficacy of infestation formation, as observed in mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Logan et al. 1998, Powell et al. 2000). This second hypothesis predicts that southern pine beetle population growth rates will be a humped (quadratic) function of minimum winter temperature, peaking when winters are neither lethally low nor unusually warm.

We standardized both climate variables to a mean of zero before analysis.

**Analysis.** Southern pine beetle population dynamics have previously been described as following the linear delayed density-dependent relationship,  $N_{t+1} = N_t \exp[r_0(1 - N_t/K)]$ , where  $N_t$  is population density at time  $t$ ,  $r_0$  is intrinsic population growth rate, and  $K$  is the carrying capacity (Turchin et al. 1991). The model can be expressed in terms of population growth,  $r_t$ , and expanded to include climatic effects such that

$$\ln\left(\frac{N_t}{N_{t-1}}\right) = r_t = r_0 - cN_{t-1} + \sum_{i=1}^j \alpha_i V_i + \varepsilon \quad [1]$$

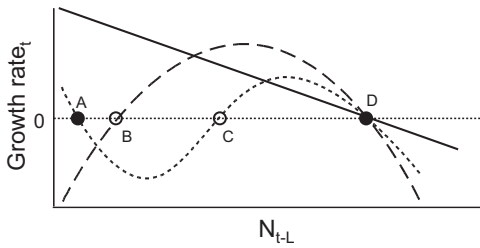
where  $\alpha_i$  and  $V_i$  are linear coefficients and climatic variables, respectively, and  $c = r_0/K$ . Residual environmental or demographic noise is assigned to the term  $\varepsilon$ . Equation 1 can be parameterized by linear multiple regression. Note that our terminology differs from that used in some other time series analyses (Turchin et al. 1991, Royama 1992, Perry et al. 2000). Growth,  $r_t$ , refers to population change from time  $t$  to time  $t + 1$  rather than the retrospective change from time  $t - 1$  to time  $t$ . Our terminology emphasizes the goal of predicting population growth (i.e., change in number of southern pine beetle spots).

A more general second-order population growth model takes the form

$$r_t = r_0 + f(N_t) + f(N_{t-1}) + \sum_{i=1}^j \alpha_i V_i + \varepsilon \quad [2]$$

where  $f(N_t)$  and  $f(N_{t-1})$  are functions describing direct and delayed density dependence, respectively, that can themselves take any form, and the summation includes all effects of climate. There are biologically reasonable motivations for using nonlinear terms in the density dependence functions, ranging from the general observation that population dynamics are inherently nonlinear (Turchin and Taylor 1992, Perry et al. 2000) to more specific hypothesis about population regulation such as positive density dependence (Allee 1931, Stephens and Sutherland 1999) and multiple equilibria (May 1977), both of which are particularly relevant to bark beetle ecology (Raffa and Berryman 1983, Berryman et al. 1985). Figure 2 shows three examples of density-dependent growth functions.

The general formulation in Equation 2 lacks a potentially important feature: the ability of climate to alter the form or strength of density dependence. Models with static terms for regulation produce strongly periodic population dynamics, even with the introduction of reasonable levels of random noise into their simulation. In contrast, most natural populations are not strictly periodic in their dynamics (Dwyer et al. 2004). Changes in equilibrium population size or the periodicity of dynamics around that equilibrium might result from variation in the mechanism, timing, or strength of density dependence with variation in climate (Berryman and Lima 2006). Hence, popula-



**Fig. 2.** Three theoretical forms of population regulation. Growth rate is a function of population size,  $N$ , at time  $t - L$ . For direct density dependence,  $L = 0$ . A population equilibrates where growth is equal to zero and further increases in population size reduce growth rate (filled circles). Linear negative density dependence (solid line) produces a single equilibrium point (D). A quadratic growth function that initially increases with population density to produce a hump (dashed curve) has a threshold (B) below which the population goes extinct. Cubic density dependence (dotted curve) can have up to two stable equilibria (A and D) separated by a threshold (C). Nonlinear growth curves can arise from nonlinear species interactions, such as saturating predator responses or cooperative resource utilization.

tion regulation might be a function of both population density and climate variables, as in

$$r_t = r_0 + f(N_t, \mathbf{V}) + f(N_{t-1}, \mathbf{V}) + \sum_{i=1}^j \alpha_i V_i + \varepsilon, \tag{3}$$

where  $\mathbf{V}$  is a vector of climatic effects on density dependence.

We used the general framework in Equation 3 to explore biologically reasonable endogenous processes and their interaction with temperature extremes. For each significant endogenous process, we compared models that included linear effects of high temperature, quadratic effects of low temperature, and interactions between endogenous and exogenous components. We chose the best model for each endogenous process using Akaike Information Criterion (AIC), a common information-theoretic approach to choosing among regression models (Quinn and Keogh 2002, Gotelli and Ellison 2004, Grossman et al. 2006) while favoring parsimony (Burnham and Anderson 2002).

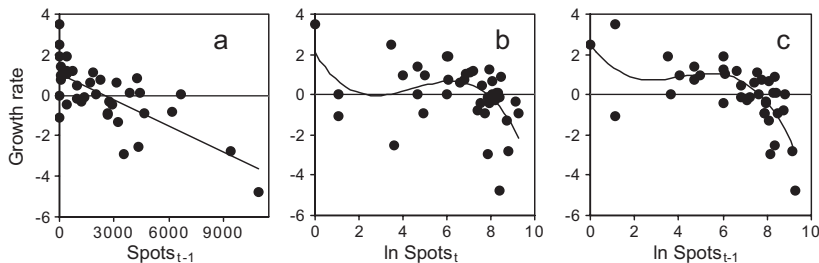
To evaluate the behavior of the resulting best models, we simulated population dynamics through 2003 from observed initial conditions in 1958 and 1959, introducing climate information and random error in population growth at each iteration.

