Quantitative Ecology and Resource Management
APPLIED QUALIFYING EXAMINATION INSTRUCTIONS
Spring Quarter 2012 (June 13-19, 2012)

This exam includes:
- 4 examination questions, hard copy of data and 1 reference article
- one data set (text file attachment) was emailed to you

Please open the attachments immediately and confirm by email that you are able to open all attachments.

INSTRUCTIONS:

1.   Your unique ID number is: *(emailed to you)*. Please list this ID number on the top of each page.
     DO NOT INCLUDE YOUR NAME ON THE EXAM.

2.   Number each page of the exam. Appendices should also be numbered so that any reference to the appendix refers to a particular set of pages.

3.   Provide a 1-3 page summary at the beginning of your exam.

4.   Your write-up should include a narrative (including any pasted in tables, graphics, etc.) for each question showing the thought process of the analysis, the results at each step, and how that leads to the next step.

5.   Clearly describe in your text the points that any diagrams or tables demonstrate.

6.   All graphs should be clearly labeled and computer output annotated as need be.

7.   Please send an electronic copy of your exam (PDF format) and any appendices, *directly to Joanne* at jbesch@u.washington.edu, **no later than 12:00 p.m. on Tuesday, June 19th**. She will forward an electronic copy to each exam committee member.

LIBRARY HOURS:

REMEMBER libraries will most likely be CLOSED Saturday and Sunday, so any reference materials you may need should be checked out before then.

QUESTIONS?

Hong Qian (Question #1): By email at hqian@u.washington.edu

Vladimir Minin (Question #2): By email at vminin@u.washington.edu. Cell phone: 310-254-6101

Loveday Conquest (Question #3):
- Between 8:00 a.m. and 5:00 p.m. weekdays (6/13-15 and 6/18-19) email Loveday (conquest@u.washington.edu) or call on her office phone (206-543-1708).
- After 5:00 p.m. weekdays and all-day on the weekend it is best to reach her at her home number (206-325-7237) since she does not have email at home.

Sandor Toth (Question #4): Please note that Sandor will be leaving for Europe on Monday, June 18th. If you need to contact him it would be best to do so by Friday, June 15th. He can be reached by email at toths@u.washington.edu, office phone: 206-616-2738, cell: 206-518-4978.

If you need to reach Joanne you may email her at jbesch@u.washington.edu, office phone (206-616-9571), or cell phone 206-661-5054.

Good luck!

Beetles and Trees

Question 1

Background

We shall be interested in a problem that is motivated by the bark beetle *Ips typographus* attacking Norway spruce *Picea abies*. The mathematical model will focus on the dynamics during the initial attacking phase, a few hours to a few days, rather than the later tree conquering stage. In the early phase, the ecological struggle is between the amount of resin flowing and the number of beetles at the surface of a tree trunk or branches.

   We shall let $R(t)$ denote the surface density of resin on a tree, and $A(t)$ denotes the number of attacking beetles on a tree, the trunk or branches, at time t.

   Quantifying the resin. Let $f_2(A)$ be the rate of resin loss, due to the holes on a tree resulted from beetle attack, per unit amount of resin. It is a function of the number of attacking beetles. f_2 is called *specific rate*; the total rate then will be $f_2(A) \times R$.

   The production of resin is determined by the physiological state of a tree, called *vigour*, which in turn is a function of the A. We shall assume that this rate is not a function of the amount of surface resin; the physiological state of the tree, however, is a function of A, the number of attacking beetles.

   Combining the production and loss, one has

$$\frac{dR}{dt} = f_1(R) - f_2(A)R. \tag{1}$$

   The dynamics of beetle population. We assume there is a constant source of beetles in the environment with density N_0. They are attracted to a tree due to pheromone signaling from the attacking beetle A. The production of pheromones by attacking beetles is tiggered by the tree resin: Bark beetles utilize host-tree monoterpenes, a class of organic compounds

1

and the major components of resin. It is a biosynthetic building blocks for the pheromones. Therefore, the "per capita birth rate" is given be $N_0 b(R)$.

On the other hand, the beetles die (or drown) in resin. We denote the per capita death rate as $d(R)$.

The population dynamics of attacking beetles, then is

$$\frac{dA}{dt} = \Big(N_0 b(R) - d(R) \Big) A \tag{2}$$

The simple Stenseth model.

$$
\begin{align}
f_1(A) &= a_0 - a_1 A, \tag{3} \\
f_2(A) &= b_0 - b_1 A, \tag{4} \\
b(R) &= c_1 R - c_2 R^2, \tag{5} \\
d(R) &= d_1 R, \tag{6}
\end{align}
$$

in which a's, b's, c's and d_1 are all positive. Stenseth further assumed that

$$\frac{b_0}{b_1} > \frac{a_0}{a_1}. \tag{7}$$

Questions Part A: Deterministic dynamics

Please analyze the beetle-tree dynamic model given by Eqs. 1-7. You should consult and evaluate the attached paper by N.C. Stenseth ["A model for the conquest of a tree by bark beetles", *Holarctic Ecology*, vol. 12, 408–414 (1989).] Please compare your results with those in the paper. Please include the following items in your answer:

(a) Will the dynamics given by Eqs. 1-7 remain in the frist, positive quadrant? If yes, please show it; if not, what does it mean?

(b) Briefly describe the ecological meaning of the terms in this model, as well as the biological implications for the functional forms and parameters.

(c) Non-dimensionalize the system of differenetial equations and simplify it into the form

$$\frac{dx}{d\tau} = (\rho - y)\, xy, \tag{8}$$

$$\epsilon \frac{dy}{d\tau} = 1 - x - (1 - \sigma x)\, y. \tag{9}$$

Give the new parameters ϵ, σ and ρ in terms of the original parameters. While all the original parameters are non-negative, which, if any, of these new parameters can be negative? What does Eq. 7 correspond to?

