

A RESOURCE-DEPLETION MODEL OF FOREST INSECT OUTBREAKS

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Abstract. Detailed analyses of thresholded ecological interactions can improve our understanding of the transition from aperiodic to periodic dynamics. We develop a threshold model of the population dynamics of outbreaking bark beetle populations that alternate between non-epidemic and epidemic behavior. The model involves accumulation of resources during low-density periods and depletion during outbreaks. The transition between the two regimes is caused by disturbance events in the form of major tree felling by wind. The model is analyzed with particular reference to the population dynamics of the spruce bark beetle (*Ips typographus*) in Scandinavia for which a comprehensive literature allows full parameterization. The fairly constant outbreak lengths and the highly variable waiting time between outbreaks that are seen in the historical records of this species agree well with the predictions of the model. The thresholded resource-depletion dynamics result in substantial variation in the degree of periodicity between stochastic realizations. The completely aperiodic tree colonizations are partly predictable when the timing of the irregular windfall events are known. However, the predictability of inter-outbreak periods is low due to the large variation of cases falling most frequently in the middle between the extremes of purely nonperiodic (erratic) and periodic (cyclic) fluctuations.

Key words: aperiodic disturbances; bark beetle; epidemic; fluctuations; log-spline density analysis; outbreak; population dynamics; spectral analysis; time series; waiting time; windfall events.

INTRODUCTION

A variety of organisms exhibit episodes of explosive population growth that are triggered by disturbance events. This behavior can be found in the dynamics of pathogen, predator, and herbivore populations, as for example in several bark beetle species that show tree-killing outbreaks at regional scales. Various approaches have been used to model the interactions between bark beetles and host trees or tree stands (Berryman et al. 1984, 1985, 1989, Raffa and Berryman 1986, Stenseth 1989). Essential in this work is the formulation of a threshold in beetle numbers that enables the bark beetle populations to switch between non-epidemic and epidemic dynamics (Berryman 1982, 1999). Also, the phenomenon of accumulation of susceptible hosts has been recognized as a critical part of the dynamics of host-pathogen interactions, and great advances have been made using models that incorporate this (e.g., May 1977, Berryman and Stenseth 1984).

Previous exploratory models (sensu Taylor 2000) have been important for the conceptual understanding of bark beetle population systems, such as the intrinsic metastability of bark beetle population systems that are constrained by accumulating resources (May 1977, Berryman and Stenseth 1984, Berryman et al. 1984).

Building on the previous theory, we present here a more detailed model involving thresholded resource accumulation–depletion dynamics as triggered by disturbance events. Our goal is to develop a model that can be parameterized with data, thus enabling us to do more realistic quantitative analysis of model behavior and comparisons with historical outbreak records (re-description sensu Taylor 2000). We parameterize the model based on the extensive literature on the dynamics and biology of the spruce bark beetle, *Ips typographus* L. The model is made as realistic as possible by incorporating pertinent biological detail. A sensitivity analysis of predicted dynamics with respect to key parameters is also presented in order to understand the significance of important interactions and uncertainties in parameter estimation.

We evaluate the long-term behavior of the model with particular reference to predictability of tree colonizations and outbreaks, and the transition between periodic and nonperiodic oscillations. Neither historical records nor previous characterizations of bark beetle outbreaks (Berryman 1987, Berryman and Stenseth 1984, Berryman et al. 1984) suggest strict periodicity that can be described by periodic functions based on exact periods (e.g., Gurney and Nisbet 1998, Tong 1990). Analyzing the degree of periodic behavior is of special interest because periodicity is connected with the level of predictability in the outbreak dynamics. However, completely aperiodic behavior can also provide predictability when it is closely tied to an aperi-

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odic factor (e.g., windstorm events), but then with a shorter reaction time. To analyze the degree of periodicity in dynamics, we apply spectral analysis on time series and logspline density estimation of period lengths and waiting times between periods of both tree colonization periods and outbreak periods. Finally, we compare model realizations with historical data on *I. typographus* outbreaks.

