



Simulation Modeling as a Tool for Understanding the Landscape Ecology of Southern Pine Beetle Infestations in Southern Appalachian Forests

David Martin Cairns^{*1}, Charles W. Lafon¹, Andrew G. Birt², John D. Waldron³, Maria Tchakerian², Robert N. Coulson², Weimin Xi² and Kier Klepzig⁴

¹Department of Geography, Texas A&M University

²Department of Entomology, Texas A&M University

³Department of Environmental Studies, University of West Florida

⁴US Department of Agriculture, Forest Service Southern Research Station

Abstract

The forests of southeastern North America are influenced by a variety of disturbances including fire and insect outbreaks. In this paper, we discuss the role of disturbances in structuring forest landscapes with particular emphasis placed on the reciprocal interaction between forest structure and outbreaks of the southern pine beetle (*Dendroctonus frontalis* Zimmermann). We highlight work in which we are currently involved to illustrate the importance and utility of using spatially explicit forest modeling as a tool for understanding forest–insect interactions and its potential role in determining management strategies.

Introduction

Forest landscapes are structured by the interaction of topography, climate and multiple disturbances. In a landscape ecology context, structure refers to the arrangement and number of discrete patches of distinctive ecosystems that exist within some surrounding matrix (Forman and Godron 1986). Disturbances typically generate spatially heterogeneous patterns of vegetation damage, rather than homogeneously damaged swaths (Turner 2005; Turner and Dale 1998). This patchiness in forest damage imparts structure that can persist for decades or centuries over the course of vegetation succession (the replacement of one community by another over time). The vegetation structure itself can, in turn, influence the spatial pattern and severity of subsequent disturbances (e.g. via influences on the spread of contagious disturbances among forest patches). In this paper, we explore influences of insect outbreaks on forest landscape structure, and of landscape structure

on the extent and severity of insect outbreaks. We focus specifically on the case of the southern pine beetle ('SPB', *Dendroctonus frontalis* Zimmermann) in yellow pine (*Pinus* L.) stands of the southern Appalachian Mountains, where we are conducting a simulation modeling study on the reciprocal interactions of SPB outbreaks, fire, and landscape structure.

The role of disturbances in structuring landscapes has been investigated for most of the major biomes and for a range of disturbances. For example, Parker and Bendix (1996) reviewed the effects of geomorphic disturbances in structuring vegetation communities in four different environments, and Malanson (1993) discussed their importance in riparian systems. The importance of fire on forested ecosystems around the world has been investigated extensively (Foster et al. 1998; Gromtsev 2002). Climatic disturbances such as hurricanes (Foster et al. 1998) and ice storms are known to have significant impacts on landscape pattern (Millward and Kraft 2004; Stueve et al. 2007). Similarly, the impacts of human activity such as logging have received considerable attention in a variety of forest systems (Gautestad et al. 2005; McGarigal et al. 2001; Staus et al. 2002).

The role of insects as the 'engineers' of landscapes, however, has not been investigated thoroughly. Some studies have taken a landscape ecological approach to insect disturbances (e.g. Howe and Baker 2003). However, by and large, the research into insect–forest interactions are relatively simple. Entomologists tend to view the forest as only a resource for the insects that are their primary concern and conversely, vegetation ecologists and biogeographers tend only to investigate the effects of an insect outbreak on the landscape without considering the complexity of the insect's life cycle and resource needs. In this paper, we discuss how insects have the potential to impact landscape structure, and we present one approach to studying forest–insect interactions based on our own work with the SPB. The approach that we discuss here relies heavily on simulation modeling and serves as a way to attempt a holistic investigation of the role of the SPB in structuring the forest landscape of the southeastern USA.

Background

DISTURBANCE INFLUENCES LANDSCAPE HETEROGENEITY

In most cases disturbances increase the heterogeneity of a landscape (e.g. Mladenoff et al. 1993). However, in some instances, a disturbance is so large that it can create a homogenous landscape. Although fires are the most obvious example of disturbances that can grow so large as to homogenize a landscape, floods, severe droughts, and extreme snowfall events can have the same homogenizing effect (Forman 1995). In contrast to homogenizing disturbances, most disturbances tend to be smaller and more disjunct thereby increasing the landscape heterogeneity (Forman 1995).

In general, disturbed landscapes exhibit heterogeneity through the presence of significantly more small forest patches and fewer large matrix patches than a comparable intact forested landscape (Mladenoff et al. 1993). Furthermore, in the disturbed landscape, patches tend to have simpler shapes represented as a lower fractal dimension (Mladenoff et al. 1993).

Landscape structure is influenced by both patterns of ownership and varying management regimes as well as the interaction of multiple disturbances. Nonaka and Spies (2005) used a simulation modeling approach to study the landscape structure of the Oregon Coast Range. They found that contrasting patterns of ownership and management within the forests they simulated perpetuated a landscape structure outside the historical range of variability when subjected to wildfire. Furthermore, even if management of this region ceased and wildfires were to occur, the past management of the region has left a legacy on the landscape that would take centuries to erase.

The interaction of multiple disturbances can have significant effects on landscape structure. For example, the subalpine forests of Colorado are subject to insect outbreaks, blowdowns and fires. Each of these disturbances has potentially different signatures on the landscape with regard to pattern and extent of the disturbance, and each type of disturbance can be influenced by the existing heterogeneity of patch age within the forest (Howe and Baker 2003). For example, in the Rocky Mountains, fire and blowdown disturbances interact because each disturbance is dependent upon the structure of the forest. If there has been a recent fire, that part of the forest is relatively young, which means that the amount of fuel at the site is also relatively low so fire is not as likely as at other locations where the stand is older and more fuel is present. Also, if there are only young trees at a site, the risk of blowdown is significantly lower (Howe and Baker 2003). Similar disturbance interactions between fire and insect outbreaks have been demonstrated for Douglas-fir-dominated forests in Rocky Mountain National Park, Colorado (Hadley and Veblen 1993) and in Switzerland (Bouget and Duelli 2004).

HETEROGENEITY (LANDSCAPE STRUCTURE) INFLUENCES INSECT OUTBREAKS

The importance of the structure of the landscape in affecting insect populations has been addressed using both theoretical and empirical approaches. Gripenberg and Roslin (2007) make a theoretical case for the importance of landscape structure influencing insect populations. Their work relies heavily on results from studies of metapopulations (series of interacting local populations) and the roles of immigration and emigration, and how these processes vary spatially across a landscape. They also relate the spatial variability in insect populations to the variability across a landscape in predators of those insects.