(d) What and where are the isoclines for the system of Eqs. 8 and 9? When is the y-isocline non-monotonic?

Where in the phase plane does the beetle population increases and/or decreses; and for the amount of resin?

(e) What is the nature (focus, node, saddle point, etc.) and the stability of each steady state?

(f) Is there the possibility of bistability? Under what condition?

(g) Assuming $\epsilon \ll 1$, try to simplify the mathematics. Thoroughly study the simplified mathematical model for different scenarios including at least

[i]: $0 < \sigma, \rho < 1$,

[ii]: $\sigma \rho > 1$.

Questions Part B: Stochastic dynamics

We shall now re-interpret the x and y in Eqs. 8 and 9: We assume that resin, y, is produced and lost by discrete particles, with production rate $\frac{1}{\epsilon}(1+\sigma xy)$ and degradation rate $\frac{1}{\epsilon}(x+y)$. Similarly, the immigration (birth) and death rates for attacking beetles, x, are ρxy and xy^2, respectively.

(h) Let $N(t)$ and $M(t)$ be the integer random variables representing the number of resin particles and number of beetles, respectively, at time t. Draw the *state transition* diagram for the stochastic model, and lable all the transitions.

(i) What is the relation between the interior steady state obtained in Part I, and the stationary probability distribution $\Pr\{M = m, N = n\}$ for the stochastic model? Justify your answer(s).

(j) Again assuming $\epsilon \ll 1$, try to reduce the stochastic model to a one-dimensional birth-death process.

(k) Obtain the stationary distribution for the one-dimensional system you obtained in (i); also discuss the *conditional probability* for surviving population.

Question 2

Consider the first stochastic model for the bark beetle and Norway spruce dynamics from Question 1. According to this model, the number of attacking beetles, M_t, and the number of resin particles, N_t, evolve in time as a continuous-time Markov chain (CTMC), (M_t, N_t) on the state space $\{0, 1, 2 \ldots\} \times \{0, 1, 2 \ldots\}$. The infinitesimal rates of the process are

$$\lambda_{(m,n),(k,l)} = \begin{cases} \rho mn & \text{if } k = m+1, l = n, \\ mn(n-1) & \text{if } k = m-1, l = n, \\ \delta(1 + \sigma mn) & \text{if } k = m, l = n+1, \\ \delta(m+n) & \text{if } k = m, l = n-1, \\ 0 & \text{otherwise.} \end{cases}$$

(a) Write a computer program to simulate random paths of the above process on a finite time interval. Set $\rho = 50$, $\sigma = 1.0$, $\delta = 100$, $(M_0, N_0) = (100, 20)$ and plot 10 random paths of both variables on the interval $[0, 4^{-4}]$.

(b) Using the same parameter values, estimate the probability of attacking beetles going extinct during the time interval $[0, 4^{-4}]$.

(c) Suppose we observe the bark beetle and Norway spruce dynamics continuously on the time interval $[0, T]$. Write down the log-likelihood of such a fully observed CTMC in terms of the following sufficient statistics:

$$R = \sum_{m=1}^{\infty} \sum_{n=1}^{\infty} d_T(m, n) mn,$$

$$Q = \sum_{m=0}^{\infty} \sum_{n=0}^{\infty} d_T(m, n)(m + n),$$

$K_m^+ = $ number of $m \to m+1$ transitions,

$K_n^+ = $ number of $n \to n+1$ transitions,

$K_n^- = $ number of $n \to n-1$ transitions,

where $d_T(m, n)$ denotes the amount of time the process spent in state (m, n) during the time interval $[0, T]$.

(d) Assume that σ is known and equal to 1. Derive analytic formulae of the maximum likelihood estimators of ρ and δ in terms of the above sufficient statistics.

(e) Derive the observed Fisher information matrix for the estimators in part (d).

(f) Use one of the simulated paths from part (a) to estimate ρ and δ, fixing $\sigma = 1$. Use the derived Fisher information matrix to compute asymptotic 95% confidence intervals for ρ and δ.

Question 3

Scientists wish to investigate the relationship between mortality from a particular type of beetle disease, the size of a tree (female beetles seem to like to attack larger trees), whether a tree has been subjected to low intensity burning, and mortality from beetle disease. Pine trees of a particular species have been subjected to low intensity burning (a management practice which kills the understory but allows the pine trees to survive—this may, however, make them more susceptible to beetle attacks). There are also controls which have not been subjected to burning. Trees with similar characteristics have been "binned" to obtain denominators > 1 when computing mortality.

Build a statistical model that relates beetle disease mortality to the given predictor variables: whether trees underwent low intensity burning or not, and a size index based upon DBH (diameter at breast height). Be sure to include diagnostics that justify your choice of model.

Summarize your results by describing what happens to mortality from beetle disease as one moves along the size index, and the effects of the burning treatment.

Question 4

Bark beetles (*Scolytinae*) can cause significant damage to forestlands both in North America and Europe. The Mountain pine beetle (*Dendroctonus ponderosae*), as an example, has destroyed most of the Lodgepole pine (*Pinus concorta*) forests in interior British Columbia, Canada and in some of the Rocky Mountain regions in the United States. Once the beetles appear in a forest stand of one of their two primary host species, Lodgepole or Ponderosa pine (*Pinus ponderosa*), the population grows exponentially (say at rate r) until the threshold capacity of the host (τ) is reached. When this happens, the beetles move on to a different stand (if one is available) during their host selection flight, and the process starts over again. The only economically viable method that is available for forest managers to fight the beetles is to cut or thin the stands that are susceptible to damage. Let x_{nt} (binary) denote the decision whether to treat (i.e., to cut) stand n in time period t or not. Let p_{nt} (positive continuous) denote the expected population level of the beetles in stand n in time t. When a treatment action occurs in a stand in say time t, it is assumed that the population of beetles in that stand will be zero in the subsequent period.