PREAMBLE: THE FOCAL SPECIES

Ips typographus is among the most destructive of the bark beetles in Palearctic coniferous forests (Christiansen and Bakke 1988, Wermelinger 2004). At low population densities this species breeds in fresh wind-caused tree-falls (hereafter “windfalls”) or dying trees of Norway spruce (*Picea abies* (L.) Karts.). Natural defense mechanisms of healthy spruce trees usually repel or kill any assailants (Franceschi et al. 2005). At high densities, in contrast, the beetles can overcome these defenses through mass attack coordinated through aggregation pheromones. The number of beetle attacks must exceed a threshold for a tree to be killed and beetle progeny to be produced (Berryman 1982, Christiansen 1985). Field data show that colonization of healthy trees is only successful once the beetle numbers in standardized pheromone traps exceed about 4500. Above this threshold, the volume of trees killed appears to increase linearly at least in the range up to 45 000 beetles (Weslien et al. 1989, Lindelöw and Schroeder 2000). The resource base of *I. typographus* can be divided in two groups with different characteristics and influences on beetle population dynamics. The first group is fresh windfalls, which represent an immediately available but transient resource—the resource value will degrade within a year. Such windfall events appear to occur sporadically in time and space, sometimes including large amounts of bark beetle substrates. The second resource, which requires high beetle numbers to be utilized, is living trees that are susceptible to beetle attacks. There is a high variation among trees not just in quality but also fundamentally in whether they can or cannot be colonized (by a given population level). Defense capacity and relative resistance of conifers depend on both the genetics and the physiological status of the individual (Franceschi et al. 2005). During periods of low beetle numbers, this second resource base will tend to accumulate.

Intermittent outbreaks over the past two centuries have caused catastrophic timber loss in Central and Northern Europe (Annala 1969). The last outbreak (1971–1981) killed the equivalent of 5×10^6 m³ of spruce timber within a 140 000-km² area of southeast Norway (Bakke 1989). Pheromone trapping in the final two years of the last outbreak period revealed that beetles numbered about 15 000 insects/trap in this late outbreak period. The numbers dropped well below 15 000 in the postepidemic period (Økland and Berryman 2004). Historical records (Reventlow 1811, Asbjørnsen

1861, Hagemann 1891, Herre 1925) testify to three major outbreak periods (1799–1810, 1850–1858, and 1971–1980) in Norwegian spruce forests during the last 250 years. The outbreak periods are typically relatively short with a roughly decadal duration, while the waiting time between outbreaks appears to be long and highly variable.

A RESOURCE-DEPLETION MODEL

We represent beetle numbers in terms of counts in standardized pheromone traps. These traps are widely used to measure beetle abundance and therefore trap counts are a convenient unit for parameterizing the population model; several studies have used mark–recapture methods to estimate dispersal capabilities and sampling area of traps (Botterweg 1982, Helland et al. 1989, Weslien and Lindelöw 1989). These provide detailed methods for converting trap counts to density measures of beetles per square kilometer. Motivated by previous studies (Berryman 1982, Økland and Bjørnstad 2003, Økland and Berryman 2004), we formulate the dynamics as a thresholded, discrete-time, first-order, density-dependent process, governed by Gompertz-type density dependence (Royama 1992) in the growth:

$$R_t = \log(N_t/N_{t-1}) = a(1 - \log(N_{t-1}/\log(K_t))) \quad (1)$$

where R_t is the per capita growth rate in year t , a is the intrinsic maximum rate of increase, K_t is the carrying capacity (as determined by the resource base), and N_t is the population size of the local population in year t . With given bark beetle parameters (Appendix A), a linear relationship (i.e., logistic or Ricker models) predicts a strong period-2 component that is inconsistent with observed long-term dynamics (see for example Økland and Berryman 2004). Thus, in agreement with the analyses of empirical data (Økland and Berryman 2004), we chose a log-linear Gompertz-like relationship. Rewriting Eq. 1, the population size in year t is given by

$$N_t = N_{t-1} \exp[a + b \log(N_{t-1})] \quad (2)$$

where $b = -a/\log(K_t)$. The carrying capacity may be highly variable over time, as determined by the two resource bases: K_L , which is the carrying capacity of newly windfelled trees, and K_S which is the living trees that are only available at high densities, such that

$$K_t = K_L + K_S. \quad (3)$$

Here K_L is proportional to the volume of wind-felled spruces in a given year (W_t):

$$K_L = b_w W_t \quad (4)$$

where b_w is the number of beetles produced per cubic meter windfall of spruce. Years of large windfall episodes are rare, and previous studies indicate that only years of large windfall episodes have a significant influence on the population level (Økland and Bjørnstad

2003, Økland and Berryman 2004). Thus, a simplified model for the windfall dynamics is

$$W_t = W_{B,t}k_w + W_0 \quad (5)$$

in which $\{W_{B,t}\}$ may be taken to be a sequence of independent random Bernoulli (0/1) variates with a probability of ~ 0.0625 of large windfall events that are sufficiently large to make a significant increase in the beetle population in any given year (Økland and Berryman 2004). The parameter k_w is the average volume of wind-felled spruces per square kilometer in such years, and W_0 is an average background level of wind-felled spruces per square kilometer occurring in all years (smaller and scattered windfalls, top breaks, etc.).

