

Simulating the reciprocal interaction of forest landscape structure and southern pine beetle herbivory using LANDIS

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Abstract The reciprocal interaction of landscape structure and ecological processes is a cornerstone of modern landscape ecology. We use a simulation model to show how landscape structure and herbivory interact to influence outbreaks of southern pine beetle (*Dendroctonus frontalis* Zimmermann) in a landscape representative of the southern Appalachian Mountains, USA. We use LANDIS and its biological disturbance agent module to simulate the effects of landscape composition (proportion of landscape in host area) and host aggregation on the size and severity of insect outbreaks and the persistence of the host species, Table Mountain Pine (*Pinus pungens* Lamb.). We find that landscape composition is less important in the modeled landscapes than host aggregation in structuring the severity of insect

outbreaks. Also, simulated southern pine beetle outbreaks over time tend to decrease the aggregation of host species on the landscape by fragmenting large patches into smaller ones, thereby reducing the severity of future outbreaks. Persistence of Table Mountain pine decreases throughout all simulations regardless of landscape structure. The results of this study indicate that when considering alternative restoration strategies for insect-affected landscapes, it is necessary to consider the patterns of hosts on the landscape as well as the landscape composition.

Keywords Disturbance · LANDIS · BDA · Insect outbreak · Table Mountain pine

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Introduction

The reciprocal interaction between spatial pattern and ecological processes is a central tenet of contemporary landscape ecology (Turner 2005b). Spatial pattern influences the lateral fluxes of matter across landscapes (Peterjohn and Correll 1984), the movement of animals, and the spread of disturbance (Turner 1989; Turner et al. 1989). Disturbances such as fire, insect outbreaks, and disease respond to landscape pattern (Coulson et al. 1999; Gilbert et al. 2005; Jules et al. 2002). The reciprocal interaction of spatial pattern and disturbance processes is an important topic in landscape ecology and also

influences forest management planning and decision making (Coulson and Stephen 2006). Because they are spatially structured, insect outbreaks create excellent conditions for investigating the interaction of spatial pattern and ecological processes. Insect herbivory is influenced by both the composition of the landscape (i.e. what types of landscape elements are present and how many) and the configuration of those landscape elements (Coulson and Wunneburger 2000). Of particular interest is the impact of insect herbivory occurring in mesoscale forest landscapes over successional time.

The influence of spatial structure on insect outbreaks can be approached either from the point of view of the insects or from the plants upon which they feed. Classical insect population models ignore spatial heterogeneity, but recently, metapopulation models have been used to investigate the impacts of landscape heterogeneity on population dynamics (cf. Gamarra 2005). Although metapopulation approaches have advanced our understanding of insect populations, by nature of being insect-centered, they do not easily consider the reciprocal nature of the relationship between insects and landscape structure. The explicit linkage between landscape structure and insects has been addressed through correlational studies (Powers et al. 1999; Radeloff et al. 2000; Roland 1993) and simulation modeling (Sturtevant et al. 2004). Often the linkage between pattern and process in these studies has been based on a simple relationship between a measured property of the landscape and a dependent variable describing either the population size or the impact of insect activity (e.g. Gilbert et al. 2005; Radeloff et al. 2000; Roland 1993).

Questions in landscape ecology often are addressed using simulation models. Simulation models provide the benefit of analyzing large areas, multiple landscapes, and/or relatively long time periods while controlling initial conditions and the processes included. Thereby, the relative importance of particular processes and their interactions can be investigated. An important step in a simulation modeling effort to understand disturbances within a landscape ecological context is to explore model projections of a single disturbance agent without the interacting influences of other disturbances. In this paper we explore how simulated insect outbreaks interact with landscape structure within the context of

the LANDIS model (He et al. 1996; Mladenoff et al. 1996). Our investigation is based on outbreaks of southern pine beetle (SPB, *Dendroctonus frontalis* Zimmermann (*Coleoptera:Curculionidae*)) in Table Mountain pine (*Pinus pungens* Lamb.) forests of the southern Appalachian Mountains. Table Mountain pine is endemic to the Appalachian Mountains, and is the most common pine species in mid-elevation ranges. SPB attacks various pine species throughout southeastern North America. It occasionally infests other conifers, but never hardwoods. The Appalachian pine-SPB system provides a useful case for examining interactions between landscape structure and insect outbreaks because of the host specificity of SPB and the contagious nature of SPB infestations, combined with a patchy distribution of pine stands on xeric sites within a hardwood forest matrix. More generally, this modeling exercise should be relevant to insect outbreaks in landscapes where patches of host vegetation are interspersed with non-host vegetation.

We previously applied LANDIS to simulate successional dynamics on hypothetical landscapes representative of the southern Appalachian Mountains, and to investigate the interacting influences of fire and SPB on succession (Lafon et al. 2007; Waldron et al. 2007). The work presented here extends our previous efforts by considering implications of spatial patterns for insect-host interactions on simulated (neutral) landscapes with varying configurations of host vegetation. Clearly, any modeling endeavor, particularly one using neutral landscapes, involves simplification and abstraction of the actual system. However, this work is a step toward understanding potential interactions between landscape structure and SPB herbivory on actual Appalachian landscapes, where the varying configurations of pine offer potential opportunities for modeling experiments and empirical studies to investigate such interactions.