a. Your first task is to develop a spatially and temporarily explicit linear-integer programming model that would optimally allocate treatments to a set of stands (say set N, indexed by n) over a set of planning periods (set T indexed by t). The objective of the model is to minimize the sum of expected pine beetle infestations (population) over all stands at the end of the planning horizon (at time $|T|$) subject to a budget constraint. Assume that the population level in a given stand at time t, p_{nt}, depends on three things: (1) whether stand n was treated in time t-1, (2) whether the population has reached the host capacity in time t-1, and (3) on the population levels in time t-1 in both stand n and in all of the other stands. If stand n was treated in time t-1, or if the host capacity in stand n was reached in t-1, $p_{nt} = 0$. Otherwise, p_{nt} will be equal to the population that is expected to remain in stand n plus the expected immigration into stand n from all of the other stands, compounded by the exponential growth rate of r. Let $0 \le \pi_{mn} \le 1$ represent the probability that, in any time t, beetles in stand m will disperse to stand m in the subsequent period (π_{nn} represents the probability that the pest stays in stand n). Assume that $\sum_m \pi_{nm} = 1$ for each $m \in N$, and that the initial population levels in each stand (p_{n0}) are given based on data from field traps and remote sensing. Make sure that you clearly define the variables and parameters that you use in your model. Explain in detail how your objective function and the constraints work. (**10 pts.**)

b. Apply the model you developed in Part a.) to the hypothetical forest outlined below (Fig. 1). Assume that $p_{10} = 2$, $p_{i0} = 0$ $\forall i \in N \setminus \{1\}$, $r = 9$, and $\tau = 8$ for all 25 stands. Mimmiccing a northwesterly predominant wind direction, assume also that $\pi_{mn} = 0.3$ if $n = m$, $\pi_{mn} = 0.15$ for the 3 stands that are located south and east of stand m,

$\pi_{mn} = 0.05$ for the 5 stands that are one removed but still located south and east of stand m, and $\pi_{mn} = 0$ for stands that are further removed.

1	2	3	4	5
6	7	8	9	10
11	12	13	14	15
16	17	18	19	20
21	22	23	24	25

Fig. 1. A hypothetical forest landscape (the numbers index the stands)

```
case.id deaths trees treatment size
1 1 47 burn 10.1
2 3 63 burn 10.3
3 7 80 burn 10.5
4 4 75 burn 10.7
5 3 76 burn 10.9
6 5 83 burn 11.1
7 1 98 burn 11.3
8 7 57 burn 11.5
9 5 51 burn 11.7
10 3 60  burn 11.9
11 5 62  burn 12.1
12 3 68  burn 12.3
13 6 79  burn 12.5
14 7 61  burn 12.7
15 8 85  burn 12.9
16 5 79  burn 13.1
17 15 81 burn 13.3
18 17 89 burn 13.5
19 15 71 burn 13.7
20 11 74 burn 13.9
21 8 66  burn 14.1
22 5 51  burn 14.3
23 8 60  burn 14.5
24 10 71 burn 14.7
25 17 77 burn 14.9
26 16 83 burn 15.1
27 17 82 burn 15.3
28 10 69 burn 15.5
29 18 85 burn 15.7
30 14 86 burn 15.9
31 12 49 burn 16.1
32 16 65 burn 16.3
33 14 61 burn 16.5
34 18 76 burn 16.7
35 12 89 burn 16.9
36 13 59 burn 17.1
37 19 76 burn 17.3
38 14 64 burn 17.5
39 23 89 burn 17.7
40 26 88 burn 17.9
41 15 75 burn 18.1
42 1 53 control 10.1
43 3 68 control 10.3
44 1 62 control 10.5
45 3 56 control 10.7
```

```
46 3 85 control 10.9
47 2 50 control 11.1
48 1 80 control 11.3
49 2 70 control 11.5
50 3 47 control 11.7
51 2 56 control 11.9
52 5 82 control 12.1
53 2 59 control 12.3
54 3 65 control 12.5
55 6 67 control 12.7
56 6 87 control 12.9
57 2 60 control 13.1
58 8 51 control 13.3
59 9 57 control 13.5
60 12 77 control 13.7
61 8 73 control 13.9
62 8 82 control 14.1
63 5 65 control 14.3
64 8 78 control 14.5
65 7 73 control 14.7
66 12 69 control 14.9
67 11 76 control 15.1
68 11 70 control 15.3
69 5  53 control 15.5
70 14 83 control 15.7
71 19 75 control 15.9
72 12 62 control 16.1
73 16 84 control 16.3
74 9  50 control 16.5
75 12 67 control 16.7
76 9  55 control 16.9
77 13 75 control 17.1
78 15 77 control 17.3
79 14 81 control 17.5
80 17 83 control 17.7
81 14 77 control 17.9
82 9  59 control 18.1
```

A model for the conquest of a tree by bark beetles

Nils Chr. Stenseth

Stenseth, N. C. 1989. A model for the conquest of a tree by bark beetles. – Holarct. Ecol. 12: 408–414.

A model for the interaction between attacking bark beetles and a tree is developed and discussed. It is shown that in addition to the more intuitive outcomes where the tree wins or the beetles win, it is also deduced that under certain conditions there may exist a stable coexistence (at least for some period of time) between the beetles and a living tree. Finally, it is demonstrated that the outcome of the tree-beetle interaction often depends on initial conditions such as the number of colonizing beetles.

These results are discussed with reference to empirical findings, as well as to the development of proper population dynamics models for bark beetles in a forest stand, and models developed for assisting forest managers in avoiding bark beetle outbreaks and for minimizing the damage caused by a bark beetle outbreak.

Nils Chr. Stenseth, Division of Zoology, Dept of Biology, University of Oslo, P.O. Box 1050, Blindern, N-0316 Oslo 3, Norway.