The carrying capacity constituted by living susceptible trees (K_S in Eq. 3) is only available in years with a beetle density higher than the threshold for tree killing (called L here), and is then proportional to the volume of susceptible spruces per km^2 . Thus, K_S can be formulated as the threshold function:

$$K_S = \begin{cases} S_{\text{acc},t}b_a & \text{for } N_t > L \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

where b_a is the number of beetles produced per cubic meter of killed susceptible spruce and $S_{\text{acc},t}$ is the accumulated volume of susceptible spruces per square kilometer in year t . The susceptible spruce, $S_{\text{acc},t}$ can be expressed as the accumulated volume up to the previous year ($S_{\text{acc},t-1}$) less the volume consumed by beetles in the previous year (A_{t-1}) plus the added volume in the current year (S_{add}):

$$S_{\text{acc},t} = S_{\text{acc},t-1} + S_{\text{add}} - A_{t-1}. \quad (7)$$

The added volume in the current year (S_{add}) is a positive function of stand aging because the beetles mainly colonize mature trees. S_{add} is proportional to the total volume of mature spruce trees in the current year ($V_{m,t}$):

$$S_{\text{add},t} = k_s V_{m,t} \quad (8)$$

Being dependent on beetle density, A_t will clearly also be a threshold function. Density of colonized spruces has previously been shown to be linear in the numbers of beetles captured in pheromone traps (Lindelöw and Schroeder 2000). We thus model A_t according to

$$A_t = \begin{cases} h_s N_t - h_s L & \text{for } N_t > L \\ 0 & \text{otherwise} \end{cases} \quad (9)$$

in which h_s is the slope and $-h_s L$ is the intercept in the linear relation. In this way we assume that the total population of susceptible trees in intercolonization periods depends purely on the time elapsed since the previous period of colonizations, but the actual population of those colonized depends linearly on beetle density when above the threshold L .

Using *I. typographus* as a model system, the model parameters were estimated from monitoring data, empirical surveys, and former experiments. Details about

the parameter estimates and their sources are given in Appendix A.

STATISTICAL ANALYSES

We focused on two key statistics: the predicted average length of outbreaks ($N > E$) and the inter-outbreak waiting-time distribution. In order to quantify the waiting-time distributions predicted by the model we used logspline density estimation on outbreak lengths and intervals between outbreaks in simulated time series. This method applies maximum-likelihood estimation to estimate the density function $\log(f)$ using cubic splines with a finite number of prespecified knots (Koopman and Stone 1991, R Development Core Team 2004). Large data sets were needed to achieve precise estimates of waiting-time distributions and distributions of outbreak lengths. This was done by simulating one long time series (20 000 years), because the results of our analyses by the present ergodic model will not be different from that using several small time series.

The resulting logspline density plots were used to analyze the degree of randomness or regular periodicity of waiting times and outbreak lengths; a narrow distribution indicates periodic behavior (in fact strictly periodic dynamics are represented by zero variance and all waiting times entered on a single value). In contrast, completely randomly timed outbreaks (e.g., completely aperiodic behavior) have an exponential distribution of the waiting time between outbreaks. The same method was also used to analyze the distribution of periods above threshold of colonizing trees ($N > L$) and intercolonization periods ($N < L$).

We further used spectral analysis to analyze the degree of periodicity in simulated time series (100 years) in the following way: the variation attributed to various period lengths was estimated by calculating the amplitude as a function of period length. An index of periodicity was set as the maximum amplitude divided by the sum of amplitudes, which will approach 1 for a perfectly periodic time series and 0 for a time series without any sign of periodicity. The periodicity indices from 1000 simulations were used to prepare a density plot using kernel density estimates.

RESULTS

The general behavior of the model is illustrated in Fig. 1. Periods of low insect population size are characterized by smaller peaks of population increases reflecting the irregular occurrences of large windfall events. Since windfalls are only suitable as breeding substrate during one season, the population most often declines to a low level that is given by the scattered dying trees in the spruce forest stands (W_0 in Eq. 5). However, in some cases the large windfall episodes induce a population increase above the threshold for colonizing susceptible trees (L ; dotted line in Fig. 1). As a consequence, the population increases quickly due