Throughout our study, we assumed that other potentially important environmental factors such as forest composition remained constant over the course of the observed population dynamics.

**Results**

Climate variables showed no clear temporal trends over the duration of the population dataset (Fig. 1a-c). The southern pine beetle population in east Texas ceased forming multi-tree infestations after 1997 (Fig. 1d). Individual beetles were likely still present at extremely low densities, but the cessation of mass attack behavior caused the appearance of a sudden extinction in the dataset. From the years 1958 to 1997, the population fluctuated around a high mean number of spots per year—dropping and then recovering once in the early 1980s. A second decrease from the high mean occurred in 1994, from which the population has yet to recover (Fig. 1d). In all of the population models we tested, the extinction event in 1998 was an extreme outlier and was excluded along with all following years of data (see Discussion).

Plotting annual growth ( $r_t$ ) against the number of spots in either the current or past year, only three forms of density dependence seemed to be valid hypotheses for population regulation (Fig. 3). As in previous analyses (Turchin et al. 1991, Reeve and Turchin 2002), the pure delayed density-dependent model was a good descriptor of spot dynamics from 1958 to 1997 (Fig. 3a). It would be reasonable to expect some positive density dependence in southern pine beetle dynamics because of the need to mass attack hosts (Berryman et al. 1985) and the theoretical increase in aggregation formation with population density that characterizes pheromone-mediated host location (Byers 1996). The endogenous function that includes both positive density dependence and a stable equilibrium is quadratic. However, neither direct nor delayed density dependence appeared to be quadratic in form. Bark beetle populations are often described as having two states, endemic and epidemic (Wallin and



**Fig. 3.** Three forms of population regulation fit to the east Texas southern pine beetle time series. (a) Linear delayed density dependence ( $r^2 = 0.51$ ;  $df = 1,36$ ;  $F = 39.88$ ;  $P < 0.0001$ ). (b) Cubic direct density dependence ( $r^2 = 0.18$ ;  $df = 3,35$ ;  $F = 3.8$ ;  $P = 0.018$ ). (c) Cubic delayed density dependence ( $r^2 = 0.49$ ;  $df = 3,34$ ;  $F = 12.76$ ;  $P < 0.0001$ ).

**Table 1.** Comparison of four competing models fit to dynamics of the southern pine beetle, *D. frontalis*, in east Texas for the period 1958–1997

Model	Endogenous process		Exogenous factors		Exogenous/endogenous interaction <sup>d</sup>				Goodness of fit	
	Form of density dependence <sup>a</sup>	Intrinsic growth	No. hot days <sup>b</sup>	Min. temp. <sup>c</sup>	Direct		Delayed		<i>r</i> <sup>2</sup>	AIC
					Hot days	Min. temp.	Hot days	Min. temp.		
1(a)	Delayed linear <i>N</i>	1.07 <sup>e</sup>	—	—	—	—	—	—	0.51	8.4
1(b)		0.99 <sup>e</sup>	-0.17 <sup>f</sup>	—	—	—	—	—	0.56	5.0
2(a)	Direct cubic ln( <i>N</i> )	2.12	—	—	—	—	—	—	0.18	29.9
2(b)		2.24 <sup>f</sup>	-0.023 <sup>f</sup>	—	—	—	—	—	0.29	24.8
3(a)	Delayed cubic ln( <i>N</i> )	2.50 <sup>f</sup>	—	—	—	—	—	—	0.49	12.0
3(b)		4.84 <sup>g</sup>	-0.12 <sup>e</sup>	-0.099-0.029 <sup>f</sup>	—	—	0.045 <sup>f</sup> -0.0042 <sup>h</sup>	—	0.73	-7.7
4(a)	Direct cubic ln( <i>N</i> ), delayed	3.35 <sup>f</sup>	—	—	—	—	—	—	0.51	12.8
4(b)	cubic ln ( <i>N</i> )	4.95 <sup>e</sup>	-0.12 <sup>e</sup>	-0.11 <sup>f</sup> -0.034 <sup>e</sup>	—	—	0.048 <sup>f</sup> -0.0046 <sup>h</sup>	—	0.79	-15.7

For each endogenous process, the coefficient of determination and AIC score are given (a) excluding climate and (b) for the best model with climate.

<sup>a</sup> Estimates of pop density, *N*, are the no. of southern pine beetle infestations (spots) on nonfederal lands.

<sup>b</sup> Days >32°C: hypothetical mechanism = high summer temperatures reduce survival.

<sup>c</sup> Quadratic function: hypothetical mechanism = cold winters cause mortality and warm winters decrease new infestation formation.

<sup>d</sup> Hypothetical mechanism = climatic conditions alter the strength or form of density dependence.

<sup>e</sup> *P* < 0.0001.

<sup>f</sup> *P* < 0.05.

<sup>g</sup> *P* < 0.001.

<sup>h</sup> Interaction is with ln(*N*<sub>*t*-1</sub>) and ln(*N*<sub>*t*-1</sub>)<sup>2</sup>.

