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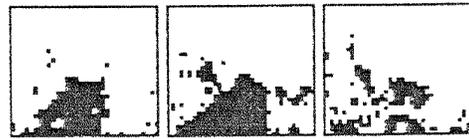
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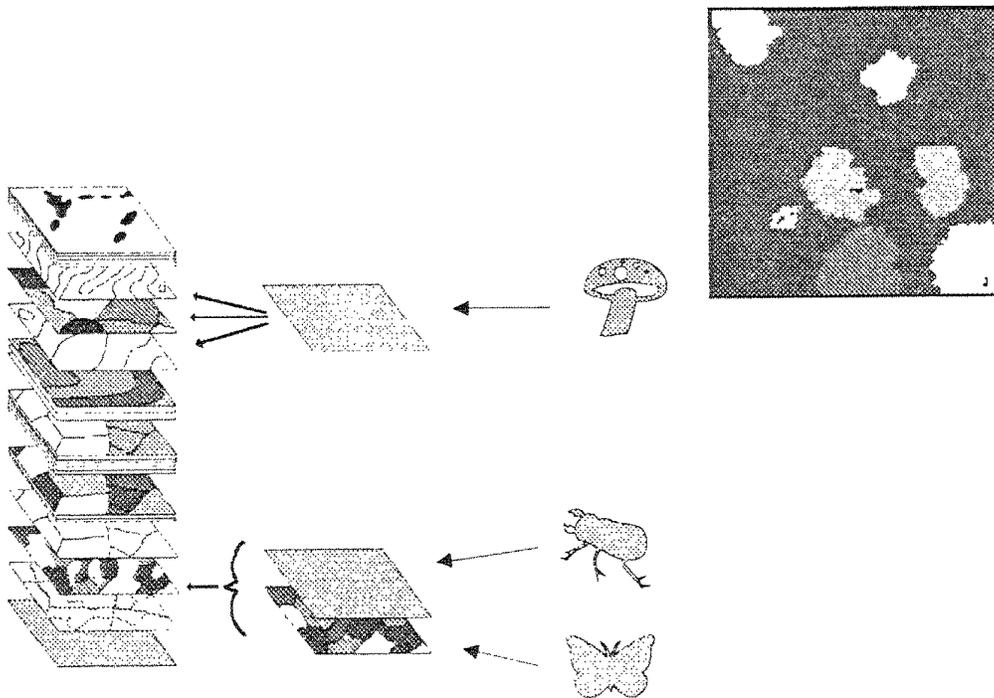


# Proceedings

## Spatial Analysis and Forest Pest Management



$$N_{x,t} = \frac{N_{0,0} e^{-\pi x^2/4Dt}}{4\pi Dt}$$



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June 1993

PROCEEDINGS  
SPATIAL ANALYSIS AND FOREST PEST  
MANAGEMENT

April 27-30, 1992  
Mountain Lakes, Virginia

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Virginia Polytechnic and State University



## FOREWORD

Over the last 20 years technologies have been developed that provide new tools for analyzing and modeling spatial processes. These tools have allowed scientists to overcome the conceptual problems and data management complexities that in the past prohibited exploration of spatial problems. These new technologies include geographic information systems (GIS), which are software for managing and manipulating spatial data, more powerful computer systems that are able to handle the computationally intensive needs of spatial data analysis, and new numerical procedures that allow analysis and modeling of spatial data. These technologies have been embraced in a variety of disciplines ranging from mining engineering to biomedical research but one field where these tools are being rapidly applied is forestry. Typically, forest management entails making decisions on land use over large, heterogeneous landscapes. This decision making typically involves the integration of multiple data themes (such as vegetation, topography, hydrology) over large geographical areas and is therefore a prime candidate for application of GIS.

The U.S. Forest Service is currently implementing a national GIS plan that will integrate GIS and other spatial analysis technologies into many aspects of forest management. This technology is similarly being applied by state and private forest management organizations around the world. In 1990 the Computer Sciences and Telecommunication staff of the US Forest Service headquarters realized that during the implementation of this plan, there was a need to bring together university and Forest Service scientists from a variety of disciplines to discuss accomplishments and future needs in spatial analysis.

In early 1991 a team of scientists working in the field of forest insect and disease management and research began to organize a workshop that would address accomplishments and future needs in the spatial analysis of forest pest problems. This group included Andrew Liebhold, Northeastern Forest Experiment Station, Donald Jameson, Computer Sciences and Telecommunications, Ross Pywell, Forest Pest Management, Patrice Janiga, Forest Pest Management, J. Robert Bridges, Forest Insect and Disease Research, Brian Geils, Rocky Mountain Forest and Range Experiment Station, Jesse Logan, Virginia Polytechnic and State University, and Lukas Schaub, Virginia Polytechnic and State University. The objectives of the workshop that they organized were:

1. Exchange information on current and near-future needs and opportunities for application of spatial analysis to describe and predict the dynamics of insects and pathogens as well as their affects on forest ecosystems.
2. Identify critical gaps in our understanding of ecosystem properties or processes that require spatial analysis to describe, maintain, and improve forest health.
3. Develop a strategic plan whereby emerging concepts and technologies using spatial relationships could be better incorporated into forest planning, monitoring, and research.

The workshop was held April 27-30, 1992 at Mountain Lakes, Virginia. The first two days of the meeting were used by the participants to make presentations on current accomplishments in spatial analysis. The last day was spent in break-out groups, discussing gaps in our current knowledge and setting priorities for future research and development.

These proceedings contain papers authored by workshop participants and a final report at the end of this volume summarizes the conclusions made by the participants in the break-out groups. The purpose of publishing these proceedings was to allow individuals who were not at the workshop to learn about what research and development is underway in the area of spatial analysis of forest pests and to communicate the participants' conclusions about future research and development needs.

SPATIAL ANALYSIS AND FOREST PEST MANAGEMENT  
April 27-30, 1992  
Mountain Lakes, Virginia

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# SPATIAL ANALYSIS AND INTEGRATED PEST MANAGEMENT IN A LANDSCAPE ECOLOGICAL CONTEXT

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*Abstract.* Integrated pest management (IPM), forest management, and environmental management are levels of focus in an increasingly complex spatial and temporal hierarchy of land use. Evaluating and projecting the consequences of actions and activities taken at each of these levels involves use of spatial analytical methodologies. In this paper we (i) describe the concept and practice of IPM in a landscape ecological framework and (ii) consider the utility and limitations of geographic information systems for spatial analysis at the landscape scale of ecological integration. The architects of IPM used a holistic approach in their initial definition of the concept and the ecosystem was identified to be the appropriate level for abstraction. However, the ecosystem concept is inherently vague about scale and boundary. We suggest that the landscape ecological concept of *ecotope* (which embraces ecosystem functionality within the context of a land unit that has discrete boundaries) is the appropriate unit of abstraction. The ecotope concept permits consideration of land units (chorology) as well as land attributes (topology) in structuring analyses to evaluate and project the consequence of management actions. Although the procedures for landscape analysis are in an evolutionary state, all require use of spatially referenced data. For this reason, the geographic information system (GIS) has proven to be a useful tool. The GIS provides a "tool box" of functions that are helpful in landscape analysis and interpretation: map generalization/simplification, map overlay, spatial query/browsing, spatial statistics, spatial relationships, spatial reasoning.

## INTRODUCTION

Integrated pest management (IPM) has been a dominant theme in forestry for more than two decades. The social, economic, and ecological impacts of insects and diseases are no less significant today than in the past. However, IPM has taken on a new significance, since forest management practices are now linked directly to larger environmental issues (e.g., deforestation, sustainable production, loss of biological diversity, global warming, cultural heritage). IPM, forest management, and environmental management are levels of focus in an increasingly complex spatial and temporal hierarchy of land use. Evaluating and projecting the consequences of actions and activities taken at each of these levels involves use of spatial analytical methodologies, which are only just beginning to be developed. Conclusions from the analyses are interpreted within the context of principles of ecology and management science. In this paper our specific objectives are (i) to describe the concept and practice of IPM in a landscape ecological framework and (ii) to consider the utility and limitations of geographic information systems for spatial analysis at the landscape scale of ecological integration.

## FOREST PEST MANAGEMENT IN A LANDSCAPE ECOLOGICAL CONTEXT

### *Integrated pest management*

The formal beginning of IPM can be traced to the symposium proceedings *Concepts of Pest Management* (Rabb & Guthrie 1972). Since then, fundamental principles of IPM, and the forestry perspective on the subject (forest pest management - FPM), have evolved (Coulson 1981, USFS Anon. 1988). We are concerned here with both the concept and practice of IPM. Initially, IPM was a research and development activity. Emphasis was placed on issues of concept. Several specialized definitions were formulated. An example follows:

...the maintenance of destructive agents, including insects, at tolerable levels by the planned use of a variety of preventive, suppressive, or regulatory tactics and strategies that are biologically and economically efficient. It is implicit that the actions taken must be fully integrated into the total resource management process in both planning and operation. This means that pest management must be geared to the life span of the tree crop as a minimum and to a longer span where the resource planning horizon so requires...(Coulson & Witter 1984).

Implementation of this concept into forest management practice has proven to be a challenging task. Although the definition includes cryptic reference to a time frame, missing is any direct consideration of spatial scale or boundary. Pest management activities associated with suppression and prevention have quite different time and space constraints. The difficulty associated with merging concept and practice begins to be evident when we recognize that FPM is a site-specific activity, i.e., actions are directed to discrete land units of varying size. Furthermore, projecting the probable consequences of FPM practices involves interpretation based on ecological principles from several levels of integration, i.e., populations to landscapes. Simply stated, FPM practice embraces a hierarchy of land units and ecological levels of abstraction.

### *Landscape ecology and integrated pest management*

Landscape ecology is the academic discipline that provides a scientific base for problem-solving and decision making in land-use management. Basic principles of landscape ecology are described in Forman & Godron (1986), Kolasa & Pickett (1991), Navch & Lieberman (1984), Pickett & White (1985), Turner (1987), Turner & Gardner (1991), and Zonneveld & Forman (1990). This science deals with the study of landscape structure (components of the landscape and their linkages and configurations), function (quantities of flows of energy, materials, and species within and among landscape elements), and change (alteration in the structure and function of the ecological mosaic over time). Also included within the realm of landscape ecology are the actions and activities of humans relative to their environment.

From the onset, the developers of the IPM concept recognized the importance of a holistic approach and, therefore, identified the ecosystem (the biotic community together with the abiotic environment) as the appropriate level of focus (see Watt 1968 and Van Dyne 1969). The approach was appealing in that researchers could examine functionally how insect populations and communities influenced, or perhaps regulated, ecosystem level processes such as primary production, consumption, decomposition, or abiotic storage.

The fundamental problem with this approach is that the ecosystem concept is inherently vague about scale and boundary. In fact, ecosystems are often described simply as environments around special organisms of interest, e.g., the forest ecosystem, the cotton ecosystem, the apple orchard ecosystem. The term *ecotope* is used in landscape ecology to address ecosystem functionality within the context of a land unit that has discrete boundaries. Therefore, a landscape consists of a mosaic of ecotopes, i.e., tangible ecosystems (Figure 1).

With the ecotope serving as the basis for abstraction, landscapes can be viewed to have both horizontal and vertical dimensions. Horizontal (chorological) dimension refers to land units, which can be aggregated at different scales. For example, the convention used by the US Forest Service on national forests consists of a hierarchy beginning with the forest stand (the ecotope). Stands are combined to make compartments. Compartments are further clustered into a district. Districts form national forests (Figure 2). Vertical

(topological) dimension refers to land attributes, e. g., flora, fauna, soil, landform, etc. One function of landscape ecological research is to integrate information on land units and land attributes (Zonneveld 1990).

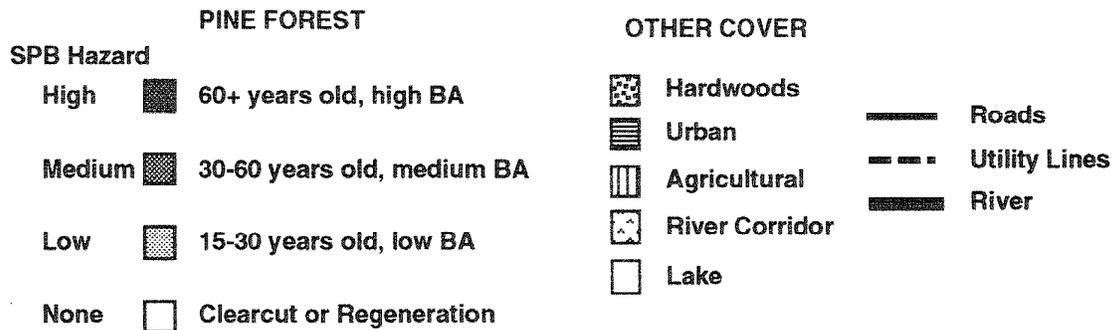
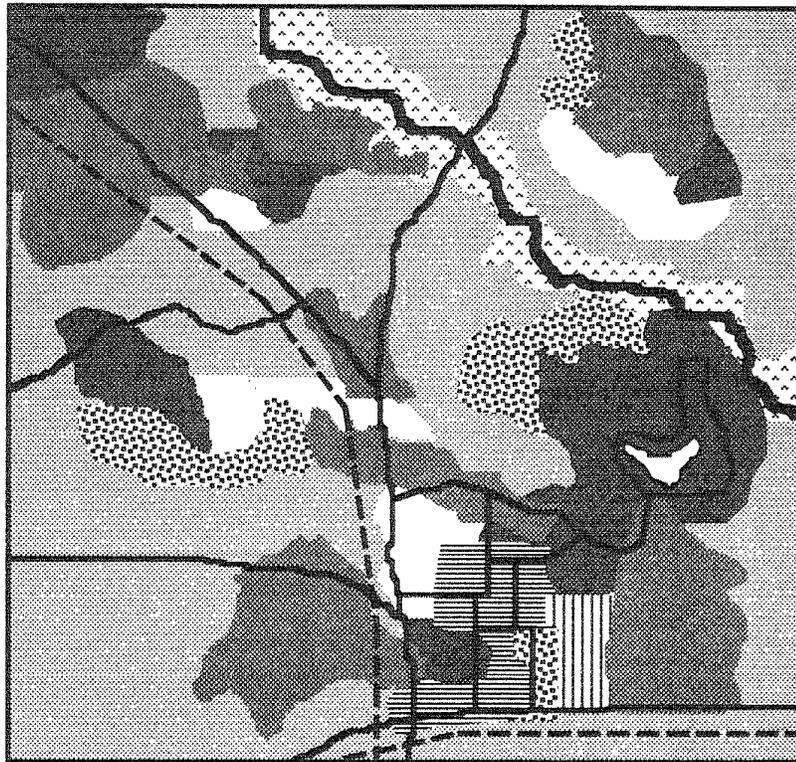


FIG. 1. forested landscape consisting of a mosaic of constituent ecotopes. The ecotope is the fundamental unit for IPM. One important function of landscape ecological research centers on integrating chorological (land unit) and topological (land attribute) information.

LANDSCAPE ANALYSIS, IPM, AND GIS

*Geographic information systems and landscape ecology*

One of the fundamental topics of study in landscape ecology centers on understanding how and why organisms are distributed across complex mosaics of ecotopes. Of course, this subject is of paramount importance to IPM as well. Changes in the distribution and abundance of a pest species can be assessed when studies of large-scale patterns and processes are interpreted within an ordered framework. The

hierarchy of land unit classification, with the ecotope serving as the base, is a useful way to organize landscape level analyses. Examination of the distribution and abundance of a pest insect species (or guild) requires analytical techniques that include the interaction of the horizontal and vertical dimensions of a landscape in the context of a specific landscape characteristic. For example we may be interested in how herbivory by bark beetles in mature pine forests (the landscape characteristic) is influenced by land unit configuration and specific land attributes such as tree species composition, other age classes of trees, soil type, hydrography, etc. Although the procedures for landscape analysis are in an evolutionary state, all require use of spatially referenced data. For this reason, the geographic information system (GIS) has proven to be a useful tool.

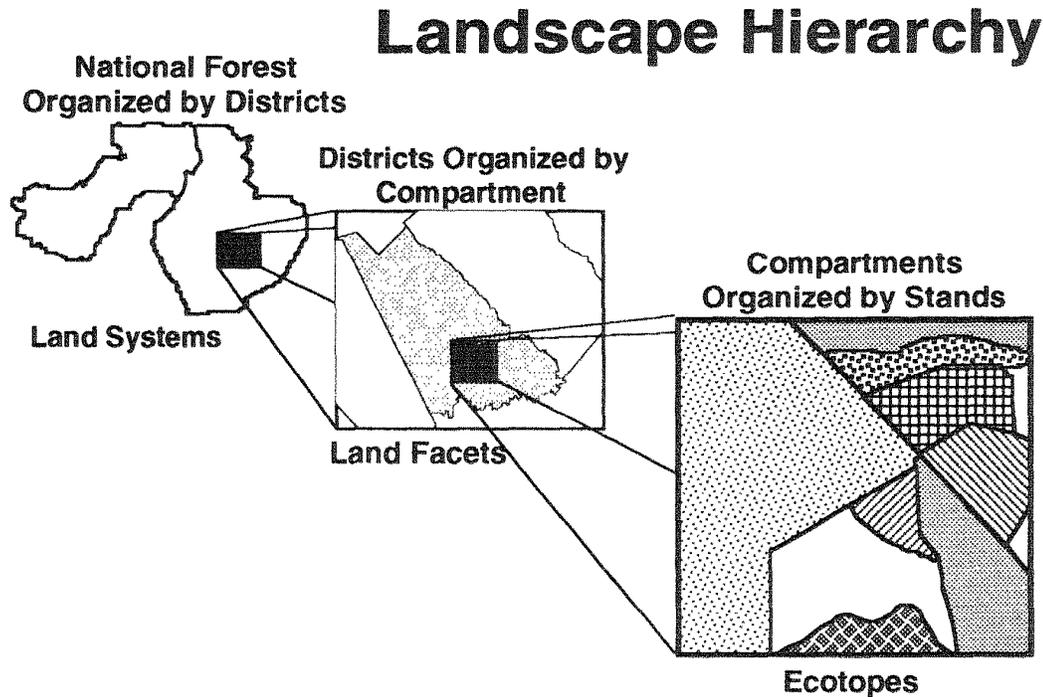


FIG. 2. With the ecotope serving as the basic level of abstraction, landscapes can be viewed at different scales. The convention used by the USDA Forest Service for national forests consists of a hierarchy beginning with the forest stand. Stands are combined to make compartments. Compartments are further clustered into a district. Districts form national forests.

Contemporary developments in GIS and the companion technologies of remote sensing and image processing are treated in Aronoff (1989), Buhyoff (1988 & 1990), Burrough (1988), Davis (1986), Laurini and Thompson (1992), Maguire, et al. (1991), Peuquet & Marble (1990), Star & Estes (1990), and Tomlin (1990). The appeal of GIS software is that it provides access to and display of geographically referenced databases. Interest in cartography provided the motivation for early GIS development. Potential practitioners looked beyond cartographic uses of GIS. Their expectation was that GIS could be used as a tool to address problems of spatial analysis and landscape modeling. However, the initial GISs had modest utility in this regard, with analytical functionality limited to Boolean operations, polygon overlay, buffer zones, and some statistical computation (Coppock 1989, Davis et al. 1988). This circumstance is beginning to change, as there is considerable research activity currently being directed to development of methods for spatial statistical analysis and landscape modeling (Turner & Gardner 1991).

#### *Functionality of geographic information systems*

GIS software and hardware usually consist of five subsystems (Burrough 1986). They are the: (1) data input subsystem, (2) data storage and management subsystem, (3) data visualization and output subsystem, (4) data manipulation and analysis subsystem, (5) user interface subsystem. Capabilities of the data manipulation and analysis subsystem determine how the GIS can be used to characterize landscapes.

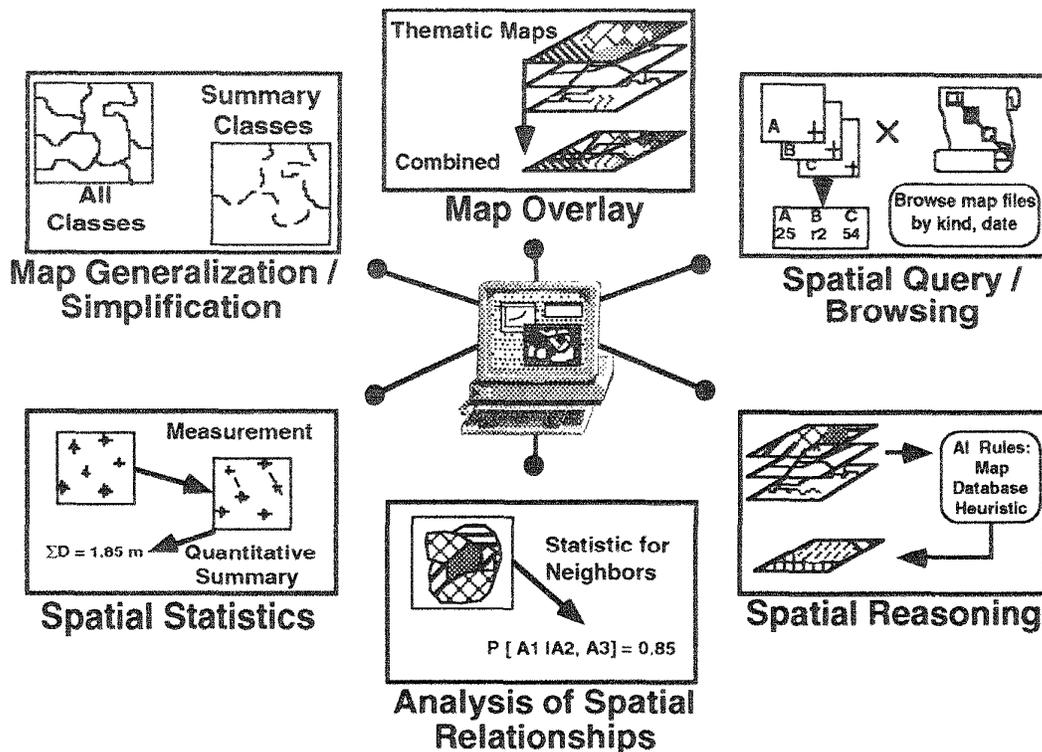


FIG. 3. The analytical functionality for most GISs includes utilities for map generalization/simplification, map overlay, spatial query/browsing, spatial statistics, analysis of spatial relationships, and spatial reasoning.

The data manipulation and analysis subsystem provides a "toolbox" of functions used to transform thematic map data. Manipulation and analysis either add value to the spatial database or solve spatial problems. The added value may come from creation of new thematic maps or visualizing spatial distributions. Spatial problems are solved using measurements of objects in space, by determining spatial relationships, and by creating predictive spatial models. Typical spatial analysis functions provided by GIS are (Burrough, 1986 and Laurimi and Thompson, 1992) (Figure 3):

- (1) *Map generalization and simplification*: These functions permit re-classification of spatial objects. The procedures allow the user to isolate the specific variables needed for analysis.
- (2) *Map overlay*: Map overlay techniques can be used to combine thematic maps. These procedures allow for the synthesis of maps consisting of novel data themes.
- (3) *Query and browse*: Query functions facilitate extraction of information from a spatial database. Browse functions permit exploring the contents of a spatial database.
- (4) *Spatial statistics*: Usually, a GIS can provide descriptive statistics and histograms for attributes of spatial objects. Also, GIS usually provide for correlation analysis to compare spatial relationships that exist between and within thematic maps.
- (5) *Analysis of spatial relationships*: A GIS can measure spatial arrangement of objects on a map. Spatial relationship measurements include proximity, distance, and trend.
- (6) *Spatial reasoning*: Some systems provide tools for decision-making, incorporating both spatial information and heuristic knowledge. Human deductive reasoning can be imitated using expert systems techniques. The simplest systems use rule based reasoning to interpret within and among landscape data themes.

The GIS technology has improved dramatically in recent years. The suite of analytical tools has been broadened considerably. However, further development in statistics for spatial analysis and modeling is needed.

#### ACKNOWLEDGMENTS

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## A MECHANISTIC APPROACH TO UNDERSTANDING AND PREDICTING SOUTHERN PINE BEETLE DYNAMICS

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*Abstract.* Despite extensive research on the behavior and ecology of the southern pine beetle (SPB) and its natural enemies, our understanding of its populations dynamics remains incomplete. In particular, it is unknown what role natural enemies play in the regional outbreaks seen in the SPB, nor what effect they have on the growth of local SPB infestations. In this article, we discuss how recent ecological theory can be adapted to address these questions in the SPB system. Our approach is based on a conceptual model which divides the system into two components, the first involving the movement of the SPB and its natural enemies between trees, and the second the interaction of the SPB and enemies once they arrive on a tree under mass-attack. We discuss what sort of experiments are necessary to investigate each component of this conceptual model, and review our results to date. We then show how the two components can be combined to generate predictive mathematical models of the system, and describe how the models can be empirically tested.

### INTRODUCTION

The cyclic population outbreaks of the southern pine beetle (SPB), *Dendroctonus frontalis*, cause significant economic damage to pine forests in the South. During the outbreak year of 1985, for example, losses in the region due to the SPB exceeded \$120 million (USDA 1987). Despite extensive research on the behavior and ecology of the SPB and its associates, however, our understanding of its population dynamics remains incomplete. On a regional scale, for example, it is unknown what mechanism causes SPB populations to regularly cycle between outbreak and endemic phases. Although there is circumstantial evidence that natural enemies may contribute to this cycling (Billings 1988; Stephen *et al.* 1989; Turchin *et al.* 1991), this hypothesis has not been critically examined. Much also remains to be learned about SPB dynamics on a local scale, at the level of individual SPB infestations, or "spots". It is unclear why some spots naturally cease growth, while others grow unchecked until control measures are applied. Another critical but unanswered question is the extent to which SPB dispersal connects different spots, and contributes to their early growth, before local reproduction has occurred.

What sort of information would be necessary in order to understand SPB dynamics, on both a regional and local scale? Recent ecological theory suggests that several different types of information are required to understand the dynamics of insect populations, and in particular predator-prey systems, like SPB and its natural enemies (Hassell 1978; Chesson and Murdoch 1986; Kareiva and Odell 1987; Murdoch and Stewart-Oaten 1989; Taylor 1988; Hassell *et al.* 1991; Ives 1992). First, information is needed on the movement of the organisms involved across a range of spatial scales, ranging from local to regional, and with respect to local concentrations of prey or predators (e.g. movement of the predators toward their prey). Second, we also need to know how the predator and prey interact once they reach the same location or patch. This will be determined by the attack rate and functional response of the predator, and by competition among the prey, as well as the predators. Finally, it is critical to know the duration of the life history stages of both predator and prey, especially those prey stages which are invulnerable to attack, since this can strongly influence the dynamics of the system (Murdoch *et al.* 1987; Godfray and Hassell 1989). Given these different types of information, one can construct mathematical models of a system which predict its behavior in some detail.

In this article, we outline how the above approach can be applied to investigate the dynamics of the SPB and its natural enemies, with the eventual goal of developing a predictive model of the system. To do this, we divide the system conceptually into two components. The first component involves all movement of the SPB and its natural enemies between trees, beginning when the SPB brood and natural enemies emerge from their natal tree, and ending when they arrive on new trees under mass attack by SPB. The second component involves the interaction of the SPB and its natural enemies once they arrive on the tree, which we call the "within-tree" interaction. For example, an arriving SPB will compete with other individuals for space within the phloem, and its progeny will be consumed by predators and parasitoids. After these interactions occur, SPB and natural enemy progeny are produced and emerge from the tree, entering the movement component of the system and completing the circle.

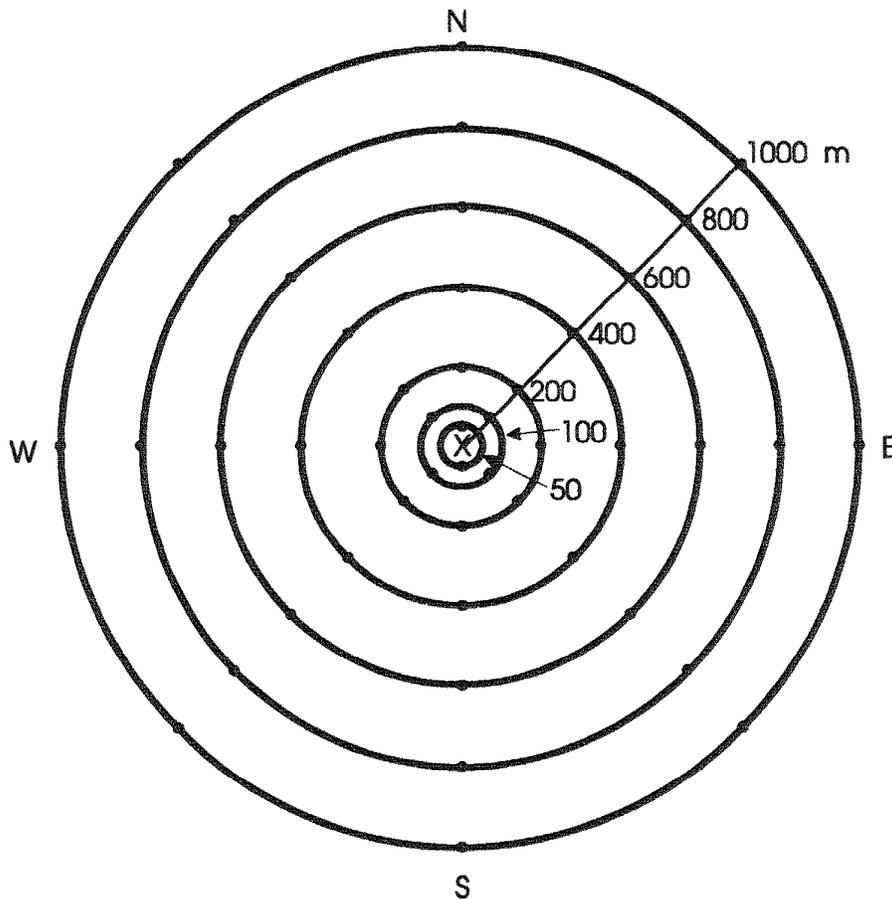


FIG. 1. Recapture grid. Each solid circle indicates the position of a trap. X indicates the point of release.