Empirical treatments of the importance of landscape structure on insect outbreaks have been undertaken for a variety of insects and landscapes. For example, Perkins and Matlack (2002) reconstructed the pre-settlement structure of the southeastern forest landscape and found that the present day landscape structure is considerably different from pre-settlement conditions. Current loblolly and slash pine clusters are smaller and more circular than in pre-settlement times, but they are more extensive and separated by shorter distances. Perkins and Matlack (2002) infer that this change in landscape structure facilitates the spread of insect pests and pathogens such as SPB and fusiform rust due to an increase in landscape connectivity.

In Rocky Mountain forests, Hadley and Veblen (1993) illustrated that variability in age structure expressed as a patchwork of stand characteristics of Douglas-fir forests in Rocky Mountain National Park, Colorado, had a significant effect on the severity of outbreaks of western spruce budworm (*Choristoneura occidentalis* Free.) and Douglas-fir bark beetle (*Dendroctonus pseudotsugae* Hopk.) in the late 20th century. The net effect of these simultaneous outbreaks was to slow the successional trend toward a steady-state Douglas-fir forest (Hadley and Veblen 1993).

Weslowski and Rowinski (2006) found that more fragmented stands suffered less defoliation due to winter moth (*Operophtera brumata* L.) outbreaks in Poland than did more contiguous forest stands. They hypothesized that this was the result of greater dispersal mortality of early stage larvae in the fragmented stands. Similarly, Ryall and Fahrig (2005) illustrated that a bark beetle (*Ips pini*) in red pine (*Pinus resinosa*) was more abundant in isolated stands of a more fragmented landscape. The reasons for this were that there were higher numbers of predators in the surrounding contiguous forest than in the isolated stands thereby increasing the number of the *Ips* beetles. They postulate that outbreaks will become more severe as habitat becomes increasingly isolated. In contrast, stand size and mortality due to the hemlock woolly adelgid (*Adelges tsugae*) are positively correlated in New England forests and indicate that either populations of the insects reach large stands more quickly or that they increase and spread more rapidly in large stands relative to smaller ones (Orwig et al. 2002). These contrasts in findings about the responses of different insects to landscape structure underscore the difficulty in making generalizations about the way that insect outbreaks interact with spatial structure of their environment. Therefore, each insect must be analyzed independently.

At course spatial scales, encompassing regions, heterogeneity in outbreak activity occurs due to environmental controls. For example, forest insect outbreaks are often linked to drought conditions (Carter et al. 1998; Mattson and Haack 1987; Smith et al. 2002). Drought conditions stress trees thereby reducing vigor and their ability to withstand insect attack and consequently increasing tree mortality (Mattson and Haack 1987; Smith et al. 2002).

Other aspects of forest structure, including roads, trails and riparian areas, can increase connectivity of forests thereby facilitating the spread of insects across the landscape (Koch et al. 2006). Gypsy moths are one example of how anthropogenic structures (roads) can influence the direction, distance and mode of dispersal across a landscape.

LANDSCAPE STRUCTURE AND THE SOUTHERN PINE BEETLE

The range of the SPB is extensive, encompassing most of the southeastern USA as well as parts of Central America and the southwestern USA (Lafon and Kutac 2003). The insect attacks a number of economically and ecologically important pine species in the southeastern USA. Southeastern US landscapes vary from the Atlantic and Gulf Coastal Plains, where large areas are covered with virtually monospecific pine plantations, to the more heterogeneous southern Appalachian Mountains, where pine populations are fragmented by topography into smaller patches within a hardwood forest matrix. Most of the Appalachian forests are the result of natural regeneration. Throughout the Southeast, the SPB is a component of complex disturbance regimes that involve storms, anthropogenic activities (e.g. logging), and fire. Fire played an important role historically, and is thought to have interacted with SPB infestations to maintain open, pine-dominated woodlands on dry upland sites (Schowalter et al. 1981a).

At a regional (county) scale SPB outbreaks occur periodically through time. Outbreaks typically persist for between 1 and 3 years (Payne 1980) and are characterized by heterogeneous patterns of tree mortality and locally abundant populations (Coulson 1979). However, between outbreaks, SPB populations decline to densities that cause minimal tree mortality and in some cases make them practically undetectable in the forest environment. Populations may persist at these low, 'non-outbreak' densities for extended periods (5–15 years) that vary considerably across the range of the insect (Mawby and Gold 1984; Pye 1993). In a quest to characterize, predict and understand SPB damage, many researches have reported this pattern of pestilence as cyclical – suggesting that the temporal pattern (timing) of outbreaks is to some extent regular (Turchin et al. 1991, 1999). However, an alternative viewpoint is that outbreaks occur unpredictably through time (Kroll and Reeves 1978; Price et al. 1998).

Disturbances, including SPB outbreaks, contribute to the structure of southeastern US landscapes. Timber harvest and the associated stand regeneration exert a strong control on forest patterns across much of the region, particularly the Coastal Plain. SPB outbreaks impose additional heterogeneity onto this human-generated template. At the regional scale, large outbreaks lead to an excess of salvaged timber and deflated timber prices, which may in turn influence management decisions that precipitate changes in land use (Prestemon and Holmes 2004; Redmond and Nettleton 1990). At smaller spatial scales, large patches of tree mortality

may stimulate foresters to regenerate damaged stands and to redefine stand boundaries. In less intensively managed forests (e.g. National Forest Wilderness Areas), SPB outbreaks can fragment and restructure formerly homogeneous patches of pine (Coulson and Stephen 2006). SPB outbreaks in the southern Appalachian Mountains may augment the fragmentation associated with the physical structure of the landscape.

Landscape structure, in turn, may influence the dynamics of SPB populations and consequently the extent and severity of pine mortality. At the most basic level, the aggregate composition of the forest across a landscape is important for determining the potential number of hosts available to SPB. However, the ability of SPB to find potential hosts is also a function of the interaction between forest configuration – especially the location of suitable habitat – and SPB life history (e.g. dispersal). SPB population biology is driven by the obligate mortality of its natal host, such that successive generations (between four and eight throughout most of its range (Ungerer et al. 1999)) must locate, attack, and overcome the defenses of fresh trees. One conceptual model of SPB population dynamics is that during non-outbreak years, beetles exist at low population densities and are regulated by their ability to find a limited supply of susceptible hosts, e.g. trees weakened by lightning (Coulson et al. 1983), overcrowding (Brown et al. 1987; Lorio 1980), wind or mechanical damage (Fredericksen et al. 1995), or biotic damage such as disease (Conner et al. 2001). According to this hypothesis, low level, ambient populations exist for extended periods until population densities reach levels capable of overcoming the defenses of more numerous, healthy trees. Once this occurs, a rapid population growth rate is possible and may lead to large multi-tree infestations (Figures 1, 2), elevated regional population densities, and ultimately the



Fig. 1. A large multi-tree infestation of southern pine beetle. Orange trees in the photograph have been killed by the southern pine beetle.