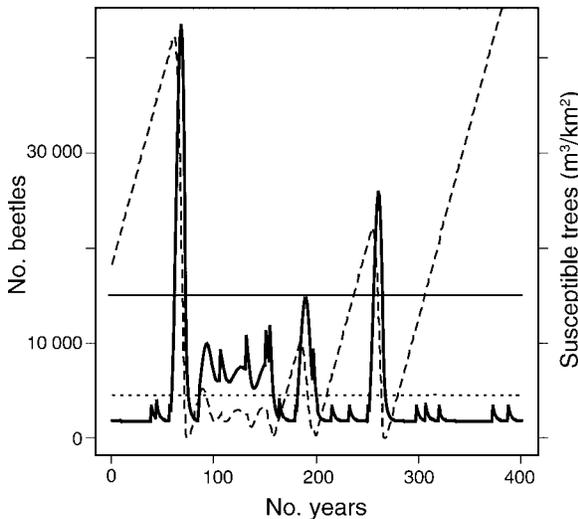


FIG. 1. General behavior of the model: a selected sample from the simulated population time series (solid curve, left axis), including accumulation of susceptible trees (dashed curve, right axis), threshold of tree colonization (horizontal dotted line), and threshold of epidemic outbreak (horizontal straight line).

to its access to both resources of windfall and susceptible trees. Depending on the availability of accumulated susceptible trees (S_{acc} ; dashed curve in Fig. 1), the population may continue to increase beyond the outbreak threshold (E ; horizontal dotted line in Fig. 1). A large population size results in a rapid depletion of the susceptible trees (S_{acc}), leading to a population decline below the threshold of tree colonization (L). Large windfall episodes within the outbreak period may prolong the outbreak period. However, such prolongations are short because additional population increases during outbreaks speed up the depletion of susceptible trees. Conversely, there is a large accumulation of susceptible trees after long periods below the threshold of tree colonization, leading to extra-large outbreak populations when the population finally passes the threshold. When depletion of all susceptible trees is associated with high frequencies of windfalling, the population level may for a period be maintained above the threshold of colonizing trees (L) without rising to outbreak levels (E) (Fig. 1). Similar to previous models (e.g., Raffa and Berryman 1986), the dynamic of the present model is insensitive to initial population size. The same kind of dynamics was found when the initial population size was low (100), high (20 000), equal to the threshold L (4500), or equal to the threshold E (15 000).

The model simulations indicate the periods between tree colonizations are completely aperiodic ("erratic"). The logspline density plots show a near-exponential distribution for the waiting time between periods above the threshold for colonizing trees, L (broken curve in Fig. 2a).

The characteristics of waiting times and period lengths differ between outbreak ($N > E$) and colonization dynamics ($N > L$). The waiting time between outbreaks was neither strictly periodic nor completely aperiodic. Logspline density plots of the waiting-time distributions had a long tail and a mode around 75 years (solid curve in Fig. 2a). In contrast, most outbreaks were 6–10 years long. The logspline density distribution of the outbreak durations reveals a skewed peak with a mode around 10 years (Fig. 2b).

The highly variable behavior of the model may in some cases produce near-periodic or completely aperiodic dynamics even without changing parameter values. The density plot of the periodicity based on spectral analyses of 1000 simulated time series of 100 years showed that the time series range from nonperiodic to near-periodic patterns with an optimum of intermediate cases (Fig. 2c). For the simulated time series, 5% yielded an index higher than 0.5, and 0.4% of the indices exceeded 0.75. Allowing parameter changes, certain parameter combinations (beyond realistic values of *I. typographus*) exhibited narrow logspline waiting-time distributions indicative of near-periodic behavior (Fig. 2d).

Changes in the magnitude of the parameters p_w , S_{add} , L and E did not change the qualitative model behavior, but did significantly impact waiting times and outbreak lengths. The results of the sensitivity analyses are presented in Appendix B. The original model parameters that were based on the empirical and experimental data show that outbreak lengths and waiting times of historical data fall nicely within the range predicted by the model (Fig. 3).

DISCUSSION

The present model sheds light on the difficulty of using analysis of a single short time series for classification of insect outbreaks as aperiodic or periodic (noncyclic or cyclic). Due to the substantial underlying variability inherent in thresholded resource-based dynamics, various time-series may occasionally appear to be anything from completely aperiodic to near-periodic with identical model parameters. Our quantitative analysis of inter-outbreak periods and time-series patterns demonstrated that the majority of the model realizations were intermediate cases between the extremes of purely periodic or nonperiodic. Thus, we argue that in thresholded ecological interactions (e.g., Grenfell et al. 1998, Stenseth et al. 1998), it may be fruitful to consider the transition from aperiodic to periodic dynamics using waiting-time analysis in addition to the more classic time-series methods, such as periodograms and autoregression (see previous debates on methods; e.g., Hunter and Price 2000). Even though the present model does not include an underlying autoregressive component that may result in the classic ecological phase-forgetting cycles (Nisbet and Gurney 1982), the indices based on spectral analyses revealed a potential for near-