#### THE MOVEMENT COMPONENT

Although a number of different methodologies have been used to investigate and model the movements of insect populations, we have chosen the framework of diffusion equations to describe the movement of SPB and its enemies, an approach used with significant success in many other systems (Okubo 1980; Kareiva 1983; Kareiva and Odell 1987; Turchin 1989). For the SPB and its natural

enemies, movement seems to occur essentially in a two-dimensional plane within the forest, because the insects are usually found flying in a narrow range of heights above the forest floor. Given that the insects move in only two dimensions, an appropriate general diffusion equation for the SPB is

$$\frac{\partial S}{\partial t} = -\frac{\partial}{\partial x}(\beta S) - \frac{\partial}{\partial y}(\beta S) + \frac{\partial^2}{\partial x^2}(DS) + \frac{\partial^2}{\partial y^2}(DS) - \delta S \quad (1)$$

Here  $S(x,y,t)$  is the density of flying SPB at a particular location in space and time,  $\delta$  is their mortality rate, and  $\beta$  and  $D$  are the drift and diffusion coefficients of the diffusion process. The drift coefficient  $\beta$  controls the tendency of the beetles to move in particular direction (if it is zero there is no tendency). For example, if beetles are biasing the direction of their movement towards a tree producing attractive volatiles, then there will be a non-zero population drift towards the attractive tree.  $D$  encapsulates the undirected component of beetle movement. To complete this model of SPB movement it is necessary to specify the form of  $\beta$  and  $D$ , which in general could be functions of the position of the beetles in space (their  $x,y$  coordinates) and other variables in the system. Given  $\beta$  and  $D$ , the above equation can be solved to give the density of flying SPB at any point in space and time, given an initial distribution of beetles, and appropriate boundary conditions. Similar equations can be defined to describe the movement of the natural enemies in the system.

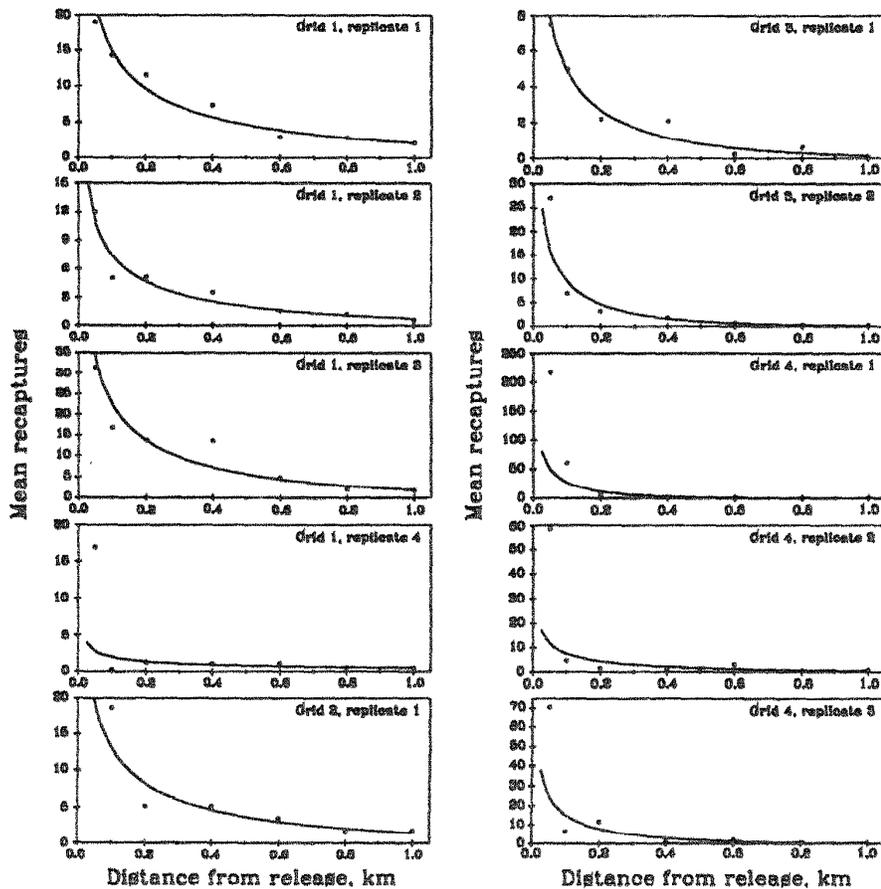


FIG. 2. Recaptures-with-distance curves for each replicate release, at four different locations (grids). The data points are the cumulative recaptures averaged over all traps at a given distance from the release point. The solid lines are the fitted diffusion model.

The next step in using the diffusion framework is to experimentally determine  $\beta$  and  $D$  for SPB and its natural enemies. With SPB, this problem is complicated by the fact their movement seems to involve two distinct phases; the dispersal of brood beetles from the tree in which they developed, followed by their congregation on trees undergoing mass attack, in response to the release of the attractive pheromone, frontalin (Gara and Vité 1962, Vité *et al.* 1964). Different experiments and methods of analysis are necessary to measure beetle movement in each phase. To examine movement purely in the dispersal phase, a series of mark-recapture experiments were conducted in areas of the forest cleared of all trees attacked by SPB, thus eliminating any potential foci for beetle congregation (Turchin and Thoeny, in press). In these experiments, bolts containing SPB brood were transported to a central point and then coated with a fluorescent powder, which marked the beetles as they emerged. The marked beetles were then recaptured using an array of pheromone-baited funnel traps (Lindgren 1983) located at different distances and directions from the center (Fig. 1). Analysis of the resulting information indicated that a simple diffusion model incorporating in-flight mortality provided a good fit to the data (Fig. 2), and yielded estimates of the quantity  $D/\delta$ , the ratio of the diffusion coefficient and the mortality rate.

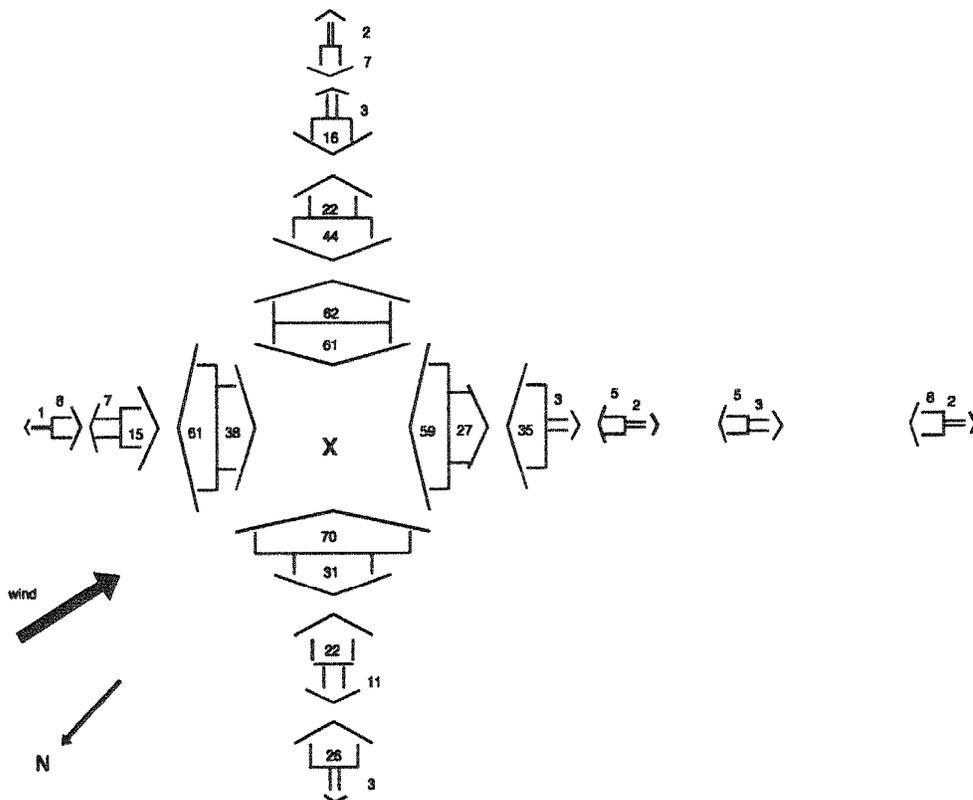


FIG. 3. The spatial structure of a beetle swarm around a focal tree. X indicates the focus of congregation (the mass-attacked pine tree). Arrows pointing towards (away from) the focus show how many beetles hit the  $1 \text{ m}^2$  sticky screen going towards (away from) the tree. The width of the arrow and the number inside it indicate the actual number of beetles captured. Summing the numbers of beetles hitting both sides of the screen, we obtain an estimate of the swarming density at the spatial position of each screen. Taking the difference we obtain an estimate of net flux with respect to the congregation focus.

A second study, using different experimental methods, was necessary to examine SPB behavior during the congregation phase of movement. The basic premise of the study was that beetles flying in the vicinity of a mass-attacked tree use chemical (pheromones and host volatiles) and visual (the vertical shape of the tree, see Gara, Vité and Cramer 1965) cues to bias their movements towards the tree. This

bias results in congregation and mass attack. The attractive bias is assumed to be a function of the distance and direction from the tree to the flying beetle. In addition, the bias is modified by the total number of beetles boring into the tree. At the beginning of mass-attack, the strength of the bias should increase with the number of attacking beetles, since more beetles are congregating on the tree, releasing frontalin. As the tree begins to fill with attacking beetles, however, the bias should decrease in strength, possibly even becoming negative, due to the release of the repellent pheromone verbenone (Payne 1980).

The approach of the second study was to quantify attractive bias by measuring the flux of flying SPB at various spatial points, around a single tree under mass-attack by SPB. Flux in relation to the mass-attacked tree is defined as the number of SPB crossing a unit of surface area ( $1 \text{ m}^2$ ) per unit of time (1 day) toward the tree, minus the number crossing the surface away from the tree. To begin the experiment, a single loblolly pine (*Pinus taeda*) was baited with frontalin and turpentine, to initiate SPB attack. As soon as mass attack was underway, these artificial volatiles were removed, allowing the attack to proceed naturally. To measure the flux of flying SPB toward the tree,  $1 \text{ m}^2$  sticky screens were erected at different distances and directions from the tree. The course of the mass attack was monitored by counting the number of entrance holes of boring beetles on 16 smoothed areas of bark ( $1 \text{ dm}^2$  in area) on the focal tree. Analysis of the resulting data has shown that the flux of beetles toward the tree is a function both of the number of beetles attacking, and the distance from, the focal tree (Fig. 3).

Given information on the fluxes of SPB, our eventual goal is to determine the form of  $\beta$ ,  $D$ , and  $\delta$  for this phase of SPB movement, and so fully define equation (1). Combined with the results of the dispersal phase experiment, the resulting diffusion model will provide a complete description of beetle movement (see Fig. 4 for a conceptualization of how this model of beetle movement would work). The same experimental techniques will eventually need to be applied to key natural enemies in the system. Once diffusion equations for the SPB and natural enemies are defined, they can then be solved to determine the total number of SPB and natural enemies which arrive on the surface of the tree during attack. These inputs to the tree are the inputs to the second half of our conceptual model of the SPB system, involving the interaction of the SPB and its natural enemies once they arrive on the tree.

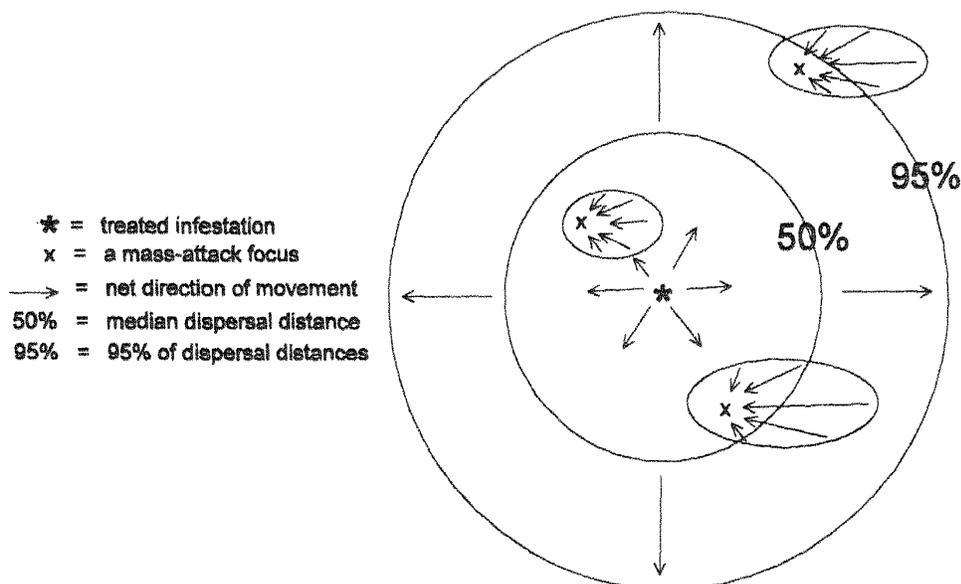


FIG. 4. A conceptual model of intraforest dispersal in the SPB. Arrows indicate net population fluxes. Thus, individual beetles may be moving in randomly chosen directions, but the average population flow will occur in the direction indicated by arrows. Solid concentric circles indicate the spatial scale of dispersal, enclosing 50% and 95% of all dispersers, respectively. Ovals delineate attractive areas of mass-attack, or congregation, foci. These foci, which could be either single trees or spots, are indicated by X.

## THE WITHIN-TREE INTERACTION

To complete our model of SPB dynamics, we now focus on the interaction of the SPB and its natural enemies once they have arrived on a tree under mass-attack. Many different aspects of the biology and behavior of the SPB and its enemies could, in theory, influence this interaction. These include the attack rates and functional responses of the different enemy species, and any interference or competition between them. Unfortunately, there is almost no information of this kind for the enemies of SPB, especially under natural conditions. In petri dishes, adults of the SPB predator *Thanasimus dubius* (Coleoptera: Cleridae) have been shown to have a Type II functional response on SPB adults (Turnbow *et al.* 1978; Mizell 1980; Nebeker and Mizell 1980), but no information exists on the behavior of clerid larvae, which are thought to consume large numbers of SPB brood underneath the bark (Thatcher and Pickard 1966). Dix and Franklin (1974, 1981, 1983) have observed aggressive encounters among SPB parasitoids, an indication that interference is occurring among them. While this could potentially affect the dynamical behavior of the system, no measurements of the degree of interference were made. In general, although the basic ecology and life histories of many SPB natural enemies are known, we lack the quantitative information necessary to understand their effects on SPB dynamics.

Perhaps the main reason why we lack quantitative information on natural enemies is that much of the interaction takes place beneath the bark surface, making direct observation of natural enemy and SPB behavior difficult. Because we cannot easily use observational methods, we have adopted a more practical, if indirect, approach by quantifying the interaction between the SPB and its natural enemies at the level of the tree. At this level, one has an initial set of inputs to the tree, consisting of the number of SPBs and natural enemies arriving on the tree. Once there the organisms interact (the "within-tree" interaction), generating a set of outputs, which are the number of SPB and enemies eventually emerging from the tree (the progeny of the arriving individuals). This idea can be written mathematically as

$$\begin{aligned} S' &= S \cdot f_S(S, X_1, X_2, \dots) \\ X_1' &= X_1 \cdot f_1(S, X_1, X_2, \dots) \\ X_2' &= X_2 \cdot f_2(S, X_1, X_2, \dots) \\ &\text{etc.} \end{aligned} \tag{2}$$

where  $S$  is the number of SPB attacking the tree, and  $X_1, X_2, \dots$  are the number of natural enemy species 1, species 2, etc., arriving on the tree.  $S', X_1', X_2', \dots$  are the number of SPB and natural enemy progeny later emerging from the tree. The within-tree interaction is described by the functions  $f_S, f_1, f_2, \dots$ , which are essentially per capita growth rates. The particular shape of each function would be determined by the details of the behavior and biology of each enemy, and the SPB. For example, if enemy 1 (say *Thanasimus*) possessed a Type II functional response, then one would expect  $f_S$  to increase as arriving SPB density ( $S$ ) increases, because the clerids would become saturated at high prey densities (assuming all other densities ( $X_1, X_2, \dots$ ) remain the same). If there were also significant competition for food among clerids, in addition, then one would expect  $f_1$  to decrease as clerid density increases on the tree.

We are currently using two different but complementary approaches to determine the within-tree interaction. The first, a field study of trees within SPB infestations, employs naturally-occurring variation in enemy and SPB numbers to determine the within-tree interaction (i.e., the form of  $f_S, f_1, \dots$ ), with all the enemy species present. The study involves measuring the number of natural enemies and SPBs arriving on the tree, using sticky-traps. Bark samples are then taken to estimate the density of successful SPB attacks, and then emergence traps attached to catch both the emerging SPB brood and natural enemies.

Response surface methodology (RSM) will then be used to estimate the within-tree interaction functions. The RSM approach is similar to polynomial fitting of the data, but also permits nonlinear transformation of the variables to be fitted (Box and Cox 1964), and thus provides greater flexibility. In essence, RSM is a phenomenological, and hence model-independent, approach to fitting a function to

ecological data (Turchin and Taylor 1992). Because of the typical residual structure in ecological data, we will not fit Equation (2) directly to the data, but instead will use the statistical model

$$\log S'/S = g(S, X_1, X_2, \dots) + \epsilon \quad (3)$$

where  $\epsilon$  is the error term, and  $g$  is the response surface to be fitted using Box and Draper (1987) methods. Stepwise regression of  $\log S'/S$  on the numbers of natural enemies visiting the tree (i.e.  $X_1, X_2, \dots$ ) will be used to determine which natural enemy species have a significant effect on the SPB, and so should be included in the response surface model. It should also be possible to fit analogous response surfaces for each of the natural enemy species, which would describe how the number of emerging individuals of each species is related to the number arriving on the tree, and SPB density.

The second natural enemy study, a field experiment using tree cages, manipulates the density of *Thanasimus* and SPB within enclosures which exclude all other natural enemies, to examine the contribution of *Thanasimus* to the total within-tree interaction. This experiment will allow us to examine the pairwise interaction between the SPB and one natural enemy species, in contrast with the field study, which involves the interactions among all the species. *Thanasimus* is an abundant natural enemy of the SPB, making it a logical first choice for this type of experiment. The same methods could, however, be used to study the effects of many of the other natural enemy species.

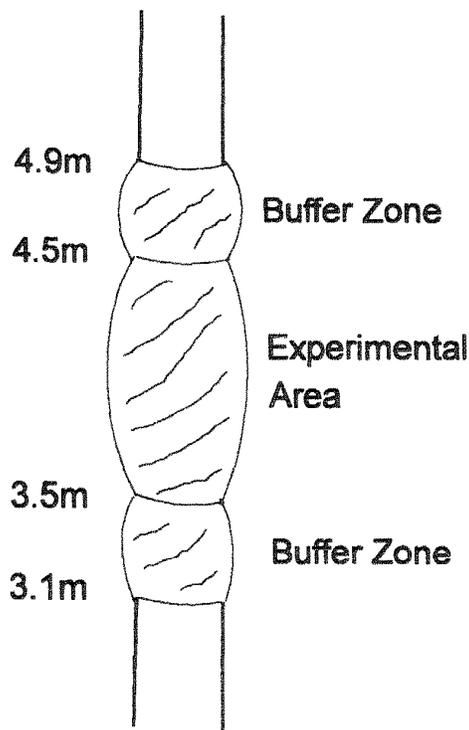


FIG. 5. Tree cage used to manipulate the densities of *Thanasimus* and SPB, while excluding other natural enemies.

The experiment has eight different treatments, four clerid densities crossed with two SPB densities. The first step in the experiment is to choose loblolly pines in an area where SPB are prevalent, and then install the cages (see Fig. 5). These are 1.8 m long cylindrical enclosures, made from fine-meshed saran screen, divided into a 1 m experimental area in the center (to which the SPB and clerids are added), and buffer zones above and below the experimental areas (no insects added). The buffer zones act as barriers to the within-bark movement of SPB and natural enemies from outside the cages. The trees are then baited with frontalinal and turpentine, to induce SPB attack on the tree outside of the cage. As the tree

succumbs to attack, the required number of SPB and clerids may then be added to the cage. Bark samples are then taken after several weeks to estimate the attack density of SPB. Just before SPB emergence, the tree is felled and the caged area removed and held within a rearing can, to measure the number of SPBs and clerids emerging. Response surface methodology will again be used to analyze the outcome of the experiment. Because only one natural enemy species is involved, however, the model simplifies to

$$\log S'/S = g(S, X) + \varepsilon \quad (4)$$

Here  $S$  and  $X$  are the inputs of SPBs and clerids to the cage, while  $S'$  is the number of SPB emerging.

#### SYNTHESIS

Once the movement and within-tree interaction components of the SPB system are known, it should be possible to construct and test quantitative mathematical models of the system. We plan to construct a hierarchy of models, beginning with one of a single tree under mass attack. Starting with an initial distribution of SPB and natural enemies in space, the model would first predict the number and temporal pattern of insects arriving on the focal tree, and then using the within-tree interaction component, predict the number of SPB and natural enemy progeny later emerging from the tree. The next step in modeling the system would be to construct a spot dynamics model. Again, the model would take an initial distribution of organisms in space and predict the number arriving on one or more focal trees. The progeny emerging from these trees would then be fed back into the movement part of the model, after an appropriate developmental delay, where they could potentially attack new trees or disperse away from the spot. To test these two models, one would need an estimate of the density of flying SPB and natural enemies in the vicinity of the focal tree or spot, since this provides the initial condition of the model. The predictions of the model could then be compared with the growth of actual spots, under different initial conditions. The final model in the sequence would be a regional one, which would predict where spots would occur within a large geographic area, and would also predict how densities of the SPB and its natural enemies fluctuate through time. An important test of this model would be its ability to predict the amplitude and period of SPB oscillations seen in nature.

#### CONCLUSION

A number of different hypotheses have been advanced to explain the occurrence of SPB outbreaks. These include the influences of climate (King 1972), systematic shifts in individual quality between endemic and epidemic populations (Hayes and Robertson, in press), an interaction between hosts (possibly involving cyclic changes in host quality) and SPB populations (Berryman 1976), and a cycle driven by natural enemies. We have focused on the predator-prey aspect of SPB population dynamics, because we believe this is currently the most fruitful direction, given the indirect evidence supporting this hypothesis. Our goal is to either refute or provide support for the enemies hypothesis. However, other hypotheses could be included within the general modeling framework we have advanced in this paper. For example, if there are in fact cyclic changes in the quality of SPB populations (perhaps in their fecundity), we could incorporate this in the model, and then see if it predicted oscillations in SPB density similar to those seen in the field. By proceeding in this way, our modeling approach should allow us to test each of the above hypotheses.

A key feature of our approach is its explicit consideration of the spatial dimension of SPB dynamics. Until recently, very little quantitative information was available about the spatial scale and factors affecting SPB dispersal (Turchin and Thoeny, in press). Without such information, we would never be able to explain such puzzling spatial features of SPB dynamics as the apparent synchronization of outbreaks over large spatial scales (e.g. at the level of states). Are regional SPB outbreaks synchronized by SPB and/or natural enemy movement? Or are they synchronized by correlated weather patterns?

It is clear that both data and models are required to answer questions of the sort raised above. However, the dynamics of SPB outbreaks have traditionally been studied either purely empirically, or with phenomenological models (e.g., Gold *et al.* 1980). There has been little, if any, interaction between the models and data. Theory is needed to indicate what sorts of data must be collected. For example, by writing down the diffusion model of SPB movement, we have identified the key parameters that need to be measured in field experiments. On the other hand, models unrestrained by data are not helpful in eliminating competing hypotheses that purport to explain SPB outbreaks. We believe that a mechanistic framework combining modeling and empirical work, such as the one proposed here, is necessary for sorting out various hypotheses explaining SPB outbreaks.

#### CONCLUSION

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## REGIONAL DYNAMICS OF SOUTHERN PINE BEETLE POPULATIONS

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**Abstract.** Critical analysis of a dataset on southern pine beetle activity assembled by 11 states and spanning 31 years reveals broad scale patterns and variability of beetle outbreaks and resulting tree mortality. Spatial and temporal patterns are explored at both regional and state scales, and decadal and annual time steps. These analyses indicate that outbreaks can be initiated simultaneously at multiple sites and across multiple states. Outbreaks also appear to cycle through an initial, intensive phase of damage and then to spread into a more extensive phase where damage is less concentrated. However, because the data are assembled from operational records, critical appraisal of data quality is essential to proper interpretation of results. For this reason, methodological artifacts may be contributing in some degree to the observed patterns. Two analyses are illustrated where inconsistencies in data definitions currently prevent credible analysis (merchantability shifts during outbreaks, and the contribution of National Forests to surrounding outbreaks). By clarifying broad scale variability and processes, spatial and temporal analyses at these regional scales can be a crucial complement to finer scaled analyses of pest dynamics. Because beetle dynamics are extremely variable over time, work on initiating collection of more methodologically defensible data cannot begin too soon.

The principal objective of this paper is to explore broad scale southern pine beetle (SPB) dynamics for processes which might be responsible for initiating outbreaks, based on a recently published 31 year dataset of regional scope (Price and others 1992). Initiating factors are focussed on because 1) factors initiating outbreaks may differ from those which terminate them, and 2) suppression efforts at this early phase of outbreak may be more effective than efforts during outbreak peaks.

This paper has a secondary objective. While an earlier compilation of southern pine beetle outbreaks (Price and Doggett 1982) was used in numerous investigations (Mawby and Gold 1984; Mawby and Hain 1985; Mawby and Gold 1984; Mawby and others 1989; Michaels and others 1986), little attention was given to the origins and limitations of the underlying data. Because these data were originally collected by various State forest pest specialists for operational rather than scientific purposes, data comparability is an important concern. Explicitly addressing such issues is the best means to minimize its misinterpretation.

The paper will thus describe first how the data were derived. This will be followed with discussion of the patterns implied by the data, and the implications of data quality on proper interpretation of these patterns.

### DATA DERIVATION AND METHODS

The data on southern pine beetle used here are annual measures of outbreak status and timber volume damage. The data from 1960 to 1980 were solicited from State forest pest specialists near the end of this period and first published as Price and Doggett (1982). Data extending the series through 1990 were collected in 1989 and 1991 and the full series published as Price et al. (1992) along with some discussion of how the data were derived. Two types of data are discussed below, both at an annual time step: outbreak status and damage (mortality) estimates. The dataset also contains separately derived estimates of salvage amounts, but these are not addressed here.

### *Outbreak Status*

The severity of SPB infestations is usually characterized for some area as a ratio of the number infestations ("spots") over the amount of potential host. The former is based on detection flights and ground checks. The latter is obtained by summing Forest Inventory and Analysis estimates of acres in loblolly/shortleaf and oak/pine forest types. When the ratio equals or exceeds 1.0 the region is termed "in outbreak." Data on outbreak status are available South-wide by county for 1960 through 1990.

### *Damage Estimates*

States estimate annual volumes of pulpwood and sawtimber mortality caused by SPB from spot data using a variety of extrapolation methods. The pulpwood estimates are reported in cords and sawtimber in MBF. However, these separate estimates have been combined and reported here as total damage in cubic feet. These estimates are available at the State rather than county level. For some States the estimates extend from 1990 all the way back to 1960, but South-wide coverage has only been available since 1972.

Because the data on outbreak status report infestation frequency adjusted for amount of available host, this measure helps inform forest owners on the historical infestation risk experienced by susceptible forests in their area. Damage estimates on the other hand provide a rough indication of the impact of beetle populations on the State's economy. Additionally, because successful reproduction by the beetle requires killing the host tree, volume of timber killed also provides our best region-wide proxy for SPB population levels by reflecting variations in both spot numbers and spot size.

Difficulties with these two types of data can arise in four areas: aerial survey and ground checking intensity, determinations of susceptible acres, extrapolation from spot counts to volume estimates, and assignment of damage to merchantability class.

### *Aerial Survey and Ground Checks*

Two details are relevant to spot detection. First, not all patches of dead or dying pine trees are infested by southern pine beetle. Patches located on aerial sketch maps must be checked on the ground to confirm SPB as the cause of mortality. Second, because small spots are far more likely than large spots to cease expanding on their own (Hedden and Billings 1979), States disregard spots smaller than 5 or 10 trees.

Flights to detect beetle spots suffer understandable technical limitations. Observers may miss seeing a spot for a variety of reasons: proximity to the flight line, poor weather, or lack of development of crown discoloration on infestation. Spot locations may be inaccurately sketched on maps, preventing ground truthing and allowing double counting of the spot the next flight. The ability of observers to control these problems will likely differ within and across states. Technologic improvements in navigation have likely reduced some sources of error over time (Dull 1980) but may have introduced a temporal bias.

Aerial detection flights are conducted for pragmatic reasons to help landowners protect their forests from damage. Such motivations are in practice constrained by budgets, budgets which vary by state and from year to year. Concentrating limited efforts where they will do the most good, agencies tend to fly less intensively when beetle activity is judged low, and not fly in those areas where beetles are not thought a problem. Judgments on where and when to fly can be based on pheromone sampling (Billings 1992), previous population levels (Mawby and others 1989), and reports from ground personnel, aerial fire control operations, and concerned landowners. More bothersome is how varying budgets can affect flight intensity and therefore thoroughness of spot detection. Additional concerns about varying coverage of detection flights include those surrounding interpretation of missing data (Mickler and Dwire 1992), and the impact of varying survey intensity on our ability to support spot suppression during critical endemic-epidemic transitions (Mawby and others 1989).

Budgets also can affect the thoroughness of ground checking, despite evidence of their importance in correcting aerial estimates (Mayyasi and others 1975). Data on the intensity and consistency of ground checks are not available across the scope of this dataset. However, lack of ground checks in South Carolina in 1989 and 1990 resulted in limiting all infested counties to the lowest outbreak category (.1 to less than 1 spot per thousand).

#### *Susceptible Acres*

Acreage estimates used as the denominator in spots per thousand are also subject to uncertainties, principally arising from the temporal and spatial resolutions of the data. The only regionally compatible data source available for estimating acreages of susceptible host material is collected by the Forest Inventory and Analysis (FIA) units of the US Forest Service's Southeastern and Southern Stations. Although FIA samples approximately forty five thousand locations region wide, county-level estimates of acres by forest type strain the spatial resolution of the sampling design, and intervals between surveys mean estimates can be up to nine years out of date (Ray Sheffield and Joanne Faulkner, Southeastern and Southern FIA respectively, personal communication 1992). The temporal and spatial limitations of the data mean that host acreage estimates must be viewed as only approximate indicators of actual amounts of host material available in any given county and year.

Because SPB estimates are reported on an annual basis, a method is needed to interpolate county-level host acreages between FIA survey years, and two were employed with these data: step and linear. In step interpolation, acres from a given survey are assumed to continue unchanged until replaced by data from the next survey. Because this approach is simple to use and can produce ratings each year as new spot counts become available, it was the most common method used in the dataset.

Linear interpolation assumes that host acres change gradually between surveys. Linear interpolation was employed between 1972 and 1990 and only for Georgia. FIA surveys were conducted three times in Georgia during this period (1971-1972, 1981-1983, and 1988-1989). For each year and county between these survey dates host acreages were estimated by linearly interpolating between adjacent survey years. If for a given county a year lay outside the survey dates, the acreage figure from the nearest survey year was used.

Of course, actual host acreage dynamics are more complex than either interpolation method. However, comparing how interpolation methods affect assignment to outbreak intensity classes sheds some light on the sensitivity of this measure to host acre change. Outbreak classes were recalculated for all counties in Georgia for 1973 to 1988 based on step interpolated acres and compared with the ratings calculated using linearly interpolated acres.