Introduction

To a large extent, ecology is the study of dynamic interactions and their emerging dynamic behaviour. It is a difficult field of study, particularly because our intuition often fails. By its nature, ecological dynamics is an abstract field, incorporating such abstract concepts as density, density dependence, etc.; in this field, mathematical modelling is often of great help (e.g., Roughgarden 1979, Stenseth 1984). It is often easier to describe the anatomy of a species or to quantify and describe the nature of pheromones: these fields of study do not often involve such abstract quantities. The relative ease of study does not, of course, say anything about the importance of the various fields. In fact, the various fields of study often depend mutually upon each other. The description of bark beetle pheromones represents, for instance, an essential basis for theoretical studies on bark beetle populations dynamics (e.g., Berryman et al. 1984, Berryman and Stenseth 1989, Stenseth 1989). Theoretical studies, on the other hand, often help us understand how the pheromones produced by a group of beetles affect the future development and dynamics of the beetle population.

Even though mathematical modelling is, to most of us, of great help in our efforts to understand the dynamic consequences of a set of assumptions about the

way the world is organized, it is of course important to realize that mathematics is not essential for understanding the nature around us. It can only help us in our reasoning. The best proof of that is Darwin: he never developed a mathematical model as part of his work on the dynamics of evolution; nevertheless, he did get most of it right. Mathematics is of *help*, however, in our efforts to see patterns in the world around us, and in our efforts to deduce null hypotheses to be tested against empirical observations. Such hypotheses may then be compared by applying various statistical methods. Hence, mathematical modelling and statistical hypothesis testing become important quantitative *tools* in ecology, as in several other fields of study.

In this paper I present a simple mathematical model describing the dynamic interactions between bark beetles (Coleoptera: Scolytidae) attacking a living tree and the tree trying to fight off such an attack. The success of the beetles depends to a large extent on their cooperation, mediated by the pheromones being produced and the vigor of the tree. The success of the tree depends, on the other hand, on its ability to respond to an attack, an ability which itself depends upon the tree's vigor. In this paper, I am in particular concerned with finding the conditions which favour the beetles being able to conquer the tree and those conditions which favour the tree winning. Earlier we have discussed a related problem
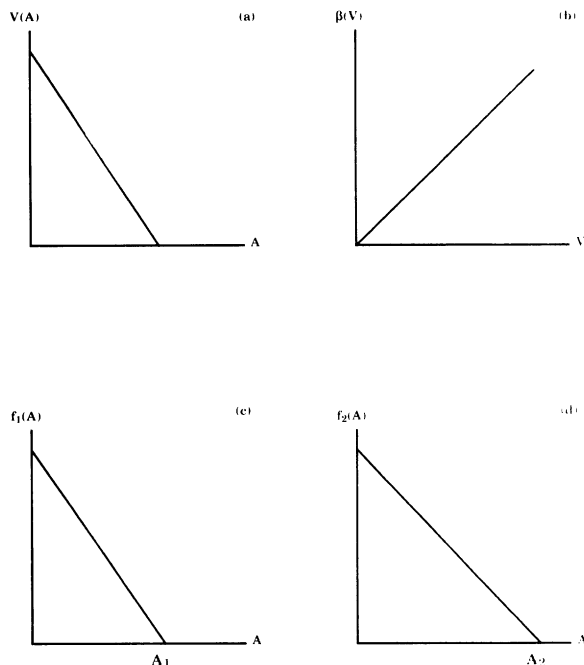
Fig. 1. Components of the model (Eq. (3)) describing the dynamics in the tree-equation. (a): The tree's vigor as a function of bark beetle density on the tree. (b): Production rate of resin as a function of tree vigor. (c): Combining a and b gives a function f, see Eq. (2) and the main text. (d): The rate of resin leaking out on the tree.

also with reference to bark beetles (Berryman et al. 1985): given that the tree wins, what should the optimal attack density be. Consequently, in the present paper I need to be less concerned with the actual value of the beetle density in a successfully conquered tree. Rather, I focus on whether or not the tree is conquested and on the dynamics during the initial attack phase.

Bark beetles are a kind of parasite. In contrast to many other types of parasites, bark beetles do not seem to have the ability to inhibit host defensive reactions (e.g., Raffa and Berryman 1983). Instead the so-called "aggressive" or "primary" bark beetle species seem to rely on behaviours resembling cooperation in order to overwhelm host defense. By rapidly concentrating on selected trees in response to aggregation pheromones, bark beetles are capable of intensifying the strength of their attack and thereby possibly exhausting the host's defensive systems (Miller and Keen 1960, Vité et al. 1972, Safranyik et al. 1975, Berryman 1976, Christiansen 1985). It is assumed that the outcome of the interaction between the attacking beetles and the tree depends on whether the number of attacking beetles exceeds a certain tree-specific threshold (Thalenhorst 1958, Wood 1972, Berryman 1978, Mulock and Christiansen 1986). It is furthermore known that resistance capacity varies between trees, and sometimes within trees, depending on the energy available for defensive metabolism (Wright et al. 1979, Miller and Berryman 1985, Chris-

tiansen and Ericsson 1986). The dynamic properties of these interactions are, however, very poorly understood. This is particularly so because the beetle-tree interaction involves several positive and negative feedback loops.

The model

Preamble

I consider the bark beetle *Ips typographus* attacking Norway spruce *Picea abies*.

A tree under attack tries to fight off the beetles by secreting resin and by actively synthesizing and/or mobilizing additional defensive compounds at the attack site (Miller and Keen 1960, Smith 1963, Berryman 1969, 1972). By so doing, the tree either drowns the beetles or forces them to leave the attacked tree. The beetles, on the other hand, may overcome this resistance by producing pheromones and thereby attracting more beetles. Bark beetles utilize host monoterpenes as precursors and synergists to their attractant pheromones (e.g., Silverstein 1969, Borden 1974). As stated in the Introduction, it is not at all clear what the outcome of the beetle-tree conflict will be under various conditions. That is why it is worth while to develop a mathematical model for studying this process.