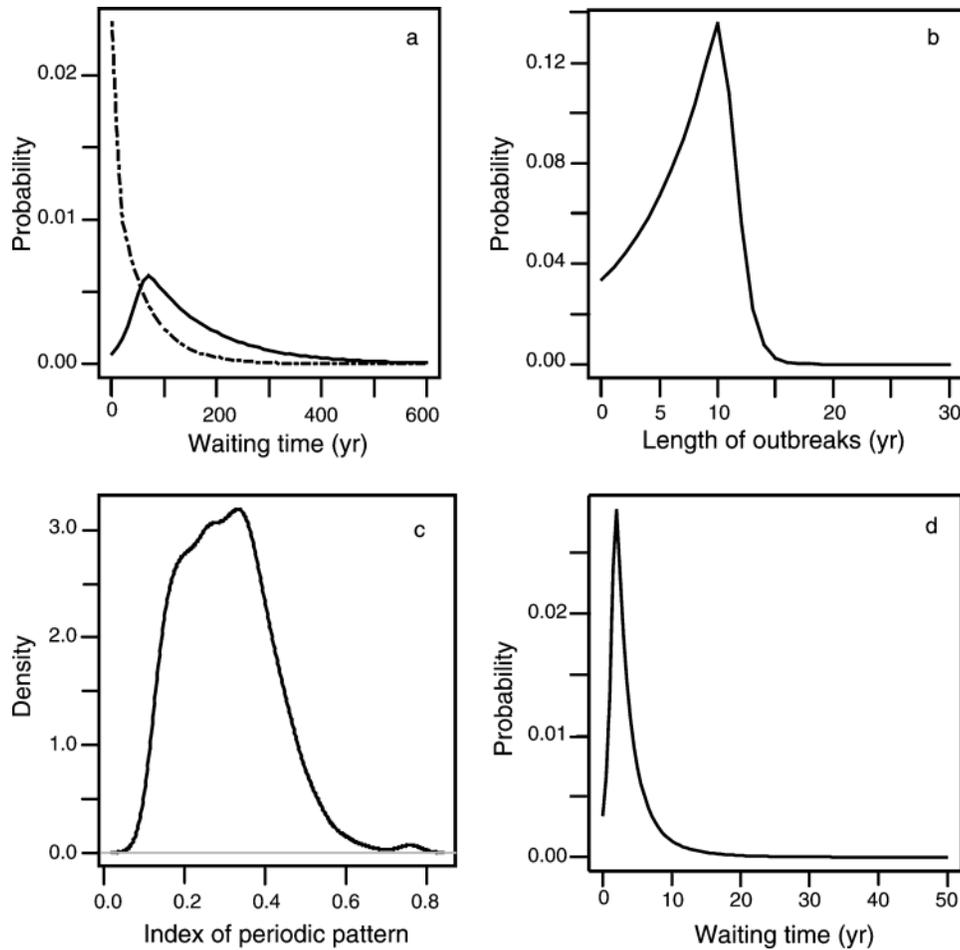


FIG. 2. Density plot results: logspline density plots based on simulated time series (a, b, and d) and density plot periodicity index (c). (a) Logspline density plot for waiting time between outbreaks (solid curve) and periods above threshold for colonizing trees (broken curve). (b) Logspline density plot for length of outbreak periods. (c) Density plot of periodicity index (spectral analysis) calculated from simulated time-series sequences. The index will attain 1 for a perfectly periodic time series and 0 for a time series without any sign of periodicity. For more details on the index, see *Statistical analysis*. (d) Logspline density plot for waiting time between outbreaks within simulated time series using the parameter values p_w (yearly probability of big windfall event) = 0.15, S_{add} (added volume of susceptible spruce trees in the current year) = 31, and L (beetle density threshold for killing trees) = 6000.

periodic patterns in addition to highly irregular time-series patterns (Fig. 2c). This potential was also reflected in the waiting-time analyses that showed a distribution between completely aperiodic and strict periodic inter-outbreak periods (Fig. 2a: solid curve), as well as narrow distributions indicative of quasi-periodism when parameters were adjusted (Fig. 2d; Nisbet and Gurney 1982). Strict periodic behavior of time-series sequences or inter-outbreak periods were not observed, even though the variation in outbreak lengths was small.

When model parameters were confined to realistic values for *Ips typographus* in Scandinavia, our results show that the large windfall events (Fig. 1) and the time between starts of colonizations are completely aperiodic (indicated by near-exponential distributions; Fig. 2a: broken curve), while the distribution of waiting

times between outbreaks (Fig. 2a: solid curve), and the time-series patterns by spectral analyses (Fig. 2c) fall somewhere between purely aperiodic and purely periodic (the majority of the simulated cases were closer to the middle than to the extremes). This gives some predictability of the start of colonizations when we know the windfall events, while the predictability of outbreaks and time-series patterns is generally low. In contrast, the variation in outbreak length was relatively small, implying that the outbreak durations are quite predictable.