TABLE 1. Comparison of outbreak class ratings determined using two methods for interpolating host acres between survey years (see text). The comparison here is for 159 Georgia counties for the years 1973 through 1988.

	No. observations	Ratings Using Step Interpolation				Total
		0	1	2	3	
Ratings	0	1790	2	0	0	<b>1792</b>
Using	1	7	464	2	0	<b>473</b>
Linear	2	0	15	147	1	<b>163</b>
Interpolation	3	0	0	8	108	<b>116</b>
	<b>Total</b>	<b>1797</b>	<b>481</b>	<b>157</b>	<b>109</b>	<b>2544</b>

Table 1 shows the two approaches produced identical ratings in 2509 of the 2,544 possible comparisons (159 counties times 16 years). The 35 differences involved adjacent ratings, but with a bias. Linear interpolation rated 30 more severely, presumably due to a reduction in host acres occurring during the period (data not shown). The 98.6% agreement in ratings between the two approaches is comforting, but the more important error associated with year to year acreage fluctuations remains unknown.

Another inconsistency concerns how states have handled National Forest lands. Because the USDA Forest Service has responsibility for controlling spots in National Forests, many states do not bother flying detection flights over them, and do not count spots there. For these States, adding State and National Forest spots is difficult because National Forest tallies are not broken out by county. Compounding the difficulty, standard FIA reports of susceptible acres by county do not distinguish Federal from other ownerships. Thus several states exclude Federal spots but include Federal acres when calculating outbreak intensities and classes, tending to understate the true severity of outbreaks. Table 2 shows how eight of the states treated National Forest spots and/or National Forest susceptible acres in their calculations of county level outbreak status.

TABLE 2. How different States handled inclusion of National Forest acres and spots in calculating outbreak status.

		spots	
		yes	no
acres	yes	AL, GA, MS	NC, SC, TN, TX
	no	none	LA

#### *Damage Estimates:*

Little information is available on the methods employed by states to estimate pulpwood and sawlog volume damages. Ideally each spot would be visited by ground crews and estimates made of the sawtimber and pulpwood volumes killed by the beetle. Volumes by the two product classes could then be summed to the state level. However, measuring volumes of all killed trees is expensive. Some states count trees killed and apply state average tree volumes to these counts to obtain statewide pulpwood and sawtimber volume damages. Estimates of amounts salvaged (not reported here) are typically obtained by a separate survey of mills or other log purchasers.

#### *Overview of Potential for Error*

The methods and concerns discussed above suggest that errors in the data are particularly likely at certain spatial and temporal scales. Because methods are most likely to differ between rather than within states, comparisons between counties within a state are more robust than comparisons across state borders. Similarly, to the extent that changes in personnel and methods occur only sporadically over time, year to year changes are probably safer than comparisons between decades. Rankings and relative shifts are probably on safer ground than determinations of absolute amounts.

#### PATTERNS AND RESULTS

This paper takes a graphical, exploratory approach to data analysis rather than applying statistical tests of hypotheses. Statistical approaches were avoided for three reasons: 1) the data describe full spatial coverage of the population of interest, not a random subsample, 2) the data appear both spatially and temporally autocorrelated, and 3) statistically rigorous formulations for most of the comparisons are elusive. The purpose is thus not to statistically test the importance of specific causal factors but to suggest hypotheses for more specific tests. The analyses below progress from broad to narrower scales, and progress from spatial to temporal comparisons and then to a combination of the two.

#### *SPB range and host availability*

Figure 1 shows how frequently counties have been in outbreak status during the period 1960-1990. Southern pine beetle outbreaks have been reported to occur at one time or another across most of the South. A total of 559 counties from east Texas to North Carolina and from Tennessee to the Gulf coast have reported SPB outbreaks during this period. Areas suffering particularly chronic outbreaks include

east Texas, southwest Mississippi, and the South Carolina uplands. Indeed, twenty-one counties South-wide were reported to be in outbreak more years than not.

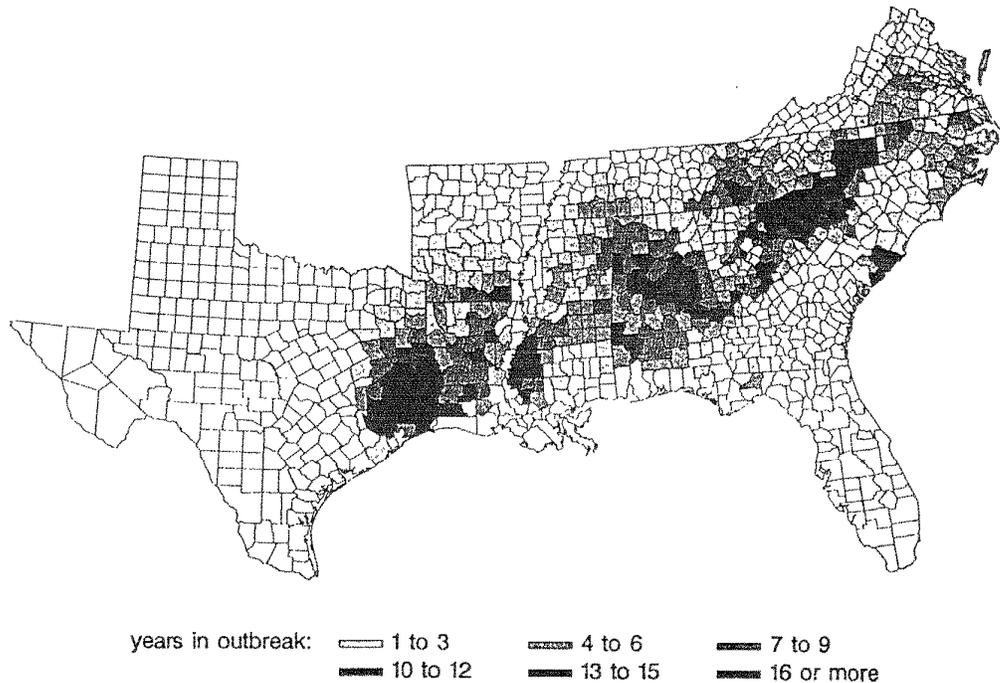


FIG. 1. Total years in SPB outbreak status during the period 1960-1990 as reported by State forest pest specialists. Outbreak is defined as one or more SPB spots per thousand acres of susceptible host type.

Other distinguishing spatial features include gaps in outbreak incidence along the Mississippi River and Gulf Coast, and an isolated area with outbreaks in the Florida panhandle. Also visible is a trough in outbreaks along the upper Atlantic coastal plain. That is, outbreaks are rare in the upper coastal plain but occur in counties nearer the coast.

The spatial distribution of SPB outbreak frequency closely follows the distribution of its major hosts. Figure 2 shows the combined timber volumes of loblolly, shortleaf and Virginia pines, expressed as cubic feet of wood per land acre (per Census Bureau figures). The timber volumes were collected by Southern and Southeastern Forest Inventory and Analysis Units (Eastwide Database) and describe conditions in the last decade, although it is very similar to that of loblolly and shortleaf from the 1960's (Pye 1992).

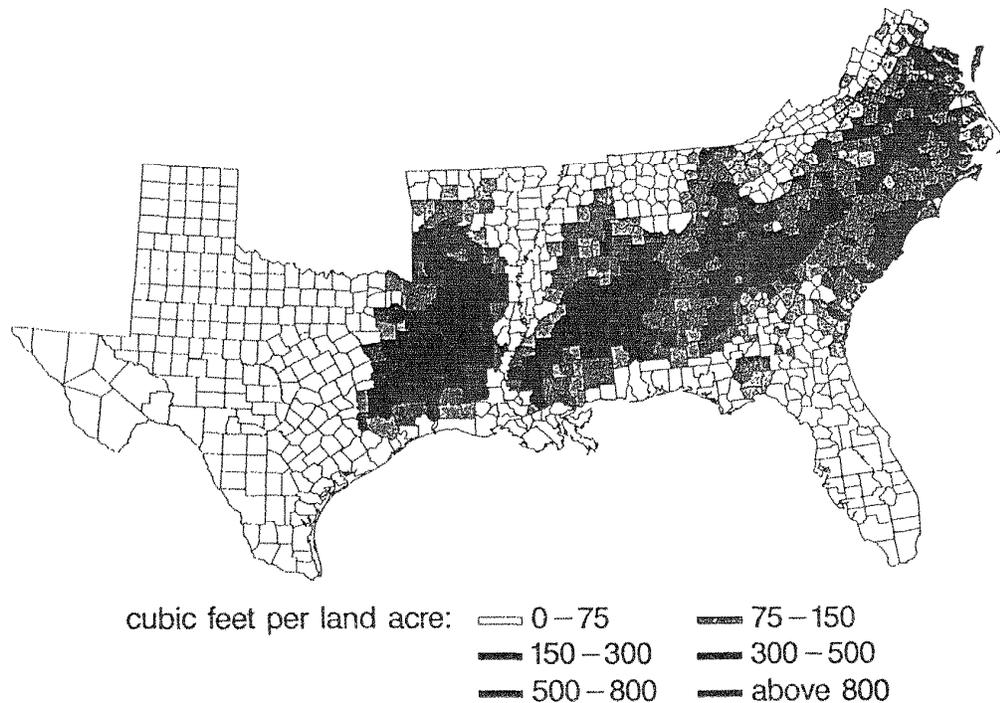


FIG. 2. Combined volumes of three SPB host species: loblolly, shortleaf and Virginia pines, expressed as cubic feet per acre of land. Data were collected by the Forest Inventory and Analysis units of the Southern and Southeastern Forest Experiment Stations and assembled as part of their Eastwide Database. These data were graciously forwarded by the Asheville office of Forest Pest Management. The data describe conditions from FIA's most recent survey cycle for each state and thus report conditions in the late 1980's to about 1991.

The two distributions suggest that, in the long run, southern pine beetle is able to take advantage of susceptible species throughout their range. The absence of outbreaks along the Gulf Coast, the Mississippi River, and upper Atlantic Coastal Plain all agree with reduced availability of these three host species. Areas with large concentrations of host (east TX, southwest MS, and piedmonts of GA and SC) show greater frequency of outbreak, even when adjusted for host acres. Patterns along the northern range of the distribution show lesser agreement. Both Virginia and northern Louisiana/southern Arkansas show disproportionately fewer outbreaks than their host material might indicate, suggesting that climatic factors may be responsible for reduced populations at the beetle's northeastern and northwestern ranges. In contrast, outbreaks in the southern Appalachians appear higher than the three host species might suggest, and may be due to pitch pine, whose southern distribution extends into this region (Burns and Honkala 1990).

These conclusions must be checked against alternative, methodological explanations. Two considerations are particularly relevant: State differences in detection intensity, and omission of areas which do not have these host species.

Abrupt changes in outbreak frequency along State lines are not uncommon. The bulk of the range limits occur within and not along state borders, and most changes in outbreak frequency do coincide with

change in host availability. However, two cases are apparent where outbreak frequencies change along state borders in ways not readily explainable by simple changes in host volume: northwest South Carolina, and the borders of Alabama with Mississippi and Georgia. Such differences do not affect the overall interpretation of beetle range but might need to be considered in other evaluations.

Areas with particularly older, stressed pines might be particularly at risk to SPB. Because National Forests manage stands on longer rotations than most private land owners, pine stands in National Forests are often thought particularly vulnerable to attack by southern pine beetle (Carter and others 1990). Indeed, the three areas of most chronic outbreak shown in Figure 1 all include National Forests: east Texas (Sabine, Angelina, Sam Houston and Davey Crockett National Forests), southwest Mississippi (Homochitto NF), and northeast Georgia-western South Carolina (Chattahoochee and Sumter NF's). It would be tempting to use these data for explicit testing of the influence of National Forest holdings on frequency of outbreak, but the different handling of Federal lands across the region dictates particular care in interpreting the outbreak classification of any county which contains National Forest lands.

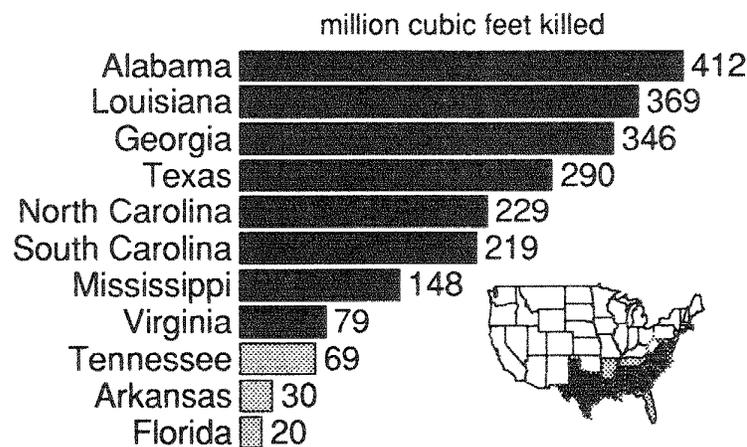


FIG. 3. Reported volumes of timber killed by SPB during the period 1972 through 1990, by state. The three States shown in gray reported the least amounts of damage. The remaining eight states thus conveniently represent a curving transect from southwest (Texas) to northeast (Virginia), made use of in Figures 4 and 5.

Damage estimates provide another view of how long term impacts of SPB may differ spatially across the region. Figure 3 shows total reported damages by state for the period 1972 and 1990. Not surprisingly, states with greater amounts of host species (and therefore near the heart of the outbreak range) report greater amounts of damage than states near the northern, southern and eastern peripheries.

As noted above, comparisons between states are particularly risky with this dataset. The rankings between states are much safer than absolute estimates of damage, but conclusions are safest when bolstered by other data, as are those in the above paragraph. For example, it would be imprudent to conclude that Alabama in truth has suffered greater damage than, say, Texas, but it does appear safe to conclude that Georgia has suffered more than Virginia. Although no quantitative estimates of error are available, a reasonable course might be to assume a factor of two error on the estimates for purposes of ranking between states, and perhaps a larger factor for determining absolute damages.

Relative shifts between years should be more reliable than absolute measures of damage. Figure 4 shows how damage estimates have varied by year, both by state and across the region. During this 19 year period there were three large outbreaks and 2-3 lesser ones. A regular cycle of 6-7 years apparent at this regional scale is not reflected in damages by state. Different sets of states are responsible for

different regional outbreaks. The first regional outbreak occurred across virtually the entire South, but the outbreaks in 1979-80 and again in 1988 were strictly mid-South events, and the extreme outbreak of 1985-86 was limited to Louisiana and Texas. The smaller outbreak in 1982 was only apparent in Virginia.

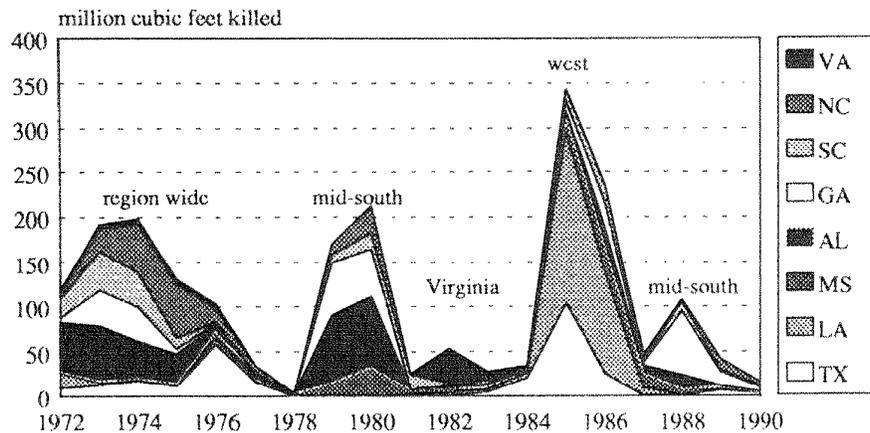


FIG. 4. Area graph of reported volumes of timber killed by SPB as reported by the eight highest reporting states (see Figure 3). Labels above peaks indicate subregions where damage occurred.

At least for the period spanned here, most outbreaks appear to occur simultaneously in adjoining states, suggesting that outbreaks can operate across distances of 500 to 1500 km. Comparisons of timing between different states is complicated however by differences in absolute damage between states. One way to account for these differences is to normalize the damages of each state to vary between that state's own maximum and minimum during this period. That way the relative variations for each state can be compared for characteristics such as timing of outbreak initiation and recession.

Figure 5 shows these relative variations in SPB damage for each of the eight states suffering the largest total damages. The temporal pattern for each state is stacked one above the other, and ordered to reflect their spatial distribution from southwest to northeast. In this arrangement, the synchrony of outbreaks in adjoining states can be seen as parallel deflections in adjoining lines. The single state outbreaks of Texas (1976) and Virginia (1982) appear as isolated blips, but the remaining three major outbreaks clearly span multiple adjoining states. Such outbreaks may peak in different years in different states, but for the major outbreaks beginning during this time period, each outbreak is initiated in the same year. That is, outbreaks during the seventies and eighties apparently started simultaneously across large parts of the region, rather than beginning in one state in one year and subsequently spreading to the next state.

This spatial temporal pattern of simultaneous initiation argues against beetle dispersal or host maturation as factors triggering outbreaks at these broad scales. Rather it suggests a large scale process such as weather is responsible for synchronizing populations across large portions of the region. Of course, methodological explanations should be considered as well. By sharing information among themselves, forest pest specialists in adjoining states might become mutually concerned an outbreak was underway, and in response intensify their monitoring and find more spots. In theory, synchronizing shifts in sampling intensity (or volume extrapolation parameters) could make the resulting state observations appear more synchronous than the underlying populations. This would suggest the unlikely situation that State forest pest specialists respond strongly to information derived from outside their borders and less strongly to information available from within.

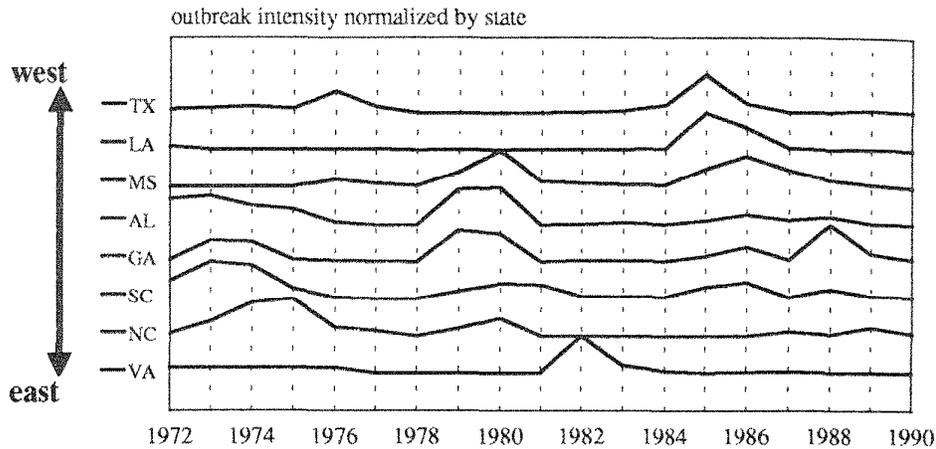


FIG. 5. Relative temporal dynamics of reported state level SPB damage between 1972 and 1990. Chart was constructed by normalizing each state's annual damage to vary between 0 and 1, based on that state's maxima and minima during the period. The resulting series for the states were stacked one above the other, with their order reflecting each state's relative spatial arrangement from southwest to northeast. Parallel deflections graphically indicate a broad scale spatial autocorrelation in timing of outbreak.

Another potentially useful analysis involves how damage is distributed between the two different product classes, pulpwood and sawtimber. Estimates of economic damage should be quite sensitive to merchantability assumptions, and biologic concerns are involved as well. During low outbreak years spots are believed to be primarily restricted to the highest risk, older stands, but during severe outbreaks spots develop more equally in stands of different age classes (Mason and others 1981). Such shifts in host size classes killed might therefor appear as shifts between the two product classes, so long as assignment of damage to the two merchantability classes were based on consistent criteria such as stem size.

Indeed, as illustrated in Figure 6, some states do show large swings in merchantability class with outbreak cycle. The southcentral states of Texas, Louisiana, Mississippi and Alabama showed pulpwood share expanding dramatically during outbreaks, often with a modest lag. The southeastern states of Georgia, North Carolina, and South Carolina however showed little relationship between outbreak intensity and pulpwood share.

Unfortunately, such patterns cannot be so clearly interpreted. Checks on data definitions and extrapolation methods used by the different States reveal that many States evaluate merchantability based on salability of the spot as salvage rather than its potential value had the infestation not occurred. Thus product degrade, market depression and small sale volume confound biologic shifts toward smaller stems which might have occurred. Additional extrapolation difficulties further complicate interpretation. South Carolina for example does not update its estimate of average tree size during an outbreak, missing shifts in size class which might occur from year to year. In Georgia all non-Federal damages are converted to cords to reflect the prevalence of weight-based purchasing practices.

Much of this problem arises from conflicting objectives. Those wishing to characterize potential benefits of beetle suppression need data which reflects the uses to which the trees would have been put had they not been damaged. Those wishing to emphasize mitigation opportunities for the landowner want data showing salvage opportunities given that damage has already occurred. The result is that assignments to product class are virtually useless for regional appraisals.

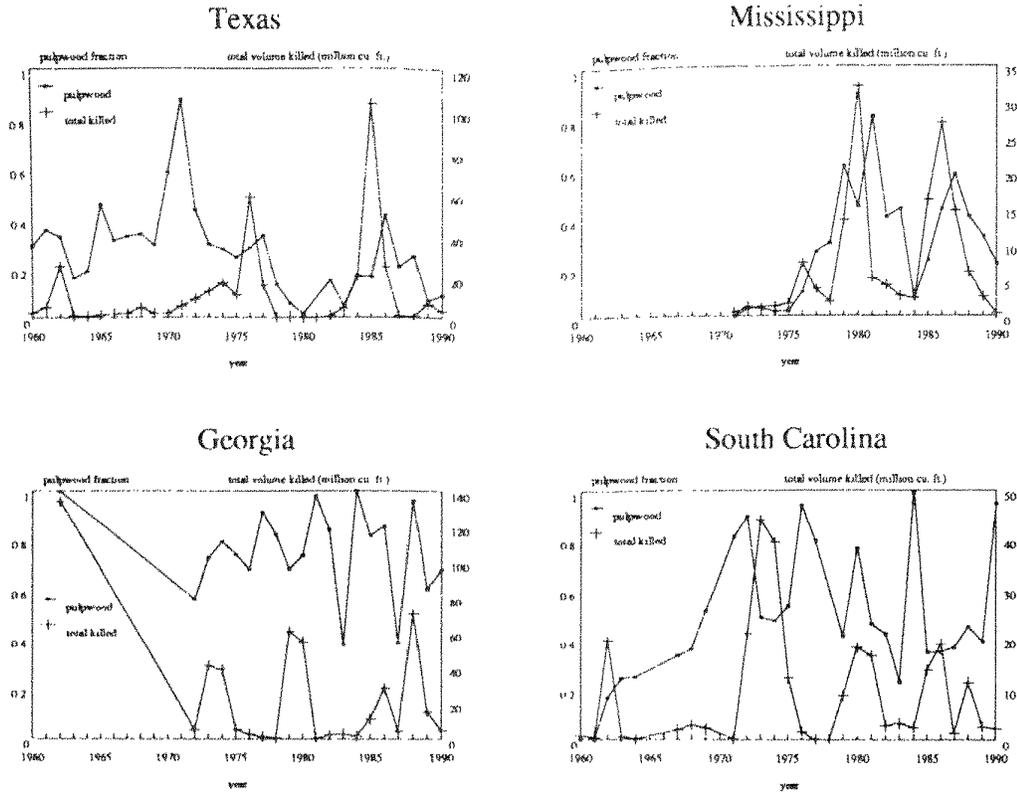


FIG. 6. Annual SPB-caused mortality (pulpwood plus sawtimber) and the fraction of this total reported as pulpwood for four states. Although for Texas and Mississippi the two measures appear correlated, merchantability definitions make its interpretation obscure. See text.

The analyses above began with outbreak status at regional scales, then examined damage estimates at regional then state scales. This last analysis involves relationships between the two types of data, and explores the relationship between the extent of an outbreak, indicated by outbreak status information, and the intensity of the outbreak, as indicated by damage estimates. Quantitatively relating the two types of data might shed light on state-level dynamics of the outbreak process, and could also provide a means for estimating damage levels prior to 1972 for those states where damage estimates are only available for more recent years.

A potential difficulty relating the two types of data is that outbreak counties may have differing amounts of susceptible forest, and their contribution to statewide damage should reflect this. For this analysis, the estimates of susceptible volumes in Figure 2 were used to weight each county's status. As these volume estimates were collected in the recent FIA survey cycle, weights were only applied to outbreak data from 1981-90. The susceptible volumes in outbreak counties in a given year and state were summed and compared to that state's total susceptible acres. Figure 7 shows the resulting annual "percent of susceptible volume in outbreak counties" plotted against damages for several representative states.

Two patterns are apparent. First, there is a rough correspondence between the extent of an outbreak across the resource and the intensity of that outbreak in terms of volume mortality. Thus when total SPB damages are high, much of a state's susceptible pines are in outbreak areas. Conversely, very little damage is reported in those years with few reported outbreak counties. This should not be surprising, although many states show a large scatter to this relationship.

Second, there is a regular progression during an outbreak from an initial intensive phase of growth to a more extensive phase. That is, in the first part of an outbreak damage increases rapidly with little increase in extent. Growth in total damage then slows but continues to expand across the resource. Finally the outbreak collapses and recedes toward the origin. On the plots this cycle appears as a counterclockwise progression, and was found in the outbreak cycles of 7 of the 10 states reporting outbreaks in the 1980's. Such a pattern is consistent with spatial expansion of outbreaks from epicenters, but the contagious spatio-temporal pattern this also implies has not yet been confirmed.

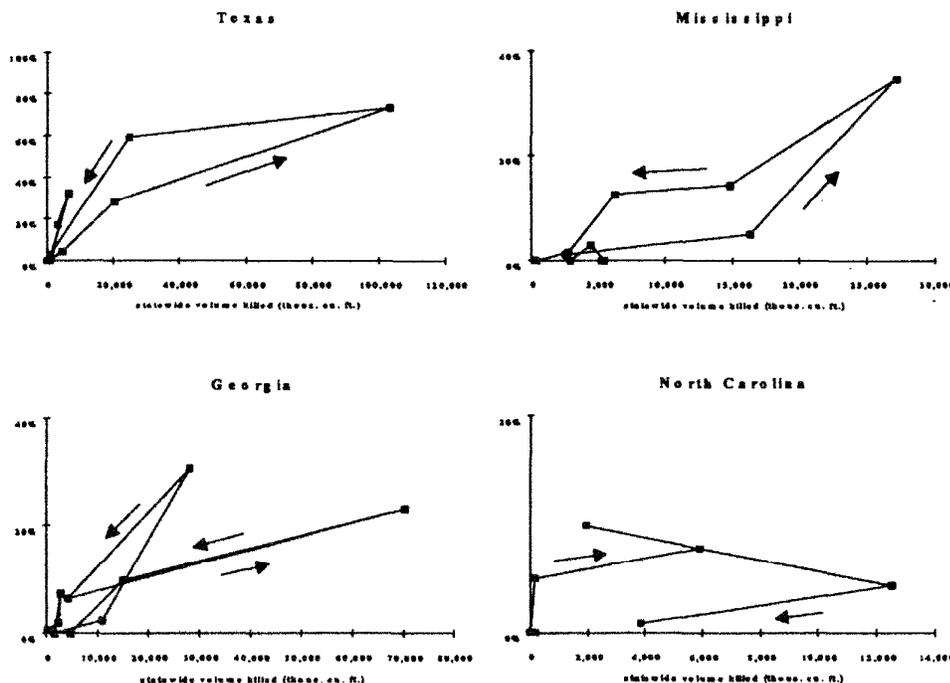


FIG. 7. The percent of each state's combined volumes of loblolly, shortleaf, and Virginia pine located in counties in outbreak status (y axis), plotted against the reported state-wide volume damages for that year (x axis). Lines connect successive years with arrows indicating direction from earlier to later. Of the four states shown, only North Carolina fails to show a counterclockwise pattern.

Examination of methods suggests a potential complementary explanation. Detection efforts during the initial phase of an outbreak might be focussed on those counties containing stands at greatest risk. Damage per acre in high risk, high volume stands could indeed be quite high, accounting for the "intense" damage observed. In following years, states might expand their detection efforts to include counties with stands of lower risk, also finding them to be in outbreak. With smaller spots and lesser basal areas, damage in these less susceptible stands might be lower and would constitute the "extensive" phase. In each case true outbreaks are found. The potential problem with this shift in detection would be that the outbreak may have begun simultaneously in both the high and low risk areas but simply was unreported in the lower risk areas until later in the outbreak, giving the appearance of expansion when none was there. Resolving the degree to which methodology amplifies true outbreak shifts requires distinguishing between when a status of "no outbreak" arises from actual detection versus when a county was not checked.

A common thread to the analyses above has been critical regard to its derivation and data quality limitations and focus on the spatial and temporal scales of methodological shifts. Thus, of the analyses shown here, estimates of statewide damage are the most uncertain, because the spatial unit of

investigation most closely matches the most probable scales of methodological change: state wide and multi-year. Similar comparisons of long term change in outbreak severity would also be questionable. Fortunately, many methods available for quantitative analysis of spatial and temporal trends remove the more suspect gradual or broad scale shifts and focus on the more credible relative, fine scale shifts.

Note that two analyses have been illustrated which are particularly in need of improved data. These are: evaluation of stem size shifts during across phases of outbreak, and tests of the role of National Forests as outbreak epicenters. Such analyses would best be conducted with data from individual states after careful appraisals for data consistency.

#### CONCLUSIONS

There are two, complementary explanations to the patterns illustrated above. The first explanation runs as follows:

- host characteristics appear to define long term risk of SPB outbreak.
- outbreaks occur across multiple, adjoining states
- outbreaks are initiated simultaneously at multiple locations in adjoining states
- outbreaks expand from multiple epicenter(s) located in multiple states

There is, however, a complementary set of explanations, one who's contribution to the patterns observed cannot fully be resolved, and which is based on a more cynical appraisal of the methods involved.

- State pest specialists in a region convince each other an outbreak is underway
- looking first in highest risk locations, they find high rates of damage
- looking later in lower risk areas, smaller trees and lower damage rates are found

Two points are relevant to appraising the relative importance of these two sets of explanations. The first involves the importance of ad hoc information sources in focussing detection efforts appropriately. The contributions of extension agents and landowners are hard to quantify, but should serve to keep efforts focussed where damages are most severe. Secondly, even an order of magnitude precision in sampling may be sufficient when populations fluctuate over several orders of magnitude (A. Berryman in (Volney 1992)). This would particularly be the case with most quantitative temporal or spatial analyses, which often focus on fine scale changes.

Although I've attempted to demonstrate those areas where useful insight can be gained, it is equally important to recognize that only through greater standardization of methods, definitions, and survey intensities can these analyses be confidently defended against methodological artifacts. Such improvements will be increasingly important for many pressing broad scale problems, such as effects of global warming on pest impacts to forests.