Raffa 2004), which might correspond to low and high equilibria, respectively. As shown in Fig. 2, the simplest function that can produce two stable equilibria is cubic. This form also includes a region of positive density dependence between the stable equilibria. Both direct and delayed cubic functions of growth versus ln-transformed numbers of spots were significant (Fig. 3). Neither partial autocorrelation analysis of population sizes or growth rates (Royama 1992) nor partial rate autocorrelation analysis (Turchin et al. 1999) suggested a significant role for lagged population size beyond 1 yr. Hence, we chose four endogenous models with which to test the role of temperature extremes in east Texas southern pine beetle dynamics. Models had the structure given in Equation 3 with the following density-dependent terms: linear delayed density dependence (model 1), direct cubic density dependence (model 2), delayed cubic density dependence (model 3), and both direct and delayed cubic density dependence (model 4).

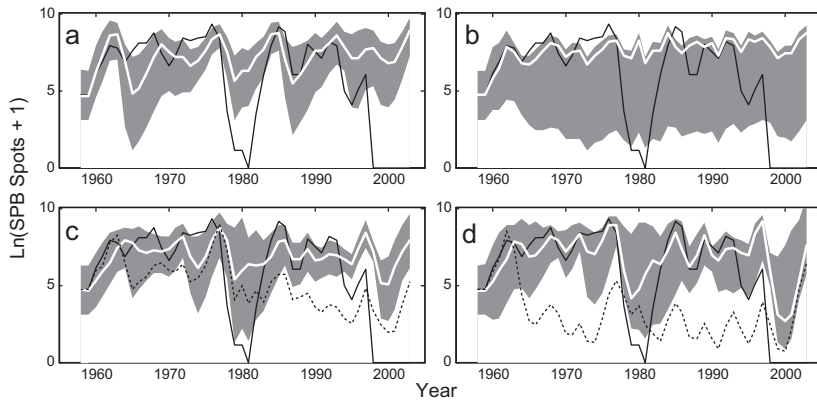
The role of temperature depended on the endogenous process of the model. As expected, growth decreased with the number of days >32°C in all cases. Only in models 3 and 4 was minimum winter temperature significant. In those cases, the effect of winter temperature on growth was quadratic, peaking in winters that were neither lethally cold nor unusually warm. Models 3 and 4 also featured a significant interaction between delayed density dependence and the number of days >32°C. Growth rate at low population size decreased in hot years.

The best combination of endogenous and exogenous components for model 1 yielded the prediction equation  $r_t = 0.99 - 0.0004N_{t-1} - 0.017V_1$ , where  $V_1$  is the number of days >32°C (*df* = 2,35; *F* = 25.01; *P* < 0.0001). The best model 2 prediction equation was  $r_t = 2.24 - 1.98X_t + 0.5X_t^2 - 0.036X_t^3 - 0.023V_1$  (*df* = 4,38;

*F* = 4.91; *P* = 0.0031), where  $X = \ln(N + 1)$ . The best model 3 prediction equation was  $r_t = 4.84 - (2.63 - 0.045V_1)X_{t-1} + (0.58 - 0.0042V_1)X_{t-1}^2 - 0.041X_{t-1}^3 - 0.12V_1 - 0.099V_2 - 0.029V_2^2$ , where  $V_2$  is minimum winter temperature (*df* = 8,29; *F* = 13.24; *P* < 0.0001). The best form of model 4 was  $r_t = 4.95 - 0.79X_t + 0.31X_t^2 - 0.025X_t^3 - (2.39 - 0.048V_1)X_{t-1} + (0.45 - 0.0046V_1)X_{t-1}^2 - 0.029X_{t-1}^3 - 0.12V_1 - 0.11V_2 - 0.034V_2^2$ , which has four variables and 13 parameters (*df* = 11,26; *F* = 13.53; *P* < 0.0001).

Despite its complexity, model 4 had the best AIC score of the four endogenous frameworks we studied (Table 1). It was also the case of greatest improvement with the addition of climate variables (Table 1). Model 2, direct cubic density dependence, had the least information content, with or without climate. The simplest endogenous process, model 1, had the best AIC score of the group when climate was not considered, but was the third best model with climate. Climate effects, coefficients of determination, and AIC scores for the four model structures are summarized in Table 1.

Stochastic simulations provided qualitative information about the match between each model and observed southern pine beetle dynamics. We iterated each model using only the first 2 yr of observed data as initial conditions. Climate observations for all years were used without resampling. Growth in each year was augmented by a small amount of random noise drawn from a normal distribution with a mean of 0 and an SD of 0.25. All models tended to fluctuate around a high mean population size (Fig. 4). In many simulations of model 2, population density switched to a lower equilibrium, producing a large confidence interval below the median projection (Fig. 4b). Visual inspection indicated that model 1 produced the most regularly periodic dynamics and that the period of the



**Fig. 4.** Stochastic simulations of southern pine beetle dynamics in east Texas from 1960 to 1998 using four different endogenous models and climate data. (a) Model 1: linear delayed density dependence and the number of hot days. (b) Model 2: direct density dependence and the number of hot days. (c) Model 3: delayed density dependence, the number of hot days, minimum winter temperature, and an interaction of delayed density dependence with hot days. (d) Model 4: cubic direct and delayed density dependence, the number of hot days, minimum winter temperature, and an interaction of delayed density dependence with hot days. Solid black lines are observed data. White lines are simulation medians. Gray areas indicate 95% CIs. For c and d, broken lines are medians of simulations without the endogenous  $\times$  exogenous interactions. For all simulations,  $N_{t+1} = N_t \exp[r + \varepsilon]$ , where  $r$  is the growth model and  $\varepsilon$  is a normal random deviate with a mean of 0 and an SD of 0.25. Initial conditions for 1958 and 1959 were drawn randomly from a normal distribution with a mean of 106 and an SD of 1.

