

The Southern Pine Beetle and Pine Forest Ecosystems

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This paper describes a rudimentary deterministic model of a pine forest ecosystem inhabited by the southern pine beetle. Intraspecific scramble competition among pine beetle larvae plays a crucial role in the model, which successfully mimics observed “outbreaks” of the beetle population.

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Introduction

Dendroctonus frontalis, the southern pine beetle (SPB), is a highly destructive species of bark beetle that inhabits pine forests in the southern United States and parts of Central America. [6] In natural pine forests, the ecological role of the SPB presumably is to hasten the demise of weak or damaged trees, perhaps creating kindling for fires that contribute positively to the long-term health of the forest ecosystem. In commercial forests and developed residential areas, SPBs are responsible for hundreds of millions of dollars in timber losses annually. Compounding the problem is the fact that the value of salvaged timber is reduced due to staining by a “blue-stain” fungus, one of several symbiotic organisms associated with the SPB.

Outbreaks

SPB populations exhibit outbreak behavior similar to other forest insect pests, such as the eastern spruce budworm in Canada [2][9] and other bark beetles such as the mountain pine beetle in the western U.S. [8][1], typically persisting at low endemic levels for a number of years before rapid increase to epidemic levels and subsequent collapse. The causes of these outbreaks are not well understood and are often correlated with weather conditions.

Over the past several decades, many natural pine forests consisting mainly of longleaf and slash pines have been replaced by commercial stands of shortleaf and loblolly pines, which are less resistant to SPB attack. [6] This and other factors have contributed to an increase in the frequency, distribution, and severity of SPB outbreaks in the southern U.S. since the mid-20th century. During that period, outbreaks typically lasting for 2 to 3 years have been separated by 4 to 10-year intervals. [7]

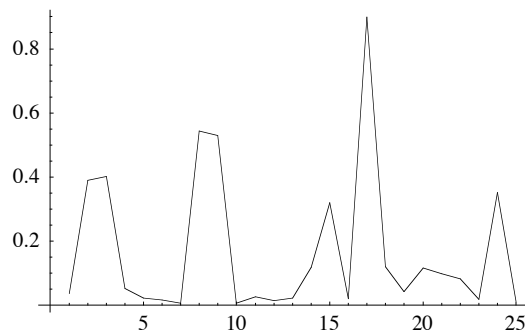


Fig. 1. Estimated SPB damage (cords / 10⁶) in Georgia between 1972 and 1996. [7]

There is no doubt that weather plays a major role in the dynamics of SPB populations. Mild winters, mild summers, and droughts are all favorable conditions for the SPB, while the opposite conditions are generally unfavorable. However, density-dependent factors are not as well understood and are likely also significant. Our goal in this work is to demonstrate that a simple, deterministic model of an SPB-forest ecosystem can exhibit outbreaks, suggesting—as hypothesized in [5]—that ecosystem-level SPB population dynamics may be the result of stochastic fluctuations superimposed on a deterministic oscillatory trend.

SPB-Tree Interaction

Female SPBs drill holes in the outer bark of host trees in order to lay eggs within the inner bark. SPB larvae then feed upon phloem tissue before emerging as adult beetles. For successful SPB reproduction, host trees must be killed in order to stop their defense mechanism, which consists of filling SPB-drilled holes with resin.

In order to achieve sufficient numbers to overwhelm a tree’s defenses, SPBs attract other SPBs by means of an aggregation pheromone. [6] The number of beetles necessary to kill a given tree depends upon the “vigor” of the tree, which typically decreases with the age of the tree and the density of the stand. Tree vigor is also negatively affected by tree wounding and environmental disruptions such as landscaping, road building, etc.

Intraspecific Scramble Competition

Recent research [4] has shown that the proportion of SPB larvae that survive to adulthood (“brood survivorship”) decreases sharply at high levels of infestation—*i.e.*, the intraspecific competition among beetle larvae is best classified as *scramble competition*. Thus, large SPB populations tend to have a low reproductive rate.

An Ecosystem Model

Variables

We let p denote a scaled average density of living trees, assumed proportional to the average attackable surface area per acre. We assume that $p = u + w$, where w represents the density of trees that are vulnerable to SPB attack, and u is the density of trees that are capable of fending off attack. A scaled average pine beetle density will be denoted by b .

Modelling Assumptions

The following assumptions are the basis of our model:

Time Scale

For convenience, our time scale is chosen so that one unit of time represents the average SPB life span, which we assume to be 8 weeks. Thus 1 year corresponds to 6.5 time units, and the per capita SPB death rate is 1.