Fig. 2. A southern pine beetle outbreak in a Table Mountain pine stand. Orange trees have been killed by the southern pine beetle.

pattern of infective, multi-spot infestations that are characteristic of SPB outbreaks. Once a multi-tree infestation occurs, its growth may depend on aspects of landscape structure such as stand size; the age, size and juxtaposition of trees in the stand; and canopy structure, which influences pheromone movement (Schowalter et al. 1981b).

Alternative models for SPB outbreak dynamics also require a consideration of spatial heterogeneity. For example, Turchin et al. (1991) proposed that delayed density-dependant regulation by insect predators is responsible for the cyclical outbreak dynamics of SPB. Central to this hypothesis is that the predators of SPB can regularly and efficiently locate SPB populations for prolonged periods, thus suppressing high growth rates and damage during non-outbreak years. They demonstrated these concepts using non-spatial models. However, there is reason to believe that these processes may be affected by landscape pattern. For example, Ryall and Fahrig (2005) found that increased fragmentation led to reductions in the predator–prey ratios in another bark beetle–predator system, as described above, implying that the predator and prey show differential responses to landscape pattern. Changes in the abundance of predators and prey, or the efficiency of prey-finding by an insect predator, are clearly important in the context of explaining spatio-temporal patterns of SPB outbreaks.

Southern Pine Beetle Modeling Case Study

The SPB is an insect pest that attacks economically important pine species in the southeastern USA. Between 2000 and 2002 a devastating outbreak of SPB occurred and was most severe in North Carolina and Tennessee. The economic effects of this outbreak were disastrous and amounted to a

loss of \$1.1 billion across eight Southern states. This loss of forests due to a known hazard was the impetus for the development of a method of analyzing the reciprocal impacts of insect outbreaks and forest landscape structure. To accomplish this, a multidisciplinary team of scientists comprised of geographers and entomologists developed a simulation modeling approach to understanding the impacts of the SPB on southeastern US forest landscapes and plan for their restoration to pre-outbreak conditions.

Modeling the effects of SPB on southeastern forest landscapes has required that we proceed in a stepwise fashion. To accomplish our goals, we have performed the following steps: (i) parameterize an existing model (LANDIS) to simulate forest behavior in the southern Appalachian Mountains in the absence of the southern pine beetle; (ii) investigate the combined roles of fire and SPB outbreaks; and (iii) investigate the reciprocal effects of landscape structure and insect outbreaks using landscapes with controlled structural characteristics.

THE MODELING ENVIRONMENT

To understand the interaction of the SPB and the southern Appalachian landscape, we have used a widely used forest simulation model, LANDIS (LANdscape DIsturbance and Succession). LANDIS is a stochastic, spatially explicit, raster-based computer model that simulates forest succession and disturbance across large areas and over long time periods (He and Mladenoff 1999a, b; He et al. 1996; Mladenoff and He 1999; Mladenoff et al. 1996). The model was originally developed to simulate succession as well as a variety of disturbances, but was not initially capable of simulating the effects of insects (Mladenoff 2004). LANDIS has recently been extended to include disturbances that are biological in nature (such as insect outbreaks) through the use of the Biological Disturbance Agent (BDA) module (Sturtevant et al. 2004). LANDIS has been used to simulate landscapes worldwide (Franklin et al. 2001; He et al. 2002; Pennanen et al. 2004; Pennanen and Kuuluvainen 2002; Schumacher et al. 2004; Shifley et al. 1998, 2000; Syphard and Franklin 2004; Wimberly 2004; Xu et al. 2004).

In LANDIS, tree species are simulated as the presence or absence of 10-year age cohorts on each cell. At the site (cell) level, LANDIS manages user-defined species life history traits (e.g. longevity, minimum age at reproduction, shade tolerance, fire tolerance, minimum/maximum seed dispersal distances, and resprout probability) at 10-year time steps. Succession in LANDIS is competitive and based on species life history attributes (He et al. 2004). Dispersal, birth, growth, and senescence are all simulated. Details of LANDIS's treatment of these life history elements can be found elsewhere (Mladenoff and He 1999).

The BDA has been tested for its sensitivity to the pattern of land types simulated, the size of the neighborhood used in calculations of site vulnerability, and the influence of species richness (Sturtevant et al. 2004).

Table 1. Species included in LANDIS simulations of the southern Appalachians.

Species	Common name
<i>Acer rubrum</i>	Red maple
<i>Cary glabra</i>	Pignut hickory
<i>Nyssa sylvatica</i>	Blackgum
<i>Oxydendrum arboretum</i>	Sourwood
<i>Pinus pungens</i>	Table Mountain pine
<i>Pinus rigida</i>	Pitch pine
<i>Pinus strobus</i>	Eastern white pine
<i>Pinus virginiana</i>	Virginia pine
<i>Quercus alba</i>	White oak
<i>Quercus rubra</i>	Northern red oak
<i>Quercus coccinea</i>	Scarlet oak
<i>Quercus velutina</i>	Black oak
<i>Robinia pseudoacacia</i>	Black locust
<i>Tsuga canadensis</i>	Eastern hemlock

Sensitivity of the BDA was measured on the number of sites disturbed by an insect. The BDA is most sensitive to the tree species richness, followed by the neighborhood effect and land type arrangement (Sturtevant et al. 2004).

For our work in the southern Appalachian Mountains, we simulated forest dynamics over a 500-year period on low and mid elevation xeric landscapes using data from Great Smoky Mountains National Park. For consistency, each landscape is comprised of a single land type represented by a 100×100 cell grid with a cell size of $10 \text{ m} \times 10 \text{ m}$. To capture xerophytic landscapes, we used four land types that correspond to two elevation zones (low: 400–915 m; and middle: 916–1370 m) and two topographic moisture classes (SE-W Facing Slopes and Ridges & Peaks) in the Great Smoky Mountains (Whittaker 1956).

We included 15 tree species in our simulations that are the current dominants on xeric sites in Great Smoky Mountains National Park (Table 1). Life history parameters were based on Burns and Honkala (1990), which has served as the basis for a number of previous forest modeling studies (Lafon 2004; Sturtevant et al. 2004; Wimberly 2004). LANDIS uses an establishment coefficient to represent the habitat suitability of each land type for each species. We based the establishment coefficients on the patterns of species abundance along elevation and moisture gradients in the Great Smoky Mountains (Whittaker 1956). Each 100-m^2 cell was then populated randomly with a single species based on its relative abundance in each of the land types.