median projection was slightly longer than that in the observed data (Fig. 4a). Models 2 and 3 had the least regular dynamics (Fig. 4b and c). Model 4 seemed to best reproduce the slightly irregular fluctuations of the observed dynamics. We also simulated models 3 and 4 without the interaction between hot days and delayed density dependence to see how important this interaction was to model behavior. In both cases, simulations with static density-dependent functions tended to switch to a lower equilibrium (Fig. 4c and d). No model predicted the end of outbreak activity in 1998, but model 4 projected (on average) the largest drop in population density for that year (Fig. 4).

Much of the complexity of the southern pine beetle's population dynamics may be driven by climate. Deterministic simulations under constant 1958–1997 average climatic conditions settled to a stable equilibrium in all four models. Deviations from average climate caused dramatic changes in equilibrium dynamics, although these effects differed qualitatively among the models. Iterating model 1 at constant temperatures over the observed range of days  $>32^\circ\text{C}$ , the long-term behavior ranged from quasiperiodicity or complex cycles to stable equilibrium (Fig. 5a). As in model 1, the equilibrium of model 4 decreased with increasing numbers of hot days, but complex dynamics arose under hot rather than cool conditions (Fig. 5b). The model 4 equilibrium peaked at intermediate minimum temperatures, dropping sharply to near-extinction levels under conditions of extreme cold or warm winters.

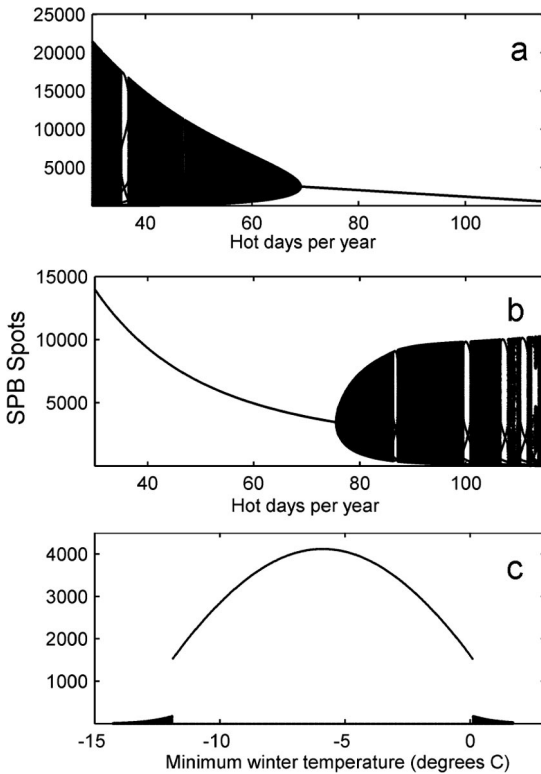
### Discussion

Although density-dependent and density-independent factors have historically been presented as alter-

native explanations for population dynamics (Andrewartha and Birch 1954, Nicholson 1954), there is increasing acknowledgment that both mechanisms contribute to the distribution and abundance of species (Ito 1972, Zhou et al. 1997, Ellner 2000, Berryman and Lima 2006, Crozier and Dwyer 2006, Esper et al. 2007, Wilmers et al. 2007). Our analysis of southern pine beetle population growth over a 39-yr period in east Texas suggests that fluctuating dynamics arise from both density-dependent population regulation and annual variation in temperature extremes.

We followed the example of previous studies that proposed growth models with straightforward biological interpretations (Turchin et al. 1991, Reeve and Turchin 2002, Berryman and Lima 2006), rather than using response surface modeling, which is aimed at identifying dynamical classes of system behavior (Turchin and Taylor 1992, Perry et al. 2000). A linear delayed density dependence model with climate (model 1) was attractive for its simplicity and explained more than one half the variation in observed growth rates (Table 1). However, climate contributed little to its explanatory power (Table 1), and the model's intrinsic periodicity was both stronger and longer than that observed in the data (Fig. 1a). Of the remaining models tested, model 4 explained the most variance in growth, had the best AIC score (Table 1), and had the most realistic intrinsic periodicity (Fig. 4d).

Southern pine beetle outbreaks are not perfectly regular. Fluctuations in southern pine beetle activity clearly have the general characteristic of lasting only several years and occurring several years apart, but our analysis also suggests that the precise timing, duration, and severity of outbreaks is determined by the simultaneous action of density-dependent and -independ-



**Fig. 5.** Long-term equilibrium population size as a function of endogenous models and constant temperatures. (a) Model 1: linear delayed density dependence and a decrease in growth rate with the number of hot days per year (days  $> 32^{\circ}\text{C}$ ). Under average temperature conditions (70 hot days), the population converges on a stable equilibrium. Cooler summers yield complex dynamics. Hotter summers decrease equilibrium population size. (b) Model 4: cubic direct and delayed density dependence with effects of hot days and minimum winter temperatures, assuming mean minimum temperature. The mean number of hot days yields a stable equilibrium in the long-term. Cooler summers lead to increased population size. Hotter summers produce complex dynamics. (c) Model 4 again, this time assuming the mean number of hot days. Minimum winter temperature near the mean ( $-4.32^{\circ}\text{C}$ ) yield the highest equilibrium population size. Extremely cold or warm winters shift the population to a lower equilibrium near extinction. Note different scales on y-axes. Graphs represent 2,000 generations for each temperature after 200,000 generations of attenuation time to avoid transient dynamics. Solid black areas indicate quasiperiodic cycles.