Logistic Forest Growth

We assume that p satisfies a logistic growth equation when $b = 0$. By fitting this model to real data (from International Paper Co.), we obtain an intrinsic per capita growth rate of approximately $1/40$ per unit time. We assume further that p is scaled so that the stable equilibrium of this logistic model is at $p = 1$. So, when $b = 0$, we have

$$p' = \frac{1}{40} p(1 - p), \tag{1}$$

i.e.,

$$u' + w' = \frac{1}{40} (u + w)(1 - (u + w)). \tag{2}$$

We assume that surface area becomes vulnerable to SPB attack at a rate that is proportional to u and independent of b . Thus,

$$u' = \frac{1}{40} (u + w) (1 - (u + w)) - \alpha u, \quad (3)$$

where $\alpha > 0$, and, if $b = 0$,

$$w' = \alpha u. \quad (4)$$

Assuming that somewhere between 2% and 10% of SPB-resistant trees become vulnerable to attack each year, the corresponding range for the parameter α is roughly 0.003 to 0.015.

Rate of Tree Death by SPB

We assume that, due of SPB attack, w decreases at a rate given by $w \gamma_h(b)$, where the predatory functional response $\gamma_h(b)$ has the form

$$\gamma_h(b) = \frac{b^4}{h^4 + b^4}. \quad (5)$$

Note that $\gamma_h(h) = 1/2$ and $\gamma_h(b) \approx 1$ for “large” b . The following is a plot of $\gamma_{1/2}$.

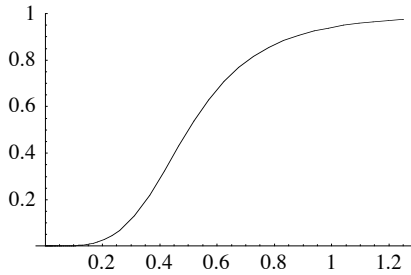


Fig. 2. Graph of $\gamma_{1/2}$.

Scramble Competition and SPB Birth Rate

We define *attack density* to be

$$\vartheta_\varepsilon = \frac{b}{\varepsilon u + (1 - \varepsilon) w}, \quad (6)$$

where $0 \leq \varepsilon \ll 1$. The parameter ε is small because SPBs are expected to have a strong preference for vulnerable trees. We assume that the per capita “birth” rate of SPBs is given by $\lambda w \sigma_\eta(\vartheta_\varepsilon)$, where $\lambda > 0$ and

$$\sigma_\eta(\vartheta) = \frac{6\eta^5 \vartheta}{5\eta^6 + \vartheta^6}. \quad (7)$$

This function is intended to model the rate of emergence of adult SPBs per unit surface area as a function of the attack density. [4] It attains a maximum value of $\sigma_\eta(\eta) = 1$, and its rapid decrease for attack densities above the threshold parameter η reflects the intraspecific scramble competition among SPB larvae. The following is a plot of σ_1 .

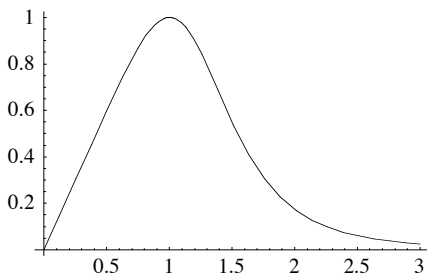


Fig. 3. Graph of σ_1 .

The parameter λ is related to the average number of eggs laid per female SPB, which can be as large as 30. [6] Since our model does not distinguish between male and female SPBs, reasonable values of λ should perhaps fall between 5 and 15. An appropriate range of values for η is not readily predictable.

SPB Immigration

We assume an SPB immigration rate given by kp , where $k > 0$. It is difficult to predict a reasonable range for k ; however, it is expected to be relatively small.

The Differential Equations

The foregoing assumptions give rise to the following system of ordinary differential equations:

$$\begin{aligned} u' &= \frac{1}{40} (u + w) (1 - (u + w)) - \alpha u \\ w' &= \alpha u - w \gamma_h (b) \\ b' &= b (\lambda w \sigma_\eta(\partial_\varepsilon) - 1) + k (u + w) \end{aligned} \tag{8}$$

Numerical Results

Periodic Outbreaks

Numerical experiments show that the b component of solutions of (8) exhibits periodic “outbreaks” for a variety of sets of reasonable parameter values. Two such cases are illustrated in Figures 4 and 5.