Historical records of *I. typographus* from Scandinavia suggest a highly variable waiting time between outbreaks and a fairly constant length of outbreaks, which is not consistent with the simple delayed autoregressive models, or predator-prey models and competition models used on many other animal species

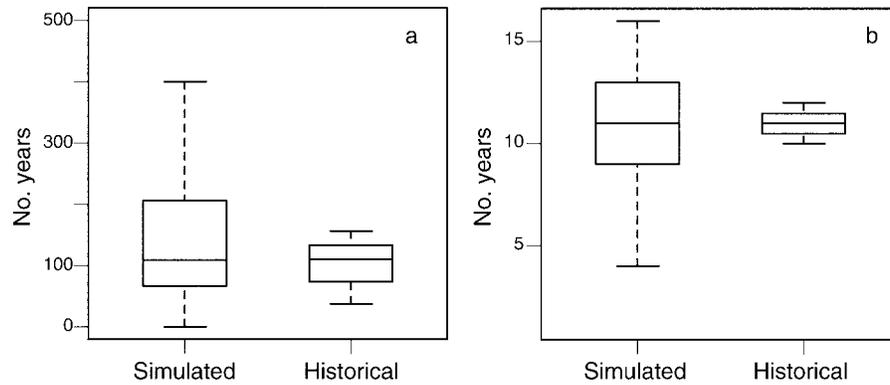


FIG. 3. Comparison of (a) waiting time and (b) outbreak length between historical records and time series simulated by the model. The central lines of the box-and-whiskers plot show the median, the box indicates lower and upper quartiles, and the whiskers show the largest and smallest observations that fall within a distance of 1.5 times the box size from the nearest quartile.

(Royama 1992, Turchin 2003). These patterns of outbreak lengths and waiting times have not been described by previous quantitative models of bark beetle dynamics. Furthermore, delayed density dependence was not significant in time-series analyses of *I. typographus*, which showed a dominance of lag 1 density dependence only (Økland and Berryman 2004). The present model appears to predict the general behavior of the bark beetle outbreak dynamics, and the results are consistent with previous exploratory models (Berryman and Stenseth 1984, Berryman et al. 1984). The waiting times and the outbreak lengths of the historical data are well within the typical range predicted by the model (Fig. 3).

The present model may need modifications to be applied in other parts of the distribution area of *I. typographus*. As illustrated by studies of numerous other species, variation in biological conditions may result in significant regional differences in population dynamics of a given species (e.g., Bjørnstad et al. 1998). For example, predators are currently believed to be the reason for noncyclic lemming populations in Arctic Canada, while they are believed to be the cause of cycles in Greenland and Scandinavia (Hudson and Bjørnstad 2003). We do not know to what extent species composition of natural enemies or differences in voltinism may lead to a higher degree of periodicity of *I. typographus* in other regions. There are still more details to learn that can be important for how the threshold of colonizing susceptible trees should be formulated as a function of population size and population-dependent responses. As indicated by the experimental studies of *Dendroctonus rufipennis* (Wallin and Raffa 2004), it could be that the number of trees that are “susceptible” increases with the population size (due to their ability to mass attack and adjust behavior as needed), even as susceptible trees are being depleted. We do not know in detail how such phenomena are manifested in the various bark beetle species and how they might impact dynamics.

The only source of stochasticity in our model is W_p , which represents the yearly occurrence of large windfall events (Eq. 5). These windfall episodes are known to represent the major trigger of outbreaks, while drought appears to have less influence on the dynamics of *I. typographus* from Scandinavia (Økland and Bjørnstad 2003, Økland and Berryman 2004). In some bark beetle–forest systems (e.g., *Dendroctonus frontalis* in the southern states of the United States), the random events of thunderstorms and lightning-struck trees may play a fundamental role for outbreak dynamics (Hodges and Pickard 1971, Feldman et al. 1981, Coulson et al. 1983). The dynamics of bark beetle species in other regions (e.g., *Dendroctonus ponderosae* in North America) appear to be more closely tied to large-scale tree aging and the random occurrence of drought events (Berryman 1999). Specifically, drought effect could be implemented in the present model via stochastic effects on the colonization threshold, L (Eqs. 6 and 9). The effects of accumulating mature forest may be added by describing the total volume of mature spruce trees $V_{m,t}$ as a function of time (Eq. 8). This variable was taken to be constant in the present system because the stand-rotation practice in Fennoscandian forests aims to keep an approximately constant age distribution of stands (Børset 1986).