The model I have developed is a differential equation, continuous time, model. The time horizon I have in mind spans from a few hours to a few days. The dynamic variables of my model are the density of beetles actually *on* the tree or underneath the bark, and the amount of resin flow per surface area of tree branch.

The tree's response to a beetle attack

In response to a beetle attack, the tree fights back by increasing its production of resin. Since the attacking beetles bore holes in the tree, the resin may, however, drain out at a faster rate than it otherwise would do.

Let R measure the amount of resin flow, and A the density of attacking beetles (i.e., number of beetles *on* the tree trunk or branch). The resin will run out of the tree as a result of bark beetle attack holes, at a *specific* rate determined by a function $f_2(A)$ which decreases with increasing values of A (Fig. 1d.); for simplicity we assume a linearly decreasing function:

$$f_2(A) = b_o - b_s \cdot A, \tag{1}$$

where b_o and b_s are fixed positive numbers. Let A_2 be defined as the solution to $f_2(A_2) = 0$.

The production of resin is given by a rate function $f_1(A)$. This function is determined by the vigour of the tree. Assume that the vigour, V, is given as a function of beetle density, A; i.e., V(A) (see Fig. 1a). Assume further that the production of resin increases with vigour according to a function $\beta(V)$ (see Fig. 1b). Then,
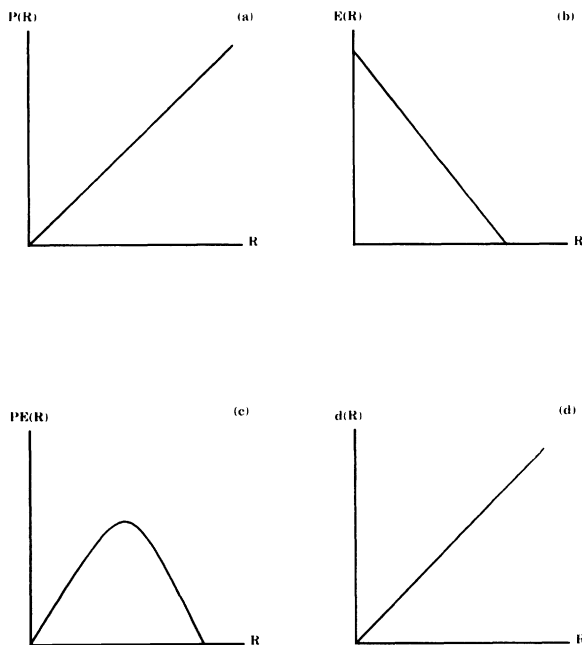
Fig. 2. Components of the model (Eq. (7)) describing the dynamics in the beetle-equation. (a): Pheromone production as a function of resin flow. (b): Inhibition effect on pheromone emission as a function of resin flow. (c): The product of the function depicted in a and b. (d): Resin-induced beetle death rate.

the production of resin as a function of beetle density, $f_1(A)$, is given by

$$F_1(A) = a_o - a_a \cdot A, \qquad (2)$$

where a_o and a_s are fixed positive numbers (see Fig. 1c). Let A_1 be defined (as the solution to $f_1(A_1) = 0$.

It is reasonable to assume that $A_2 > A_1$ (see Figs 1c and d): the production of resin will stop long before the resin stops leaking. Since $A_1 = a_o/a_s$ and $A_2 = b_o/b_s$, it follows that $b_o/b_s > a_o/a_s$. Using these definitions and assumptions, the dynamic equation describing the amount of resin is given by

$$\frac{dR}{dt} = f_1(A) - f_2(A) \cdot R. \qquad (3)$$

The beetles' response to resin flow

Attacking bark beetles are, as already pointed out, affected by resin in several ways: beetles depend on resin for their production of attraction pheromones (Silverstein 1969, Borden 1974), and they die or drown in resin; in addition resin may inhibit pheromone emission. The mechanism by which resin secretion inhibits attraction is unknown, but may involve mechanical ob-

struction, or toxicity to pheromone-producing microflora.

Let the function relating pheromone production per beetle to the amount of resin be defined by P(R); assume this to be a linearly increasing function of R (see Fig 2a). That is,

$$P(R) = p_o \cdot R, \qquad (4)$$

where p_s is a fixed positive number.

With increasing amount of resin, emission of produced pheromones becomes increasingly inhibited. Assume that the function describing this inhibition effect is given by E(R) (see Fig. 2b). That is,

$$E(R) = f_o - f_s \cdot R, \qquad (5)$$

where f_o and f_s are fixed positive numbers.

The specific effective emission of pheromones per beetle is then given by $PE(R) = P(R) \cdot E(R)$ (see Fig. 2c).

The resin-induced specific beetle death, d(R), is assumed given by a linearly increasing function (Fig. 2d). That is,

$$d(R) = d_s \cdot R, \qquad (6)$$

where d_s is a fixed positive number.

Using these definitions, the dynamic equation describing the number of beetles on the tree is given by

$$\frac{dA}{dt} = P(R) \cdot E(R) \cdot A \cdot N - d(R) \cdot A. \qquad (7)$$

That is, the number of beetles on the tree will grow as a function of the amount of pheromone emitted from the tree, $A \cdot P(R) \cdot E(R)$, and the number of beetles swarming in the forest stand under consideration, N. The number of beetles on the tree will decrease as a result of death or emigration of adults.