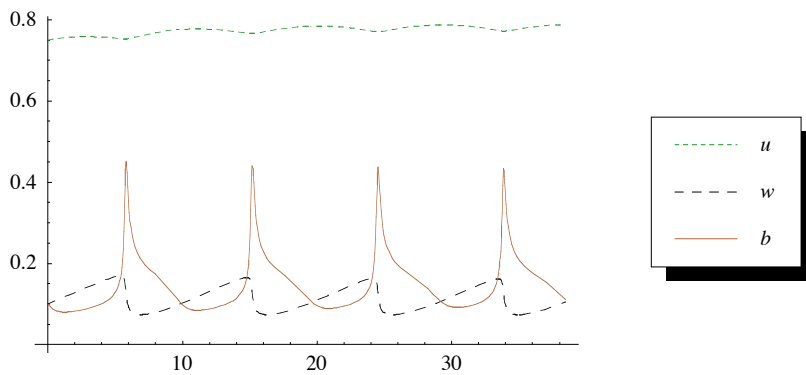


Fig. 4. A solution of (8) with $\alpha = .003$, $h = .5$, $\lambda = 10$, $\varepsilon = .05$, $\eta = 2$, $k = .057$. (Horizontal scale in years.)

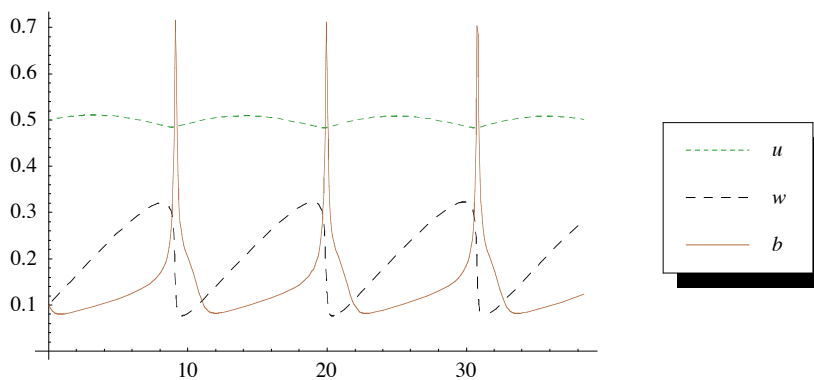


Fig. 5. A solution of (8) with $\alpha = .01$, $h = .5$, $\lambda = 9$, $\varepsilon = 0$, $\eta = 3$, $k = .09$. (Horizontal scale in years.)

Sensitivity to Parameter Values

Numerical experiments show that small changes in any of the parameters in (8) may result in the destruction or destabilization of a stable steady state. We give one illustration as follows.

The following plot shows a stable steady state for the following set of parameter values:

$$\alpha = 0.0077, h = 0.33, \lambda = 10, \varepsilon = 0.12, \eta = 1, k = 0.0185 \quad (9)$$

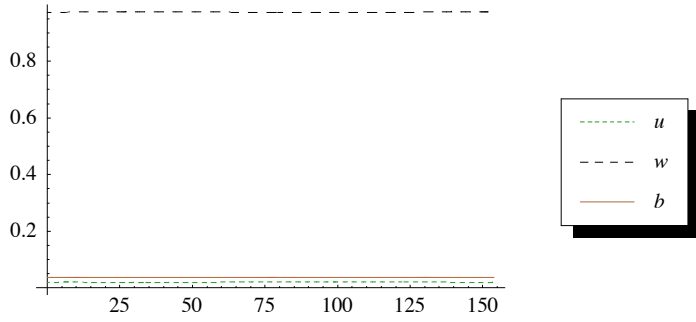


Fig. 6. A solution of (8) with the parameter values in (9). (Horizontal scale in years.)

Each plot in the following table results from a small change in *one* of the parameters from its value in (9). The changed value is indicated below each plot.