Although this paper has focussed on characterizing potential errors internal to this dataset, there is another potential error implicit to broad scale investigation of southern pine beetle dynamics. Hierarchy theory tells us that because controlling processes frequently change across scales, conclusions regarding broad scale processes should be based on observations collected at these scales, rather than on extrapolation from observations collected at other scales (Meentemeyer 1989; Urban and others 1987). This dataset represents, along with its closely allied FPM variant, the only compatible records for comparing the dynamics of SPB over multiple states and across multiple outbreaks. This broad perspective is crucial for understanding the context or representativeness of more rigorous, finer scale studies.

Broad scale analyses should also be useful for assessing the scaleability of stand level risk factors. Stand level risk factors such as slope, pine basal area, and disturbance history may continue in importance at larger scales, or be replaced by other predictive measures, such as physiographic region,

volume of susceptible hosts, or frequency of severe storms. Only by comparing data from a range of scales can we determine where shifts in controlling processes may occur. Factors which might particularly benefit from broad scale data include landscape structure, weather, and beetle/predator dynamics (Rykiel and others 1988; Lovelady and others 1991; Turchin and others 1991).

On a more pragmatic note, timber markets and government control policies are typically defined at the broad scales explored here. Evaluations of policy options for minimizing welfare damage of SPB will need to reflect the dynamics of southern pine beetle at compatible scales.

In sum, reliable, long term data on forest pests is critical to identifying ecosystem responses to changing climate, estimating long term risks to forest landowners, and determining area-wide effectiveness of control policies. The data described here provides a tantalizing view of the potential utility of rigorously collected broad scale datasets. Hopefully it will further stimulate Federal and State efforts to ensure such data will be available in the decades to come.

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# THE SPATIAL DYNAMICS OF INVASIONS BY EXOTIC FOREST PESTS

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*Abstract.* Biological invasion occurs when a species becomes established in an area disjunct from its usual range of distribution. Over the last century biological invasions have greatly increased in North America and many of these new species are damaging forest pests. The invasion phenomenon consists of three processes: 1. establishment, whereby a founding population is transported to the new environment, 2. establishment, during which the founder population either becomes established as a permanent, reproducing population or goes extinct; 3. spread, where the founder population expands its range into adjoining areas of suitable habitat. Consideration of spatial processes is important during each of these three phases. Further, any attempts to reduce the impacts of invading forest pests should be directed in an appropriate manner toward each of the three invasion phases.

Over the last century, technological advances have greatly facilitated intercontinental travel by humans and their goods. An undesirable by-product of this technology has been the dramatic increase in biological invasions caused by a breakdown of natural biogeographic barriers that once limited the interchange of the world's biota. Figure 1 demonstrates that around 1860, there was a dramatic increase in the rate of establishment of exotic species in this country. Presumably this change reflects the great increase in intercontinental mobility that occurred between 1850 and 1900.

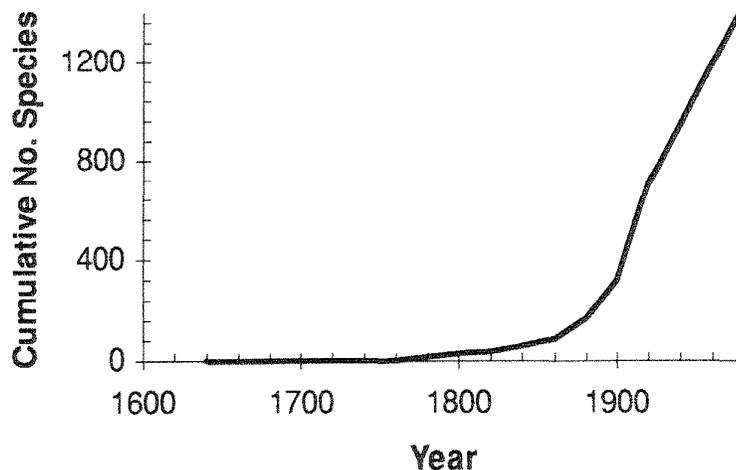


FIG. 1. Cumulative number of exotic species of insects and mites introduced to the United States (from Sailer, 1978)

This increase in the number of exotic organisms generally has resulted in a substantially greater number of forest pests. For a variety of reasons, introduced species are more likely to be pests than are native species (Simberloff 1986, di Castri, 1989). Pimentel (1986) estimated that of the 70 major insect pests of U.S. forests, 19 were introduced species. This proportion (27%) is much higher than the proportion of pests seen in native species (less than 1%). This increasing load of pest species is likely to result in spectacular and long term impacts on forest ecosystems. Introductions of major forest pests to North America, such as the gypsy moth, dutch elm disease and chestnut blight, are examples of introductions that have caused catastrophic tree mortality, and in some cases caused the virtual elimination of previously dominant tree species. Thus, the accumulation of biological invasions is a problem comparable in some respects to some of the more well-known contemporary environmental problems such as atmospheric warming and acidic deposition.

Consideration of biological invasions from a landscape ecology perspective is useful since movement through space is an inherent feature of these invasions. As a landscape process, a biological invasion can be divided into three processes: arrival, establishment, and spread (Elton, 1958; Dobson and May, 1986). Because of their economic importance and accelerating frequency, all three stages of biological invasions recently have been the object of increased scrutiny (Mooney & Drake 1986, Groves & Burdon, 1986, Drake et al. 1989, Hengeveld 1989).

#### ARRIVAL

Biological invasions have been occurring without human intervention for millions of years. Chance dispersal events as well as natural modifications of habitats such as glaciation and climate change have contributed to the natural dynamics of change in species ranges over geologic time. The field of biogeography has developed as a discipline that focuses on this natural movement of species distributions (MacArthur and Wilson 1967). Humans have greatly accelerated this natural intercontinental ebb and flow of species in two ways. First, we augmented the natural movement of organisms both by accidental transportation of species (e.g. in the ballasts of ships) and by intentional introductions (e.g. introduced natural enemies). Simberloff (1986) noted that the patterns of species introductions parallels the ongoing intercontinental commerce patterns (e.g. most introductions to North America have come from Europe). The second way in which we have accelerated the natural rate of biological invasions is by disturbance of habitats. These disturbances do not alter the arrival process but, instead, seem to enhance the establishment of certain species.

The gravity of the problems created by biological invasions was not fully realized until the early 1900's. Before this time, most governments had a rather *laissez faire* attitude about introductions. For example, many people went to great lengths to introduce and establish bird species such as the European starling, *Sturnus vulgaris*, in North America around 1890 apparently with no concern about potential ecological damages (Hengeveld 1989). In 1912 Congress enacted the Domestic Plant Quarantine Act, which gave authority to the U.S. Department of Agriculture (USDA) to regulate the movement of plant and animal material into and within the country (Weber, 1930); these regulations have been modified substantially since then. The quarantine measures were designed to decrease invasions by directly limiting the arrival process and thus represent a first line of defense against invasions.

#### ESTABLISHMENT

Every seed that falls to the ground does not develop successfully into a reproducing plant. Similarly, many invaders may arrive successfully in a new habitat but few become established. Here we define establishment as the process that results in a population that persists for many generations. Founding populations typically are very small and consequently at great risk to extinction. Generally, the smaller the founder population, the less likely is establishment. Though many scientists have referred to a "minimum viable population", there rarely is a distinct threshold. Instead, it is more realistic to consider

the *probability* of establishment as being a continuous function of the initial population. This function reflects many characteristics of the species, such as its intrinsic rate of reproduction, mate location abilities, and genetic diversity (Mooney & Drake 1986).

The dynamics of all animal and plant populations are highly stochastic and typically affected strongly by variations, such as weather, in the environment. When viewed over very small areas, even well established populations may become extinct locally as a result of this stochastic variation. When the population is established over large areas, zones of local extinction are reinfested quickly from adjoining areas. The invading population also may follow the same pattern and become extinct locally, but because its initial distribution is completely isolated, the result is total extinction (Figure 2). It is for this reason that most arrivals usually do not result in establishment.

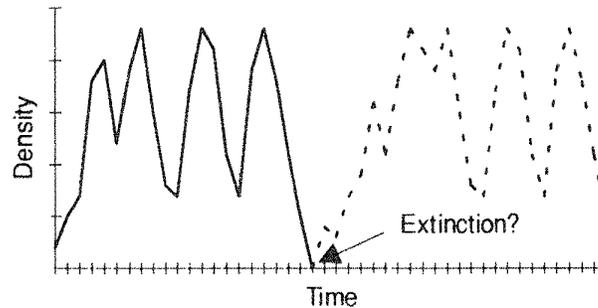


FIG. 2. Dynamic patterns in a hypothetical invading population that fails to establish (solid line) and a hypothetical established population that is re-infested from adjoining populations.

Understanding this process has important implications for management. The activity we call "eradication" is aimed at reversing the process of establishment; eradication is forced extinction. But we can see from the above description that eradication is likely to succeed only in situations where the target population is both low in density and highly restricted in its spatial distribution.

#### SPREAD

Once a population is established, its density typically will increase and it will expand its distribution into adjoining areas of suitable habitat. For most biological invasions this is the only process that we can observe directly since the arrival and establishment phases typically occur without notice by humans.

The spread process is driven by two behaviors of the species: population growth and dispersal. Most models of population spread have concentrated on these two behaviors. The simplest and probably the most widely applied population spread model was developed by Skellam (1951). Skellam's model combined Fick's law of diffusion with an exponential model of population growth.

Fick's law states that the concentration,  $C$ , of particles is normally distributed across any dimension,  $x$ , and thus the concentration at any point in time after release at point  $x = 0$  is described by:

$$C_{x,t} = \frac{M e^{-x^2/4Dt}}{2\sqrt{\pi Dt}} \quad (1)$$

where  $t$  is the time since the initial release of  $M$  particles at point  $x = 0$  and  $D$  is the "diffusivity" or diffusion coefficient" (Okubo, 1980). The diffusion coefficient is constant for any class of particles and environmental conditions (e.g. temperature);  $C$  is distributed normally at time,  $t$ , with a variance of  $Dt$ . Fick's law assumes that particles move randomly.

The exponential population growth model mathematically describes the concept of unlimited population growth:

$$N_t = N_0 e^{rt} \quad (2)$$

where  $N_t$  is the number of individuals at time  $t$  and  $r$  is the "intrinsic rate of natural increase" (birth rate - death rate under optimal condition; i.e. no crowding).

Skellam combined Fick's law of diffusion with the exponential growth model to obtain a generalized model of the spread of an invading organism:

$$N_{x,t} = \frac{N_{0,0} e^{rt-x^2/4Dt}}{4pDt} \quad (3)$$

where  $N_{x,t}$  is the density of organisms distance,  $x$ , from the point of release and time,  $t$ , from the time of release of  $N_{0,0}$  organisms at time 0. The assumption of random movement in this model implies that the population will spread radially, at an equal rate in all directions. Skellam (1951) showed that for any detection threshold,  $T$ , such that the infested area at any time  $t$  is restricted to points where  $N_{x,t} > T$ , the expansion velocity of the infested front,  $V$ , is constant and can be described:

$$V = 2\sqrt{rD} \quad (4)$$

The above model assumes that both  $r$  and  $D$  are constant through both time and space during the period of range expansion of the invading organism, an assumption that does not intuitively seem likely in many cases (i.e. spatial variation in the habitat may profoundly affect birth/death functions, as well as dispersal rates). Nevertheless, there has generally been a good congruence between predictions of this model and observed rates of spread of most exotic organisms (Levin, 1989). For example, Long (1979) found that the larch casebearer *Coleophora laricella* has been spreading in the northern Rocky Mtns. at a constant radial rate, as predicted by Skellam's (1951) model.

#### CASE HISTORY: THE GYPSY MOTH IN NORTH AMERICA

The gypsy moth, *Lymantria dispar* L. is one of the most destructive exotic organisms in North America. It is a major forest pest through-out much of the northern hemisphere: the species is associated primarily with *Quercus* species though, it is polyphagous in its feeding habits. In many areas, epidemics are common and resultant defoliation can cause substantial ecological and economic impacts.

The gypsy moth was introduced accidentally from France to Medford, Massachusetts, in either 1868 or 1869 by an amateur entomologist (Liebhold, Mastro & Schaeffer, 1989). It is an example that illustrates how long it can take from the time of arrival until damaging levels are reached. It wasn't until 1889, 20 years after arrival, that the first outbreak occurred. Eradication was attempted several times but ultimately failed, and the range of the gypsy moth has since spread through-out most of northeastern North America. The current distribution of the species includes a large area composed of the north Atlantic states of the US and parts of bordering Canadian provinces (Fig. 3). A second, discrete population exists in Michigan that is due to a secondary introduction and failed eradication efforts. The primary and secondary infested regions continue to spread; there are no current programs underway to stop this spread (though some state and federal programs are aimed at slowing the spread). In contrast, numerous isolated infestations arise sporadically (e.g. recent infestations in California, Oregon and British Columbia); considerable resources are allocated by state and federal agencies to eradicate these populations. These efforts largely have been successful.

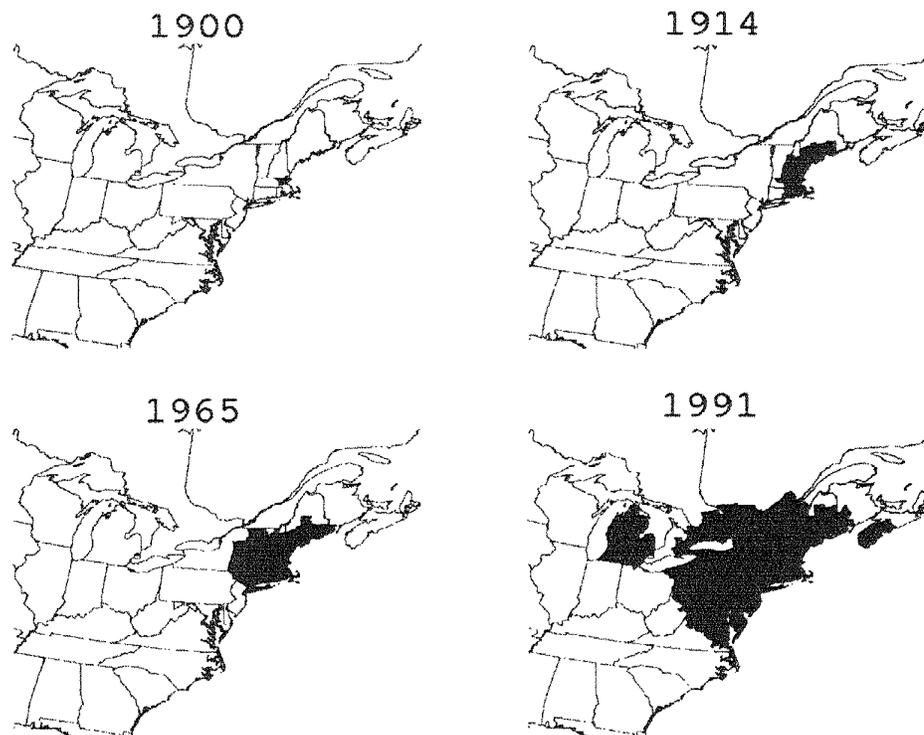


FIG. 3. Historical spread of the gypsy moth through North America (black areas indicate the generally infested area).

The relatively slow rate of spread of the gypsy moth (historically, compared with that of other organisms) is related to its biology. Females in North American populations are unable to fly, thus the primary mechanism for gypsy moth dispersal is thought to be wind-borne passive movement of first instars (Mason & McManus, 1981). The expansion of the generally infested area and the founding of isolated populations also may occur when egg masses or other life stages are transported accidentally on human-made objects (Talerico 1981).

Because the gypsy moth feeds on a wide variety of tree species, it is likely that gypsy moth populations ultimately will invade most of the US and Canada. However, the rate of spread is so slow (relative to the historical spread of other exotic organisms) that it may be many years before the full range of the potential habitat becomes infested. Figure 4 illustrates the historical rate of spread of the gypsy moth. These data indicated that three distinct periods occurred during which spread rates differed: a high rate (9.45 km/year) from 1900 to 1915, a low rate (2.82 km/year) from 1916 to 1965, and a very high rate (20.78 km/year) from 1966 to 1990. Furthermore, expansion was slower (7.61 km/year) during the period of 1966-1990 in counties where the mean minimum temperature was less than 7<sup>o</sup> C. These data are more fully analyzed in Liebhold et al. (1993). The slow rate of spread from 1916 to 1965 could be due to a variety of possible reasons. We believe the most likely reason for this slow rate of spread was that during that period, federal and state agencies were attempting to stop the spread of the generally infested area by intensive monitoring and population suppression along the leading front of the gypsy moth range. Those attempts ultimately failed to achieve the desired goal of stopping the spread, but they probably did contribute to slowing the rate of spread.

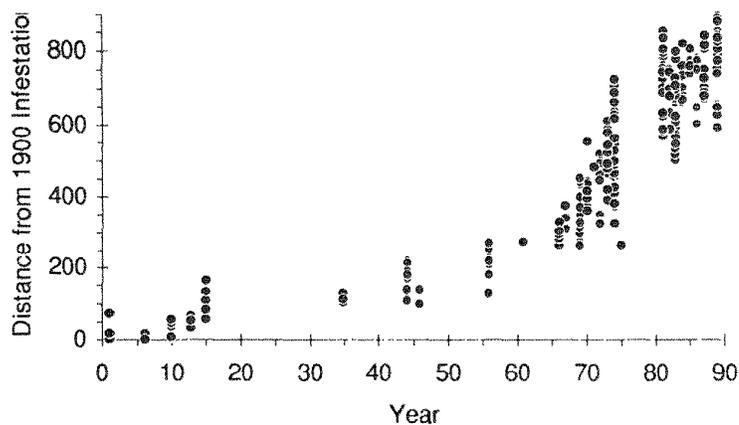


FIG. 4. Historical spread of the gypsy moth in North America. Each circle represents a U.S. county or a Canadian census district.

Liebhold et al (1993) also attempted to calculate the radial rate of spread independently from population parameters. Equation (4) was used to estimate this rate from estimates of  $r$ , the intrinsic rate of increase, and  $D$ , the diffusion coefficient (dispersal magnitude). They obtained approximate estimates of  $r$  from observations of maximum population growth in the field. Estimates of  $D$  were derived from a field experiment of natural dispersal of wind-born first instars (Mason & McManus 1981). The resulting estimate, 2.5 km/yr, was substantially less than the current empirically derived expansion rate of 21 km/yr. The higher observed rates of expansion may be due to human-caused movement of gypsy moth life stages which was not incorporated in estimates of  $D$  made here.

#### SUMMARY

Considering the acceleration of international commerce and travel, biological invasions will increase and result in new, more damaging forest pest problems. Attempts to minimize these impacts should be directed at the three phases of the biological invasion process: arrival, establishment, and spread. For these actions to be effective, attention should focus on applying a management strategy appropriate to the condition of the current phase of the invasion process. During the arrival phase, damages can be mitigated largely through quarantine procedures. Eradication is an appropriate management strategy only during the establishment phase. During the spread phase, procedures designed to slow the spread are the only remaining mitigation procedures that may be feasible.

#### ACKNOWLEDGMENTS

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# FOREST HEALTH MONITORING WITH AIRBORNE VIDEOGRAPHY

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*Abstract.* Airborne videography is emerging as another remote sensing tool available to forest resource managers. The U.S. Forest Service has been developing and evaluating video image capture and analysis technology for use in monitoring forest health. Combining a high-quality Super-VHS video camera system with Global Positioning System (GPS) navigation, and image processing and geographic information systems (GIS), forest health specialists are able to detect and monitor forest pest activity over large areas. Videography offers many advantages over more traditional methods of pest detection and monitoring, including lower cost than ground methods, higher accuracy than conventional aircraft-based sketch mapping, and faster turnaround time than conventional remote sensing methods. Video data can quickly be converted to a digital form for analysis and integration into a GIS environment. This paper presents an evaluation of videography for detecting and monitoring forest insect and disease conditions. Integration of video with other technologies and its application to resource inventories are discussed.

## INTRODUCTION

To discuss the importance and utility of airborne videography for forest health monitoring applications, it is essential to understand the scope of insect and disease problems and the land manager's information needs. It is also important to understand the role videography can play in the forest health monitoring arena and its relationship to existing aerial survey technologies.

Insect and disease damage is one of the most serious causes of tree mortality and growth loss in North American forests. Insects and diseases as a group damage commercial forests, reducing both the amount of timber harvested and the quality of the products. Approximately 2.4 billion cubic feet of timber is killed by insects and diseases each year in the United States. This is 24 times the amount of forest fire-caused mortality (Ciesla, 1983). Outbreaks of insects and diseases can occur in destructive proportions at any time on forested lands. The frequency of occurrence, intensity and duration are difficult to predict. Surveys of forested lands are essential to determining insect and disease presence, population trends, and the need for control measures.

The USDA Forest Service, Forest Pest Management (FPM) is responsible for the detection, evaluation, and control of insect and disease impacts upon the Nation's forest resources. Only through prompt discovery of damaging forest pests, can timely, effective action be taken to prevent or suppress damage, or salvage timber. Resource managers require estimates of the location and intensity of pest damage to plan and conduct suppression or salvage programs. Often, these estimates are obtained from aerial detection surveys conducted to discover pest outbreaks when they first appear and to monitor changes.

## TRADITIONAL AERIAL MONITORING METHODS

Insect and disease surveys are usually flown as part of an ongoing systematic monitoring plan. The methods and procedures used for aerial detection surveys have been developed in considerable detail but may vary from one region of the country to another. Historically, aerial detection surveys have been of two types: 1) visual sketchmapping surveys, and 2) aerial photographic surveys.

*Sketch mapping surveys*

Visual sketchmapping is the technique of delineating the area of pest-caused damage onto maps based on observations by an entomologist or pathologist flying in a small aircraft. Aerial sketchmapping has been the most efficient and economical method of detecting and appraising recognizable pest damage over large remote forest areas. Sketchmapping is highly subjective, however; the resulting data can be no more accurate than the competence of the sketchmapper and the conditions under which the data were obtained. No two sketchmappers will or can be expected to record the same pest outbreak in exactly the same way. For this reason, sketchmapping should be regarded more as an art than as an exact science (Klein et al., 1983).

When an outbreak is detected its causal agent and host are identified, and its location is marked on the survey map. Large outbreaks are drawn as polygons while very small infestations, usually less than 10 trees in a group, are designated as a dot. Sketchmap surveys are used to record current year defoliation and mortality, locate new infestation areas, detect new and potential pest problems for ground evaluation, stratify damage intensity for aerial photographic surveys, and provide historical records of insect and disease outbreaks and their rate of spread. Most of this work is done when insect activity and the resultant damage is at the peak of visible symptoms, usually judged by vegetation color change. Although annual sketchmap surveys supply resource managers with current and useful information about the status of pests, more reliable remote sensing techniques could provide improved data on the location and extent of the pest damage.

*Aerial photographic surveys*

Aerial photography is another available survey tool for forest health monitoring. Color and color-infrared (CIR) photography are valuable tools for assessing insect and disease activity on forest lands. Photography has been used to estimate current and/or total levels of damage and mortality from pests. Photos provide a historical record of pest activity and have been used to monitor the rate of spread and trends of a pest over time. Chemical, biological, and cultural treatment methods can be evaluated with the use of aerial photography to determine the vegetation damage prevented.

Most aerial photography applications in pest management can be divided into two broad classes - mapping photography and sampling photography. Mapping photography can be defined as a block of continuous photo coverage that, when assembled into a photo mosaic, could be termed a photo map. Mapping photography is generally used for mapping the total extent of a pest problem (delineating polygons of damage), or mapping a pest's vegetation type. This type of photography usually covers a large ground area and therefore enables the photointerpreter to observe various patterns, or trends, and distribution of the pest activity. Sampling photography can be defined as photo coverage of a small area that is representative of a larger unit or type. Sampling photography is generally used with some type of survey sampling design. This type of photography is used when it is not operationally feasible or cost effective to evaluate 100 percent of the area of concern. A sampling design utilizing aerial photos can be used to obtain an estimate of pest activity and the photo estimate can be strengthened by ground sampling. Since most sampling photography is acquired at larger photo scales, the interpreter can obtain more reliable data, such as tree counts, identifiable pest symptoms and tree species, etc. (Myhre, 1988).

The use of aerial photography as a detection method has certain advantages and is very useful, but it has some disadvantages and limitations. The primary advantages of photography are that a permanent

image record is preserved for a point-in-time and that photography provides a source of detailed information. Through the use of photointerpretation techniques and equipment, aerial photos can provide more accurate information than sketchmapping methods. One of the main disadvantages of using photography over sketchmapping is the high cost and the amount of time required in processing film and prints, interpreting photos, and transferring information from photos to a map. This delay can severely impact suppression and control decisions.

#### DEVELOPMENT OF AIRBORNE VIDEOGRAPHY

Airborne videography is emerging as a remote sensing tool available to resource managers. Recent changes in this technology have made video a viable sensor for the acquisition of timely information for resource management applications. Video technology has been evaluated by FPM for forest health monitoring applications. As a result of these evaluations, the Methods Applications Group (MAG) of FPM has developed an airborne video system to support a variety of aerial survey needs. The overall system consists of two major components - an airborne video image acquisition component and a video image processing component.

#### *Background*

Television or video (Latin word meaning "I see") has existed for many years. It was not until recent years that this technology moved into the remote sensing arena. In the early 1980s, a variety of research and development efforts began to evaluate videography as a potential remote sensing tool for natural resource management. During this time, a variety of airborne cameras emerged; a few were commercially available and the rest were still in the research and development stage.

Because of improvements made in the mid-1980s in image quality, affordability, and portability, video equipment became increasingly viable as a remote sensing tool. A joint project with the Forest Service (FPM/MAG) and the University of Minnesota/Remote Sensing Laboratory began in 1986 to assess the operational feasibility of a color-infrared (CIR) video camera for forest health monitoring. The camera used in this test was a prototype CIR camera developed by the University of Minnesota, and is now marketed under the trade name Biovision. The camera was a three-tube color camera which had been modified to simulate the spectral response of color-infrared film. The objective of this assessment was to determine if CIR video imagery obtained with an airborne video camera was capable of detecting aerially visible tree defoliation and mortality caused by forest insects. The assessment tests were conducted over areas containing mountain pine beetle, *Dendroctonus ponderosae* Hopkins, mortality in Wyoming and forest tent caterpillar, *Malacosoma disstria* Hubner, defoliation in Minnesota (Munson et al., 1988). Two general conclusions were apparent from the examination of the video imagery, sketch map data, and aerial photography. First, the degree of detail possible in mapping classes of defoliation from video is superior to that obtainable via the sketch mapping technique. Second, the positional accuracy of polygons (map locations) of insect damage appeared to be greater when using video imagery than when using sketch mapping. The discouraging part of the tests was the poor resolution of the color-infrared tube camera. However, the assessment provided enough positive results to justify the continued evaluation and development of this technology.

Airborne videography should not be viewed as a replacement for aerial photography, but can be substituted for photography where the needs do not demand the quality and cost of photography. There are many resource activities where remote sensing and aerial photography data are not being used, primarily due to cost. These gaps could be filled by using airborne videography techniques (Myhre et al, 1990b). Listed below are attributes of videography that offer advantages over conventional aerial photographic film and camera systems.

1. Imagery is available immediately, making video particularly useful in applications requiring rapid turnaround time such as pest surveys and disaster assessment (i.e., fires, flooding, etc.).

2. The operator can view "live" imagery on a monitor in the aircraft concurrent with the acquisition, making the video acquisition process less subject to error than that of photography. The image display allows camera exposure settings to be adjusted interactively.
3. The audio track permits notation of pertinent information, which may be of use in future analysis, directly on the video tape while in flight.
4. A straightforward pathway is provided from the videotape to digital format for computerized image processing and incorporation into a geographic information system (GIS).
5. Video cameras and videotape are lower in cost relative to conventional aerial photography cameras and film.
6. Airborne video improves the success rate of acquiring the desired coverage at a given point in time. This is especially important when narrow biological windows are involved.
7. Video cameras have higher light sensitivity than film cameras allowing useable imagery to be acquired under less than ideal weather conditions.
8. Video is useful in locations where aerial film and processing may be difficult to obtain.

In 1988, following the CIR video test previously discussed, MAG employees evaluated the status of commercially available video technology that could be adopted for airborne use. Our intent was to eventually deploy video systems to multiple field locations, so we restricted our evaluation to commercially available "off-the-shelf" technology. The evaluation produced the following information:

1. New solid-state cameras using charged couple device (CCD) sensors are superior to tube cameras. Solid-state cameras are less prone to damage from vibration making them more suitable for aircraft operation.
2. Shuttered video cameras are available that produce higher quality imagery by reducing blur from image motion and vibration that arise in airborne operations.
3. A new recording system called Super-VHS (S-VHS) is now available. S-VHS has several advantages over VHS, including increased resolution (700 lines of horizontal resolution for S-VHS vs 400 lines for VHS), improved color quality, and improved signal-to-noise ratio through an increased band width.

Based on the new advancements in video, FPM/MAG personnel developed an airborne video package suitable for addressing forest pest management applications. This package consists of an airborne video image acquisition module and a video image processing module (Myhre et al., 1990a.)

#### *Video acquisition system*

The airborne video acquisition system currently in use by FPM consists of the following components:

Video Camera - The camera system features S-VHS format, three CCD sensors (one each for red, green, and blue), high-speed shutter system for reducing image motion and blurring, remote-controlled 9.5 mm to 143 mm zoom lens that allows both zooming and image brightness to be controlled from within the aircraft.

Video Recorder - A portable S-VHS recorder used for recording both video imagery and audio notes during the flight mission.

Video Monitor - A 10-inch S-VHS color monitor used for observing both what is being recorded and the image quality so that necessary adjustments can be made in flight.

Caption Generator - This unit links the video camera, video recorder, and an aircraft navigation system (GPS or LORAN-C). Through this linkage, aircraft positional information (latitude, longitude, bearing) can be recorded on the video frames for future use in determining the location of video frames.

Electronic Navigation Unit - A Long Range Navigation (LORAN-C) or Global Positioning System (GPS) navigation system can provide positional data, as well as time, date, and aircraft heading, through an RS-232 interface to the caption generator.

Camera Mount - A mount suitable for holding the camera in a relatively stable, level, and vibration-free state over the aircraft camera hole.

Additional Equipment - This includes all cabling to link all components and the power converters and inverters needed to match equipment power demands to the aircraft's power supply.

Together these components provide a compact and versatile image acquisition system. They fit easily into almost any small, single engine aircraft having a 6-inch or larger camera hole. As the system provides instant feedback on image coverage and quality, users can quickly become proficient in its use.

#### *Consolidated procurement package*

To simplify the transfer and implementation of this technology, a consolidated procurement package was established for the video image acquisition system. The consolidated package ensures that the users of the video system have all the correct components, and that the system will function as it was designed and field-tested.