dent processes. Of particular interest, we found that the strength and form of density dependence can vary with climatic conditions, altering the timing and especially the magnitude of predicted outbreaks (Fig. 4c and d). Such variation in regulation means that the population is affected by multiple or moving equilibria and might help explain the dynamics of the large number of species with less periodic dynamics (Dwyer et al. 2004) and has already been successfully applied to a long-term dataset of sheep abundance (Berryman and Lima 2006). In the case of southern pine

beetles, hot summers change regulation from generally negative to a humped function characteristic of Allee effects, increasing the potential for both extinction and complex dynamics.

Taken in isolation from its abiotic environment, it does not seem that southern pine beetle is inherently an outbreaking pest. The long-term behavior of the east Texas southern pine beetle population under constant mean temperature conditions is a stable equilibrium approached through damped oscillations (midpoints of the x-axes in Fig. 5). Each year's unique temperature profile perturbs the population away from this equilibrium toward a different long-term state. For instance, a hotter than average summer pushes the population toward a lower equilibrium abundance. Southern pine beetle dynamics can be inherently complex when summers deviate from average temperatures, but the expected effect of climate depends on our understanding of the underlying endogenous process. Under model 1, complex cycles arise when summer temperatures are below average (5a). Under model 4, complexity arises in hot summers (Fig. 5b). Minimum winter temperature also affects model 4 behavior; southern pine beetles can only maintain outbreak levels within a discrete range of winter temperatures (Fig. 5c). Hence, different scenarios of climate change can have different long-term effects on the population.

Our study highlights the ecological importance of temperatures at either extreme of an organism's thermal niche. A meta-analysis by Jarosik et al. (2002) of many insect and mite genera confirmed that growth rates respond linearly to temperature within what the authors termed an "ecologically relevant" range of temperatures, but the authors discarded some extreme temperatures to obtain this result. Similarly, recent efforts to relate growth rates to chemical reaction kinetics have focused on linear approximations over small ranges in temperature (Gillooly et al. 2002). The standard shape of temperature-dependent growth curves, although nonlinear at its extremes, is nearly linear over an intermediate range of temperatures (Taylor 1981). However, the correlation between southern pine beetle population growth rates and extreme temperatures highlights the importance of considering nonlinear responses to temperature as well.

The southern pine beetle's most significant predator, the clerid beetle *T. dubius*, is an obvious candidate species for driving complex population dynamics in the southern pine beetle system (Turchin et al. 1999) because of its extended development time (Reeve 1997) and potential to cause high levels of mortality among both pine beetles adults and immature stages (Reeve 1997). Warm winters may lead to higher predator survival or emergence rates. It is reasonable to expect the effect of predators to be nonlinear, both because clerids are generalist predators with the potential for prey-switching (Dwyer et al. 2004) and because southern pine beetles can swamp predation pressure at high density (Reeve 1997). Bluestain fungus, *Ophiostoma minus* Hedge., may also drive inter-annual variation in southern pine beetle growth rate

(Lombardero et al. 2003). However, *O. minus* seems to have a direct (unlagged) effect on southern pine beetle growth rates (Reeve and Turchin 2002, Hofstetter et al. 2006a). *O. minus* reduces the survival of southern pine beetle brood through competition with the beetle's mutualistic fungi (Ayres et al. 2000, Lombardero et al. 2003). The prevalence and impact of fungal associates varies with temperature and season (Klepzig and Six 2004, Hofstetter et al. 2006b, 2007). Similar relationships hold for other southern pine beetle associates, e.g., *Monochamus* wood-boring beetles. *Monochamus* galleries are not present in winter-infested southern pine beetle trees. If the relative strength of direct and delayed density dependence in southern pine beetle population growth is geographically variable, it would be valuable to test for accompanying variation in the relative importance of fungal pathogens, arthropod predators, and competitors. By influencing the prevalence of clerid predators, *Monochamus* competitors, or *O. minus*, extreme temperatures may affect southern pine beetle population dynamics not only by changing the agent of regulation but by altering the lag in dominant ecological feedbacks. The combined direct and delayed density dependence in model 4 and the interaction of climate with regulation capture this complexity in a general way. Further observations and modeling are needed to understand the explicit community dynamics.

Why have southern pine beetles remained inactive in east Texas since 1997? All of the models tested projected high growth in the years 2000–2003. However, there is a subjective aspect to any study of population dynamics. For instance, the east Texas southern pine beetle time series can be viewed as a series of short outbreaks (our approach), as two extended outbreaks spanning decades each, or as a single prolonged outbreak lasting over 40 yr with a short interruption in the middle (Fig. 1c). The very decision of how to graph the data influences whether this organism seems to exhibit dramatic outbreak dynamics (suggested by a plot of raw infestation numbers, as in Reeve and Turchin 2002) or a fairly steady, large population size with dramatic intermittent crashes (suggested by a plot of log-transformed data, as in Fig. 1d). The endogenous behaviors of models 1 and 4 favor the latter interpretation; as much attention should be focused on the periods of low abundance between outbreaks as on the outbreaks themselves, because both phases are deviations from the system's "natural" state. Furthermore, the "natural" state seems to change with time. None of the models tested captured both the increase in the first half of the southern pine beetle time series and the decrease in its second half. Forest dynamics may be influencing southern pine beetle population growth. Likewise, both the depletion of suitable hosts in wilderness areas (Clarke and Billings 2003) and control efforts on managed land may have contributed to the sudden end of spot formation after 1997. Regardless of the explanation, it is important to recognize that the most stark fluctuation in southern pine beetle population size is at a scale greater than decades. At an even greater time scale,