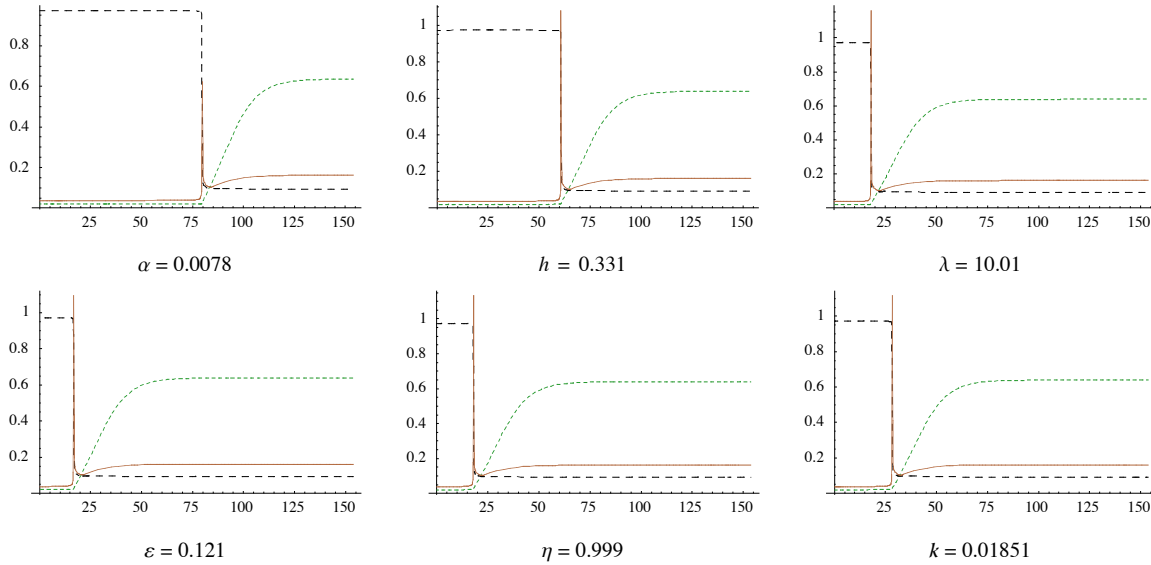


Fig. 7.

Reduction to a Two-component Model

Some insight into the behavior of solutions of (8) can be gained by reducing (8) to an approximating pair of differential equations for w and b and viewing the resulting phase portrait. To accomplish this, we will assume that surface area becomes susceptible to SPB attack at a constant rate, which is tantamount to assuming that u is constant in the preceding development.

Thus we have the following differential equations for w and b , where u is treated as a parameter:

$$\begin{aligned} w' &= \alpha u - w \gamma_h(b) \\ b' &= b(\lambda w \sigma_\eta(\partial_\varepsilon) - 1) + k(u + w) \end{aligned} \quad (10)$$

The diagram on the left below shows the nullclines associated with (10) for parameter values $\alpha = .003$, $u = 1$, $h = .5$, $\lambda = 12$, $\varepsilon = .04$, $\eta = 2$, and $k = .03$. The graph on the right shows the same nullclines along with an orbit that approaches the stable equilibrium point.

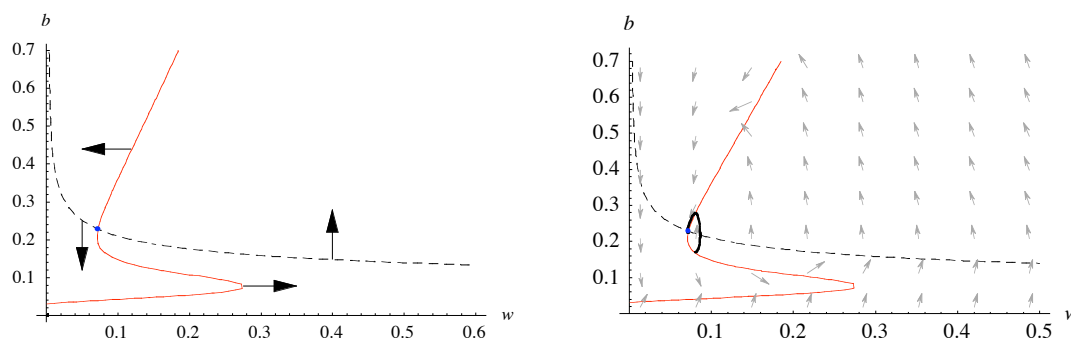


Fig. 8.

The diagram on the left below shows the nullclines associated with (10) for parameter values $\alpha = .003$, $u = 1$, $h = .5$, $\lambda = 10$, $\varepsilon = .05$, $\eta = 2$, and $k = .035$. The graph on the right shows the same nullclines along with a stable limit cycle.

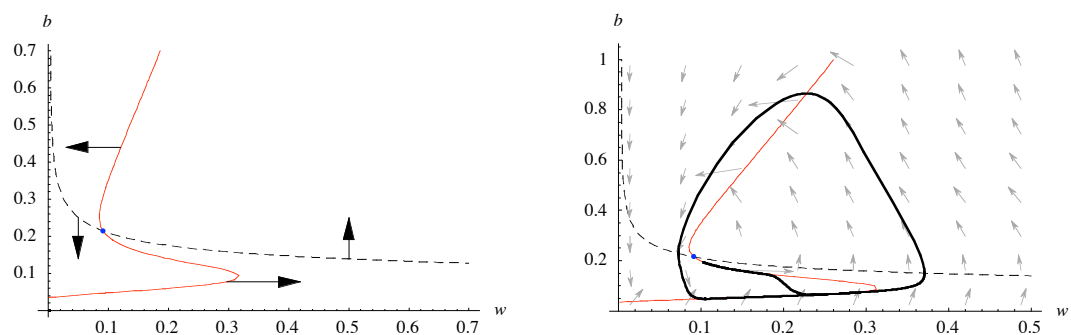


Fig. 9.