Prior to the establishment of the consolidated procurement package, four systems were purchased with technical assistance from MAG. The Forest Service groups which first obtained the systems include:

NE Area/FPM Field Office - St. Paul, MN  
Region 8/National Forests in Texas - Lufkin, TX  
Region 8/FPM Field Office - Alexandria, LA  
Nationwide Forestry Applic. Program - Salt Lake City, UT

Under the procurement package established for fiscal year 1991, six systems were purchased and delivered to the following groups:

Region 2/FPM - Denver, CO  
Region 3/Kaibab N.F. - Williams, AZ and Region 3/FPM  
Region 4/FPM Field Office - Boise, ID  
NE Area/FPM Field Office - Durham, NH  
NE Area/FPM Field Office - Morgantown, WV  
FPM/MAG - Fort Collins, CO

A second consolidated procurement package has been initiated for 1992. A call letter has gone out from the Washington Office (Director of Forest Pest Management) to Forest Service units requesting information from them and their State cooperators.

### *Video image processing system*

Once video imagery has been successfully captured on tape, it can be used immediately in management applications. This use can be as simple as viewing the video tape on the monitor or using the imagery to do sketchmapping in the office. There are, however, more sophisticated tools for using video imagery. MAG has been using the Map and Image Processing System (MIPS), a product of MicroImages Inc. of Lincoln, Nebraska. MIPS runs in a DOS operating environment on any 80386 microcomputer with a math coprocessor. The software supports an array of peripheral devices including digitizers, plotters, color printers, scanners and optical disc drives.

MIPS offers the advantage of being able to capture video frames from tape and convert them to a digital form. In MAG's case, the frames are captured as TARGA files, but other formats are supported. Once the frames are stored as digital images, they can be geometrically corrected to a map base and mosaiced. The software permits the user to annotate polygons of insect activity using a cursor on the screen or do automated classification based on color composite pixel values (Myhre et al., 1990a). This digital data can be moved easily to a variety of geographic information systems for use and analysis with other data. There are a number of other image processing systems in the market place with similar capabilities.

### APPLICATION OF AIRBOURNE VIDEOGRAPHY

FPM/MAG has acquired airborne video imagery of a variety of pest activities and host types and examined or evaluated this imagery to various degrees. The list of video coverage acquired to date includes the vegetation impacts of the following forest insects and diseases: gypsy moth, *Lymantria dispar* (L.), mountain pine beetle, *Dendroctonus ponderosae* Hopkins, southern pine beetle, *Dendroctonus frontalis* Zimmermann, spruce beetle, *Dendroctonus rufipennis* (Kirby), spruce budworm, *Choristoneura fumiferana* (Clemens), Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, and oak wilt, a systemic, lethal disease caused by *Ceratocystic fagacearum* (Microascales, Ophiostomataceae).

The most vigorous test of videography as applied to forest health monitoring was conducted in July 1991 to compare the effectiveness and cost of airborne video to conventional sketchmapping and CIR aerial photography for classifying and mapping gypsy moth defoliation in Michigan (Buffington, 1991). For the purpose of this test, 1:11,000 scale 9 inch by 9 inch CIR aerial photography and 1 mile swath width color video were acquired over 35,000 acres in central Michigan. The area was almost completely forested in upland oak and pine forest types. To minimize the impact of ongoing insect activity and refoliation on the study results, the photographic and video imagery were taken within 24 hours of each other. Due to logistical and weather problems, sketchmapping was done 4 days later, but it is felt that this had little effect on the study results.

### *Procedures*

Sketchmapping was done by a trained entomologist with 3 years experience in sketchmapping. Areas of defoliation were delineated on a 1:24,000 scale topographic map using a classification of heavy (100 percent to 75 percent defoliation), moderate (40 percent to 75 percent defoliation), and light/none (less than 40 percent defoliation). This work required 2 hours to complete.

Office sketchmapping was done using the video imagery. Sitting in front of the monitor, an analyst viewed the imagery and delineated the same defoliation classes described above on a 1:24,000 scale topographic map. The analyst was able to pause, rewind, and fast forward the video tape to help determine location and severity of defoliation. This work required 2.5 hours to complete.

The CIR aerial photography was used as the standard against which the first two methods were compared. The photography was interpreted in stereo using the same defoliation classes. The resulting defoliation polygons were then transferred to a 1:24,000 scale topographic map using a Bausch and Lomb Zoom Transferscope. The interpretation and transfer process took 40 hours to complete.

The three maps were then digitized and put into a GIS for comparison and analysis. All defoliation polygons smaller than 5 acres were determined to be not meaningful and were discarded prior to analysis.

### Results

A visual inspection of the three map products showed them to be very different. Even with the polygons smaller than 5 acres removed, the map produced through interpretation of the CIR photography had very fine detail and many small polygons. The map produced through conventional aerial sketchmapping was very broadly drawn with large polygons. The video office sketchmap was more closely aligned with the map produced from CIR photography, but did not have the same level of detail. Locational accuracy relative to the map produced from aerial photography was better on the office sketchmap than the conventional sketchmap. The GIS was used to compute the number of defoliation polygons and the minimum, maximum and average size. These data are presented in Table 1 for each of the three mapping processes. Table 2 presents the total acreage by defoliation class for each of the three mapping processes. It is believed that the differences between the CIR photography data and the office sketchmapping data are a result of the better spectral response of the CIR imagery. Defoliation was more easily detected in the CIR imagery, while on the true color video, bare ground, wetlands, and stands with low stocking densities were sometimes confused with defoliation.

TABLE 1. Number of polygons and average size of polygons based on five-acre minimum mapping unit (Buffington, 1991).

Map Type	Number of Polygons	Min. Size (acres)	Max. Size (acres)	Ave. Size (acres)
Aerial Sketch	43	20.7	1,454.8	266.4
Office Sketch	141	5.1	562.3	37.6
Aerial Photo	159	5.1	735.7	42.9

TABLE 2. Acres of each defoliation class by map type (Buffington, 1991).

Map Type	Defoliation Class in Acres		
	Heavy	Moderate	Light/None
Aerial Sketch	7,219	4,283	24,944
Office Sketch	2,587	2,619	31,298
Aerial Photo	3,912	2,949	29,642

Table 3 presents cost comparisons between the three remote sensing procedures. All costs are actual costs incurred in the process and presented in U.S. dollars. Depreciation of equipment is not included in the cost analysis. It should be pointed out that the aircraft used for video and photo acquisition was a twin engine aircraft with a higher operating cost than the aircraft used for aerial sketchmapping. This is a logistical artifact of this particular study. The smaller aircraft with the lower operating cost could be used for video acquisition, making the cost of office sketchmapping of this area almost identical to conventional aerial sketchmapping.

TABLE 3. Cost analysis of remote sensing techniques used to define and map gypsy moth defoliation. All monetary values in U.S. dollars (Buffington, 1991).

Technique	Time (hrs.)	Plane/Pilot	Mapper/Analyst	Film/Processing	Total
Aerial Sketch	2.0	\$105/hr	\$9.68/hr	0	\$229.36
Video Acquisit.	1.5	\$250/hr	\$20.90/hr	\$12.95	\$419.30
Office Sketch	2.5	---	\$10.00/hr	---	\$25.00
					\$444.30
Photo Acquisit.	2.0	\$250/hr	\$20.90/hr	\$1100.00	\$1641.80
Photo Interp.	40.0	---	\$10.00/hr	---	\$400.00
					\$2041.80

### CONCLUSIONS

Videography will not replace any existing remote sensing systems. We do feel however that enough evaluation has been done to document its usefulness as an additional tool for the resource manager. The technology is relatively inexpensive to acquire and use. Field-level personnel with little or no remote sensing background can be quickly trained to operate the equipment efficiently. In the last year, FPM has placed six video acquisition systems in the field. Almost as soon as these units became operational, field personnel began finding new applications for the systems. While the systems were initially purchased for forest health monitoring activities, they have also been used for post-fire mapping, site preparation planning, stand prescription maps, timber sale activities, watershed inventory, riparian habitat mapping, law enforcement and storm damage assessment. Videography is also being applied to a number of resource problems in other government agencies. U.S. Fish and Wildlife Service personnel have several years experience in using airborne videography to monitor wetland changes and conditions. They have integrated video data into a GIS environment and use the resulting data base to drive waterfowl production models (Cowardin et al., 1989, Sidle et al., 1990).

Videography has demonstrated the following advantages over conventional aerial survey techniques (sketch mapping) for monitoring forest health: 1) the system can be installed in most of the survey aircraft now used for conventional sketchmapping; 2) videotape provides a permanent record of conditions as they exist at the time of the survey; 3) eliminates the subjective evaluation of the observer while in flight; 4) provides improved positional accuracy of the data collected, and 5) provides more accurate estimates of the areal extent and severity of pest damage. The major advantages of videography over aerial photography are: 1) imagery is available to be viewed and analyzed the same day it is acquired; 2) video can be acquired under high overcast or broken cloud conditions where photography cannot be obtained; and 3) the cost of video imagery is far less than conventional frame photography.

Video technology is continuing to change rapidly as equipment vendors and resource managers begin to realize its potential as a remote sensing tool. As it changes, MAG will continue to evaluate its utility in forest health monitoring.

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# REVIEW OF SPATIAL ANALYSIS TECHNIQUES

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*Abstract.* This paper reviews some common techniques for analyzing spatial patterns. Topics include quadrat and distance sampling for describing point distribution patterns (uniform, random, and aggregated) and geostatistical techniques such as Moran's I statistic, spectral analysis, the Mantel test, and wavelet analysis for characterizing spatial structures of populations. The various methods described differ in both the kinds of data to which they may be appropriately used and in the information which they provide.

## INTRODUCTION

The problem of assessing spatial patterns has assumed considerable importance within the past few decades (Moore 1954, Morisita 1959, Matern 1960). The first attempts to analyze spatial patterns used simple, visual description (Curtis and McIntosh 1950). These methods were adapted because of the spatial complexity encountered in various ecological studies and the need for relevant information over extensive areas (Curtis and McIntosh 1950). Direct, visual characterization of spatial pattern is influenced by subjective, personal interpretation and is now seldom used for quantitative or comparative studies. Although individuals in many natural plant communities are not randomly distributed (Ashby 1935), many early sampling methods were developed under the simplifying assumption that populations were randomly distributed (Clark and Evans 1954). If sample distributions departed significantly from random, resulting statistics and estimates of their reliability could be seriously flawed (Cole 1946). Several methods based on quadrats or distance measurements were developed to determine which statistical distributions best approximated observed spatial point patterns. Likewise, many inference tests require that observations be statistically independent. Whereas in fact, observations close to each other may be spatially correlated due to factors and processes such as soil fertility or propagule dispersal. In addition to displaying spatially related trends in the data, geostatistical methods enable investigators to detect complex patterns and to compare several data sets as transects or surfaces.

## ANALYSIS OF SPATIAL POINT PATTERNS

The recognition of nonrandom patterns in biological populations has led to the development of numerous mathematical models based on assumptions essential in the formation of particular spatial patterns (Clark and Evans 1954). In general, departures from randomness have been tested by assessing the degree and direction that observed distributions deviate from various known statistical distributions. Agreement between theoretical and observed distributions, however, does not require that the observed spatial distribution was formed under the same assumptions as the theoretical distribution (Morisita 1959, Pielou 1959). Discrepancies among various models may be attributed to the sensitivity of the tests employed in detecting the various degrees of nonrandomness (Blacksmith 1958). Two of the most frequently applied methods of expressing nonrandomness in spatial distributions are described below.

### *Quadrat Sampling*

The quadrat method is used primarily to study vegetative characteristics other than spatial patterns (Mawson 1968). Quadrats are used extensively in forestry and ecology to sample such vegetative characteristics such as frequency, density, abundance, and presence (Curtis and McIntosh 1950). Although quadrat methods can detect nonrandom patterns, results may vary significantly with quadrat size (Pielou 1957). This affect can be alleviated to some extent with the use of contiguous quadrats.

Several frequency distributions have been used to test the results obtained from the quadrat method. These are: the negative binomial, Neyman's type A, and Thomas' double Poisson distribution. Of the three distributions, the negative binomial distribution has the most desirable properties for modeling contagious distributions. It has two parameters which can be interpreted in a biological sense as a density parameter and a heterogeneity parameter. As the latter increases to infinity, the negative binomial distribution will converge to a two-dimensional Poisson distribution (Daniels 1978).

### *Distance Sampling*

Distance sampling, the second method of determining nonrandomness, is used primarily to study the spatial relationships of biological populations (Mawson 1968, Pielou 1959, Holgate 1965, Clark and Evans 1954, Moore 1954). This method depends partly or wholly on distances from randomly selected points to the nearest tree, or from randomly selected trees to their nearest neighbor. The underlying assumption is that the observed distance distribution in a randomly distributed population conforms to a Poisson distribution with population entities randomly located within an infinitely large area (Cottam et al. 1953).

As with the quadrat method, several frequency distributions such as the normal, binomial, Poisson, negative binomial, and Neyman's type A distribution are used to test results obtained from distance sampling methods. Mawson (1968) compared the frequency distribution of point-to-tree and tree-to-tree distance measurements with the above mentioned theoretical distributions and concluded that the observed distributions differed significantly from the reference distribution. He found the normal distribution to be good for random spatial patterns and poor for uniform spatial patterns, and the binomial distribution good for uniform spatial patterns. Mawson (1978) showed, however, that point-to-tree and tree-to-tree distances may appear to be random, aggregated, or uniformly distributed. Therefore, it is essential that the distribution of distance measurements should not be the only method used to detect nonrandom spatial patterns in biological populations (Pielou 1959).

Five of the more promising distance sampling methods include Clark and Evans (1954) nearest neighbor index, Holgate's ratio and Holgate's correlation index (1965), Pielou's index of nonrandomness (1959) and Hopkins and Skellam's coefficient of aggregation (Pielou 1977, Payandeh 1970).

Clark and Evans (1954) developed an index for detecting nonrandom spatial patterns based on the average distance between randomly selected trees and their nearest neighbor. This index has been used to estimate the density of randomly distributed populations or to describe the spatial aggregation of populations of known density. Thompson (1956) modified Clark and Evans nearest neighbor index by comparing the mean distance to the  $n$ -th nearest neighbor, thus eliminating the need for an independent estimate of the population density. He concluded that this test is better suited to detect larger-scale heterogeneity than Clark and Evans' nearest neighbor index.

Holgate (1965) introduced two indices for detecting nonrandom patterns based on distances between randomly selected points to the  $s$ -th and  $t$ -th nearest neighbors. He examined these methods on three populations with known spatial distributions and concluded that both indices were valid for random spatial distributions. Holgate argued that the ratio index was more sensitive in detecting aggregated distributions and the correlation index was better in detecting uniform distributions.

Pielou (1959) devised an index of nonrandomness based on distances between randomly selected points and their nearest neighbor. This index has been used to evaluate departure of spatial distributions from completely random distributions (Mountford 1961).

Hopkins and Skellam developed a test for detecting nonrandom spatial patterns in plant populations based on the assumption that a population has a random spatial distribution if the distribution of distances from randomly selected points to their nearest neighbor were identical to the distribution of distances from randomly selected trees to their nearest neighbor (Pielou 1977, Payandeh 1970).

Indices derived from distance sampling have certain advantages over quadrat sampling when estimating the spatial patterns of a population. Cottam and Curtis (1956) pointed out that by eliminating the use of plots, distance sampling is more efficient in terms of time and equipment needed. The authors pointed out that the major disadvantage of distance sampling is an unfamiliarity with the methods, as well as the precision and limitations associated with their use.

#### SPATIAL ANALYSIS OF MAPPED DATA SETS

Because of the difficulty in randomly selecting individual trees within a given population researchers tend to map the location of individual trees and then apply distance sampling or quadrat sampling techniques in an attempt to analyze spatial patterns. Cliff and Ord (1981) point out that if one were to examine all possible distances between observations, they would not be independent thus violating the underlying assumption of independent observations under the null hypothesis (Ripley 1981). In such instances, exact tests should be used in determining the degree of nonrandomness in the population. Some of the more common techniques used in analyzing the spatial pattern of mapped data sets include multiresponse permutation procedures and spectral analysis.

#### *Multiresponse Permutation Procedures (MRPP)*

Reich et al. (1990, 1992) discuss the merits of using distance-based permutation procedures (MRPP) for characterizing spatial relations among two or more groups in a mapped data sets. In addition to being able to characterize spatial relationships, MRPP can also be used to identify spatial patterns (e.g. random, aggregated, and uniform). Unlike distance sampling, the use of MRPP in detecting nonrandom spatial patterns requires an external reference set with known spatial pattern. This external reference set is similar to the theoretical distributions (e.g. normal, binomial, Poisson, negative binomial, Neyman's type A, etc.) used in some of the more classical distance sampling techniques. It provides a relevant reference distribution against which the observed spatial patterns may be compared.

Reich et al. (1990, 1992) points out that the application of MRPP is very efficient in estimating the spatial relationships in mapped data sets. In addition to testing for nonrandom spatial patterns and association, MRPP is flexible in the type of hypotheses that can be tested. For example, MRPP could be used to compare observed spatial patterns with hypothetical patterns generated using growth and yield models that take into consideration the degree of stand heterogeneity, competition and disease incidence. Such comparisons allow for testing of underlying assumptions or processes thought to influence spatial patterns. Other applications of MRPP include the study of space-time interactions and pattern similarities.

Another application of MRPP comes from the work by Stauffer (1978). Stauffer suggests that an aggregated distribution of trees is better characterized by the presence of holes rather than by the presence of clearly defined clusters. To test this hypothesis, an external reference distribution can be generated using Stauffer's clustering algorithm. This external reference distribution can then be compared with an observed spatial pattern using MRPP. This information could then be used to select an appropriate clustering algorithm for use in distance-dependent growth models and to model the spread and intensification of contagious diseases such as dwarf mistletoe or pitch canker.

## GEOSTATISTICAL TECHNIQUES

Pattern recognition provides important clues in understanding multi-resource spatial interactions in ecological systems. It also yields information on the likelihood of connectivity between selected points in the pattern. For example, pattern disturbances over time may be spatially correlated with management practices and/or changes in environmental conditions. In spite of the interest in ecological pattern recognition and comparisons, a relatively small amount of work has been reported on spatial patterns over large geographical areas (e.g.,  $10^6$  to  $10^7$  ha). Most of the work has been limited to a relatively small area ( $10^0$  to  $10^3$  ha).

Geostatistical techniques, such as Moran's I statistic (Cliff and Ord 1973), spectral analysis (Ripley 1981), the Mantel test (1967), and wavelet analysis (Bradshaw and Spies 1992), are just a few procedures which permit tests of hypotheses regarding spatial patterns. They describe the structure of the pattern including the presence of directional components at various scales (Legendre and Fortin 1989).

*Moran's I*

Moran's I statistic has been used by ecologists and geographers alike to test for the presence of spatial autocorrelation in a two-dimensional plane (Cliff and Ord 1973, Jamars et al. 1977, Legendre and Fortin 1989, and Ripley, 1981). A variable is said to be spatially autocorrelated when it is possible to predict the value of this variable at some point in space from the known values at other sampling points whose locations are known (Legendre and Fortin 1989). Moran's I is generally thought to be an extension of the Pearson product moment correlation coefficient with a weighted sum of squared cross products in the numerator divided by a weighted sum of squares. Thus, Moran's I generally varies over the range of -1 to 1, but may exceed these values depending on the characteristics of the weights used in the analysis.

In a review of techniques for analyzing spatial patterns, Jamars et al. (1977) points out that the choice of weights plays an important role in the ability of Moran's I to detect spatial autocorrelation. If for example, one were to choose a specific set of weights such as the Euclidean distance separating two points, autocorrelations at other weights may not be apparent, while if more general weights were to be used (e.g. 0,1) the test for spatial autocorrelation may be weak (Jamars et al. 1977). Cliff and Ord (1973) discusses the choice of weights and suggests that the most powerful test of no spatial autocorrelation is provided when the weights correspond with the autocorrelation pattern under the alternative hypothesis.

*Spectral Analysis*

Spectral analysis is very similar to time-series analysis (Ripley 1981) in that it can be applied to both one- and two-dimensional data. In analyzing spatial patterns using spectral analysis it is assumed that the variable of interest can be meaningfully represented by sinusoidal waves summed over different frequencies, with a different amplitude and phase at each frequency (Bartlett 1964). The spectral analysis is obtained by Fourier transforming data from a rectangular or triangular lattice (to obtain the coefficients of the sinusoids at a discrete set of frequencies), grouping neighboring frequencies into frequency bands, and estimating various quantities from the Fourier transformed data in one frequency band at a time (Bartlett 1964). Frequencies are grouped into bands to enhance the statistical stability of the estimates (Bartlett 1964, Ripley 1981, Legendre and Fortin 1989).

Spectral density is estimated by computing the average squared amplitude of the sinusoids within a frequency band (Ford and Renshaw 1984). This estimated spectral density is then plotted as a function of frequency. The spectral density indicates how the variation exhibited by the data is distributed over the different frequency bands (Ford and Renshaw 1984, Legendre and Fortin 1989).

The four main components of spectral analysis include (Ford and Renshaw 1984):

1. The autocorrelation function which estimates the correlation between points and their nearest neighbors,
2. The periodogram which shows the extent to which the data contains periodicities at different frequencies,
3. The R-spectrum which highlights the frequency of pattern repeats, and
4. The 0-spectrum which highlights directional components in the data.

While spectral analysis has been used primarily to analyze the spatial pattern of data from a systematic grid it can also be used to analyze point patterns of mapped data sets. In this instance, a fine grid is laid over the map and each cell is coded as a zero or one depending on whether or not it contains an individual. Spectral estimators are then computed in the usual way.

#### *Mantel's Test*

Another problem arises in practice when one is given a set of variates  $X_i$ ,  $Y_i$  and wishes to determine whether variates are spatially correlated with one another. In an attempt to answer this question, researchers have frequently resorted to some method for reducing the dimensionality of the variable space, and then employing one of the several tests for spatial autocorrelation (Orloci 1978, Legendre and Fortin 1989).

Legendre and Fortin (1989), for example, advocate the use of the Mantel test (1967) as one method of analyzing the spatial relationship between biological variables such as species abundance and productivity and environmental factors (e.g., drainage, slope, aspect, rainfall, climate, etc.). The test statistic involves two distance matrices, similar to the proximity matrix used by Moran. The first is a matrix of geographical distances ( $x_{ij}$ ) describing the spatial location of the sample plots from one another; the second is a matrix of ecological distances ( $y_{ij}$ ). To account for the spatial interaction of the multivariate data the authors advocate combining the data in such a fashion as to derive a quantitative index, or coefficient of association which defines the likeness of sample points as a composite of data collected at the sample points (Orloci 1978). Orloci (1978) points out that the resemblance of a given pair of sample points should be independent from the resemblance of any other pair in the sample. An example, would be the use pest risk and hazard indices to indicate the likelihood of an outbreak occurring and the expected losses that would result. Other techniques for reducing the dimensionality of set of data are described by Orloci (1978).

The Mantel statistic given by

$$z = \sum_{(2)} x_{ij} y_{ij} \quad (1)$$

can be standardized as follows:

$$r = \frac{\sum_{(2)} (x_{ij} - \bar{x})(y_{ij} - \bar{y})}{(n-1)s_x s_y} \quad (2)$$

where  $s_x$  and  $s_y$  are the sample standard deviation of the geographical and ecological distances respectively. The P-value under the null hypothesis is obtained using permutation procedures to generate the sampling distribution of Mantel's statistic under the null hypothesis. This is accomplished by randomly assigning the response variables (i.e. coefficient of association) to the geographical location of the sample points and computing the test statistic,  $r$  (Legendre and Fortin 1989). The realized statistic is then compared to the simulation distribution of the statistic under the null hypothesis. If the observed

statistic is likely under the null hypothesis, then  $H_0$  is accepted, and one would conclude that there is no spatial relationship among the sample data points. If the test statistic is extreme under the null hypothesis, then  $H_0$  is rejected, and one would conclude that there is a spatial relationship among the sample points. If a significant spatial pattern is observed Legendre and Fortin (1989) advocate doing a series of posteriori tests with Mantel's index to determine which of the environmental response variables are important in describing the spatial trend.

Unfortunately, this approach does not address the question of whether or not two or more response variables are spatially correlated with one another. Legendre and Fortin (1989) discuss a procedure referred to in the literature as a partial Mantel test as possible procedure for detecting spatial autocorrelation among two response surfaces. In this test the matrix of geographical ( $x_i$ ) and ecological ( $y_i$ ) distances are replaced by residuals from a regression model of the values of two response variables corrected for their geographical proximity to one another. The two residual matrices are then used to compute the Mantel test. The partial Mantel test implicitly assumes a spatial relationship among the two response surfaces which makes it difficult to interpret the test statistic (Legendre and Fortin 1989).

#### *Wavelet Analysis*

The wavelet transform and wavelet variance (Bradshaw and Spies 1992) provide additional techniques for examining pattern and scale in spatial data. Wavelet analysis is especially suitable where spatial patterns are irregular (non-cyclic) and trended (non-stationary). The transformation function (Eq. 3) acts as a "moving window" of a given size and amplifies certain pattern features depending on the selected function. Wavelet functions can be selected to identify features such as edges or gradients. Because the analysis preserves information on the relative location of data points (e. g. distance along transect), interpretation is direct; and multiple comparisons can be easily made. By computing a series of transformations with an increasing window size ( $a$ ), the analysis can resolve the spatial scale at which patterns occur and display how patterns at different scales are nested. The wavelet variance (Eq. 4) is a useful technique for simplifying complex, multi-scale patterns and for comparing alternate data sets. At each data point, a wavelet variance is computed as the squared average of the coefficients of the transformation function across scales or between alternate data sets. Wavelet analysis is usually performed on one-dimensional (transect) data, but development of two-dimensional (surface) techniques is proceeding (Bradshaw, per. comm.).

A one-dimensional, discrete wavelet transform can be defined as:

$$W(a, x_j) = \frac{1}{a} \sum_{i=1}^n f(x_i) g\left(\frac{x_i - x_j}{a}\right) \quad (3)$$

where  $x_i$  is distance along a transect and  $g(x/a)$  is a window function of scale  $a$  centered at  $x_j$ .

The wavelet variance for  $n$  data sets is computed as:

$$V(a) = \frac{1}{n} \sum_{i=1}^n W^2(a, x_j). \quad (4)$$

## SUMMARY

Given the complexity of biological populations and the disparity in the methods of collecting and reporting information, no single approach may be sufficient for a thorough description and analysis of the spatial structures present in a sampled population. Various techniques provide information on point dispersal distributions, spatially relevant trends and patterns, and comparisons between populations. These methods can provide insights on prevailing ecological processes and suggest efficient sampling schemes.

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## FORECASTING THE SPATIAL DYNAMICS OF GYPSY MOTH DEFOLIATION USING 3-DIMENSIONAL KRIGING

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*Abstract.* This paper introduces 3-dimensional kriging as a method for forecasting pest outbreaks. The technique is illustrated with the prediction of defoliation caused by the gypsy moth, *Lymantria dispar* (L.). Forecasts are based on the statistical autocorrelation (persistence) of defoliation through space and time. Spatial and temporal autocorrelation of defoliation in historical data was first quantified at a variety of scales using semivariograms. These semivariograms were then used to parameterize the geostatistical estimation technique, 3-dimensional simple kriging. Kriged estimates are weighted averages of values from nearby locations and typically are used to interpolate 2-dimensional data. In this study, we used the procedure to extrapolate future defoliation maps into a third dimension, time. Kriged estimates were expressed as probabilities of detectable defoliation. The procedure usually performed well in predicting the spatial distribution of outbreaks in a given year, but the region-wide outbreak magnitude generally lagged a year behind actual values. Though not currently suitable for operational use, this approach represents a novel approach to landscape-level forecasting of insect outbreaks and these models may ultimately outperform current forecasting systems.

Geostatistics are a family of statistical tools for describing and modeling spatial variation in data. These procedures originally were developed for applied problems in mineral and petroleum geology (Journel & Huijbregts 1978, Hohn 1988). In a typical problem there exists a set of spatially scattered points at which there are sample values (e.g. oil yield) and the problem is to interpolate those values at unsampled locations within the same general area. "Kriging" is a geostatistical procedure that provides estimates that are linear models of values at nearby sample locations. As such, Kriging is based on the notion that values at nearby locations are more similar than values at more distant points. This assumption, while generally true for most geological data, also is valid for most biological data. Consequently, many of these techniques have been adapted to ecological problems that involve modeling of spatial patterns (Robertson 1987, Rossi et al. 1992, Kemp et al. 1989, Liebhold et al. 1991).

Most applications of kriging have involved interpolation among data scattered in a single 2-dimensional plane. Kriging also can be used to extrapolate by providing estimates in areas beyond the areas where sample data exist. Furthermore, kriging also can be applied to 3-dimensional data. Using 3-D kriging, estimates are made among sample points located in a 3-dimensional space. These may be dimensions in euclidean space, such as estimation of the boundaries of an oil reservoir in 3-dimensions, or the dimension may be in time. In the latter situation, estimates are provided by interpolating or extrapolating among or beyond points scattered through space and time (Bilonick 1988). In this paper we demonstrate the use of 3-dimensional kriging for extrapolation of a temporal sequence of gypsy moth, *Lymantria dispar* (L.), defoliation maps.

The gypsy moth is an example of an eruptive species (Price et al. 1990): population densities vary through several orders of magnitude, often reaching epidemic densities that have spectacular effects on their habitat (i.e., total defoliation of host trees). It is not uncommon for gypsy moth populations to persist for many years at densities so low that it may be difficult to detect any life stages except male moths. Occasionally, for unknown reasons, population densities increase, often to defoliating levels in excess of 6000 egg masses/ha, within only a few generations. These outbreak populations may persist for several years before collapsing.

Gypsy moth outbreaks often occur over very large areas and are notoriously difficult to predict (Liebhold & Elkinton 1989). Previous models developed for predicting defoliation have been based primarily on pre-season counts of egg masses (Gansner & Herrick 1982, Williams et al. 1991, Montgomery 1990, Liebhold et al. 1993a). Though there is a significant relationship between egg mass density and subsequent defoliation at the stand level, the variance about this relationship is great. Consequently, considerable error is encountered in using this method for prediction of defoliation. The lack of a more precise method for prediction of defoliation can have a devastating impact on the efficiency of the gypsy moth management program (Ravlin et al. 1987).

Previous models for predicting outbreaks have relied on data collected at a single point and largely have ignored spatial processes. Nearly 25 years ago, Campbell (1967) recognized that the dynamics of gypsy moth populations are affected by population conditions in nearby areas; there is often considerable synchronicity in the yearly fluctuations of gypsy moth outbreaks (Liebhold & McManus 1991). In an attempt to capture these spatial relationships quantitatively, we have adapted 3-dimensional kriging for modeling the spatial dynamics of gypsy moth outbreaks. Historical defoliation data from Massachusetts were used to parameterize a model that is used to extrapolate defoliation maps into the future. This is a novel approach and may provide a useful way of increasing our ability to predict insect outbreaks.