The BDA module was parameterized to be representative of SPB outbreaks in the southern Appalachians. Each of the pine species in the

model (*Pinus pungens*, *Pinus rigida*, *Pinus virginiana*, and *Pinus strobus*) was assessed for its vulnerability to SPB attack. Vulnerability of southern Appalachian yellow pine species to attack by SPB is correlated to tree diameter (Coulson et al. 1974). Growth rates were generalized for the southern Appalachians to arrive at vulnerability ages and then rounded to the appropriate 10-year age cohort class for LANDIS input. For example, Table Mountain pine (*P. pungens*) is considered to be a minor host at age 20, a secondary host at 40, and a primary host at age 50. Increases in vulnerability for *P. pungens* occur with changes in host classification so that the 50-year-old pines are the most vulnerable to SPB.

The timing of outbreaks was determined by a uniformly distributed random number with a minimum interval of 10 years (smallest possible in LANDIS) and a maximum interval of 30 years, which is consistent with historical SPB trends in the southern Appalachians. Outbreak severity was set to include the widest possible range of values allowed by the BDA because of chronic SPB activity at a decadal interval in these environments.

SIMULATING SUCCESSIONAL PATTERNS IN SOUTHERN APPALACHIAN FORESTS SUBJECT TO INTERACTING DISTURBANCES

Simulating stand dynamics on dry slopes and ridgetops in the southern Appalachian Mountains suggests that the interacting disturbances of fire and SPB outbreaks are important for maintaining open, pine-dominated stands similar to those thought to have existed prior to industrial logging and fire control (Harrod et al. 2000; Lafon et al. 2007; Waldron et al. 2007). Simulation modeling permitted us to explore multiple disturbance scenarios, including combinations of fire and SPB as well as each disturbance alone, or no disturbances at all. Modeling also afforded a long-term perspective not achieved readily with field data.

Modeling projections and field studies indicate that fire is critical for maintaining yellow pine dominance in the southern Appalachian Mountains. Without frequent burning, yellow pines and xerophytic (drought-tolerant) oaks would be replaced over time by various hardwood species and/or white pine (Figure 3). Indeed, field data match the modeling projections (Figure 3) and reveal that such changes already are occurring after several decades of reduced fire activity.

Despite the primary role of fire in maintaining pine and pine-oak stands, the interaction of SPB outbreaks with fire also appears to be important. First, SPB outbreaks can favor pine regeneration by opening the canopy and permitting light to reach pine seedlings on the forest floor (Brose and Waldrop 2006; Lafon and Kutac 2003). Pine regeneration in these gaps is not favored, however, unless they are burned periodically. Burning prevents encroachment of competing species that are less tolerant of fire than are the pines (Lafon et al. 2007; Waldron et al. 2007). Without

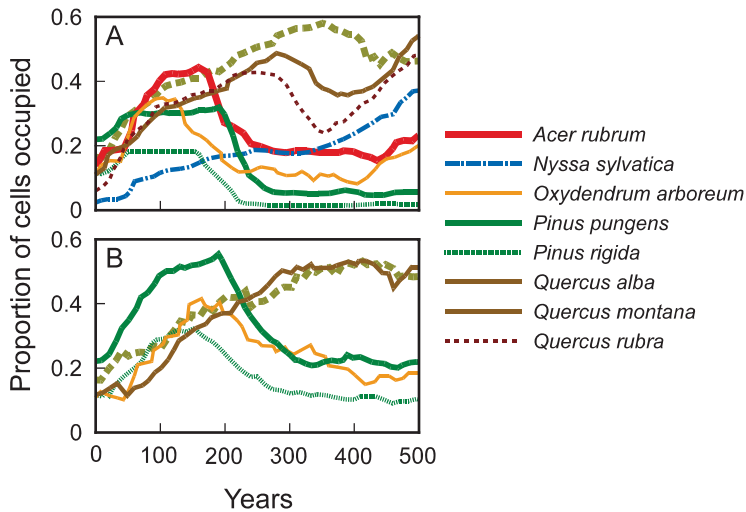


Fig. 3. Changes in tree species on south- and west-facing slopes at middle elevations in Great Smoky Mountains National Park. Results are derived from a LANDIS simulation in the absence of fire (A), and also with fire (B).

burning SPB outbreaks actually would accelerate the successional replacement of pines.

Second, when combined with fire, periodic SPB outbreaks may help maintain the mix of pine and oak that is typical on dry slopes and ridgetops in the southern Appalachian Mountains. Projections of the simulation study by Waldron et al. (2007) suggest that fire acting alone would result in a greater abundance of pines and fewer hardwoods than is typical for actual landscapes. Conversely, SPB acting alone would reduce the abundance of pines and favor hardwoods. The combination of both disturbances on the same landscape, however, results in a relatively stable coexistence of pines and hardwoods.

Third, the combined influence of fire and SPB outbreaks is projected to maintain open woodlands instead of continuous closed-canopy forests (Waldron et al. 2007). Such open woodland conditions are thought to have been typical on dry sites in the Appalachian Mountains in the past (Delcourt and Delcourt 1998; Harrod et al. 2000). Although burning alone may promote open conditions (Lafon et al. 2007), the combination of fire and SPB outbreaks appears to be particularly effective at maintaining such conditions (Waldron et al. 2007). The maintenance of open woodland conditions demonstrates how insect outbreaks may affect landscape structure at a fine spatial scale. In turn, the arrangement and spacing of trees and other vegetation within the stand likely influences the magnitude of insect outbreaks as well as the behavior of fires (Schowalter et al. 1981a).

RECIPROCAL INTERACTION OF LANDSCAPE STRUCTURE AND SOUTHERN PINE BEETLE OUTBREAKS

The modeling environment that we have developed is capable of simulating both the successional trajectories of the forests of the southern Appalachians and the response of these forests to disturbances acting singly and in concert. The next step in understanding the landscape ecology of SPB outbreaks is to understand the importance of landscape structure to both the severity and extent of outbreaks. Because LANDIS is a spatially explicit model we were able to extend the work that we have done on small landscapes to larger ones and explicitly test for the influence of landscape structure on simulated outbreaks and the maintenance of pine communities. We were specifically interested in answering questions about whether landscapes with more aggregated pine stands were more susceptible to SPB outbreaks, how landscape structure influenced the persistence of pine stands, and how persistent the initial landscape structure was over time (Cairns et al. 2008).

To accomplish these goals, we used the same version of LANDIS described above (Waldron et al. 2007). We reduced the number of species from 15 to 11 and included only one species vulnerable to SPB (*P. pungens*). We then created a series of landscapes with controlled structural characteristics so that tests of the influence of landscape structure could be undertaken. In this case, landscape structure refers to the proportion of the landscape occupied by pines and to the aggregation of those pines. Each landscape represented a 2621.44 ha area (512×512 cells with dimensions $10 \text{ m} \times 10 \text{ m}$). LANDIS simulations lasted 150 years and output maps of the forest were generated every 10 years. A variety of landscape metrics were calculated for each landscape at each year to allow the tracking of changes in landscape structure.