the role of southern pine beetles as a primary agent of pine mortality likely increased after anthropogenic alteration of forest structure that followed indigenous and then European settlement of the area (Schowalter et al. 1981, Clarke et al. 2000). The current extent of pine forests on the National Forests in Texas was from reforestation programs of the 1930s after widespread deforestation early in that century (Wakely 1954). By 1960, stands were reaching the age class of highest susceptibility to southern pine beetle infestation (Lorio and Sommers 1981, Friedenber et al. 2007).

Our approach assumed a constancy of host availability and species interactions, except as indicated phenomenologically by the change in regulation with climate. As noted above, forest dynamics have surely driven the timing and magnitude of southern pine beetle outbreaks to some degree. Moreover, we know that key species interactions have not been constant over the entire study period. The abundance of clerid predators declined significantly through the 1960s and early 1970s because of the application of chemical treatments to southern pine beetle infestations (Williamson and Vite 1971). Chemical control was replaced by mechanical suppression methods (cut-and-remove and cut-and-leave) in east Texas in the early 1970s, allowing predator populations to recover. The loss of predators can increase the role of climate in population dynamics. For instance, climate has a greater influence on moose demography when wolves are rare (Wilmers et al. 2006). Even in light of the disparities between idealized models and reality, evidence for a role of extreme temperatures indicates that the southern pine beetle is a model system for exploring the response of local population dynamics and geographic ranges of insect pests to a changing climate.

### Acknowledgments

We thank E. Stange for useful comments on the manuscript. This work was supported by CSREES NRI 2004-35302-1482 to M.P.A. and Kier Klepzig and USDA Forest Service cooperative agreements with Lanworth, M.P.A., and N.A.F.

### References Cited

- Allee, W. C. 1931. Animal aggregations: a study in general sociology. University of Chicago Press, Chicago, IL.
- Anderson, R. M., and R. M. May. 1981. The population dynamics of microparasites and their invertebrate hosts. *Phil. Trans. Roy. Soc. Lond. B.* 291: 451–524.
- Andrewartha, H. G., and L. C. Birch. 1954. The distribution and abundance of animals. Chicago University Press, Chicago, IL.
- Ayres, M. P., R. T. Wilkens, J. J. Ruel, M. J. Lombardero, and E. Vallery. 2000. Nitrogen budgets of phloem-feeding bark beetles with and without symbiotic fungi (Coleoptera: Scolytidae). *Ecology* 81: 2198–2210.
- Beal, J. A. 1933. Temperature extremes as a factor in the biology of southern pine beetle. *J. Forestry* 31: 329–336.
- Berryman, A. A. 1996. What causes population cycles of forest Lepidoptera? *Trends Ecol. Evol.* 11: 28–32.
- Berryman, A. A., and M. Lima. 2006. Deciphering the effects of climate on animal populations: diagnostic analysis