#### METHODS

**DATA.** A raster-based geographic information system (GIS), IDRISI, was employed to assemble and collate gypsy moth defoliation data. (Eastman 1987, 1989). A base-map of county boundaries in Massachusetts was used to define the study area; coordinates were projected using the azimuthal equal-distant projection (Snyder 1987). This projection conserves true distance linearly from a designated point (Boston, Massachusetts). A  $2 \times 2$  km grid cell size was selected as standard for all map layers in the GIS. Each map layer was comprised of 198 by 93 cells. The grid size was selected because it represented the minimum dependable spatial resolution of the available defoliation maps.

The Massachusetts Department of Environmental Management annually maps gypsy moth defoliation in all parts of the state using aerial sketch mapping. Mapping processes may vary from region to region and year to year in these sketch maps, resulting in the possibility of data errors from systematic and non-systematic sources (Talerico 1981, Chrisman 1987). The likely presence of these errors dictated the coarse spatial resolution of the data used in this study ( $2 \times 2$  km rasters).

The compilation of the defoliation map layers from 1960-1990 resulted in a  $198 \times 93 \times 30$ , 3-dimensional matrix of binary (0, 1) data. Because the data were coded as either 0 or 1, depending on whether defoliation exceeded a threshold (30%), the variable is considered an "indicator" variable. A variety of geostatistical procedures is available for quantifying and modeling spatial dependence in indicator values (Issaks & Srivastava 1989, Kemp et al. 1989, Liebhold et al. 1991).

**Variography.** The entire field of geostatistics is based on the concept that values at nearby points are more similar than values at more distant points. The term "autocorrelation" is used to describe this phenomenon. In order to perform kriging and other geostatistical estimation procedures it is first necessary to quantify the nature of autocorrelation present in the sample data. We quantified spatial and temporal autocorrelation first by dividing the data into distance classes (i.e. sets of pairs of points

separated by approximately  $h$  distance units) and then calculating the "semi-variogram" value for each distance class:

$$\gamma(h) = \frac{1}{2n_h} \sum_{k=1}^{n_h} [i(x_k) - i(x_k+h)]^2 \quad (1)$$

where  $\gamma(h)$  is a measure of variance;  $i(x_k)$  is a value of the indicator variable at location  $x_k$ ;  $i(x_k+h)$  is the value (in this case the value is the binary defoliation indicator variable) at a location  $h$  units from  $x_k$ ; and  $n_h$  is the number of pairs used in calculating  $\gamma(h)$  for a given value of  $h$  (Kemp et al. 1989, Liebhold et al. 1991, Ross et al. 1992). Because of the divisor 2,  $\gamma(h)$  has been called the "semivariogram" (e.g., Hohn 1988, Liebhold et al. 1991); recent literature simply refers to  $\gamma(h)$  as the "variogram" (Isaaks & Srivastava 1989). The variogram was calculated for several values of  $h$ , and  $\gamma(h)$  was plotted on the vertical axis vs  $h$  on the horizontal axis.

Use of the variogram in subsequent estimation by kriging requires fitting a variogram model. We used the exponential model:

$$\gamma(h) = C(1 - e^{-h/a}) \quad (2)$$

and a nugget effect model:

$$\gamma(h) = C_o \quad (3)$$

where  $a$ ,  $C$  and  $C_o$  are constants. The exponential model approaches  $C$ , the "sill" asymptotically, but to all appearances, reaches  $C$  at  $h = 3a$ , the "range". The nugget effect represents variability in values at a scale smaller than the minimum distance between sample locations; this variation includes both actual small-scaled spatial variation, and measurement error in the data. The nugget effect appears on the sample variogram as a non-zero intercept when values of  $\gamma(h)$  corresponding to small  $h$  are projected back to  $h = 0$ . The complete variogram model had the form:

$$\gamma(h) = \gamma_1(h) + \gamma_2(h) \quad (4)$$

where  $\gamma_1(h)$  is the nugget effect and  $\gamma_2(h)$  is the exponential model.

Variograms were calculated for a number of directions in space: east ( $0^\circ$ ), northeast to southwest ( $45^\circ$ ), north ( $90^\circ$ ), and northwest to southeast ( $135^\circ$ ), by partitioning pairs  $i(x_k)$ ,  $i(x_k+h)$  among four angle classes, each  $45^\circ$  wide and 20 distance classes, each 1 raster unit (2 km) wide. We also computed a variogram along the time axis of the data using 20 distance classes, each 1 raster unit (1 yr) wide. Variogram models were fit by eye using procedures described in Hohn (1988, chapter 2).

**Estimation.** Kriging is a geostatistical procedure for estimating a value at a particular location as a weighted average of values at nearby locations. These weights are derived from the variogram; nearby locations generally have greater weights than points farther away, reflecting the underlying spatial structure of the data. Much like linear regression, kriging minimizes the estimation error variance (Journel & Huijbregts 1978).

As stated earlier, defoliation status was a binary indicator variable; the value was coded as 0 if it was less than the 30% threshold level, and 1 if it was greater than the threshold. Consequently, kriged estimates of this variable were calculated as probabilities of exceeding the defoliation threshold. We write the defoliation probability at each cell (position in space and time is identified as  $x_k$ ) in the 198 x 93 x 30 grid as  $P(x_k)$ ; note that location  $x$  has two spatial components and a time component. A kriged estimate for  $P^*(x_k)$  is a linear combination of the  $n$  observed values of  $i(x_k)$  in spatial and temporal proximity to location  $x_k$ , i.e.:

$$P^*(x_k) = F^*(x_k) \left[ 1 - \sum_{j=1}^n w_j \right] + \sum_{j=1}^n w_j i(x_j) \quad (5)$$

in which  $P^*(x_k)$  is an estimate of  $P(x_k)$  and  $F^*(x_k)$  is an estimate of the expected frequency that  $i(x) = 1$ .

The weights  $W_j$  are computed by means of a system of  $n$  equations:

$$\begin{aligned} \sum_{m=1}^n W_m \rho(x_m - x_1) &= \rho(x_1 - x_k) \\ \sum_{m=1}^n W_m \rho(x_m - x_2) &= \rho(x_2 - x_k) \\ &\vdots \\ \sum_{m=1}^n W_m \rho(x_m - x_n) &= \rho(x_n - x_k) \end{aligned} \quad (6)$$

where:

$$\rho(a-b) = \rho(h) = 1 - \gamma(h) / \sum_{v=1}^v (C_v) \quad (7)$$

and  $C_1, C_2, \dots, C_v$  are constants in the variogram model, and  $h$  is the distance between locations  $a$  and  $b$ . The system of kriging equations is written in matrix form:

$$B \bullet W = D \quad (8)$$

and is solved with:

$$W = D \bullet B^{-1}$$

The geostatistical literature calls the estimation method used here "simple kriging" (Journel & Huijbregts 1978). It differs from the more commonly used procedure, "ordinary kriging" in that it requires a prior estimate of frequency  $F(x_k)$  for each candidate grid cell.

Kriging methods have several desirable features regarding the weights,  $w_j$ . In general, points closest to  $x_k$  have the largest corresponding weights. Variogram models can be anisotropic, that is, component variograms are damped in certain directions, or ranges vary with orientation (Issaks & Srivastava 1989, Rossi et al. 1992). Because the kriging system of equations depends upon variograms fitted to observed data, weights are greatest for directions of least variation. Hence, kriging captures consistent directional trends in variability (see discussion in Hohn, 1988, p. 107).

The effect of anisotropic variograms in kriging is to stretch the coordinate base perpendicular to the direction of minimum variation, and to weight values at points proximal to  $x_k$  by distance from  $x_k$ . Resulting estimates are mapped in the original coordinates. We exploited this feature of kriging to solve the problem accounting for separation in time relative to distance in space. A single variogram model was fitted in all three dimensions, with different ranges specified for space and time.

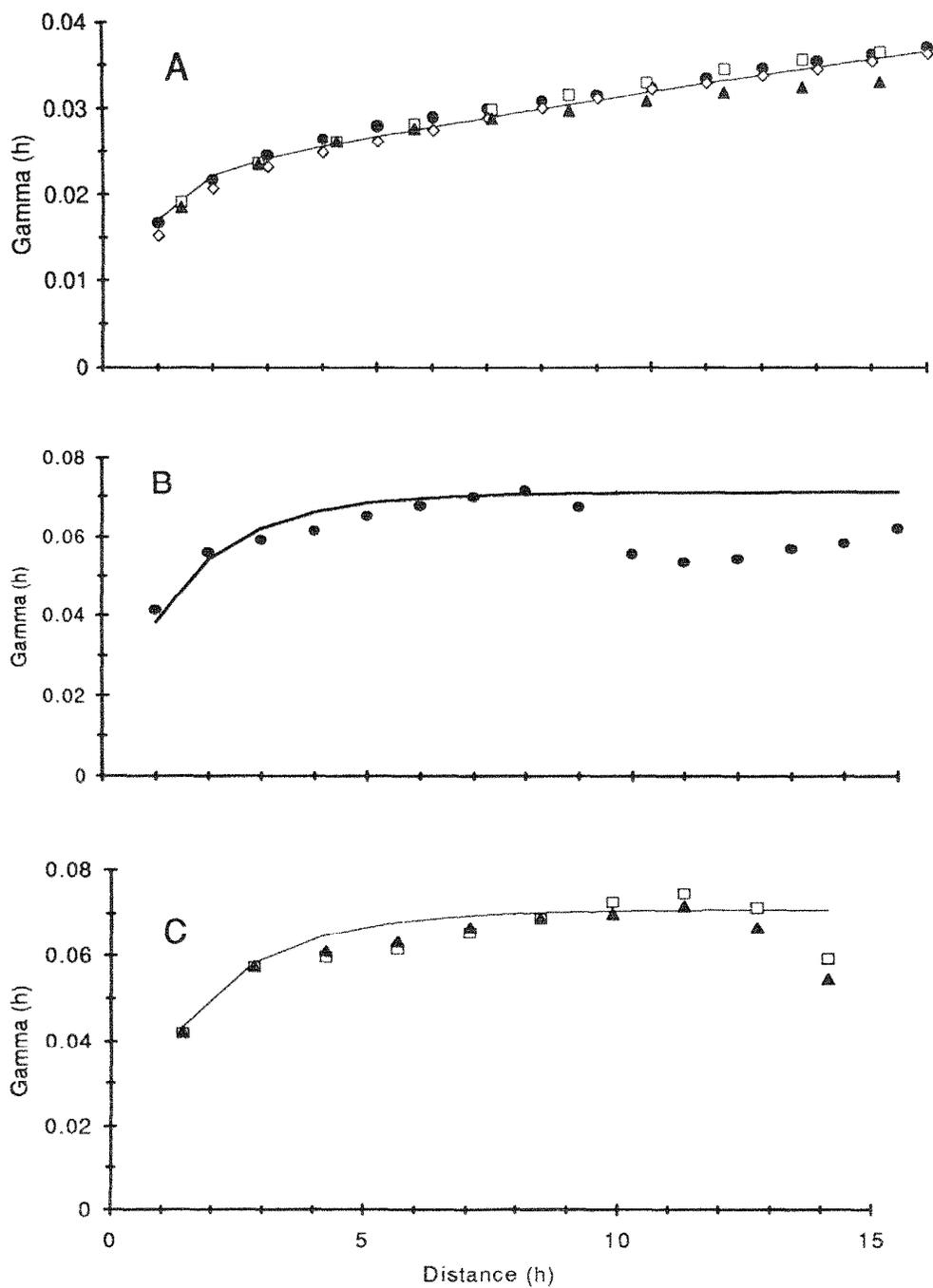


Fig. 1. Sample indicator variograms calculated in various directions from 1960-1990 defoliation data. Units on horizontal axes are numbers of cells ( $2 \text{ km} \times 2 \text{ km} \times 1 \text{ year}$ ). A. The spatial domain in each of four directions: east-west ( $0^\circ$ ), northeast-southwest ( $45^\circ$ ), north-south ( $90^\circ$ ), northwest-southeast ( $135^\circ$ ). B. The time domain. C. The space-time domain (this is the  $45^\circ$  angle in the time  $\times$  east-west plane).

## RESULTS AND DISCUSSION

Observed variograms (Fig. 1a) in the spatial domain exhibited nearly the same shape, and could be fitted with a single, isotropic model; we used a nested exponential model:

$$\gamma(h) = 0.021(1 - e^{-h/0.7}) + 0.050(1 - e^{-h/40}) \quad (9)$$

Although no nugget effect was used in the model, the range of the first exponential term (0.7) is less than the intermodel spacing of one. The small-scale variability in defoliation was not large; the ratio of the sill for this first term (0.021) to the total of the variogram (0.021 + 0.050) was only 30.

The variogram for the time domain (Fig. 1b) manifests an effective range of about five years ( $3 \times 1.7$  years), reaches a sill, then declines briefly. This "hole" in the variogram results from the episodic nature of gypsy moth outbreaks; defoliation in an area was usually low to zero, and outbreaks persisted for several years (Fig. 2a). The variogram model for time was identical to that for space except for the shorter range of the second exponential term:

$$\gamma(h) = 0.021(1 - e^{-h/0.7}) + 0.050(1 - e^{-h/1.7}) \quad (10)$$

Together, the two models comprise a single, anisotropic model in both space and time:

$$\gamma(h) = 0.021(1 - e^{-h/0.7}) + 0.050(1 - e^{-h/r}) \quad (11)$$

where

$$r = \frac{r_s r_t}{\sqrt{r_s^2 \sin^2 \phi + r_t^2 \cos^2 \phi}} \quad (12)$$

and  $r_s$  = range of spatial variogram = 40.0,  $r_t$  = range of temporal variogram = 1.7,  $\phi$  = azimuth of vector separating two locations relative to the spatial plane.

As a check,  $r$  for the variogram in the spatial plane is calculated from equation (12):

$$r = \frac{r_s r_t}{\sqrt{r_s^2 \sin^2 0 + r_t^2 \cos^2 0}} = \frac{r_s r_t}{\sqrt{0 + r_t^2}} = r_s \quad (13)$$

Similarly,  $r$  for the variogram in the time domain is equal to  $r_t$ . The expression for  $r$  in terms of  $r_s$  and  $r_t$  [equation (12)] follows from the definition of a geometric anisotropy (Journel & Huijbregts 1978). Combined space-time variograms (e.g.  $45^\circ$  in the space-time plane) need not be fitted; the space-time model (calculated from equation (12); Fig. 1c) shows an excellent fit to observed variograms in two directions.

The use of an anisotropic variogram model (equation 11) for both spatial and temporal directions avoids the assumption of any innate equivalence between spatial and temporal measurement units. In addition, separate spatial and temporal variogram models can lead to non-unique solutions of the kriging systems of equations (Myers and Journel 1990, Rouhani and Myers 1990)

Before kriging could be performed, a value for  $F^*(x_k)$  in equation (1) had to be selected. This term represents an *a priori* expectation of the frequency of defoliation which is adjusted to local conditions in time and location. A number of options exist for calculating  $F^*(x_k)$ . One approach would be to predict  $F^*(x_k)$  from variables that are associated with each grid cell. Examples of such variables include characteristics of the biological or physiographic landscape (Liebhold et al. 1993b), or the frequency could be calculated from census counts [e.g. egg mass counts (Liebhold et al. 1993a, Williams et al. 1991)]. A second approach was used in this study: frequencies were calculated as averages from historical defoliation data. The total number of years of defoliation was divided by the total number of years (30) for each of the 6,075 grid cells falling within the state of Massachusetts. The resulting map

(Fig. 2) shows clearly that some areas tend to be defoliated more often than others, reflecting the association of gypsy moth defoliation with specific forest types and physiographic features (Liebhold & Elkinton 1989, Liebhold et al. 1993b).

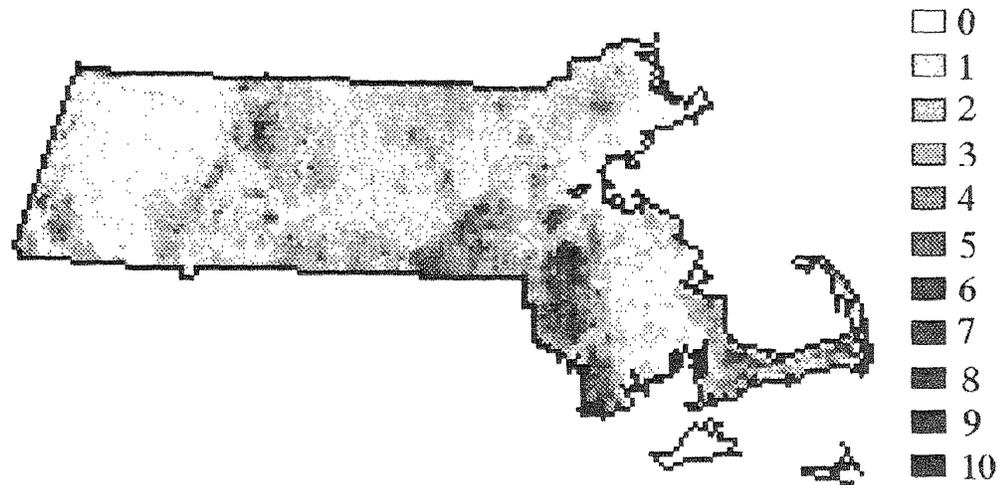


Fig. 2. Defoliation frequencies in Massachusetts from 1961-90 (no. years out of 30 with detectable defoliation).

A kriged estimate for each location  $x_k$  in a given year was computed from observed defoliation in the two previous years, and the 49 locations within a  $7 \times 7$  grid centered on  $x_k$ . This configuration of cells, or "search radius", was selected because the spatial variogram range [equation (9)] was larger than the temporal range [equation (10)], and locations approaching and beyond the range had near-zero weights and make little contribution to the final estimates. In this manner, defoliation probability maps were estimated from 1963-1990 (Fig. 3).

The sequence of estimates graphed by year (Fig. 3) show that kriging has modified the cumulative defoliation frequencies of Figure 2 to more accurately reflect particular spatial patterns in defoliation during the previous years. In addition, the maps of probabilities often have about the same appearance as the observed maps in the sense that areas of high defoliation probability typically corresponded to areas of observed defoliation (Fig. 2).

The kriging procedure performed best, in terms of delineating areas of predicted defoliation, during the peak years of defoliation (Fig. 3). It showed limited success for the initial years of gypsy moth outbreak. The modeling approach presented here is completely empirical; as such it is completely based upon the persistence and spread of defoliation through time. While specific biological processes are not explicitly modeled, the persistence and spread of defoliation reflects the emergent properties of a multitude of ecological factors. The statistical persistence of defoliation reflects a certain level of stability in high density populations that causes outbreaks to persist for several years (Liebhold 1992). Liebhold and McManus (1991) described the apparent spread of defoliation and presented several mechanisms that might cause it. They concluded that it was unlikely that the observed spread of outbreaks was caused by the dispersal of gypsy moths from high to low density areas. Instead they concluded that populations may rise synchronously over large areas, and the apparent "spread" of defoliation actually was caused by the spatial distribution of susceptibility.

The 3-dimensional kriging procedure described here probably is not suitable for operational use; even though the spatial distribution of outbreak predictions often coincided well with observed defoliation patterns, the region-wide outbreak magnitude generally lagged behind actual values. Nevertheless, we feel that this is a novel approach to forecasting insect outbreaks and that these types of landscape-level

models ultimately may outperform traditional forecasting systems. Incorporation of yearly census data into these time-space models should result in forecasts that more closely track actual year-to-year population levels.

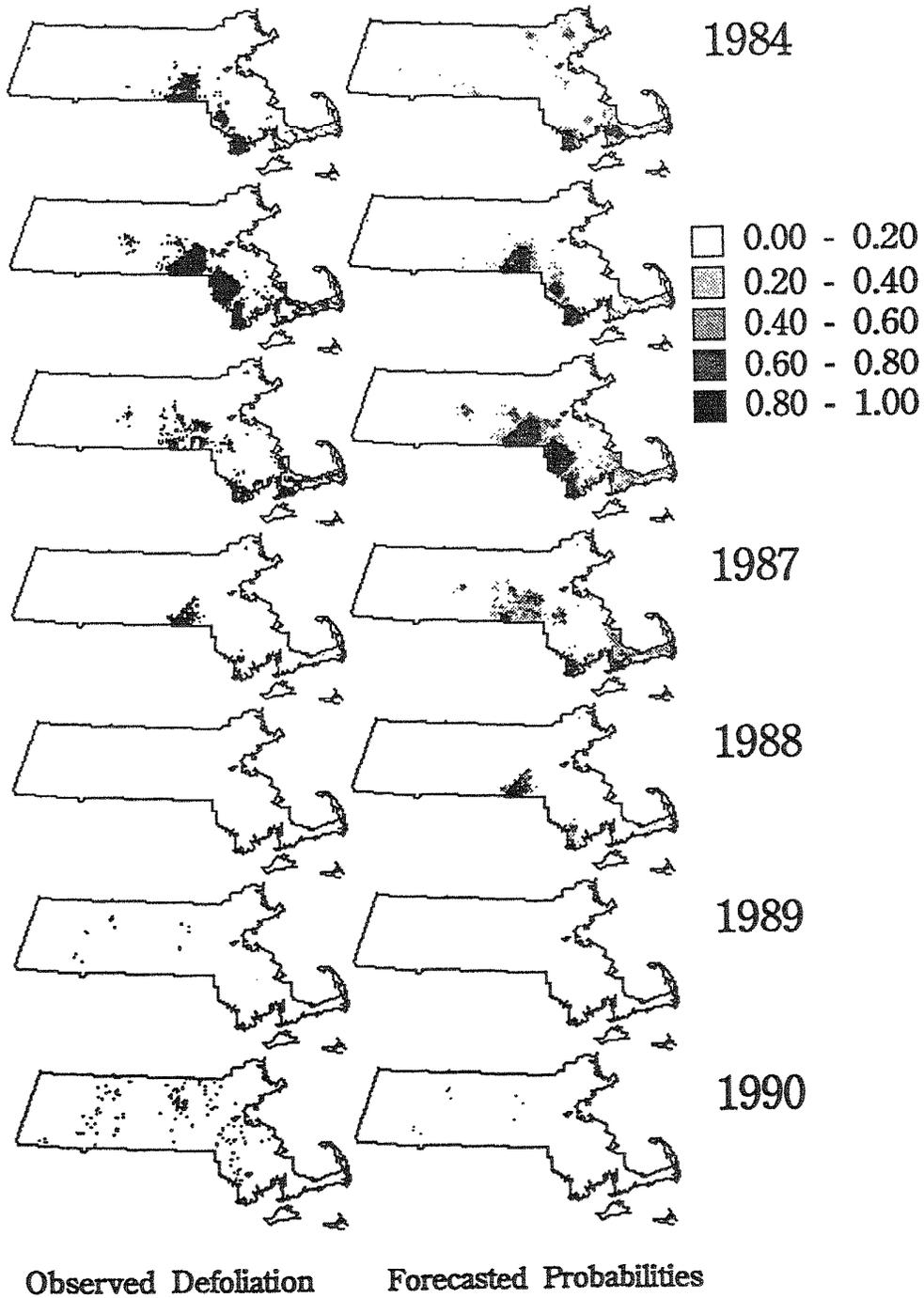


Figure 3. Predicted defoliation probabilities in Massachusetts: 1984-90.

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# A SPOT-GROWTH MODEL FOR SOUTHERN PINE BEETLE

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*Abstract.* Currently available models of the growth of southern pine beetle spots are either spatially naive or too complex for regional generalization. By spatially applying spot growth rates from an aspatial spot growth model, interactions between landscape structure and SPB spot growth can be simulated. Because the stochastic, aspatial model is driven by readily available, regional data, model results are explicitly linked to statistically compatible location and ownership measurements, and incorporate key sources of variability. By simulating SPB impacts under several scenarios of landowner response to infestation, the impact of different intensities of suppression on landscape structure can be evaluated. Spatial analysis is performed outside the model through output of generic raster landscapes. Spatial measures illustrated here using IDRISI include change in amount of pine edge and frequency with which spots spill over into adjoining stands. Although empirically obtained landscapes could be used by the model, a module was constructed which generates artificial landscapes. Southeastern stand size by age distributions are used to construct replicate landscapes of varying cover densities and complexities.

## INTRODUCTION

Over the past decade the forestry community has seen dramatically increasing pressure on both ethical and budgetary fronts. On the ethical side, we are increasingly challenged to incorporate broader ecosystem impacts into forest management decisions, including impacts on wildlife, recreation, and water quality. On the budgetary side, public involvement in forestry must increasingly be justified based on physical externalities or efficiencies of scale.

Key to addressing these concerns is understanding how stand level processes propagate upward to the surrounding landscape and in turn are controlled by their broader surroundings. Effects of forest fragmentation on bird populations is one example of a forest management impact which can only be understood through landscape scale study. A parallel issue relevant to policy is that of potential long term benefits of area-wide pest control, where a landowner's risk of infestation this year may rely on suppression activities undertaken by neighbors in years past.

Spot growth represents one of several behaviors of the southern pine beetle with potential to alter landscape structure and to cross stand borders. For analysis of southern pine beetle policies it would be useful to obtain quantitative estimates of how SPB alters landscape structure, and how frequently spots spill over from one stand to the next. The former measure is important to assessing how spots perforate or simplify landscapes under varying levels of suppression, while the latter might shed light on how frequently suppression of a spot prevents damages by that spot to adjoining stands and ownerships.

Direct empirical data on these questions is scarce. No direct measures have been found, although comparison between sizes of stands and spots might shed indirect light. Figure 1 shows frequency distributions from two sources. On the left are shown the frequency distribution of potential host stands in the Southeastern U.S. by area of stand, obtained by the Southeastern Forest Experiment Station's Forest Inventory and Analysis Unit. The bars show the relative amount of pine and oak pine acres which occur in stands of different sizes (extent). Data were collected in the late 1980's to early 1990's.

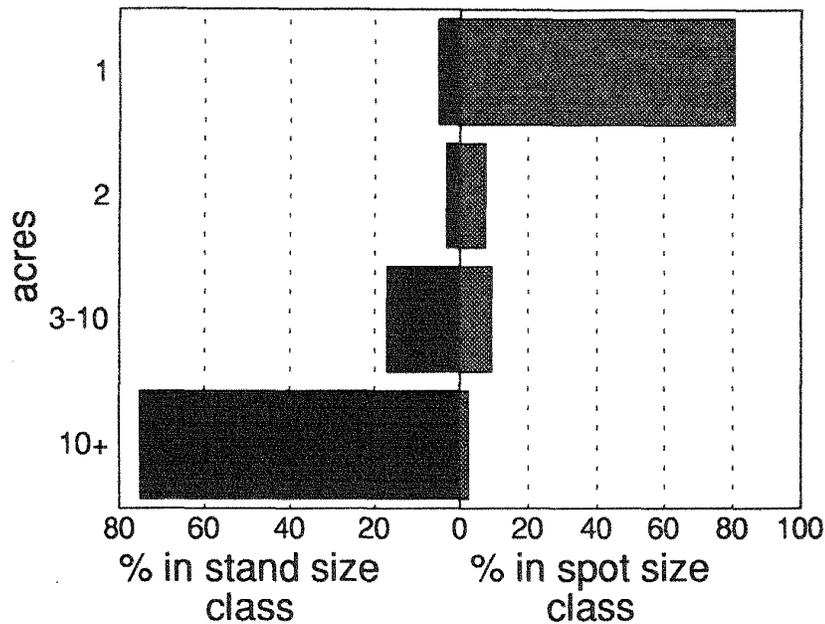


FIG. 1. Comparison of frequency distributions for stand size (left) versus spot size (right). Stand size data describes pine and oak-pine types in the five Southeastern states, as obtained from the Forest Inventory and Analysis Unit, Asheville, NC. Spot size data were obtained from Porterfield and Rowell (1981).

On the right side of the graph is the frequency distribution of SPB spot sizes in acres (Porterfield and Rowell 1981). As shown by this and other data on spot size (Leuschner and others 1976), most SPB spots are much smaller than most host stands. On the face of it this would suggest that spots crossing stand borders would be relatively rare. However, large spots may occur disproportionately in small stands, or spots may prefer stand borders to interiors. Neither of these can be ruled out, but there are more fundamental limitations to the comparison.

Most data describing spot size are obtained from detection programs, which focus on observing spots soon after they are initiated. Such observations would not show how large spots might ultimately become. Secondly, broad scale observations of spots understandably cannot require private landowners to withhold spot suppression or salvage operations. There are no empirical with-and without suppression comparisons available. In the absence of clear empirical information, simulation appears the most promising route to evaluating spot and suppression effects on landscape structure.

This paper describes the rationale, approach, and preliminary results of a spatially explicit model of southern pine beetle (SPB) spot growth in modern landscapes. Called SPBLAND, it is designed to estimate how spot growth responds spatially to landscape structure and how spot growth in turn alters those characteristics. Because the model seeks to describe processes in modern landscapes, it also estimates how impacts of spot growth on landscape structure are in turn affected by spot suppression or other landowner responses. In order to address regional policy concerns, a key requirement for the model is generalizability to conditions across the region.

SPB has been a popular subject of modelers (Stephen and others 1980). However, none of the existing models include all four of these characteristics: SPB spot growth, landscape structure, landowner response, and regional generalizability. CLEMBEETLE (Hedden 1985) and the Arkansas spot model (Hines and others 1980) both simulate spot growth but do not incorporate spatial characteristics of host

stands. TAMBEETLE incorporates the spatial arrangement of host trees (Feldman and others 1980), but cannot readily be generalized due to detailed data and processing requirements. Two models have simulated SPB populations regionwide but neither incorporated spatial characteristics of stands or landscapes (Reed and others 1980; de Steiguer and others 1987). Coulson and others (1993) describe a conceptual model of SPB which explicitly addresses the spatial characteristics of landscapes but focuses on processes which initiate new spots and maintain area-wide populations (Coulson and others, 1993; Rykiel and others 1988). Several landscape models are available which simulate generic disturbances, but these do not explicitly simulate SPB processes or landowner responses (Turner and others 1989; Graham and others 1991).

#### MODELING APPROACH

There are several additional criteria which influence the modeling approach employed.

1. Driving variables should be obtained from regional scale data sources whenever possible, and ideally should permit explicit disaggregation to more narrowly defined groups.
2. While simplifications are inevitable, aggregation methods should recognize key nonlinear and stochastic processes. Extreme cases may dominate overall effects.
3. As a research tool, flexibility of construction and analysis take preference over user friendliness. Flexibility in spatial analysis is particularly important due to the pace of development in this field.
4. Extensive data collection is not feasible at this phase. Should preliminary efforts prove promising, later collection of new data for validation or model refinement might be undertaken.

To meet these criteria and objectives, a raster-based, stochastic simulation approach was chosen, to be implemented as a collection of modules of code linked via ASCII format files. The two principal modules were written in the Interactive Matrix Language (IML) of the Statistical Analysis System version 6.04 (SAS, Cary, NC). These modules respectively construct the initial landscapes and simulate beetle behavior on landscapes. Modified landscapes are output in raster format for analysis. Spatial analyses have thus far been performed using IDRISI GIS (Clark University, Worcester, MA), although other spatial analysis tools may be used in future.