We have found that there is a strong relationship between landscape structure and SPB outbreaks. First, the proportion of pines infested with SPB is positively correlated with the aggregation of the pines on the landscape (Figure 4). We measured aggregation using the clumpiness metric (McGarigal and Marks 1995). As the aggregation of pines increases, so does the proportion of pines infested with SPB. We also found that regardless of the initial proportion of the landscape occupied by pines, the proportion of pines on the landscape decreases over time in the presence of SPB. Finally, we were able to show that there does appear to be some landscape memory (*sensu* Peterson 2002) associated with the initial pattern of the landscape. Specifically, we found that although pines are decreasing on the landscape and that highly aggregated pine stands become more dissected over time, the general outlines of the initial patches remain on the landscape over the span of the 150-year simulations (Figure 5).

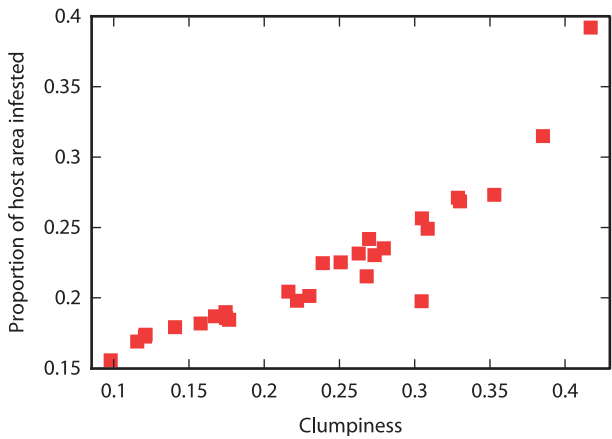


Fig. 4. Influence of patch aggregation (clumpiness) on the area infested by southern pine beetle. Points are the average clumpiness value for pine patches from 10 replications of the model with different initial aggregations of pines. The results shown here are from year 150 of LANDIS simulations which began with 25% of the landscape occupied by pine.

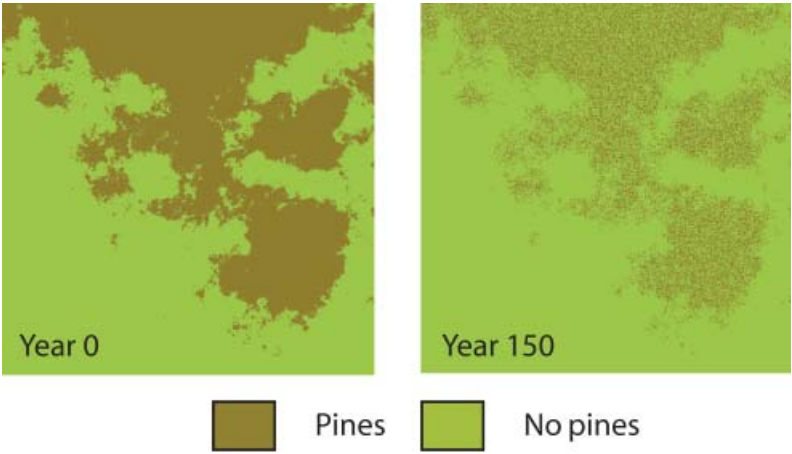


Fig. 5. Pattern of pines on a sample landscape in years 0 and 150. At year 150, the pines have become more fragmented but retain the same general configuration as at the beginning of the simulation. These maps each represent a 2621.44 ha area with 40% pines that are highly aggregated at the beginning of the simulation.

Discussion

In this paper, we have discussed the importance of disturbances in general and insect outbreaks in particular for structuring forest landscapes. The impact of the SPB has been highlighted to illustrate the ways that an insect pest can impact a landscape in ways that are important both ecologically

and economically. The simulation modeling approach that we have highlighted here is a powerful one that can be utilized to answer a wide variety of questions in both the realms of pure science and forest policy. However, the LANDIS model is not the only example of simulation modeling being applied to landscapes to understand a disturbance. Landscape models can be used to address a range of disturbance ecology topics.

Landscape simulation models are those models that seek to represent ecological processes over large areas in a spatially explicit manner. Investigation of landscape ecological theory and the application of such theory to management over large spatial extents has necessitated the use of such models (Mladenoff and Baker 1999a). The need for the inclusion of time horizons outside of the span of normal funding cycles has also facilitated the use of landscape modeling.

Landscape models have been used to address a large variety of disturbance-related questions within landscape ecology. The interaction of fire with forest succession has been the focus of many simulation models (e.g. He et al. 2004; Keane et al. 2007; Shang et al. 2007) as has the effect of logging (Baker 1999). Of particular relevance to the research summarized here are landscape models that are capable of simulating the effects of insects on the landscape. The HIBECO (Gautestad et al. 2005) and LANDIS (Sturtevant et al. 2004) models are two examples of landscape models that include insect disturbances.

In contrast to the general LANDIS model, HIBECO is a less general model that was designed to simulate Nordic mountain birch forests and includes climate change, insect and mammalian herbivory, and logging (Gautestad et al. 2005). Both LANDIS and HIBECO are capable of simulating multiple disturbances in a spatially explicit manner.

In both the case of HIBECO and LANDIS, the development of the models was driven by a desire to not only understand the ecology of disturbed landscapes, but to use the models as tools for managing the landscapes in an ecologically informed way. The integration of landscape ecology and management is a natural one and has been suggested in the USA since the 1980s (Forman and Godron 1986). The use of landscape models in management has been increasing lately (e.g. Mladenoff and Baker 1999b) and shows promise for the future.

FUTURE MODELING OF THE SPB IN THE SOUTHERN APPALACHIAN MOUNTAINS

The results that we have summarized here are all from hypothetical or synthetic landscapes. The next step in this process is to apply these same analytical tools to an actual landscape in the southern Appalachians to determine how well the model represents reality. The results up to this point are, therefore, largely heuristic, but have given us confidence in the model's ability to simulate the development of these forests over time and space while being disturbed by the SPB.

In addition to using the suite of modeling tools that we have developed so far, we also are in the process of continually improving our modeling capabilities (Xi et al. 2007). We have concentrated on using the LANDIS model to perform our simulations. However, this model does have some limitations. Primary among these limitations is the way that LANDIS and the BDA simulate the effects of insects on the landscape. The model requires that the user supply parameters that describe the outbreak cycle of the pest being simulated. We are fortunate that data are available to allow us to develop these parameters and thereby simulate outbreaks of SPB. However, the model does not explicitly have the capability of simulating the growth of the insects and their populations in response to prevailing environmental conditions. Therefore, its ability to predict when outbreaks may occur on real landscapes in the future, especially under altered climate scenarios, is extremely limited. To address this limitation, we are in the process of using previously collected life history and developmental rate data on SPB to create a model that is much more responsive to environmental conditions. The life history–environment relationship data can be collected under controlled conditions for short time-frames, but are prohibitive over large space and time regimes. Vegetation dynamics are necessarily collected over long time-frames. Consequently, the only way to integrate these kinds of data is through the use of simulation modeling. In this paper, we have illustrated the necessity of simulation modeling for elucidating the impacts of insects on forest and landscape structure. This kind of work can only be accomplished by interdisciplinary teams pooling their knowledge and expertise. We expect that geographers will play an important role in these interdisciplinary endeavors in the future.