The set of dynamic equations

Combining the equations developed in the previous two sections yields:

$$\frac{dR}{dt} = f_1(A) - f_2(A) \cdot R$$

$$(8)$$

$$\frac{dA}{dt} = PE(R) \cdot A \cdot N - d(R) \cdot A.$$

This set of equations then defines the dynamics of the beetle-tree interaction. Some aspects of the analysis of this model are reported in Appendix A. All major points are, however, discussed and summarized in the
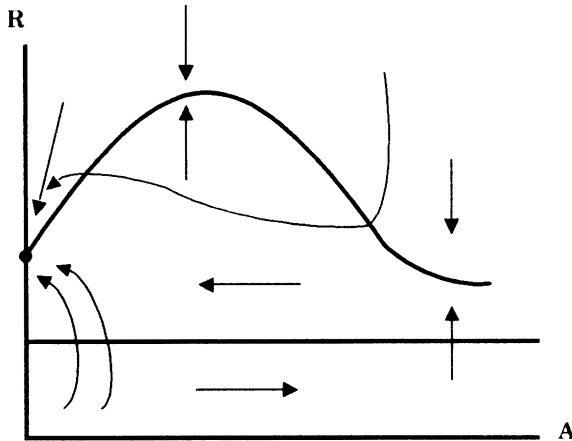
410

R

Fig. 3. An example of the isoclines and the dynamics in the R-A space, where A is the beetle density and R the resin flow. The R-isocline is the humped curve, whereas the A-isocline is the horisontal line. Arrows parallel to the R-axis depict the dynamic component caused by changes in the resin flow. Arrows parallel to the A-axis depict the dynamic component caused by changes in the beetle density. Curved lines – or trajectories – indicate the resulting dynamics of the system described by Eq. (8) and a given set of conditions on the component functions. The resulting equilibrium is depicted by a dot. The form of the isoclines is deduced in Appendix A. See that appendix and the main text for further details.

Result section. The model defined by Eq. (8) involves several simplifications. For instance, I only consider one type of resin; I do not distinguish between primary and secondary resin. Furthermore, I only consider pheromone production implicitly. I do, however, believe that the deduced dynamics of the beetle-tree system do not depend on such simplifications. Only further theoretical and empirical work can tell whether this in fact is so. In Appendix B I briefly discuss a more detailed model incorporating an explicit term for pheromone production. Analysis shows, however, that no new pattern results from this complication.

The model described by Eq. (8) is, however, only meaningful to analyze with respect to dynamic behaviour for an initial short period immediately following the beetles' attempted attack. This is so because the parameters in the various functions entering Eq. (8) will change after the initial period of attack. However, since these change at a much slower rate than the variables considered to be the dynamic ones in this paper (i.e., A and R), it is indeed meaningful to study the initial dynamics of the system as defined by Eq. (8). By so doing, we may be able to deduce the conditions under which the tree is expected to overcome the attack of the beetles, and those under which the beetles will overcome the resistance of the tree. That is, we may use the model for exactly the purpose given in the Introduction – assisting us in deducing the dynamic consequences of the architecture of the system. This is the topic of the remaining part of the paper.

Results: The dynamics of the bark beetle-tree system

Knowing the isoclines (i.e., the combinations of R and A for which dR/dt = 0 and dA/dt = 0) makes it possible to deduce the dynamics of the system defined by our model (e.g., Maynard Smith 1974). The form of the isoclines for the model defined by Eq. (8) is deduced in Appendix A. The results are depicted in Figs. 3 and 4. In Fig. 3 the basic form of the isoclines are given together with the emerging dynamics. In Fig. 4 the resulting changes due to changes in parameters (or functions) are depicted. In the following, reference is primarily made to Fig. 4.

By a *vigorous tree*, we mean one with a high a_0 (see Eq. (2)) and a low b_0 (see Eq. (1)): such a tree produces much resin and looses only a small fraction of it as a result of an attack by beetles. A *non-vigorous tree* is one with a low a_0 and a high b_0. As can be seen from Appendix A and Fig. 4, the dynamics of the beetle-tree system depends on the vigour of the tree. Obviously that is of no surprise to forest entomologists.

It appears also, again consistent with the intuition of forest entomologists, that the dynamics of the system depend on the number, N, of beetles, swarming in the forest stand. The more beetles swarming in the forest, the easier it is for the beetles to win over the tree (Fig. 4).
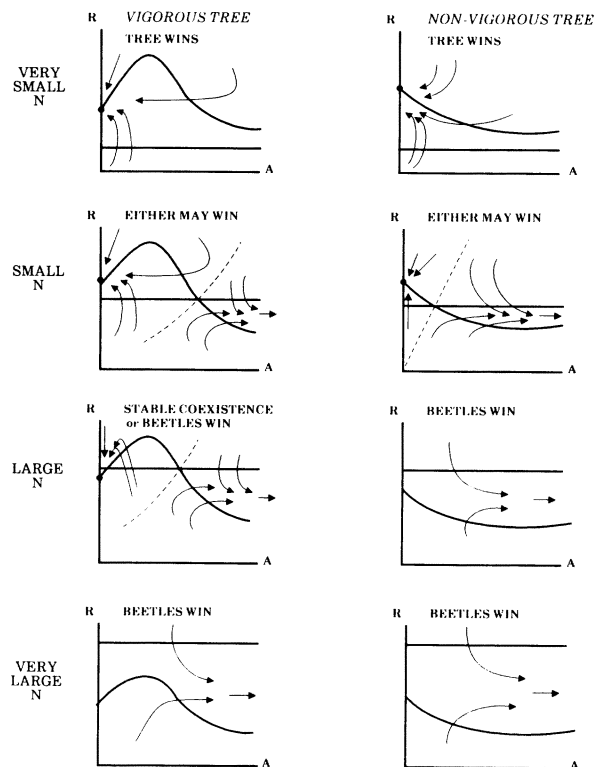

Fig. 4. Emerging dynamics under a variety of conditions of beetle abundance in the forest stand and the vigor of the tree. See the main text for further details and further interpretation.