Temporal and spatial scales are critical characteristics of the model. The following extents and resolutions were chosen based on physical and logistic criteria:

TABLE 1. Spatial and temporal resolution of simulations.

	Extent	Resolution
temporal	one year	one month
spatial	1080 acres	1/30th acre

Temporal scale was chosen based on a combination of beetle and human factors. Growth of most SPB spots ceases in the late fall as temperatures decline, and new spots are created beginning in the early spring and continuing through the fall. Detection flights and subsequent suppression activities respond to this pattern, with intervals between spot initiation and suppression separated by months rather than days (de Steiguer and Hedden 1988). A temporal resolution of one month is sufficient to capture these processes.

The spatial resolution employed in the model is dictated by availability of data on spots. Spots of less than 10 trees are typically unreported in regional surveys because they are more likely to go inactive and create little damage (Hedden and Billings 1979; Pye 1993). Small spots should also show short lived effects on the landscape due to rapid ingrowth by surrounding trees. Based on the average densities of pine in the Southeast (Bechtold and Ruark 1988) 10 trees corresponds to an area of about 1/30th acre.

Spatial extent is to some degree a logistic determination. Larger landscapes pose fewer problems with border effects. However, in version 6.04 of SAS/IML for the PC, arrays are constrained to 180 by 180 cells, resulting in landscapes of 1080 acres. This is large enough to include multiple stands and minimize border interactions for most scenarios of interest, with necessary replication achieved through multiple landscapes.

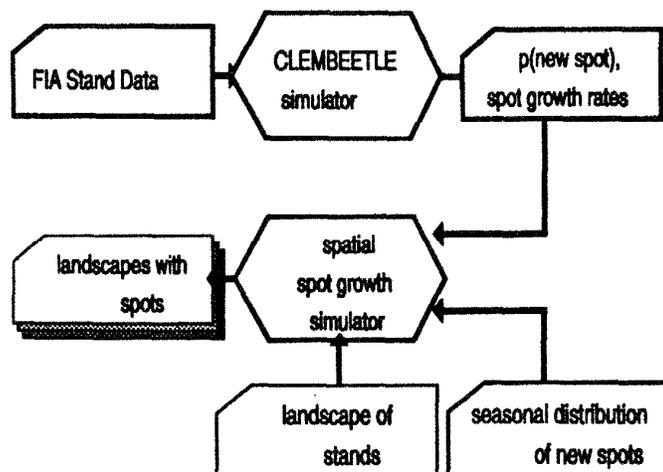


FIG. 2. Components of SPBLAND's spatial spot growth simulation module. See text for explanation.

#### *Beetle Module*

The principal components of spot growth in the beetle module are summarized in Figure 2, and consist of the following four features:

1. initiation
2. growth rate
3. growth direction
4. growth duration

**Spot initiation-** Spots are initiated randomly within the beetle season but following a seasonal pattern identified by expert survey (de Steiguer and others 1987). SPBLAND does not simulate processes of spot creation or proliferation. In SPBLAND the total number of spots in a landscape is exogenously determined. The model does determine where in that landscape spots occur using a randomization procedure. The model randomly selects a location within the landscape. If the location is pine or oak-pine the model then either accepts or rejects that location by comparing the relative risk of the host type at that location with a randomly drawn number. This is repeated until the indicated number of spots are established. Simulations thus far have included two spots per landscape.

**Spot growth rate-** The model described here is not so much a spot growth model as a spatial addition to an existing, aspatial, spot growth model--CLEMBEETLE (Hedden 1985). CLEMBEETLE assumes a homogeneous stand where spot growth is unaffected by spatial characteristics of the stand. SPBLAND takes CLEMBEETLE projections of areal rates of spot growth and applies them in a spatial context. CLEMBEETLE also provides the relative risk of spot formation in stands of different susceptibilities.

The projections of CLEMBEETLE were obtained as part of a previous simulation project which estimated regional costs and benefits of SPB suppression (de Steiguer and others 1987). For that effort, CLEMBEETLE projected spot initiation probabilities and growth rates for each of over 16,000 pine and oak-pine stands in the South. Although three levels of regional outbreak were simulated, only projections

for one level are used, that of two spots per thousand acres of susceptible host type. The variables describing stand risk factors were drawn from Forest Inventory and Analysis (FIA) surveys of the Southeastern and Southern Forest Experiment Stations (Asheville, NC and New Orleans, LA respectively).

By basing spot growth projections on FIA data, projections were generated for a statistically defined and well replicated population of stands from across the region. These linkages between each projection and its state, survey unit, and ownership characteristics allow hooks to economic models of landowner behavior, as well as permit comparison of results between different subregions or ownership assemblages.

To reduce data storage needs, 500 plots for each of three susceptibility classes were selected randomly from those in the Southeast and their predicted spot growth rates stored in a table. As each spot is initiated in SPBLAND, the susceptibility class of that location is checked and a growth rate randomly drawn from the 500 values for that class. Growth is assumed constant throughout growth of that spot.

Spot growth direction- Spots in SPBLAND are assumed to grow in a contagious fashion but with direction determined randomly each spatial step. Addition of cells is restricted to (non-spot) host cells. In short, growth is assumed to follow a self-avoiding random walk, with direction randomly redrawn for each new cell. The contagious nature of spot growth is a well recognized consequence of aggregation pheromones. Less certain is its direction, although random direction is consistent with one publication (Coulson 1981). Prolonged winds may in reality impart a greater consistency of direction, particularly for rapidly growing spots, although data to confirm this has not been located.

There are three exceptions to random direction of growth. Spots:

1. avoid expanding outside of landscape
2. avoid expanding into non-host cells
3. turn toward an adjacent cell of higher susceptibility

In all cases the spot only responds to conditions in immediately adjacent cells. Validity of this "myopic" behavior would likely depend on reception distances for both host and aggregation pheromones. Should host pheromones be important at distances greater than a cell (about 12 yards) then spots might in practice preferentially turn toward stand centers. This model provides a neutral model for such comparison.

More suspect than myopic host response is the model's assumed lack of response to aggregation pheromones from nearby spots. It is more likely that at some separating distance aggregation clouds of nearby spots overlap and the spots cease to behave independently. This simplification in the model's present structure may be a particular problem in extremely severe outbreaks. Comparing the spatial patterns it predicts under assumed spot independence with empirical observations should provide a test of spot independence. Nonindependence should appear as a greater degree of convergence of nearby spots over that predicted by the model.

spot growth duration- Landowner response to beetle infestation can take three forms: no control, spot suppression, or stand harvesting and regeneration. Spot suppression is assumed here to occur two months after the spot is formed, allowing for lags for both detecting the spot and actually implementing salvage or cut and leave actions. For simplicity at this phase, these actions are assumed fully effective.

Under the no control scenario, once spots are initiated they are assumed to grow at a constant rate until the end of the year. Under the suppression option, spot growth is stopped two months after it starts. For the harvest option, the entire stand is assumed reset to the youngest age class. Each of the first two options is simulated for the same input landscape, producing output of three matched landscapes: initial, no control, and with suppression. The harvest option has minimal impact on the spatial characteristics of landscapes, and is therefor handled externally via recoding in IDRISI of infested patches to the lowest risk class. For measures of landscape characteristics which do not distinguish risk classes, the harvest option is assumed to yield measures identical to those of the initial landscape, and this recoding is unnecessary.

### *Landscape Module*

The beetle module requires raster-based landscapes with cells classified using three strata of susceptible host plus one of non-host. In these simulations age class has been used as the stratifying variable of susceptibility. As explained above, the full variability of spot growth rates are maintained through the randomization process. The "susceptibility class" designation merely serves to link the spatial characteristics of the stand (eg. size, shape, etc.) to the beetle module.

Landscapes meeting the above criteria could be obtained through remote sensing or GIS, so long as suitable susceptibility strata can be determined. Existing cell classifications might be reclassified to match the age classes already employed in the spot growth tables (0-20, 20-40, and 40+ years). Alternatively, tables could be constructed based on some other stratifying characteristic, so long as a common characteristic can be derived from both FIA and landscape sources. Age was chosen here for its relevance to both stand size and economic value, although pine BA might be a useful alternative.

One difficulty with using remote sensing or GIS sources is the expense of broad scale data, and particularly data which includes information useful for predicting landowner response. Digitized data on National Forests are increasingly available, but these lands make up a small percentage of the SPB range (USDA Forest Service 1988) and have spatial characteristics quite different from those of privately held forestlands (Pye and Lee 1992). An alternative approach was undertaken where simulated landscapes were created based on FIA data from the Southeast.

Most measures in FIA surveys are point-based and therefore unsuitable for landscape scale analyses. However, several measures are collected which shed light on surrounding characteristics. In the Southeastern states, one particularly useful item is "extent of forest condition," shown in Figure 1. Basing landscapes on these data provides several benefits:

1. direct compatibility with risk measures from CLEMBEETLE
2. a statistically defined, regional population
3. compatibility with a standard unit of management
4. linkage to ownership class

Simulating the landscapes also allows independent manipulation of various landscape characteristics, such as patch size distribution, patch shape, and percent cover.

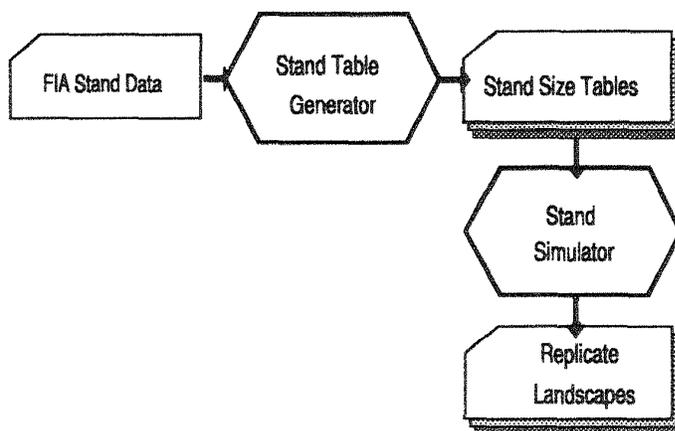


FIG. 3. Components of SPBLAND's landscape simulation module. See text for explanation.

Figure 3 shows the basic components of the landscape simulation process: generation of target stand characteristics, and locating and "growing" stands.

The module creates each landscape by randomly picking an initial point in the landscape and contagiously expanding outward from that point, assigning the susceptibility class assigned to the stand. Expansion continues until the target stand area is reached, incorporating only non-host cells into the stand. Previously established stands are avoided, as are landscape boundaries. Each stand is created in turn.

#### *target stand characteristics*

SPBLAND uses stand tables to tell it how many stands are required in a landscape and the age and target size of each stand. Although replicate stands can be generated from a single table, in these simulations new tables were randomly created for each initial landscape. The number of stands in a landscape is calculated from the target total acreage of host stands in the landscape divided by the average stand area.

To randomly assign each stand a final area and susceptibility class, frequency distributions were generated from FIA data for the five states in the Southeast for which stand area data is available. Area-weighted frequencies were generated by six classes of "size of forest condition" and three classes of age. Midpoint sizes were assigned to each size class, with a maximum allowable stand size of 55 acres.

#### *locating and "growing" stands*

SPBLAND uses the values in the stand table to sequentially generate stands, following the contagious expansion sequence outlined in the landscape module overview. However, it is the details of this procedure which determine the shape of each stand. FIA data provides no quantitative information on the shape of stands, even though this may have an important effect on landscape structure and spot growth.

The model addresses this lack of shape information through sensitivity analysis. Two alternative contagious expansion algorithms are provided, each with different implications for patch shape. Altering the fraction of a stand's area constructed with each of these algorithms creates landscapes with different degrees of complexity. This capability permits SPBLAND to predict the influence of shape complexity on spot behavior, and may allow calibration of shape complexity to match empirically observed values.

The two algorithms are referred to as branching and widening. The branching algorithm uses the self-avoiding random walk employed in the beetle module. Starting at an initial point, the algorithm creates a string of host cells. In contrast to spot growth, this algorithm periodically jumps to a different existing stand cell and starts a new branch. This produces complex, branching patches. The widening algorithm is a simpler contagious approach which randomly selects existing stand cells and tries to add an adjacent cell to the stand. This widening approach produces patches of simple shape. The branching algorithm is first applied until either the branch approach cannot continue or the switch point is reached. Then the widening algorithm continues until the target stand size is reached.

By using average stand size to determine the total number of stands in a landscape, stand size has precedence over total cover amount. That is, for a given target cover amount, each replicate landscape will be composed of the same number of stands. However, as the actual size of each of these stands is drawn randomly from regionwide distributions, some landscapes will be composed of smaller stands and some larger, with variation in realized cover percent for each landscape. The randomization procedures ensure that stand size distributions and cover percent over all simulated landscapes converge on the target amounts.



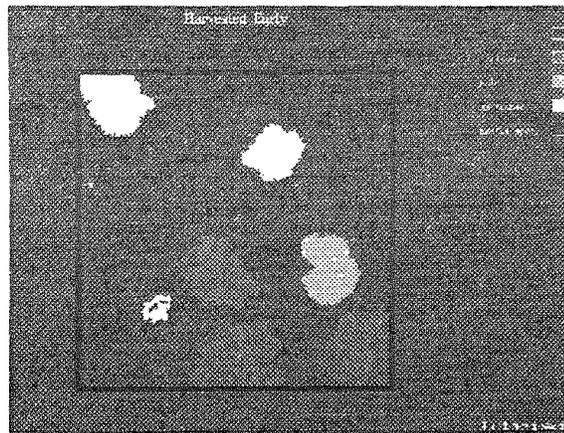


FIG. 7. Screen-shot of display from IDRISI showing the landscape from figure 5 after the harvest and regeneration scenario, where infested spots are cut and regenerated.

#### *scenarios of cover and shape*

Most of the simulations conducted thus far have used a switch point of 0.7. This level was chosen based on visual comparison of shape complexity from different switch points. Unfortunately, there is little directly comparable data available for calibration of stand shape. Most landscape scale data distinguishes patches of conifers (Turner and Ruscher 1988) but not stands, and shape characteristics of stands may differ from those based on coarser categories of forest.

Two levels of host cover have been simulated thus far: 20% and 50%. The lower was chosen as regionally representative of pine types, based on data for the Southeast (USDA Forest Service 1988; Bechtold and Ruark 1988). The higher fraction was used to represent more localized concentrations of host, such as might occur in areas where SPB outbreaks are more common.

#### PRELIMINARY RESULTS

Thus far only twenty sets of landscape have been simulated for each of the two cover amounts, so results are only preliminary. Figures 4 through 7 illustrate one sequence of treatments based on 20% cover and a switch point of 0.7. Figure 4 is the initial landscape from which the other three landscapes were derived. In this case the landscapes are composed of seven stands, with representatives from each susceptibility class. Note that the smaller spot in the bottom left has an inclusion of the non-host matrix. Figure 5 shows the landscape after simulating unrestrained spot growth. Two relatively lengthy spots can be seen in the bottom center and bottom right. By suppressing the spots after only two months of growth, damages were considerably reduced (Figure 6). Figure 7 illustrates the impact of harvesting and regeneration of the two infested stands, although this operation was not evaluated for the full set of simulations.

The resulting 120 landscapes (2 cover levels x 3 responses x 20 replicates) were imported into IDRISI. Amount of non-pine to pine edge were calculated by IDRISI for each landscape and converted into percentage increase above edge in the initial landscape. Figure 8 illustrates the results. As both the 20 and 50% cover levels received the same number of spots, the 20% landscapes began with less edge and saw a greater relative increase in edge. However, in both the 20 and 50% scenarios, suppression of spot growth cut the relative increase in edge in half.

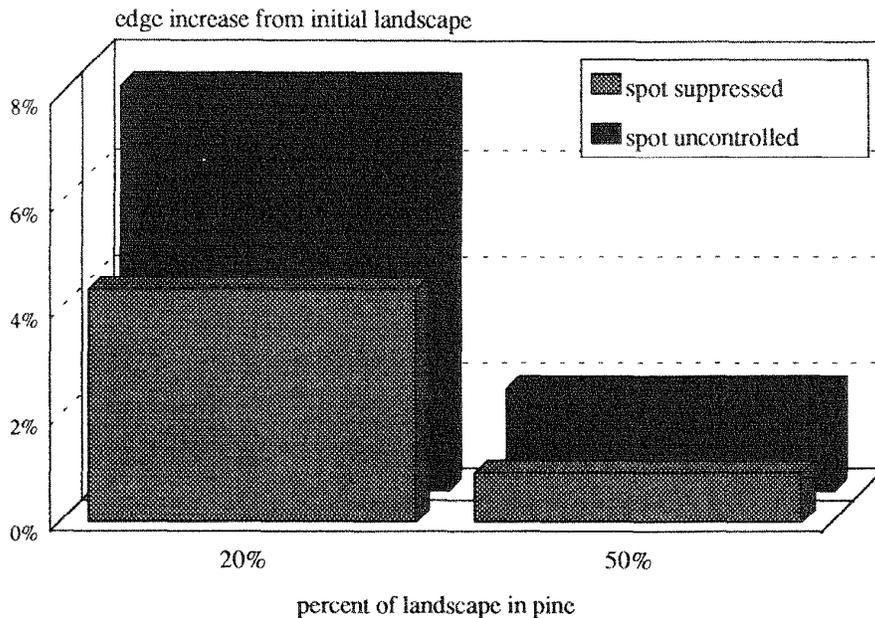


FIG. 8. Impact of spot growth with and without suppression on amount of pine forest edge for landscapes of two pine cover densities. Results are expressed as a percent of pine edge before spot growth.

Perhaps more important than the means is the variability of these estimates. The coefficient of variation for these twenty replications averages 78%, reflecting the high stochasticity of the driving variables. Greater number of replicates will be needed in future.

Visual inspection of resulting landscapes allowed tallying the number of times spots reached stand-to-stand borders. Table 2 below shows that at least for the limited replications available, increasing the frequency with which stands border one another also increases the likelihood of "border incursions" by spots. It is interesting that suppression did not prevent any of the high cover incursions, although it did prevent one in the lower cover runs.

TABLE 2. Number of times when 40 simulated spots reached a stand-to-stand border, by percent of landscape occupied by susceptible stands. Two scenarios are shown: "No control" where spot growth continues to end of season, and "with suppression" where spot growth is stopped after two months.

	20%	50%
no control	3	5
with suppression	2	5

#### DISCUSSION AND FUTURE DEVELOPMENT

As is often the case, preliminary results show several areas where model processes need improvement. Principal among these are scale of spot width and matrix inclusions.

Scale of spot width refers to how the width of spots should vary for spots of differing growth rates. By contagiously expanding each cell one after the other and simply varying the number of cells added per month, spots vary in length but not width. That is comparable to (incorrectly) assuming that spots grow faster by accelerating their generation time. Instead, rapid growth occurs through greater numbers of simultaneously active trees. Thus spot width should be scaled to the rate of spot growth. This will produce spots of more similar shape across different growth rates.

Matrix inclusions refers to remaining non-host matrix wholly surrounded by a stand. Although inclusions may be common in the field, FIA observations are not likely to recognize small ones. Worse, in the simulations inclusions appear principally in small stands, while in the field they should be more common in large ones. This bias appears to result from scaling changes in the spatial response to the switch point. Inclusions in larger stands are more easily removed by the widening algorithm even for the same proportional opportunity. The best remedy would be to periodically include a filter in all stand creation sequences which removes small inclusions.

Some system limitations may also prove short lived. The next version of SAS for the PC should remove limitations on size of array. While larger landscapes are one useful application of this change, a more fundamental one is use of lookup tables. At present each cell is represented in the matrix by its susceptibility class. With more than one digit permitted in each cell, cells can store their respective stand or spot number. With this change, susceptibility, age, or other factors can be referenced from an augmented stand table. This will provide greater flexibility in modeling response and also facilitate analysis by explicitly retaining original stand and spot identities.

Explicit stating of processes and linkages often proves heuristically useful, as it has here. It has revealed several gaps in data on the spatial nature of SPB behavior, such as the shape and directionality of growth of SPB spots and preference for edge versus interiors of stands. Also missed is information on the shape of pine stands and how often they adjoin other pine stands. As these data are obtained revisions will be needed to the code.

Several areas have been identified where improvements are required. Most of these are fortunately tractable. Once completed, sensitivity analyses and validation are needed. However, until the basic processes of the model have been validated, its results cannot be interpreted as more than theoretically interesting.

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## TWO APPROACHES TO LANDSCAPE CHARACTERIZATION OF SUSCEPTIBILITY TO GYPSY MOTH DEFOLIATION

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**ABSTRACT.** Susceptibility of hardwood forests to defoliation by the gypsy moth, *Lymantria dispar* (L.) is related to components of the landscape. In order to clarify processes operating at different geographical scales, results from two studies are presented: 1) at the forest community scale and 2) at the regional scale. First, a model of stand susceptibility is built on the basis of the relationship of forest species composition to topographic features. Second, a relative frequency model of susceptibility is investigated for Pennsylvania. Both approaches use geographical information system (GIS) operations as an integrative tool for environmental modeling. Because forest species composition is a difficult and expensive set of data to obtain for large areas, GIS is particularly valuable in cases where maps of forest species are deficient. Forest species groups occupy locations differentiated by growth requirements; these distinctions can be estimated from elevation, slope, and aspect. Digital elevation model (DEM) data is interpreted in a GIS, along with other pertinent information to construct most-likely species composition units. In the first study, DEM data at 1:24,000 for the West Virginia University Forest were converted to a triangular irregular network structure (TIN). Slope position and aspect were calculated separately from the TIN. An ecological unit classification was generated from a combination of slope and aspect. Forest types associated with these ecological units were used to estimate susceptibility. In the second study, susceptibility was characterized at the regional landscape scale. Maps of gypsy moth defoliation in Pennsylvania from 1969-89 were assembled in a raster-based GIS. Boolean algebra was applied to determine the total defoliation frequency for 2 by 2 km grid cells over the twenty-one year study period. Average defoliation probabilities were calculated for each of 6 major forest types occurring in Pennsylvania. Pitch pine, oak-pine, and oak-hickory types were the most susceptible to defoliation; maple-birch-beech, aspen-birch, and non-forest types were the least susceptible. Forest type areas were further cross-tabulated by elevation classes. The three most susceptible forest types exhibited decreased susceptibility at elevations lower than 200 m. Although these studies illustrate directions for landscape methods in susceptibility assessment, the quality of spatial data of forest type is a limiting factor and is an essential component for future development.

### INTRODUCTION

The concept of susceptibility is central to resource evaluation, conservation, and protection in forest pest management. Because of the widespread distribution of gypsy moth (*Lymantria dispar* L.) in North America, a number of questions have been generated about the characterization of forest susceptibility at different scales. This paper presents results from two studies of susceptibility that have particular emphasis on the influence of the landscape. In each example, defoliation by the gypsy moth is related to components of the landscape to study processes operating at local and regional scales. Knowledge of forest species association, landscape features, and defoliation patterns are integrated in geographic information systems (GIS) for analysis, hypothesis testing, and modeling. To establish links between the two approaches, we first review the botanical and geographical precursors of susceptibility. Second, we

examine topographic relationships to defoliation at the stand level, and propose a model to estimate susceptibility in the absence of detailed forest species data. Third, a regional landscape approach is reported using defoliation data collected in Pennsylvania during a twenty-year period and digital elevation data in a GIS.

Since the time of its accidental introduction near Boston in 1869, the gypsy moth has expanded its range to include all of New England and adjacent southeastern Canada, and is currently spreading across the Middle Atlantic states to Ohio, West Virginia, Virginia, and North Carolina (Liebhold et al. 1993). A second isolated defoliating infestation exists in Michigan. In 1991, an Asian variant was inadvertently introduced to the northwestern US. In many forests where this species has become established, populations sporadically reach very high densities and cause extensive defoliation of their host trees. Outbreaks increase tree mortality, reduce tree growth, decrease scenic quality, and create nuisance to residents (Campbell and Sloan 1977, Twery 1991). Scientific interests in the effects of gypsy moth range from the economic and ecological effects of losses of timber, consequences for species diversity, the level of scenic impacts, destruction of wildlife habitat, and the deleterious effects on watersheds. Because of the intensity and importance of these impacts, considerable effort is expended to reduce gypsy moth populations to non-defoliating densities. Pest control options and management options are in part dependent on the degree to which susceptibility can be estimated.

Unfortunately, although a substantial literature exists on insect-host relationships at the plant scale, little information exists on either gypsy moth dynamics or the distribution of susceptible forests at the regional level (Liebhold and Elkinton 1989).

Studies of the association of forest characteristics with gypsy moth defoliation have largely focused on site characteristics at the stand level (i.e. woodlots of 10-100 ha). Little is understood of the relationship between landscape-scale features and gypsy moth defoliation. Understanding relationships among landscape processes across spatial scales is necessary to develop more meaningful ecological models. Furthermore, emphasis is increasing on region-wide planning of natural resource management, including gypsy moth management (Forman 1988; Ravlin 1991; Reardon et al. 1987). An ability to forecast gypsy moth defoliation at different scales will be a valuable contribution to these region-wide systems.

#### MEASURES OF SUSCEPTIBILITY

The gypsy moth is a polyphagous insect; North American populations feed on over 300 different tree and shrub species (Leonard 1981) but despite this breadth of host preference, there is considerable variation within northeastern North American forests in their susceptibility to defoliation. A working definition of susceptibility begins with measures of defoliation probability. One operational definition of susceptibility, "the likelihood that a stand will be defoliated", is based on the relative frequency that stands with similar characteristics are defoliated (Gottschalk, 1986; Mason and Gottschalk, 1986). Clearly, susceptibility is insect species-specific (the same location may be susceptible to one pest and resistant to a second) but it is also location and scale dependent. Whereas locations vary in susceptibility at one scale of resolution (e.g. at the tree level), a different areal unit will result in different estimations of susceptibility. The appropriate choice of areal units depends on the information needs of resource managers. The degree of mortality or growth loss is termed vulnerability and, although both susceptibility and vulnerability are important to management decisions, the scope of this paper will be restricted to susceptibility.

For the purposes of constructing a model of forest susceptibility, the measurement of susceptibility at the stand level may be developed from botanical, geographical, and silvicultural precursors.

*Botanical Precursors*

Many studies have focused on characterization of the various components of stand susceptibility. These studies have implicated tree density, host species tree density, the abundance of tree structural features (e.g. bark flaps), and various site characteristics (e.g. soils) as important factors for predicting defoliation in a given woodlot (Bess et al. 1947; Valentine and Houston 1979; Herrick and Gansner 1986). Botanical characteristics have a significant and direct control on susceptibility at a given location, especially species (type and composition), and age (Gottschalk 1988).

Susceptibility is not equal for all tree species (Gansner et al. 1987) and is principally determined by gypsy moth larval feeding preferences (Mosher 1915; Montgomery 1991). Twery (1991) presented three susceptibility classes, *susceptible*: comprising forest species readily eaten by gypsy moth larvae during all larval stages; *resistant*: species fed upon when preferred foliage is not available or only by some larval stages; and *immune*: species that are rarely fed upon. Table 1 groups the major North American forest species according to this classification. The preference of gypsy moth for oak species (*Quercus* spp.) is well established, but it should be noted that not all oaks are equally preferred. The survival of the first instar is dependent on the availability of susceptible species (Mason and Gottschalk, 1986). Although susceptibility among and between species may vary with numerous leaf characteristics, the ratio of sugar to tannin in young foliage plays a significant role (Lechowicz 1983). As the sugar/tannin ratio is affected by various stresses (drought, previous defoliation, fire, etc.) the susceptibility of the individual tree, and even of leaves within the crown, may vary from growing season to growing season. The relationship of high tannin levels to higher susceptibility is also supported by Montgomery (1991). White oak is highly preferred by gypsy moth larvae because of its leaf chemistry and structural features of the tree. Montgomery (1991) has found that most oaks are suitable hosts with regard to larval growth, survival, and developmental progress.

TABLE 1. Categorization of gypsy moth host preferences (after Twery, 1991)

<b>Susceptible:</b>	
Overstory	apple, basswood, bigtooth and quaking aspen, gray, paper and river birch, larch, mountain ash, all oak species, sweetgum, willow.
Understory	hawthorn, hazelnut, hophornbeam, hornbeam, serviceberry, witch-hazel.
<b>Resistant:</b>	
Overstory	beech, black and yellow birch, blackgum, buckeye, butternut, sweet and black cherry, eastern cottonwood, cucumbertree, elm, hackberry, all hickory species, boxelder, Norway, red and sugar maple, pear, sassafras, black walnut, chestnut, eastern hemlock, all pine species, all spruce species.
Understory	blueberry, pin and choke cherry, paw, persimmon, redbud, sourwood
<b>Immune:</b>	
Overstory	all ash species, bald cypress, northern catalpa, eastern red cedar, balsam and fraser fir, American holly, horsechestnut, Kentucky coffeetree, black and honey locust, mulberry, sycamore, yellow poplar.
Understory	all azalea species, dogwood, elderberry, grape, greenbrier, juniper, mountain and sheep laurel, mountain, silver, and striped maple, rhododendron, all rubus species, spicebush, sarsaparilla, all viburnum species.

Relationships within the stand, including tree location, canopy position, leaf biomass, and even leaf position, have all been shown to influence susceptibility at the individual plant scale.

### *Geographical Precursors*

Site factors play a critical role in susceptibility. In most landscapes currently infested by defoliating gypsy moth populations, trees grow in mixed stands strongly influenced by growing conditions. Forest composition is influenced by the relative proportions of controlling variables such as light, growing degree days, moisture availability, and nutrients. The absolute and relative quantities of the controlling variables are themselves directly and indirectly influenced by topographic characteristics. Therefore, species composition is strongly related to topographic variables such as aspect, elevation, and slope position. Soil type, quality, and drainage properties, inherently tied to topography and vegetation, also influence susceptibility.

Forest composition with regard to the proportion and distribution of susceptible trees will directly influence the overall or areal susceptibility which is in turn influenced by the scale of analysis. Interdependence effects in time and space (spatial autocorrelation, multicollinearity, temporal lags) are not yet well understood and create significant difficulties in estimating causal relationships between variables influencing forest composition and hence susceptibility.

#### TOPOGRAPHIC APPROACH TO SUSCEPTIBILITY

In general, GIS investigation is enabled by the processing of multiple layers of geographical data (map layers) each coordinated to the others by means of geo-reference points. Digital Elevation Model (DEM) data consist of regular arrays of elevations aligned on a geographic coordinate system that can be manipulated and associated with other map layers in a GIS (Elassal and Caruso, 1983). Raster-based (grid cell) algorithms to find ridges and valleys have evolved from 2x2 moving windows to mathematically straight forward and more complex drainage basin models (Band 1986). In contrast to the raster-based approaches, Frank, Palmer, and Robinson (1986) proposed the use of edges and nodes contained in a triangulated irregular network (TIN) to define topographic features. Diffluent edges, where slopes are negative on both sides of the edge, define ridge lines; confluent edges identify valleys and transfluent edges indicate longer slope facets. Slope position and aspect are derived from the DEM through the manipulation of the attributes of edges and vertices in the TIN. The TIN partitions the DEM into irregular triangles with vertices situated at significant points. Local spatial relations depend on the elevation of the vertices and the distance and direction between them. Edge length, slope, relation to adjacent TIN facets, facet slope, and aspect are each derived from these local relations. Relations between edges and facets are established by means of relational joins between tables in the database using primary keys such as edge and facet identification labels. Selection by specific criteria is then possible using a database query language.