- provides new interpretation of Soay sheep dynamics. *Am. Nat.* 168: 784–795.
- Berryman, A. A., B. Dennis, K. F. Raffa, and N. C. Stenseth. 1985. Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera, Scolytidae). *Ecology* 66: 898–903.
- Billings, R. F., and C. A. Kibbe. 1978. Seasonal relationships between southern pine beetle brood development and loblolly pine foliage color in east Texas. *Southwest. Entomol.* 3: 89–95.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer, New York.
- Byers, J. A. 1996. An encounter rate model of bark beetle populations searching at random for susceptible host trees. *Ecol. Model.* 91: 57–66.
- Clarke, S. R., and R. F. Billings. 2003. Analysis of the southern pine beetle suppression program on the national forests in Texas in the 1990s. *South. J. Appl. For.* 27: 122–129.
- Clarke, S., R. Evans, and R. Billings. 2000. Influence of pine bark beetles on the West Gulf Coastal Plain. *Texas J. Sci.* 52: 105–126.
- Crozier, L., and G. Dwyer. 2006. Combining population-dynamics and ecophysiological models to predict climate-induced insect range shifts. *Am. Nat.* 167: 853–866.
- Dwyer, G., J. Dushoff, and S. H. Yee. 2004. The combined effects of pathogens and predators on insect outbreaks. *Nature (Lond.)* 430: 341–345.
- Ellner, S. P. 2000. Defining chaos for real, noisy data: local Lyapunov exponents and sensitive response to perturbations. pp. 1–32. *In* J. N. Perry, R. H. Smith, I. P. Woiwod, and D. R. Morse (eds.), *Chaos in real data: the analysis of non-linear dynamics from short ecological time series*. Kluwer Academic Publishers, Boston, MA.
- Esper, J., U. Büntgen, D. C. Frank, D. Nievergelt, and A. Liebhold. 2007. 1200 years of regular outbreaks in alpine insects. *Proc. Roy. Soc. Lond. B.* 274: 671–679.
- Frazier, M. R., R. B. Huey, and D. Berrigan. 2006. Thermodynamics constrains the evolution of population growth rates: “Warmer is Better”. *Am. Nat.* 168: 512–520.
- Friedenberg, N. A., J. A. Powell, and M. P. Ayres. 2007. Synchrony’s double edge: transient dynamics and the Allee effect in stage structured populations. *Ecol. Lett.* 10: 564–573.
- Gagne, J. A., R. N. Coulson, J. L. Foltz, T. L. Wagner, and L. J. Edson. 1980. Attack and survival of *Dendroctonus frontalis* in relation to weather during three years in east Texas. *Environ. Entomol.* 9: 222–229.
- Gagne, J. A., T. L. Wagner, P. J. H. Sharpe, R. N. Coulson, and W. S. Fargo. 1982. Reemergence of *Dendroctonus frontalis* (Coleoptera: Scolytidae) at constant temperatures. *Environ. Entomol.* 11: 1216–1222.
- Gillooly, J. F., E. L. Charnov, G. B. West, V. M. Savage, and J. H. Brown. 2002. Effects of size and temperature on developmental time. *Nature (Lond.)* 417: 70–73.
- Gotelli, N. J., and A. M. Ellison. 2004. *A primer of ecological statistics*. Sinauer, Sunderland, MA.
- Grossman, G. D., R. E. Ratajczak, J. T. Petty, M. D. Hunter, J. T. Peterson, and G. Grenouillet. 2006. Population dynamics of mottled sculpin (Pisces) in a variable environment: information theoretic approaches. *Ecol. Monogr.* 76: 317–324.
- Gumpertz, M. L., C. Wu, and J. M. Pye. 2000. Logistic regression for southern pine beetle outbreaks with spatial and temporal autocorrelation. *For. Sci.* 46: 95–107.
- Hofstetter, R. W., J. T. Cronin, K. D. Klepzig, J. C. Moser, and M. P. Ayres. 2006a. Antagonisms, mutualisms, and commensalisms affect outbreak dynamics of the southern pine beetle. *Oecologia (Berl.)* 147: 679–691.
- Hofstetter, R. W., K. D. Klepzig, J. C. Moser, and M. P. Ayres. 2006b. Seasonal dynamics of mites and fungi and interaction with southern pine beetle. *Environ. Entomol.* 35: 22–30.
- Hofstetter, R. W., T. D. Dempsey, K. D. Klepzig, and M. P. Ayres. 2007. Temperature-dependent effects on mutualistic, antagonistic, and commensalistic interactions among insects, fungi, and mites. *Comm. Ecol.* 8: 47–56.
- Huey, R. B., and D. Berrigan. 2001. Temperature, demography, and ectotherm fitness. *Am. Nat.* 158: 204–210.
- Ito, Y. 1972. On the methods for determining density-dependence by means of regression. *Oecologia (Berl.)* 10: 347–372.
- Jarosik, V., A. Honek, and A.F.G. Dixon. 2002. Developmental rate isomorphy in insects and mites. *Am. Nat.* 160: 497–510.
- Kalkstein, L. S. 1976. Effects of climatic stress upon outbreaks of southern pine beetle (Coleoptera: Scolytidae). *Environ. Entomol.* 5: 653–658.
- Kalnay, E., M. Kanamitsu, R. Kistler, W. Collins, D. Deaven, L. Gandin, M. Iredell, S. Saha, G. White, J. Woollen, Y. Zhu, M. Chelliah, W. Ebisuzaki, W. Higgins, J. Janowiak, K. C. Mo, C. Ropelewski, J. Wang, A. Leetmaa, R. Reynolds, R. Jenne, and D. Joseph. 1996. The NCEP/NCAR 40-year reanalysis project. *Bull. Am. Meteorol. Soc.* 77: 437–470.
- Klepzig, K. D., and D. L. Six. 2004. Bark beetle fungal symbiosis: context dependency in complex interactions. *Symbiosis* 37: 189–206.
- Kroll, J. C., and H. C. Reeves. 1978. A simple predictive model for potential pine beetle activity in East Texas. *South. J. Appl. For.* 2: 62–64.
- Lih, M. P., and F. M. Stipan. 1996. Relationship of host tree diameter to within-tree southern pine beetle (Coleoptera: Scolytidae) population dynamics. *Environ. Entomol.* 25: 736–742.
- Logan, J. A., P. White, B. J. Bentz, and J. A. Powell. 1998. Model analysis of spatial patterns in mountain pine beetle outbreaks. *Theor. Pop. Biol.* 53: 236–255.
- Lombardero, M. J., M. P. Ayres, R. W. Hofstetter, J. C. Moser, and K. D. Klepzig. 2003. Strong indirect interactions of *Tarsonemus mites* (Acarina: Tarsonemidae) and *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Oikos* 102: 243–252.
- Lorio, P. L., Jr., and R. A. Sommers. 1981. Central Louisiana, pp. 23–29. *In* J. E. Coster and J. L. Searcy (eds.), *Site, stand, and host characteristics of southern pine beetle infestations*. U.S. Department of Agriculture, Washington, DC.
- May, R. M. 1976. Simple mathematical models with very complicated dynamics. *Nature (Lond.)* 261: 459–467.
- May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature (Lond.)* 269: 471–477.
- McCann, K., A. Hastings, S. Harrison, and W. Wilson. 2000. Population outbreaks in a discrete world. *Theor. Pop. Biol.* 57: 97–108.
- Michaels, P. J. 1984. Climate and the southern pine beetle in Atlantic Coastal and Piedmont regions. *For. Sci.* 30: 143–156.
- Nicholson, A. J. 1954. An outline of the dynamics of animal populations. *Aust. J. Zool.* 2: 9–65.
- Payne, T. L. 1980. Life history and habits, pp. 7–28. *In* R. C. Thatcher, J. L. Searcy, J. E. Coster, and G. D. Hertel (eds.), *The southern pine beetle*. U.S. Department of