These examples make it clear that a bifurcation occurs as the upper extreme point on the S-shaped b -nullcline crosses over the (dashed) w -nullcline.

Discussion

We have presented a plausible deterministic model of an SPB-forest ecosystem that is capable of mimicking periodic SPB outbreaks. Numerical experiments also show that the system is highly structurally unstable in the sense that a stable equilibrium can be destabilized by a small change in any of the six parameters in the model, giving rise to an SPB outbreak. It is sensible to expect some of these parameters to vary somewhat predictably with weather conditions, while others, such as the immigration rate k , may fluctuate far more unpredictably.

It is interesting to compare this model to the well-known spruce budworm model [2], as the dynamics are quite similar. The following is a version of the spruce budworm model, in which φ and b represent foliage and budworm density, respectively:

$$\begin{aligned} \varphi' &= k_1 \varphi (1 - \varphi) - \mu b \\ b' &= k_2 b \left(1 - \frac{b}{\alpha \varphi}\right) - \rho \frac{b^2}{\beta^2 \varphi^2 + b^2} \end{aligned} \tag{11}$$

This model produces the following isoclines, direction field, and periodic orbit, which are similar to those of Figure 9.

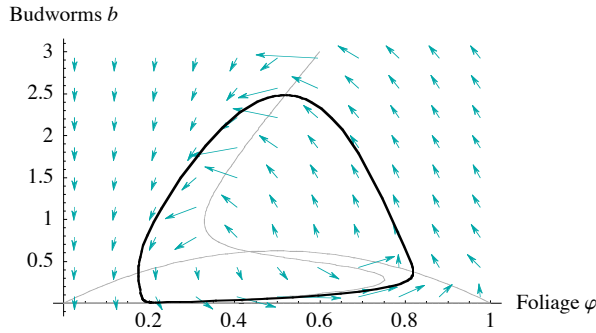


Fig. 10. Periodic solution of the spruce budworm model

In particular, an S-shaped b -nullcline (*beetle* or *budworm*) arises in both models, yet for quite different reasons. It arises in the spruce budworm model primarily due to the (saturating) predation term $-\frac{\rho b^2}{\beta^2 \varphi^2 + b^2}$, which accounts for predation by an assumed constant bird population. In our SPB model, the S-shape of the b -nullcline arises due to the SPB *birth* rate, which, as a result of intraspecific scramble competition, takes the somewhat similar form (here with $\varepsilon = 0$ for simplicity)

$$\lambda w \sigma_{\eta}(\vartheta_0) = \lambda \frac{6\eta^5 b^2 w^6}{5\eta^6 w^6 + b^6}.$$

Appendix

Mathematica Code

The following *Mathematica* code may be used to produce plots like those in Figures 4–7.

```

ϑ[t_] :=  $\frac{b[t]}{\varepsilon u[t] + (1 - \varepsilon) w[t]}$ ;
sys := {
  u'[t] ==  $\frac{1}{40} (u[t] + w[t]) (1 - u[t] - w[t]) - \alpha u[t]$ ,
  w'[t] ==  $\alpha u[t] - \frac{w[t] b[t]^4}{h^4 + b[t]^4}$ ,
  b'[t] ==  $b[t] \left( \frac{\lambda w[t] (6 \eta^5 \vartheta[t])}{5 \eta^6 + \vartheta[t]^6} - 1 \right) + k (u[t] + w[t])$ ,
  u[0] == 0.5, w[0] == 0.1, b[0] == 0.02}

Needs["Graphics`"]

makeplot[params_, tmax_] :=
  (soln = {u[t], w[t], b[t]} /.
    First[NDSolve[Evaluate[sys /. params], {u[t], w[t], b[t]}, {t, 0, tmax}]]);
  Plot[Evaluate[soln /. t -> 6.5 t], {t, 0, tmax / 6.5}, PlotRange -> All,
    PlotStyle -> {{ForestGreen, Dashing[ {.01, .01} ]}, Dashing[ {.02, .02} ]}, Sienna},
    PlotLegend -> {"u", "w", "b"}, LegendPosition -> {1.2, -.25},
    LegendSize -> {.5, .5}, LegendTextSpace -> .5])

makeplot[{α -> .004, h -> .3, λ -> 10, ε -> .12, η -> 1, k -> .027}, 250];

```

References

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