Acknowledgements

This research was supported through US Department of Agriculture, Forest Service Southern Research Station cooperative agreements SRS03-CA-11330129-168, SRS07-CA-1130129 and SRS06-CA-11330124-196.

Short Biography

David M. Cairns is an Associate Professor in the Department of Geography at Texas A&M University. His research interests are in vegetation response to climate change, ecological modeling and the influence of herbivores on forest landscapes. He has a PhD from the University of Iowa.

Charles W. Lafon is an Associate Professor in the Department of Geography at Texas A&M University. He is interested in multiple the influence of multiple disturbance on forest landscapes. He is an expert on the southern Appalachian Mountains and has recently been involved in fire history reconstructions for those environments. His PhD is from the University of Tennessee.

Andrew G. Birt is a Postdoctoral Research Associate within the Department of Entomology at Texas A&M University. His research interests center around population modeling and its practical application to landscape ecology, life history theory and the interface between humans and ecological systems. He is currently researching the population dynamics of SPB and its impacts on the forested landscape of the USA. He holds a PhD from the University of Birmingham, England, and has experience as a risk assessor and researcher in the pesticide industry.

John D. Waldron is an Assistant Professor in the Department of Environmental Studies at the University of West Florida. His research interests revolve around influences on forest landscape composition and pattern including insects, fire, anthropogenic fragmentation, seed dispersal, and multiple disturbance interactions. In addition to the work on SPB represented here, John has begun investigating impacts of hemlock woolly adelgid using a similar approach. He currently teaches Landscape Biogeography, Conservation of Natural Resources, Environmental Impact Assessment, and Seminar in Environmental Issues in addition to serving as Program Coordinator for the Bachelor of Science in Environmental Studies degree at University of West Florida–Emerald Coast.

Maria D. Tchakerian has a PhD in Geography from Texas A&M University and is currently an Assistant Research Scientist in the Knowledge Engineering Laboratory housed within the Department of Entomology at Texas A&M University. Her interests are in landscape ecology.

Robert N. Coulson is a Professor of Entomology and the director of the Knowledge Engineering Laboratory in the Department of Entomology at Texas A&M University. He holds a PhD from the University of Georgia and is one of the world's experts on the SPB. He has been influential in the fusion of landscape ecological principles with entomological research. He teaches Landscape Ecology and is currently writing an introductory landscape ecology textbook.

Weimin Xi is a Postdoctoral Research Associate in the Department of Entomology, Texas A&M University. He holds a PhD from University of North Carolina at Chapel Hill, and has teaching experience in biogeography, ecology, and GIS applications. His research interests focus on the interfaces of biogeography, plant ecology, disturbance ecology, landscape ecology and restoration ecology. He conducted research in various areas including forest gap dynamics, invasive species, GIS-based vegetation mapping, environmental assessment, and eco-informatics. He is currently using an integrated landscape modeling approach with GIS tools to study forest dynamics and disturbances, forest restoration planning and assessment for the SPB and other invasive species on the forested landscape of the USA.

Kier Klepzig is project leader of Unit of Insects, Diseases, and Invasive Plants, at the USDA Forest Service Southern Research Station. His current research focuses on the symbiotic interaction of bark beetles with fungi and mites.

Note

* Correspondence address: David Cairns, 3147 TAMU, College Station, TX 77843-3147, USA. E-mail: cairns@tamu.edu.

References

- Baker, W. L. (1999). Spatial simulation of the effects of human and natural disturbance regimes on landscape structure. In: Mladenoff, D. J. and Baker, W. L. (eds) *Spatial modeling of forest landscape change: approaches and applications*. Cambridge: Cambridge University Press, pp. 277–308.
- Bouget, C., and Duelli, P. (2004). The effects of windthrow on forest insect communities: a literature review. *Biological Conservation* 118, pp. 281–299.
- Brose, P. H., and Waldrop, T. A. (2006). Fire and the origin of Table Mountain pine – pitch pine communities in the southern Appalachian Mountains, USA. *Canadian Journal of Forest Research* 36, pp. 710–718.
- Brown, M. W., Nebeker, T. E., and Honea, C. R. (1987). Thinning increases loblolly pine vigor and resistance to bark beetles. *Southern Journal of Applied Forestry* 11, pp. 28–31.
- Burns, R. M., and Honkala, B. H. (1990). *Silvics of North America*. Washington, DC: USDA Forest Service.
- Cairns, D. M., et al. (2008). Simulating the reciprocal interaction of forest landscape structure and Southern Pine Beetle herbivory using LANDIS. *Landscape Ecology*. doi: 10.1007/s10980-008-9198-7.
- Carter, G. A., Seal, M. R., and Haley, T. (1998). Airborne detection of southern pine beetle damage using key spectral bands. *Canadian Journal of Forest Research* 28, pp. 1040–1045.
- Conner, R. N., et al. (2001). Does red-cockaded woodpecker excavation of resin wells increase risk of bark beetle infestation in cavity trees? *The Auk* 118, pp. 219–224.
- Coulson, R. N. (1979). Population dynamics of bark beetles. *Annual Review of Entomology* 24, pp. 417–447.
- Coulson, R. N., and Stephen, F. M. (2006). Impacts of insects in forest landscapes: implications for forest health management. In: Paine, T. D. (ed.) *Invasive forest insects, introduced forest trees, and altered ecosystems: ecological pest management in global forests of a changing world*. New York: Springer.
- Coulson, R. N., Hain, F. P., and Payne, T. L. (1974). Radial growth characteristics and stand density of loblolly-pine in relation to occurrence of southern pine beetle. *Environmental Entomology* 3, pp. 425–428.
- Coulson, R. N., et al. (1983). The role of lightning in the epidemiology of the southern pine beetle. *Zeitschrift für Angewandte Entomologie* 96, pp. 182–193.
- Delcourt, P. A., and Delcourt, H. R. (1998). The influence of prehistoric human-set fires on oak–chestnut forests in the Southern Appalachians. *Castanea* 64, pp. 337–345.
- Forman, R. T. T. (1995). *Land mosaics*. Cambridge: Cambridge University Press.
- Forman, R. T. T., and Godron, M. (1986). *Landscape ecology*. New York: John Wiley & Sons.
- Foster, D. R., Knight, D. H., and Franklin, J. F. (1998). Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* 1, pp. 497–510.
- Franklin, J., et al. (2001). Simulating the effects of different fire regimes on plant functional groups in Southern California. *Ecological Modelling* 142, pp. 261–283.
- Fredericksen, T. S., Hedden, R. L., and Williams, S. A. (1995). Susceptibility of loblolly pine to bark beetle attack following simulated wind stress. *Forest Ecology and Management* 76, pp. 95–107.
- Gautestad, A. O., Wielgolaski, F. E., and Mysterud, I. (2005). Landscape-scale model relating the Nordic mountain birch forest spatio-temporal dynamics to various anthropogenic influences, herbivory and climate change. In: Wielgolaski, F. E., et al. (eds) *Plant ecology, herbivory, and human impact in nordic mountain birch forests*. Berlin, Germany: Springer-Verlag, pp. 283–300.
- Gripenberg, S., and Roslin, T. (2007). Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology *Oikos* 116, pp. 181–188.
- Gromtsev, A. (2002). Natural disturbance dynamics in the boreal forests of European Russia: a review. *Silva Fennica* 36, pp. 41–55.