- Agriculture Forest Service, Combined Forest Pest Research and Development Program, Pineville, LA.
- Perry, J. N., R. H. Smith, I. P. Woiwod, and D. R. Morse. 2000. Chaos in real data: the analysis of non-linear dynamics from short ecological time series. Kluwer Academic Publishers, Boston, MA.
- Powell, J. A., and J. A. Logan. 2005. Insect seasonality: circle map analysis of temperature-driven life cycles. *Theor. Pop. Biol.* 67: 161–179.
- Powell, J. A., J. L. Jenkins, J. A. Logan, and B. J. Bentz. 2000. Seasonal temperature alone can synchronize life cycles. *Bull. Math. Biol.* 62: 977–998.
- Pye, J. M., T. S. Price, S. R. Clarke, and R. J. Hugget, Jr. 2006. A history of southern pine beetle outbreaks in the southeastern United States through 2004. (<http://www.srs.fs.usda.gov/econ/data/spb/>).
- Quinn, G. P., and M. J. Keogh. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, United Kingdom.
- Raffa, K. F., and A. A. Berryman. 1983. The role of host plant-resistance in the colonization behavior and ecology of bark beetles (Coleoptera, Scolytidae). *Ecol. Monogr.* 53: 27–49.
- Reeve, J. D. 1997. Predation and bark beetle dynamics. *Oecologia (Berl.)* 112: 48–54.
- Reeve, J. D., and P. Turchin. 2002. Evidence for predator-prey cycles in a bark beetle, pp. 92–108. *In* A. A. Berryman (ed.), *Population cycles: the case for trophic interactions*. Oxford University Press, New York.
- Reynolds, L. V., M. P. Ayres, T. G. Siccama, and R. T. Holmes. 2007. Climatic effects on caterpillar fluctuations in northern hardwood forests. *Can. J. For. Res.* 37: 481–491.
- Royama, T. 1992. Analytical population dynamics. Chapman & Hall, New York.
- Schowalter, T. D., R. N. Coulson, and D. A. Crossley, Jr. 1981. Role of southern pine beetle and fire in maintenance of structure and function of the southeastern coniferous forest. *Environ. Entomol.* 10: 821–825.
- Sillett, T. S., R. T. Holmes, and T. W. Sherry. 2000. Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* 288: 2040–2042.
- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behavior, ecology, and conservation. *Trends Ecol. Evol.* 14: 401–405.
- Taylor, F. 1981. Ecology and evolution of physiological time in insects. *Am. Nat.* 117: 1–23.
- Texas Forest Service. 1984. Texas forest pest report 1982–1983. Texas Forest Service, College Station, TX.
- Thatcher, R. C., and L. S. Pickard. 1964. Seasonal variation in activity of southern pine beetle in east Texas. *J. Econ. Entomol.* 57: 840–842.
- Tran, J. K., T. Ylioja, R. Billings, J. Régnière, and M. P. Ayres. 2007. Impact of minimum winter temperatures on the population dynamics of *Dendroctonus frontalis* (Coleoptera: Scolytinae). *Ecol. Appl.* 17: 882–899.
- Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* 73: 289–305.
- Turchin, P., P. L. Lorio, Jr., A. D. Taylor, and R. F. Billings. 1991. Why do populations of southern pine beetles (Coleoptera: Scolytidae) fluctuate? *Environ. Entomol.* 20: 401–409.
- Turchin, P., A. D. Taylor, and J. D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285: 1068–1071.
- Ungerer, M. J., M. P. Ayres, and M. J. Lombardero. 1999. Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmermann. *J. Biogeogr.* 26: 1133–1145.
- Wagner, T. L., J. A. Gagne, P. J. H. Sharpe, and R. N. Coulson. 1984. A biophysical model of southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), development. *Ecol. Model.* 21: 125–147.
- Wakely, P. C. 1954. Planting the southern pines. U.S. Department of Agriculture, Washington, DC.
- Wallin, K. F., and K. F. Raffa. 2004. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecol. Monogr.* 74: 101–116.
- White, R. A., and R. T. Franklin. 1976. Activity of the southern pine beetle in response to temperature. *J. Ga. Entomol. Soc.* 11: 370–372.
- Williamson, D. L., and J. P. Vite. 1971. Impact of insecticidal control on the southern pine beetle population in east Texas. *J. Econ. Entomol.* 64: 1440–1444.
- Wilmers, C. C., E. Post, R. O. Peterson, and J. A. Vucetich. 2006. Predator disease outbreak modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecol. Lett.* 9: 383–389.
- Wilmers, C. C., E. Post, and A. Hastings. 2007. A perfect storm: the combined effects on population fluctuations of autocorrelated environmental noise, age structure, and density dependence. *Am. Nat.* 169: 673–683.
- Zhou, X., J. N. Perry, I. P. Woiwod, R. Harrington, J. S. Bale, and S. J. Clark. 1997. Temperature change and complex dynamics. *Oecologia (Berl.)* 112: 543–550.

Received 23 August 2007; accepted 10 February 2008.