If, in Fig. 4 the equilibrium (in short as well as in the long term) is found *on* the R-axis, we conclude that the tree is predicted to win. If, on the other hand, the beetle density on the basis of Fig. 4 is seen to explode, the beetles are concluded to win. It is in this latter case that the model only is applicable to the initial period of the attack. Subsequent to this initial period, processes not incorporated into the model will come into play. These processes may change the parameters of the system at some low, but non-zero, rate.

As can be seen from Fig. 4, there are several possible outcomes of the interactions between the beetles and the tree. As already discussed, either the tree or the beetles may win; the former has a tendency to occur if the density of swarming beetles in the forest stand is low, whereas the latter has a tendency to occur if the swarming beetle density is high (i.e., the upper vs the lower panels in Fig. 4). In between these extremes, a variety of dynamic patterns may, however, result. Under certain conditions, either the tree or the beetles may win depending on the initial conditions: for instance, if many beetles suddenly happened to land on the tree, the tree may lose, whereas if only a few had landed, the tree may win. To a certain extent this is obvious. The analysis of the model makes us understand the underlaying mechanisms behind these changes in the emerging properties of the dynamic interaction studied in this paper.

One of the possible outcomes predicted by the model is somewhat more surprising: depending on initial attack densities (as described above), either the beetle may win or a stable coexistence may result. In real life this may be seen as an extended colonization period. Raffa and Berryman (1983) report, in fact, data on *Dendroctonus ponderosae* which may suggest the reality of such a low density stable equilibrium. This particular case should, of course, be further investigated both from a theoretical and an empirical point of view.

The model finally suggests that even during endemic conditions, some trees may always die due to beetle attack; this will occur if the tree's vigour is low due to, for example, drought or old age (to the right in Fig. 4), if the local density of swarming beetles in the forest stand happens to be high (due to, e.g., high temperature and no wind), and if the number of beetles that initially attacked the tree is not too small.

The biological processes underlying the predicted emerging properties may be understood more thoroughly after a parameterisation of the model. The more qualitative analysis reported in the present study provides a first approach to the study of these patterns; such a more qualitative analysis also requires less data than a parameterized model does.

Discussion and conclusion

The model analyzed in this paper suggests that optimal attack densities (as, e.g., discussed by Berryman et al.

1985) only will apply to medium high densities. Only then will there be enough beetles to overcome the resistance from the tree. At lower to medium swarming densities, there may be many trees which are able to overcome the attack: this may easily confound our results unless we have detailed insight into expected patterns.

The purpose of developing this model was to achieve a better understanding of the beetle-tree dynamics. Rather than developing a complicated simulation model, I wanted to develop a very simplistic one in the hope to see new patterns not previously being realized. One such unexpected pattern seems to have been detected; i.e., the case where a stable low density of beetles may exist on the tree without the tree dying.

The model is dominated by two positive feedback processes: the first involving pheromone emission rates, which are continually amplified as attacks accumulate; the second involving host resistance, which is continually reduced as additional attacks dilute the resin production rate. The latter process, however, can also operate in the opposite direction, causing attacks to decline to zero if the resin production rate is high enough. Although negative feedback processes are continually operating in this system, their presence becomes apparent only after a critical point is reached where either the tree or the beetle has prevailed. One negative feedback process causes the beetle attack to terminate at a density sufficient to kill the tree, the other regulates the final resin accumulation at the attack site in successfully defended trees.

Models of the kind discussed in this paper may also be used for developing more detailed population dynamics models such as, for instance, those discussed by Berryman et al. (1984), Berryman and Stenseth (1989) and Stenseth (1989). Hence, the kind of models discussed in this paper may be of help far beyond the investigation of processes *on* the tree during an attack. In particular, the results from models of this kind may also be of help in deriving the thresholds of the kinds referred to in models such as those discussed by Berryman (1982).

References

Berryman, A. A. 1969. Response of *Abies grandis* to attack by *Scolytus ventralis* (Coleoptera: Scolytidae). – Can. Entomol. 101: 1033–1042.
– 1972. Resistance of conifers to invasion by bark beetle-fungal associations. – BioScience 22: 598–602.
– 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. – Environ. Entomol. 5: 1225–1233.
– 1978. A synoptic model of the lodgepole pine/mountain pine beetle interaction and its potential application in forest management. – In: Berryman, A. A., Amman, G. D.,

Stark, R. W., and Kibbee, D. L. (eds). Theory and practice of mountain pine beetle management in lodgepole pine forests. College of Forest Resources, Univ. Idaho, Moscow, pp. 98–105.

– 1982. Population dynamics of bark beetles. – In: Mitton, J. B. and Sturgeon, K. B. (eds). Bark beetles in North American conifers. Univ. Texas Press, Austin, pp. 264–314.

– and Stenseth, N. C. 1989. A theoretical basis for understanding and managing bark beetle populations. – Holarct. Ecol. 12: 387–394.

– , Stenseth, N. C. and Wodkin, D. J. 1984. Metastability in forest ecosystems infested by bark beetles. – Res. Pop. Ecol. 26: 13–29.

– , Dennis, B., Raffa, K. F. and Stenseth, N. C. 1985. Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). – Ecology 66: 898–903.

– , Raffa, K. F., Millstein, J. A. and Stenseth, N. C. 1989. Interaction dynamics of bark beetle aggregation and conifer defense rates. – Oikos 56: 256–263.

Borden, J. H. 1974. Aggregation pheromones in the Scolytidae. – In: Birch, M. C. (ed.). Pheromones. North-Holland, Amsterdam, pp. 135–160.

Christiansen, E. 1985. Ips/Ceratocystis infection of Norway spruce. What is a deadly dosage? – Z. angew. Entomol. 99: 6–11.