- Hadley, K. S., and Veblen, T. T. (1993). Stand response to western spruce budworm and douglas-fir bark beetle outbreaks, Colorado Front Range. *Canadian Journal of Forest Research* 23, pp. 479–491.
- Harrod, J. C., Harmon, M. E., and White, P. S. (2000). Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites. *Journal of Vegetation Science* 11, pp. 465–472.
- He, H. S., and Mladenoff, D. J. (1999a). The effects of seed dispersal on the simulation of long-term forest landscape change. *Ecosystems* 2, pp. 308–319.
- . (1999b). Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. *Ecology* 80, pp. 81–99.
- He, H. S., Mladenoff, D. J., and Boeder, J. (1996). *LANDIS, a spatially explicit model of forest landscape disturbance, management and succession – LANDIS 2.0 users' guide*. Madison, WI: Department of Forest Ecology and Management, University of Wisconsin-Madison.
- He, H. S., et al. (2002). A simulation study of landscape scale forest succession in northeastern China. *Ecological Modelling* 156, pp. 153–166.
- . (2004). Simulating forest fuel and fire risk dynamics across landscapes – LANDIS fuel module design. *Ecological Modelling* 180, pp. 135–151.
- Howe, E., and Baker, W. L. (2003). Landscape heterogeneity and disturbance interactions in a subalpine watershed in northern Colorado, USA. *Annals of the Association of American Geographers* 93, pp. 797–813.
- Keane, R. E., Rollins, M., and Zhu, Z. L. (2007). Using simulated historical time series to prioritize fuel treatments on landscapes across the United States: the LANDFIRE prototype project. *Ecological Modelling* 204, pp. 485–502.
- Koch, F. H., Cheshire, H. M., and Devine, H. A. (2006). Landscape-scale prediction of hemlock woolly adelgid, *Adelges tsugae* (Homoptera: Adelgidae), infestation in the southern Appalachian Mountains. *Environmental Entomology* 35, pp. 1313–1323.
- Kroll, J. C., and Reeves, H. C. (1978). A simple model for predicting annual numbers of southern pine beetle infestations in east Texas. *Southern Journal of Applied Forestry* 2, pp. 62–64.
- Lafon, C. W. (2004). Ice-storm disturbance and long-term forest dynamics in the Adirondack Mountains. *Journal of Vegetation Science* 15, pp. 267–276.
- Lafon, C. W., and Kutac, M. J. (2003). Effects of ice storms, southern pine beetle infestation, and fire on table mountain pine forests of southwestern Virginia. *Physical Geography* 24, pp. 502–519.
- Lafon, C. W., et al. (2007). Modeling the effects of fire on the long-term dynamics and restoration of yellow pine and oak forests in the southern Appalachian mountains. *Restoration Ecology* 15, pp. 400–411.
- Lorio, P. L. (1980). Loblolly pine stocking levels affect potential for southern pine beetle infestation. *Southern Journal of Applied Forestry* 4, pp. 162–165.
- Malanson, G. P. (1993). *Riparian landscapes*. Cambridge: Cambridge University Press.
- Mattson, W. J., and Haack, R. A. (1987). The role of drought in outbreaks of plant-eating insects. *BioScience* 37, pp. 110–118.
- Mawby, W. D., and Gold, H. J. (1984). A reference curve and space-time series analysis of the regional population dynamics of the southern pine beetle (*Dendroctonus frontalis* Zimmermann). *Population Ecology* 26, pp. 261–274.
- McGarigal, K., and Marks, B. J. (1995). *FRAGSTATS: spatial pattern analysis program for quantifying landscape structure*. Portland, OR: U.S. Forest Service, Pacific Northwest Research Station.
- McGarigal, K., et al. (2001). Cumulative effects of roads and logging on landscape structure in the San Juan Mountains, Colorado (USA). *Landscape Ecology* 16, pp. 327–349.
- Millward, A. A., and Kraft, C. E. (2004). Physical influences of landscape on a large-extent ecological disturbance: the northeastern North American ice storm of 1998. *Landscape Ecology* 19, pp. 99–111.
- Mladenoff, D. J. (2004). LANDIS and forest landscape models. *Ecological Modelling* 180, pp. 7–19.
- Mladenoff, D. J., and Baker, W. L. (1999a). Development of forest and landscape modeling approaches. In: Mladenoff, D. J. and Baker, W. L. (eds) *Spatial modeling of forest landscape change: approaches and applications*. Cambridge: Cambridge University Press, pp. 1–13.
- . (1999b). *Spatial modeling of forest landscape change: approaches and applications*. Cambridge: Cambridge University Press.