The temporal frequency of important outbreak triggers may be a function of long-term climate changes. As demonstrated by the sensitivity analyses, increasing the annual probability of large windfall episodes (p_w) resulted in immediate declines in both outbreak lengths and waiting time (Appendix B); thus, a long-term increase of windfall frequency is expected to result in more frequent outbreaks of shorter duration. Such effects may come in addition to temperature changes that cause shifts in voltinism and geographical distributions of bark beetles towards higher latitudes and higher elevations (Logan and Powell 2001, Williams and Liebhold 2002, Powell and Logan 2005). More details on climate effects are given in Appendix B.

Among outbreaking insect species, eruptions are often triggered by disturbance events and then lead to exhaustion of the resource base. Thus, adjusted versions of the present model framework may potentially be useful in other regions and on other outbreak species.

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LITERATURE CITED

- Annala, E. 1969. Influence of temperature upon the development and voltinism of *Ips typographus* L. (Coleoptera, Scolytidae). *Annales Zoologici Fennici* **6**:161–208.
- Asbjørnsen, P. 1861. Om skovtørk og markaet. Steensballe, Christiania, Norway.
- Bakke, A. 1989. The recent *Ips typographus* outbreak in Norway experiences from a control program. *Holarctic Ecology* **12**:515–519.
- Berryman, A. A. 1982. Biological control, thresholds, and pest outbreaks. *Environmental Entomology* **11**:544–549.
- Berryman, A. A. 1987. The theory and classification of outbreaks. Pages 3–30 in P. Barbosa and J. C. Schultz, editors. *Insect outbreaks*. Academic Press, San Diego, California, USA.
- Berryman, A. A. 1999. Principles of population dynamics and their application. Stanley Thornes, Cheltenham, UK.
- 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.
- Berryman, A. A., K. F. Raffa, J. A. Millstein, and N. C. Stenseth. 1989. Interaction dynamics of bark beetle aggregation and conifer defense rates. *Oikos* **56**:256–263.
- Berryman, A. A., and N. C. Stenseth. 1984. Behavioral catastrophes in biological systems. *Behavioral Science* **29**:127–137.
- Berryman, A. A., N. C. Stenseth, and D. J. Wollkind. 1984. Metastability of forest ecosystems infested by bark beetles. *Researches in Population Ecology* **26**:13–29.
- Bjørnstad, O. N., N. C. Stenseth, T. Saitoh, and O. C. Lingjære. 1998. Mapping the regional transitions to cyclicity in *Clethrionomys rufocanus*: spectral densities and functional data analysis. *Researches in Population Ecology* **40**:77–84.
- Børset, O. 1986. Skogskjøtsel. II. Landbruksforlaget, Oslo, Norway.
- Botterweg, P. F. 1982. Dispersal and flight behaviour of the spruce bark beetle *Ips typographus* in relation to sex, size and fat content. *Zeitschrift für angewandte Entomologie* **94**:466–489.
- Christiansen, E. 1985. *Ips/Ceratocystis*-infection of Norway spruce: what is a deadly dosage? *Zeitschrift für Angewandte Entomologie* **99**:6–11.
- Christiansen, E., and A. Bakke. 1988. The spruce bark beetle of Eurasia. Pages 479–503 in A. A. Berryman, editor. *Dynamics of forest insect populations*. Plenum Press, New York, New York, USA.
- Coulson, R. N., P. B. Hennie, R. O. Flamm, E. J. Rykiel, L. C. Hu, and T. L. Payne. 1983. The role of lightning in the epidemiology of the Southern pine beetle. *Zeitschrift für angewandte Entomologie* **96**:182–193.
- Feldman, R. M., G. L. Curry, and R. N. Coulson. 1981. A mathematical model of field population dynamics of the southern pine beetle, *Dendroctonus frontalis*. *Ecological Modelling* **13**:261–281.
- Franceschi, V. R., P. Krokene, E. Christiansen, and T. Krekling. 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* **167**:353–376.
- Grenfell, B. T., K. Wilson, B. F. Finkenstädt, T. N. Coulson, S. Murray, S. D. Albon, J. M. Pemberton, T. H. Clutton-Brock, and M. J. Crawley. 1998. Noise and determinism in synchronised sheep dynamics. *Nature* **394**:674–677.
- Gurney, W. S. G., and R. M. Nisbet. 1998. *Ecological dynamics*. Oxford University Press, Oxford, UK.
- Hagemann, A. 1891. Vore norske Forstinstekter eller de for Skovene skadelige og nyttige Insekter, deres Opræden og Udbredelse i Norge: en Haandbog for Skovejere og Forstmænd. [In Norwegian.] Cammermeyer Forlag, Christiania, Norway.
- Helland, I. S., O. Anderbrant, and J. M. Hoff. 1989. Modelling bark beetle flight: a review. *Holarctic Ecology* **12**:427–431.
- Herre, B. 1925. En jægers erindringer. Femte utgave med tillegg: Bernhard Herre og hans forfatterskap, ved Leiv Amundsen. [In Norwegian.] Fabritius, Oslo, Norway.
- Hodges, J. D., and L. S. Pickard. 1971. Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Canadian Entomologist* **103**:44–51.
- Hudson, P. J., and O. N. Bjørnstad. 2003. Vole stranglers and lemming cycles. *Science* **302**:797–798.
- Hunter, M. D., and P. W. Price. 2000. Detecting cycles and delayed density dependence: a reply to Turchin and Berryman. *Ecological Entomology* **25**:122–124.
- Kooperberg, C., and C. J. Stone. 1991. A study of logspline estimation. *Computational Statistics and Data Analysis* **12**:327–347.
- Lindelöw, Å., and M. Schroeder. 2000. Övervakning av granbarkborre (*Ips typographus*) med feromonfällor och betade träd 1995–2000. Preliminär rapport. [In Swedish.] Institut för Entomologi, Swedish University of Agriculture, Uppsala, Sweden.
- Logan, J. A., and J. A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle. *American Entomologist* **47**:160–173.
- May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**:471–477.
- Nisbet, R. M., and W. S. C. Gurney. 1982. *Modelling fluctuating populations*. John Wiley and Sons, New York, New York, USA.
- Økland, B., and A. Berryman. 2004. Resource dynamic plays a key role in regional fluctuations of the spruce bark beetles *Ips typographus*. *Agricultural and Forest Entomology* **6**:141–146.
- Økland, B., and O. N. Bjørnstad. 2003. Synchrony and geographical variation of the spruce bark beetle (*Ips typographus*) during a non-epidemic period. *Population Ecology* **45**:213–219.
- Powell, J. A., and J. A. Logan. 2005. Insect seasonality: circle map analysis of temperature-driven life cycles. *Theoretical Population Biology* **67**:161–179.
- Raffa, K. F., and A. A. Berryman. 1986. A mechanistic computer model of mountain pine beetle populations interacting with lodgepole pine stands and its implications for forest managers. *Forest Science* **32**:789–805.