– and Ericsson, A. 1986. Starch reserves in Picea abies in relation to defense reaction against a bark beetle transmitted blue-strain fungus, Ceratocystis polonica. – Can. J. For. Res. 16: 78–83.

Maynard Smith, J. 1974. Models in ecology. – Cambr. Univ. Press, Cambridge.

Miller, J. M. and Keen, F. P. 1960. Biology and control of the western pine beetle. – USDA For. Serv. Misc. Publ. 800.

Miller, R. H. and Berryman, A. A. 1985. Energetics of conifer defense against bark beetles and associated fungi. – In: Safranyik, L. (ed.) The role of the host in the population dynamics of forest insects. Proc. IUFRO Conf., Pac. For. Res. Centr., Victoria, B.C., pp. 12–23.

Mulock, P. and Christiansen, E. 1986. The threshold of successful attack by Ips typographus on Picea abies: A field experiment. – For. Ecol. Manage 14: 125–132

Raffa, K. F. and Berryman, A. A. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles. – Ecol. Monogr. 53: 27–49.

Roughgarden, J. 1979. Theory of population genetics and evolutionary ecology: an introduction. – MacMillian Publ. Co., N.Y.

Safranyik, L., Shrimpton, D. M. and Whitney, H. S. 1975. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in Western Canada. – In: Baumgartner, D. M. (ed.). Management of lodgepole pine ecosystems. Wash. State Univ. Co-op. Ext. Serv., Pullman, pp. 406–428.

Silverstein, R. M. 1969. Terpenes and insect behavior. – In: Insect-plant interactions. Nat. Acad. Sci., Washington D.C., pp. 73–75.

Smith, R. H. 1963. Resin quality as a factor in the resistance of pines to bark beetles. – In: Gerhold, H. D., McDermott, R. E., Schreiner, E. J. and Winieski J. A. (eds). Breeding pest-resistent trees. Proc. NATO and NSF Symp. Pergamon Press, Oxford, pp. 189–196.

Stenseth, N. C. 1984. Why mathematical models in evolutionary ecology? – In: Cooley, J. H. and Gooley, F. B. (eds). Trends in ecological research for the 1980's. Plenum publ. Co., N.Y., pp. 239–287.

– 1989. A simple population model for bark beetles providing general guidelines for the application of aggregation and anti-aggregation pheromones. – Holarc. Ecol. 12: 395–407.

Thalenhorst, W. 1958. Grundzüge der Populationsdynamik des grossen Fitchenborkenkäfers Ips typographus L. – Schriftenreihe Forstl. Fak. Univ. Göttingen. No. 21.

Vité, J. P., Bakke, A. and Renwick, J. A. A. 1972. Pheromones in Ips (Coleoptera: Scolytidae): Occurrence and production. – Can. Entomol. 104: 1967–1975.

Wood, D. L. 1972. Selection and colonization of ponderosa pine by bark beetles. – In: van Emden, H. F. (ed.), R.E.S. Symp. No. 6: Insect/Plant relationships. Blackwell Sci. Publ., Oxford, pp. 101–107.

Wright, L. E., Berryman, A. A. and Gurusiddaiah, S. 1979. Host resistance to the fir engraver beetle, Scolytus ventralis (Coleoptera: Scolytidae) 4. Effect of defoliation on wound monoterpenes and inner bark carbohydrate concentrations. – Can. Entomol. 111: 1255–1262.

Appendix A: Analysis of Eq. (8)

Let A be the attacking beetle density on a tree, and R the amount of resin flow in that tree. Then, we have the dynamic system given by

$$\frac{dA}{dt} = (N \cdot p(R) \cdot g(R) - d(R)) \cdot A \qquad (A1)$$

$$\frac{dR}{dt} = f_1(A) - f_2(A) \cdot R$$

where N is the (constant) amount of swarming beetles around the tree under consideration and p, g, d, f_1, and f_2 are functions whose forms are described in the main text.

The form of the A-isocline:
The function $h(R) = p(R) \cdot g(R)$ is an unimodal function initially increasing from zero when $R = 0$. The d-function is monotonically increasing function of R. The R-value (R) for which the two functions $N \cdot p \cdot g$ and d intersect will increase with increasing N. However, as N continues to increases, R will approach an assymptote from below.

Hence, for a specified environmental condition (i.e., specified N) the A-isocline is a straight line parallel to the A-axis. Below this line, A will increase; above this line, A will decrease.

The form of the R-isocline:
The R-isocline is implicitly defined by

$$R = f_1(A)/f_2(A) = \varphi(a). \qquad (A2)$$

Differentiating yields

$$\frac{d\varphi}{dA} = \frac{(df_1/dA) \cdot f_2 - (df_2/dA) \cdot f_1}{(f_2)^2}. \qquad (A3)$$

For small A-values, $df_2/dA \leq df_1/dA \leq 0$. Assuming that the specific rates of primary and secondary resin production (i.e., f_1 and f_2) are of the same order of magnitude, we have that $d\varphi/dA \leq 0$ for small values of A. However, if $f_2 \geq f_1$ (which might actually be the case), we may have that $d\varphi/dA \geq 0$ for small values of A.

Appendix B: Analysis of a modified and extended model

Let A and R be defined as in the main text and as in Appendix A. Let, furthermore, P be the amount of pheromones produced. A model for the system discussed in the main text will then be given by

$$\frac{dR}{dt} = f_1(A) - f_2(A) \cdot R$$

$$\frac{dP}{dt} = p(R) \cdot F(R) \cdot A - \gamma \cdot p$$

$$\frac{dA}{dt} = p \cdot (N \cdot a - d(R) \cdot A, \tag{B2}$$

where p(R) and F(R) represent the pheromone production and emmision terms and γ is the disappearance rate.

Analysis show that the dynamics resulting from this extended model are the same as those emerging from the model discussed in Appendix A.