- Mladenoff, D. J., and He, H. S. (1999). Design and behavior of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: Mladenoff, D. J. and Baker, W. L. (eds) *Spatial modeling of forest landscape change: approaches and applications*. Cambridge: Cambridge University Press, pp. 125–162.
- Mladenoff, D. J., et al. (1996). LANDIS: a spatial model of forest landscape disturbance, succession and management. In: Goodchild, M., et al. (eds) *GIS and environmental modeling: progress and research issues*. Fort Collins, CO: GIS World Books, pp. 175–179.
- . (1993). Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecological Applications* 3, pp. 294–306.
- Nonaka, E., and Spies, T. A. (2005). Historical range of variability in landscape structure: a simulation study in Oregon, USA. *Ecological Applications* 15, pp. 1727–1746.
- Orwig, D. A., Foster, D. R., and Mausel, D. L. (2002). Landscape patterns of hemlock decline in New England due to the introduced hemlock wooly adelgid. *Journal of Biogeography* 29, pp. 1475–1487.
- Parker, K. C., and Bendix, J. (1996). Landscape-scale geomorphic influences on vegetation patterns in four environments *Physical Geography* 17, pp. 113–141.
- Payne, T. L. (1980). Life history and habits. In: Thatcher, R. C., Searcy, J. L., Coster, J. E. and Hertel, G. D. (eds) *The Southern Pine Beetle*. USDA Forest Service Technical Bulletin 1631, 7–28.
- Pennanen, J., and Kuuluvainen, T. (2002). A spatial simulation approach to natural forest landscape dynamics in boreal Fennoscandia. *Forest Ecology and Management* 164, pp. 157–175.
- Pennanen, J., et al. (2004). Spatially explicit simulation of long-term boreal forest landscape dynamics: incorporating quantitative stand attributes. *Ecological Modelling* 180, pp. 195–209.
- Perkins, T. E., and Matlack, G. R. (2002). Human-generated pattern in commercial forests of southern Mississippi and consequences for the spread of pests and pathogens. *Forest Ecology and Management* 157, pp. 143–154.
- Peterson, G. D. (2002). Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems* 5, pp. 329–338.
- Prestemon, J. P., and Holmes, T. P. (2004). Market dynamics and optimal timber salvage after a natural catastrophe. *Forest Science* 50, pp. 495–511.
- Price, T. S., et al. (1998). *A history of southern pine beetle outbreaks in the Southern United States*. Macon, GA: The Georgia Forestry Commission.
- Pye, J. M. (1993). Regional dynamics of southern pine beetle populations. In: Liebhold, A. M. and Barrett, H. R. (eds) *Proceedings Spatial Analysis and Forest Pest Management*, General Technical Report NE-175. Radnor, PA: US Department of Agriculture, Forest Service, pp. 111–124.
- Redmond, C. H., and Nettleton, W. A. (1990). An economic analysis of southern pine beetle suppression activity on the Gulf Coastal Plain national forests during 1985 and 1986. *Southern Journal of Applied Forestry* 14, pp. 70–73.
- Ryall, K. L., and Fahrig, L. (2005). Habitat loss decreases predator-prey ratios in a pine-bark beetle system. *Oikos* 110, pp. 265–270.
- Schowalter, T. D., Coulson, R. N., and Crossley, C. A. Jr. (1981a). Role of southern pine beetle and fire in maintenance of structure and function of the southeastern coniferous forest. *Environmental Entomology* 10, pp. 821–825.
- Schowalter, T. D., et al. (1981b). Patterns of southern pine beetle (*Dendroctonus frontalis* Zimm.) infestation enlargement. *Forest Science* 27, pp. 837–849.
- Schumacher, S., Bugmann, H., and Mladenoff, D. J. (2004). Improving the formulation of tree growth and succession in a spatially explicit landscape model. *Ecological Modelling* 180, pp. 175–194.
- Shang, Z. B., et al. (2007). Modeling the long-term effects of fire suppression on central hardwood forests in Missouri Ozarks, using LANDIS. *Forest Ecology and Management* 242, pp. 776–790.
- Shifley, S. R., et al. (2000). Modeling forest landscape change in the Missouri Ozarks under alternative management practices. *Computers and Electronics in Agriculture* 27, pp. 7–24.
- . (1998). Utilizing inventory information to calibrate a landscape simulation model in *Proceedings of Integrated Tools for Natural Resources Inventories in the 21st Century*. General Technical Report NC-212. St. Paul, MN: US Department of Agriculture, Forest Service, North Central Forest Experiment Station.

- Smith, E. L., McMahan, A. J., and Wang, G. Z. (2002). Eco-physiology approach to projecting tree stress and vigor in FVS. In: Crookston, N. L. and Havis, R. N. (eds) *Second Forest Vegetation simulator Conference, Proceedings; RMRS-P-25*. Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Staus, N. L., et al. (2002). Rate and pattern of forest disturbance in the Klamath-Siskiyou ecoregion, USA between 1972 and 1992. *Landscape Ecology* 17, pp. 455–470.
- Stueve, K. M., Lafon, C. W., and Isaacs, R. E. (2007). Spatial patterns of ice storm disturbance on a forested landscape in the Appalachian Mountains. *Area* 39, pp. 20–30.
- Sturtevant, B. R., et al. (2004). Modeling biological disturbances in LANDIS: a module description and demonstration using spruce budworm. *Ecological Modelling* 180, pp. 153–174.
- Syphard, A. D., and Franklin, J. (2004). Spatial aggregation effects on the simulation of landscape pattern and ecological processes in southern California plant communities. *Ecological Modelling* 180, pp. 21–40.
- Turchin, P., et al. (1991). Why do populations of southern pine beetle (Coleoptera: Scolytidae) fluctuate? *Environmental Entomology* 20, pp. 401–409.
- Turchin, P., Taylor, A. D., and Reeve, J. D. (1999). Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285, pp. 1068.
- Turner, M. (2005). Landscape ecology in North America: past, present, and future. *Ecology* 86, pp. 1967–1974.
- Turner, M., and Dale, V. H. (1998). Comparing large, infrequent disturbances: what have we learned? *Ecosystems* 1, pp. 493–496.
- Ungerer, M., Ayres, M. P., and Lombardero, M. (1999). Climate and the northern distribution limits of *Dendroctonus frontalis* Zimmerman. *Journal of Biogeography* 26, pp. 1133–1145.
- Waldron, J. D., et al. (2007). Simulating the impacts of southern pine beetle and fire on the dynamics of xerophytic pine landscapes in the Southern Appalachian Mountains. *Applied Vegetation Science* 10, pp. 53–64.
- Weslowski, T., and Rowinski, P. (2006). Tree defoliation by winter moth *Operophtera brumata* L. during an outbreak affected by structure of forest landscape. *Forest Ecology and Management* 221, pp. 299–305.
- Whittaker, R. H. (1956). Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26, pp. 1–80.
- Wimberly, M. C. (2004). Fire and forest landscapes in the Georgia Piedmont: an assessment of spatial modeling assumptions. *Ecological Modelling* 180, pp. 41–56.
- Xi, W., et al. (2007). Landscape modeling for forest restoration: concepts and applications. In: Stanturf, J. (ed.) *Proceedings of the IUFRO Conference on Forest Landscape Restoration*. Seoul, Korea, 14–19 May 2007. Seoul, South Korea: Korea Forest Research Institute, pp. 92–95.
- Xu, C., et al. (2004). Assessing the effect of cell-level uncertainty on a forest landscape model simulation in northeastern China. *Ecological Modelling* 180, pp. 57–72.