A set of rules derived from expert opinion has been used to predict species composition on a 3000 hectare forest in northern West Virginia. These rules, incorporated into ARC-INFO, a geographic information system, processed DEM data to generate and evaluate probable species composition. The sets of rules to relate topographic units to forest species composition encompass the topographic province (e.g. Allegheny Plateau); local topographic variables, for example elevation, aspect, slope, and slope position; Potential species associations; and most likely local species composition identified on the basis of regional and local topographic characteristics (Twery et. al., 1991).

A slope position map layer was generated with standard ARC-INFO functions, such as buffering and overlay, in combination with the rules encoded as database queries, e.g. reselection on the basis of percentage slope and slope length thresholds appropriate to the physiographic province. Five classes of slope position were established: ridge, upper slope, mid-slope, lower slope, and channel. Digital elevation data for the West Virginia University Forest at 30 meter resolution were converted to TIN structure. Database queries were conducted on the attribute tables to identify those TIN arcs having divergent and convergent slopes. First, ridge lines were identified using rules to extract divergent edges from the arc attribute table. A second query isolated divergent edges forming relatively horizontal ridge

tops. The two queries yielded a map coverage with 800 arcs which were then buffered to define ridge tops and upper slope areas. A similar set of queries was developed to extract channels from the data set. Buffer widths were chosen empirically at this stage to reflect the determination of landscape scale by the character of the topographical province, in this case the Allegheny Plateau. A boolean join operation was performed on the buffered ridge and channel coverages. Conditions for a classification of slope position based on the intersection of ridge and channel buffer zones are listed in Table 2.

TABLE 2. Slope position classification. Class, Percentage of study area, and number of polygons (in parentheses).

		CHANNEL		
		BOTTOM	MID	NOT
RIDGE	TOP	conflict 11.67 (886)	upper slope 11.76 (1484)	ridge 10.54 (763)
	MID	lower slope 6.65 (1429)	midslope 18.61 (1542)	upper midslope 20.93 m (1045)
	NOT	channel 2.30 (322)	lower midslope 6.58 (780)	neither 10.96 (174)

An aspect map generated from the DEM was also joined to slope position to produce a composite slope position-aspect map. The areal units of this map were considered to be rudimentary ecological units as they contain information about some major influences controlling forest species. Using data gathered from forestry literature a look-up table was created linking slope position-aspect units with the most-likely forest cover type (Table 3). Table 3 became the basis for a reclassification of the ecological units into an estimated forest species map, and hence of susceptibility to gypsy moth defoliation.

TABLE 3. Predicted cover type by aspect, slope position, and percentage of oak in the stand. (from Twery et al. 1991).

ASPECT	SLOPE POSITION				
	Cover Type* (percentage oak in stand)				
	RIDGE	UPPER SLOPE	MIDSLOPE	LOWER SLOPE	CHANNEL
N	55 (50)	55 (40)	59 (30)	57 (15)	58 (5)
NE	55 (50)	55 (40)	55 (40)	57 (20)	58 (10)
E	52 (60)	52 (60)	55 (50)	57 (25)	57 (15)
SE	52 (70)	52 (60)	55 (60)	59 (30)	57 (20)
S	44 (80)	44 (70)	52 (70)	55 (40)	57 (25)
SW	44 (90)	44 (80)	44 (70)	52 (50)	59 (25)
W	44 (80)	52 (60)	52 (50)	59 (30)	59 (25)
NW	55 (50)	52 (50)	59 (30)	57 (20)	58 (10)
NONE	52 (60)	N/A	N/A	N/A	58 (10)

\* SAF cover type (Eyre 1980) classifications:

44 - Chestnut oak (*Quercus prinus*)

52 - White oak (*Q. alba*), Black oak (*Q. velutina*), and Northern red oak (*Q. rubra*)

55 - Northern red oak

57 - Yellow-Poplar (*Liriodendron tulipifera*)

58 - Yellow-Poplar, Hemlock (*Tsuga canadensis*)

59 - Yellow-Poplar, White oak, Northern red oak

Attempts were made to refine the quantitative definition of ridge and channel on the basis of geographical dictionaries (Monkhouse, 1970). Dictionary definitions were found to be sufficiently imprecise to permit only arbitrary quantitative definitions. Band (1986) recognizes the need for objective criteria for ridge and valley identification. Similarly Frank, Palmer, and Robinson (1986) discuss the difficulties in describing geomorphological features in English and suggest that refined definitions are needed before quantitative analysis of these features is possible. Further experimentation and rules development for buffer size and slope criteria may provide insight for this particular study. Geographers are again faced with serious questions of the theory of landscape and the spatial language necessary for its description and analysis.

This method lends itself to an incremental approach to knowledge acquisition and is applicable across scales. Some success in validation has been achieved through the addition of digitized hydrology data. Additional sources, such as soil maps, are currently being incorporated to improve correlations with forest composition. Similar arguments can be presented for the inclusion of rules describing the control of geology, pedology, hydrology, and climate on slope form at both the meso and micro scales. A promising model using decision tree analysis has recently confirmed the value of rule based methods for predicting vegetation classes in eastern Australia (Moore et al., 1991). Modelling ecological units using topographically derived variables, combined with geological data and vegetation samples is now clearly established and may be extended to susceptibility analysis.

#### LANDSCAPE ANALYSIS OF REGIONAL SUSCEPTIBILITY

The IDRISI software (Eastman, 1987, 1989) was employed to assemble, collate, and analyze gypsy moth defoliation data at the regional scale. IDRISI is a raster-based (grid cell) GIS for capturing, storing, analyzing and displaying geographical data, designed for research applications. A base map of Pennsylvania county boundary coordinates was used to define the study area. A 2 x 2 km grid cell size was selected as standard for all map layers in the GIS. The grid size selected represented the minimum dependable spatial resolution of the defoliation data available from the Pennsylvania Department of Forest Resources.

Spatial error is unavoidably generated in the process of recording defoliation on sketch maps from aircraft (Talerico 1981). Error occurs with respect to the exact location, degree, and areal extent of defoliation, but this locational error is generally less than 1 km in magnitude. The choice of such a coarse scale of resolution raises serious issues concerning data accuracy and the cascading effect of errors as data layers are manipulated. Without corroborating evidence at a fine scale of resolution it is not possible to provide accurate estimates of the errors.

The Pennsylvania Department of Forest Resources monitors gypsy moth defoliation annually in all parts of the state using aerial sketch maps in late July when defoliation is at its peak. Thirty percent (30%) defoliation is considered the lower threshold for detection from the air. In situations where there is doubt as to the cause of the defoliation, ground checks for the presence of gypsy moth life stages are made. Initially the aerial sketch maps are overlaid on standard U.S. Geological Survey (1:24,000) topographical maps. Subsequently a composite mosaic is generated for the entire state at 1:1,000,000 scale. Mapping processes vary from region to region and year to year within Pennsylvania, resulting in a strong likelihood of significant data errors from systematic and non-systematic sources. The likely presence of these errors dictated the coarse spatial resolution of this study (2 x 2 km grid cells).

To create a uniform set of geographically referenced defoliation data, the composite maps for the period 1969 to 1989 were first transferred to mylar stable-base sheets and scanned. Data were transformed to a common base map resolution and projection by "rubber-sheeting". In transforming maps of various scales and projections, IDRISI resamples each scanned defoliation image to match the location of the four geo-reference points on the base map (Eastman 1987).

Elevation data for Pennsylvania were obtained from U.S. Geological Survey 1:250,000 Digital Elevation Models (DEM) (Elassal and Caruso, 1983). The sampling interval was 270 meters providing at least fifty (50) sampling points within each 2 km grid cell. Rubber-sheeting procedures were again used to resample these data into the same scale of resolution and projection as the base map.

Forest cover type information was extracted from a 1:7,500,000 scale map published by the Society of American Foresters (SAF) (Eyre 1980). This map delineates the distribution of the major forest types of the United States. Data collected by the U.S. Forest Service Forest Inventory and Analysis (FIA) project in 1967 were used to generate this map (Kingsley, 1985). FIA recognized six forest types in Pennsylvania: 1) Pine, 2) Oak-pine, 3) Oak - hickory, 4) Maple - beech -birch, 5) Aspen -birch and 6) non-forest ("land that has never supported forests and land formerly forested which is now developed for other uses" [Eyre 1980]). Any designation of an area as a specific forest type from these data is subject to uncertainty because the FIA map is highly generalized both in its spatial resolution and in its designation of forest types in broad categories. For example, the oak hickory type used in the FIA map within Pennsylvania encompasses at least 12 more specific forest types in the SAF system (Eyre 1980). Nevertheless, this forest type map does represent a valuable classification system of forests for a large area, such as used in this analysis. The forest type map was digitized as a vector map and converted to a raster image in the IDRISI system (Figure 1).

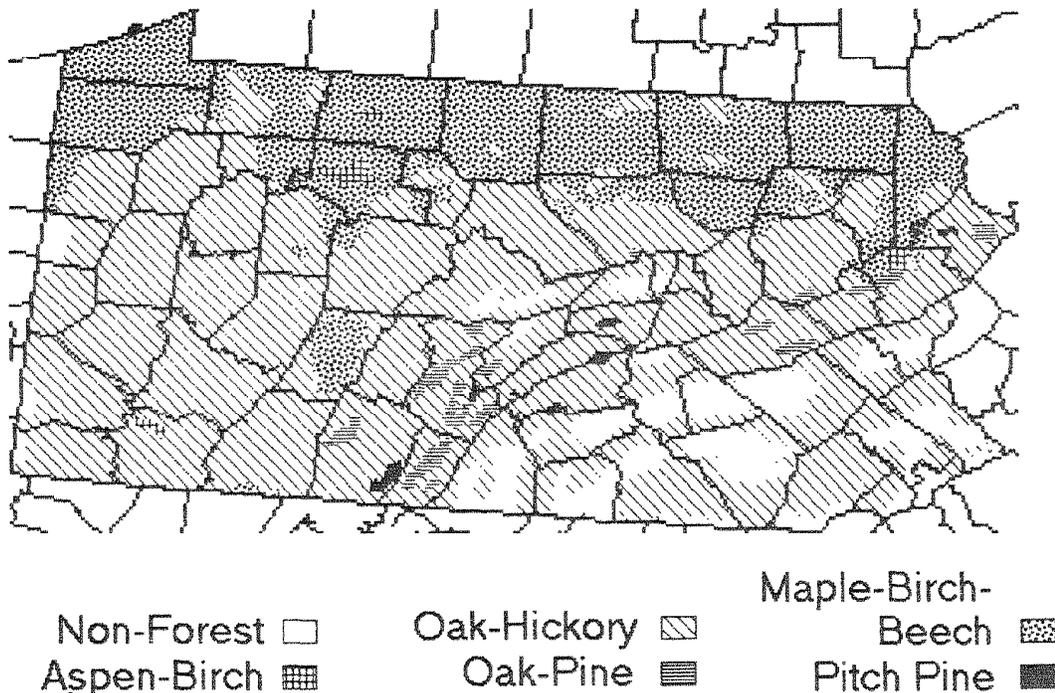


FIG. 1. Forest types of Pennsylvania (data prepared by U.S.D.A. Forest Service, Northeastern Forest Experiment Station; digitized from Eyre (1980)).

#### MAPPING SUSCEPTIBILITY TO GYPSY MOTH

Because consistent interpretation of the intensity of defoliation was unavailable, defoliation was assigned a simple binary classification (0 = no defoliation, 1 = defoliation). The modified defoliation maps from 1969 - 1989 were overlaid and coincident grid cells summed to obtain the total number of years of defoliation for each grid cell (Figure 2). Maps of cumulative defoliation derived from a relatively long time-series, such as is used here, describe the regional distribution of susceptibility to

gypsy moth. Areas having a high total number of years of defoliation are relatively susceptible to gypsy moth (Liebhold and Elkinton 1989). An unavoidable assumption of this technique is that pest management and suppression activities have not introduced any systematic bias at the chosen scale of analysis.

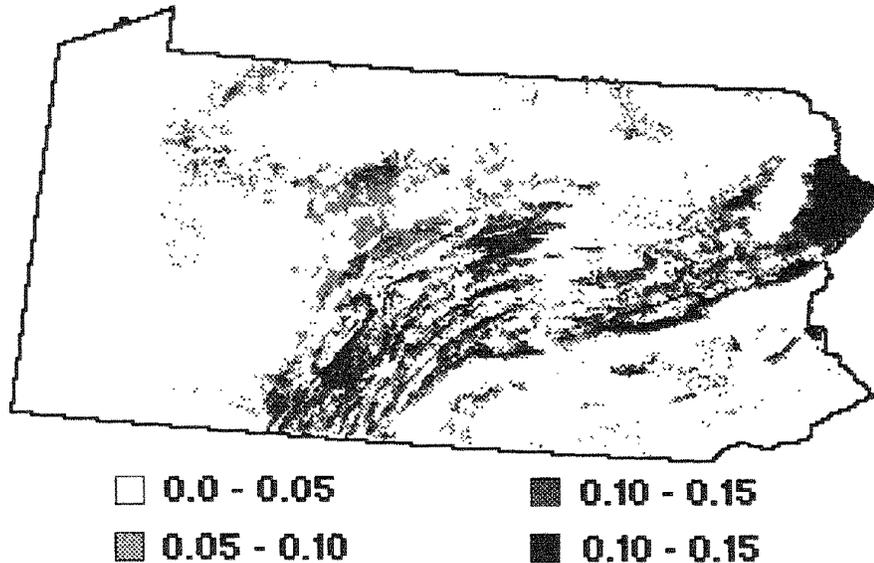


FIG. 2. Total years of defoliation in Pennsylvania (1969-89).

An identifiable potential source of bias in using the accumulated defoliation map as representing susceptibility is that gypsy moth populations have not been present in all parts of Pennsylvania over the study period. The range of gypsy moth has slowly expanded southwestward across the state during this interval. On an annual basis, the U.S. Department of Agriculture designates portions of the country that are part of the "generally infested area" for purposes of enforcement of quarantine regulations in this area. A detailed description and analysis of these data are described elsewhere (Liebhold et al. 1992). Since an area is designated as quarantined when relatively low densities of gypsy moth life stages are detected, there is arguably a lag period between the time of quarantine and the time of first defoliation in an area. We estimated this lag as the intercept,  $b_0$ , of the linear model,

$$D_i = b_0 + Q_i$$

where  $D_i$  is the year of first defoliation in county  $i$  and  $Q_i$  is the year of first quarantine in county  $i$ . By forcing a slope of 1,  $b_0$  was estimated as  $5.04 \pm 0.24$  using a linear regression procedure on the 45 counties in Pennsylvania. To maintain consistent levels of precision, we rounded this value to 5 for all further analyses.

Results from the linear model were incorporated to calculate an enhanced index of susceptibility for each grid cell (Figure 3). The value was calculated as the sum of the years defoliated divided by the number of years at risk to defoliation. Here we defined the number of years at risk to defoliation as the number of years during the sampling interval (1969-1989) during which the county in which the grid cell was located was quarantined, minus 5, the estimated value of the defoliation lag in years. Extrapolating gypsy moth susceptibility from an interval of less than 10 years leads to spurious results because of the sporadic spatial and temporal distributions of defoliation. Comparison with the simple accumulated defoliation frequencies shows that adjusting for years at risk caused many areas in the south-central portion of the state to increase susceptibility to levels similar to the northeast, as would be anticipated on the basis of forest distribution.

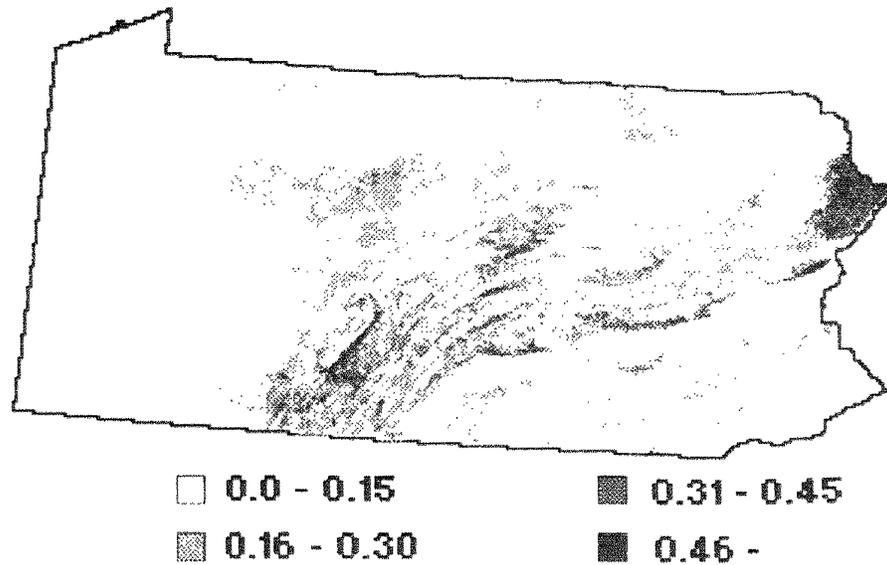


FIG. 3. Adjusted defoliation frequency (total years defoliated divided by years at risk to defoliation).

#### *Association of Susceptibility with other Landscape Features*

The relationship between forest type and gypsy moth susceptibility was determined by overlaying the susceptibility map layer (Figure 3) with the forest type layer. The relative levels of regional susceptibility reported in Table 4 agreed with previous empirical studies of susceptibility at the stand level (Bess et al. 1947, Valentine and Houston 1979, Herrick and Gansner 1986). Defoliation frequency was greatest in the pine, oak-pine, and oak-hickory types, and was least in the maple-birch-beech, aspen-birch, and non-forest types. The finding that the non-forest areas were defoliated at all reflects the coarse spatial scale of the forest type map. There are undoubtedly host trees within areas classified as "not forested".

TABLE 4. Area and gypsy moth defoliation statistics for the six major forest types in Pennsylvania. All data extracted only from portions of Pennsylvania which were quarantined by 1975 (see text for explanation).

Forest Type	No. of km <sup>2</sup>	Mean Defoliation Frequency	Adjusted Defoliation Frequency <sup>1</sup>
aspen-birch	664	0.19 ± 0.44	0.036 ± 0.084
non-forest	10,884	0.31 ± 0.76	0.044 ± 0.105
maple-birch-beech	25,750	0.33 ± 0.67	0.056 ± 0.114
oak-hickory	62,812	1.35 ± 1.52	0.200 ± 0.220
oak-pine	2,200	1.98 ± 1.74	0.286 ± 0.225
pine	380	2.64 ± 1.93	0.415 ± 0.226

<sup>1</sup> Adjusted frequency = Defoliation frequency divided by years at risk. Years at risk is defined as years quarantined - 5.

Because the forest type categories used in Figure 1 are so broad, we attempted to extend our landscape characterization of defoliation susceptibility by including elevation information. The resultant map was then combined with gypsy moth susceptibility and the average susceptibility was calculated for each forest type - elevation combination (Figure 4). Averages calculated from less than 15 raster cells (2 x 2 km) per forest type - elevation combination were not included.

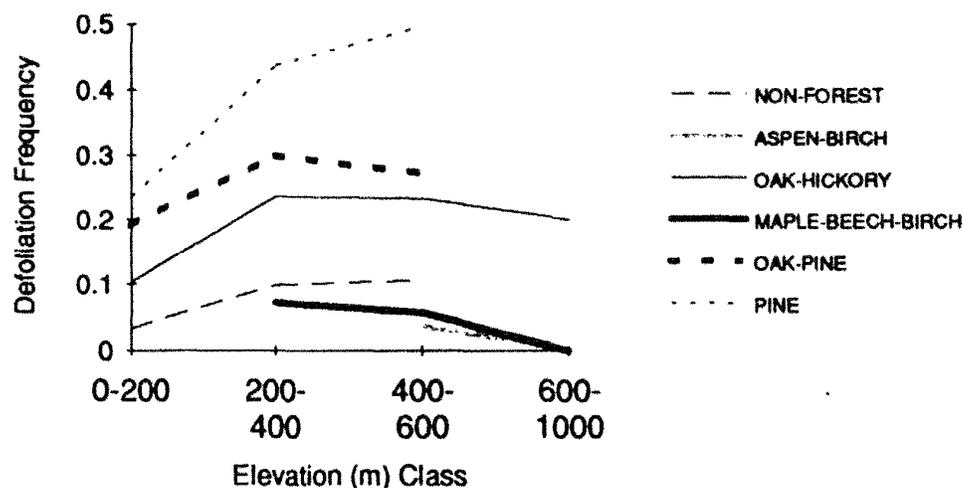


FIG. 4. Defoliation frequency of each forest type - elevation combination in Pennsylvania. OLD 9

The pine type consistently had the highest susceptibility at all elevations though this type covered a very small total area. The oak-pine and oak-hickory types both had high susceptibilities at all elevations, peaking in the 201-400 m. elevation class. The non-forest, oak-hickory, oak-pine, and pine types all exhibited reduced susceptibility at the lowest elevation class. The aspen-birch and the maple-beech-birch defoliation frequencies both declined at the highest elevation class. These patterns reflect the broad nature of the 6 forest types represented in Figure 1. Areas covered by each of these types are actually composed of many other, more detailed types, (Eyre 1980); the prevalence of these sub-types is likely different at various elevations. Furthermore, these sub-types undoubtedly vary in their susceptibility. For example, the black locust, chestnut oak, and yellow-poplar types recognized by SAF (Eyre 1980) are represented by the same oak-hickory type described by FIA. The black locust and yellow-poplar types are more common at low elevations and both are considered types resistant to gypsy moth defoliation. In contrast, the chestnut oak type is less common at low elevations and is highly susceptible to defoliation (Houston and Valentine 1977). This type of difference would thus explain the decreased defoliation frequency lower elevations within the oak-hickory type. In addition, what is recorded as a pine type in Pennsylvania is actually a mixture of chestnut oak and pitch pine, usually found on ridge tops. Although the pine itself is rarely defoliated, there is ample chestnut oak to support outbreaks of gypsy moth.

#### CONCLUSIONS

There was a high similarity between the landscape-level characterization of forest susceptibility and previous characterizations performed on a stand level (Bess et al. 1947, Valentine and Houston 1979, Houston and Valentine 1977, Herrick and Gansner 1986). At the landscape level oak-pine forests are generally the most susceptible to defoliation and, as expected on the basis of food preference, forests with a low component of oak are the least susceptible. As demonstrated by the first study, these forest types are strongly influenced by slope position and aspect. Lower susceptibility at elevations less than 200 m indicates the relationship between forest type and elevation and demonstrates how a GIS can be used to refine the representation of forest susceptibility by incorporating additional landscape characteristics. In the future, stand type characterizations derived from remotely sensed data may provide more detailed predictions of susceptibility on the landscape level. The integration of multiple types and sources of information now feasible through GIS should be useful for predicting with greater accuracy what portions of the currently uninfested portions of North America will ultimately be at higher risk to

defoliation by gypsy moth. This information, along with predictions of the future expansion of the gypsy moth-infested region, will be useful in long-range planning in currently uninfested areas and in multiple agency, regional control efforts. While these studies illustrate promising directions for research in landscape methods for susceptibility assessment, the quality of spatial data of forest type has been a limiting factor for verification and validation. Improved forest type information at a regional scale is an essential component for future developments of these approaches and for their integration into management methods.

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## SUMMARY OF WORKSHOP DISCUSSIONS ON THE FUTURE OF SPATIAL ANALYSIS AND FOREST PEST MANAGEMENT

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On the final day of the "Spatial Analysis and Forest Pest Management" workshop, discussions were held to synthesize material from the paper presentations and identify needs for future research and development in spatial analysis applications to forest pest management. These discussions were held in three groups that were assigned one of three topics: 1. use of landscape data in hazard-rating, 2. spatial structure of monitoring and decision-making systems, and 3. spatial statistics and models. The following represents a summary of discussions by workshop participants. This material documents the work and ideas of all participants. The organizers of the workshop commend the participants for their insight and dedication to this topic.

### EVALUATING HAZARD TO FOREST PESTS

Characterization of landscape susceptibility and or hazard to forest pest outbreaks is an area where spatial analysis will become increasingly useful. Several examples can be found in these proceedings where groups have used landscape-level data assembled as map layers in a geographical information system (GIS) to map pest hazard.

Spatial scale is an important consideration when studying landscape susceptibility. Susceptibility can be viewed from the individual tree level, the stand level, the district level, or even larger regional levels. Most of the examples to date have focused on the examination of susceptibility / hazard at the stand level because this is the resolution of most available data (e.g. National Forests collect compartment data). Other spatial scales may also be important, depending upon the nature of forest management. More research is needed on how pest impacts (such as water-quality, wildlife, regional socio-economic impacts) measured at the stand level manifest themselves at larger spatial scales (i.e. regional scales). There is a need to study how pest susceptibility / hazard is affected by processes operating on a variety of spatial scales. Various of multi-scale models could be developed to answer these questions. Another important area for future research is development of an understanding of how landscape heterogeneity and connectivity affect susceptibility to forest pests.

While the advent of GIS and other tools have greatly facilitated a landscape perspective of susceptibility / hazard, more landscape-level data is needed to solve these problems effectively. A major data gap exists in areas outside of National Forests. Typically, National Forest lands have available compartment data that describe each stand, but outside of National Forests the forest data is much more sparse. Forest Inventory and Analysis (FIA) plot data are designed to measure forest composition on a scale slightly larger than the typical county. Remotely sensed data are the most likely source for characterizing forests across large landscapes. While there have been isolated attempts (usually with considerable success) at characterizing forest vegetation using remotely sensed data, there are no uniformly developed maps for the entire nation. Extraction of forest composition and structure from remotely sensed data over all of the U.S. is therefore a high priority for future development.

The Forest Service National GIS Plan ("Project 615") will greatly expedite our ability to characterize hazard across complex landscapes. The availability of GIS hardware and software to forest managers should be useful tools. However, as stated above, serious data gaps still exist in many areas. Furthermore, data standards should be established so that data is collected using the same standards in different areas.

#### MONITORING AND DECISION MAKING

Spatial analysis can play a major role in forest pest monitoring and decision making processes. Increasingly, pest managers are recognizing the utility of monitoring pest populations across a network of permanent plots, spatially stratified across the management area. The actual census method (e.g. pheromone traps, visual counts, etc.) varies depending upon the pest biology and management considerations. By using these monitoring networks, managers are able to pin-point "hot spots" that merit consideration for action. The ultimate result is a pest management program that is more effective and more environmentally benign because outbreaks are halted before damage occurs and treatments can be restricted to specific areas. Without such a system, pest management has been traditionally reactive; management action typically has been initiated after the damage has occurred.

When establishing monitoring networks, there are several factors to consider. There is obviously a trade-off between sampling intensity and cost. One must consider how to stratify placement of census points relative to variation in the ecological and physiographic landscapes. Ecologists are just now beginning to explore various methods for interpolation of census data. Some of these methods allow incorporation of secondary landscape data (i.e. vegetation, elevation) when forming estimates. All of these problems provide valuable subjects for future research.

Landscape level damage assessment is also an important component of a region-wide approach to forest pest management. Examples of damage data are defoliation maps for defoliators or spot maps for bark beetles. Very often, these damage maps may be one of the best sources of information for predicting where future damage will occur. For this purpose and for purposes of large-scale regional planning, these mapping exercises are important. There is a need to develop data standards both for monitoring networks and for damage maps. The Forest Service should take an active role in defining and coordinating the collection and assembly of these data across the nation.

Pest monitoring and damage assessment should be integrated more closely with the Environmental Protection Agency Environmental Monitoring and Assessment Program (EMAP) and the Forest Service Forest Health Monitoring (FHM) program. The consensus of the workshop was that permanent monitoring of selected forest pests would be logically done at the FHM monitoring plots located throughout the country. This network of plots should provide an adequate network of plots for region-wide pest management as discussed above. If this activity is beyond the purposes of FHM then it would be logical that the Forest Pest Management field offices oversee collection of these spatially referenced data.

There are several decision support systems currently under development for use in management of selected forest pests. Each of these projects include procedures that use spatially referenced census, damage, and habitat data to guide the decision-making process. Most of these systems are intimately connected to GISs and are designed to access landscape-level data that are available in GIS format. It may be logical to ultimately combine decision support systems for different pests when they co-occur in the same area (example: southern pine beetle and gypsy moth). These decision support systems will probably evolve to a form in which they are not stand-alone systems but they will instead be integrated into general forest management procedures.

## SPATIAL STATISTICS AND MODELS

Several of the papers in these proceedings focus on how spatial data can be used in models that are useful to forest managers. There is also considerable interest in more theoretical approaches that are designed to elucidate ecological interactions through the use of spatially explicit models. Thus, there are two major approaches where incorporation of spatial relationships will be important: 1) simple analytical / theoretical models (process) and 2) Predictive models (empirical, statistical). In the past, few groups have explicitly included space in these modeling approaches.

There are two apparent approaches to modeling spatial processes: Under the first approach, the model records cells that are fixed in space. These cells might be land grid cells or trees or other fixed objects. The book-keeping in these models are such that pest numbers are added and subtracted from the summary statistics kept for each cell. Generally, there is no "memory" of pest movement.

Under the second approach, the movement of individuals is modeled more explicitly. The book-keeping records the position of each individual (or population) in space. This approach maintains a "memory" of past movement. This approach is well suited to object-oriented programming languages and is obviously computer-intensive. This approach is characterized by "emergent properties" that are evident after numerous simulation iterations.

In any spatially explicit process-oriented model movement is a very important component. Many researchers have adopted diffusion models which assume random dispersal but directed movement and advection can be incorporated. An interesting area of future development would be modeling movement which is affected by land cover and determining how landscape connectivity / heterogeneity affects redistribution.

Spatially explicit process models may also trace effects of habitat spatial heterogeneity on reproduction and survival. Predator and pathogen numbers can also be modeled as could reactions to conspecifics, such as aggregation and repulsion due to competition. An area that is largely unexplored but could be very informative is how the spatial structure of genotypic variation in host vegetation and pest populations affects changes in pest numbers over time.

Of course, spatial scale is an important consideration in spatially explicit process models. Trophic interactions change drastically among different spatial scales. Movement changes with spatial scale. More research is needed on developing our understanding of scale relationships to dynamical patterns. Certain types of nested models might be useful in this regard.

Models that are useful for actual pest management decision making are badly needed. These models should be simple, they should use empirical data, and that they should incorporate spatial statistics principles. One of the main impediments to the development and implementation of these types of models will continue to be a lack of data: insect census data, damage assessment data and habitat data.