- R Development Core Team 2004. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.r-project.org/>)
- Reventlow, C. D. F. 1811. *Min reise i Norge 1811*. Utgitt av Johannes Elgvin i 1955. [In Norwegian.] Gyldendal Norsk Forlag, Oslo, Norway.
- Royama, T. 1992. *Analytical population dynamics*. Chapman and Hall, London, UK.
- Stenseth, N. C. 1989. A model for the conquest of a tree by bark beetles. *Holarctic Ecology* **12**:408–414.
- Stenseth, N. C., W. Falck, O. N. Bjørnstad, H. Tong, M. O'Donoghue, R. Boonstra, S. Boutin, C. J. Krebs, and N. G. Yoccoz. 1998. From pattern to process: phase- and density-dependence in the canadian lynx cycle. *Proceedings of the National Academy of Science (USA)* **95**:15430–15435.
- Taylor, P. 2000. Socio-ecological webs and sites of sociality: Levin' strategy of model building revisited. *Biology and Philosophy* **15**:197–210.
- Tong, H. 1990. *Non-linear time series: a dynamical system approach*. Clarendon Press, Oxford, UK.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. Monographs in Population Biology 35. Princeton University Press, Princeton, New Jersey, USA.
- Wallin, K. F., and K. F. Raffa. 2004. Feedback between individual host selection behavior and population dynamics in an eruptive herbivore. *Ecological Monographs* **74**:101–116.
- Wermelinger, B. 2004. Ecology and management of the spruce bark beetle *Ips typographus*—a review of recent research. *Forest Ecology and Management* **202**:67–82.
- Weslien, J., E. Annala, A. Bakke, B. Bejer, H. H. Eidmann, K. Narvestad, A. Nikula, and H. P. Ravn. 1989. Estimating risks for spruce bark beetle (*Ips typographus* (L.)) damage using pheromone-baited traps and trees. *Scandinavian Journal of Forest Research* **4**:87–98.
- Weslien, J., and Å. Lindelöw. 1989. Trapping a local population of spruce bark beetles *Ips typographus* (L.): population size and origin of trapped beetles. *Holarctic Ecology* **12**:511–514.
- Williams, D. W., and A. M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology* **4**:87–100.

APPENDIX A

Model parameters and their estimates for *Ips typographus* in Scandinavia (*Ecological Archives* E087-014-A1).

APPENDIX B

Results of sensitivity analyses of model parameters (*Ecological Archives* E087-014-A2).