SPB outbreak patterns are of considerable interest in the Appalachian Mountains because of recent heavy losses of pine from SPB (e.g. Lafon and Kutac 2003), and because Table Mountain pine is a conservation priority (Williams 1998). SPB outbreaks occur cyclically with a period around 7–10 years in the Piedmont and Coastal Plain, and less frequently in the southern Appalachian Mountains (Price et al. 1998). Although the factors that lead to the initial

development of an outbreak are not completely understood, there may be relationships between outbreaks and extreme environmental conditions (Gan 2004). Also, the outbreaks in a single year appear to be influenced by spatial structure (Coulson et al. 1999). For example, the arrangement of lightning-struck trees influences the spread of infestations (Coulson et al. 1999).

The objective of this research is to study the effects of landscape pattern on the characteristics of SPB outbreaks and to show the impact of such outbreaks on the spatial pattern of forests using a spatially explicit landscape model. We are interested in the impact of spatial structure, as measured by standard landscape metrics, on the size and severity of outbreak patches and on the ability of simulated landscapes to maintain pine stands. We specifically pose the following questions: (1) Are landscapes with highly aggregated pine stands more vulnerable to severe SPB outbreaks than landscapes with smaller, less aggregated stands? (2) If aggregated landscapes are more vulnerable to SPB, is the initial landscape structure erased over time following multiple SPB outbreaks? (3) Do highly aggregated landscapes have more extensive SPB outbreaks than less aggregated ones? and (4) In the presence of SPB, does pine persist at higher levels on less aggregated landscapes than aggregated landscapes? We use a spatially explicit simulation model (LANDIS: He et al. 1996; Mladenoff et al. 1996; Mladenoff and Baker 1999) together with the biological disturbance agent (BDA) module (Sturtevant et al. 2004) on hypothetical landscapes with known landscape pattern properties to answer these questions.

Methods

LANDIS

LANDIS is a stochastic, spatially-explicit, raster-based computer model that simulates forest succession and disturbance across large areas (10^3 – 10^7 ha) and over long time periods (10^1 – 10^3 years) (He et al. 1996; He and Mladenoff 1999; Mladenoff et al. 1996; Mladenoff and He 1999). LANDIS was developed to simulate succession as well as harvesting, windthrow, and fire disturbance in the upper Midwest (Mladenoff 2004). More recently, LANDIS has been used to simulate landscapes in regions of varying ecological and

topographic complexity, e.g., the Missouri Ozarks (Shifley et al. 2000), southern California (Syphard and Franklin 2004), and the southern Appalachian Mountains (Lafon et al. 2007; Waldron et al. 2007).

In LANDIS, the presence or absence of 10-year age cohorts is simulated for each cell on the landscape. Cell size can be scaled from 10 to 500 m. For each cell, LANDIS manages user-defined species life history traits (longevity, minimum age at reproduction, shade tolerance, fire tolerance, minimum/maximum seed dispersal distances, and resprout probability) to drive competition and succession at 10-year time steps (He et al. 2004). A species establishment coefficient, which represents environmental conditions, governs establishment of each species. A landscape can be subdivided into multiple landtypes, with each landtype possessing different environmental conditions. LANDIS can simulate disturbance by fire, wind, harvesting, or biological agents (insects, disease) (Sturtevant et al. 2004).

BDA

Biological disturbances in LANDIS are modeled using the BDA module (Sturtevant et al. 2004). Biological disturbances are probabilistic at the site level and are dependent on a calculated site vulnerability value (SV). SV is a function of the quality and quantity of food resources, which are dependent on the species composition and age structure present. SV is modified by a regional outbreak status (ROS) value that represents the background level of outbreak activity and by a neighborhood modifier that accounts for the effects of landscape context (Sturtevant et al. 2004). The SV value for a cell is used to determine if an SPB outbreak occurs on that cell. The severity of an outbreak is based on the value of SV.

BDA represents some aspects of SPB outbreaks well. First, it incorporates (via the ROS) cyclic variation in outbreak occurrence across the landscape, consistent with the broad-scale periodicity of SPB activity (Coulson et al. 1999). Second, as in actual SPB outbreaks (Gumpertz et al. 2000), outbreak severity varies both spatially (during a single outbreak year) and temporally (between outbreaks occurring in different years). Third, tree susceptibility varies by species and age in BDA. In a sensitivity analysis of the BDA, Sturtevant et al.

(2004) found that the most important factor controlling probability of disturbance in BDA was the composition of species and age-cohorts in the simulated landscape. Studies of SPB outbreaks suggest that tree species and age are important factors controlling outbreak characteristics (e.g. Coulson 1981; Fettig et al. 2007). Fourth, the neighborhood modifier in BDA represents mechanisms by which the mix of tree species/ages in a forest neighborhood can influence herbivory, as observed in actual forest stands (Schowalter and Turchin 1993; Zhang and Zeide 1999; Jactel and Brockerhoff 2007). The neighborhood modifier also imparts spatial coherence in outbreak activity, which corresponds with the patchiness of actual SPB outbreaks arising from the growth of infested spots (Fettig et al. 2007).

Because the landscapes we simulate are relatively small (roughly 5×5 km) with similar macroclimatic conditions throughout, and because our emphasis is on the influence of landscape structure rather than the effects of temporal climatic variability, our analyses do not incorporate the effects of host condition resulting from climatic stress (cf. Fettig et al. 2007). Similarly, because LANDIS operates on a decadal time step, the growth of SPB infestations over the course of a growing season (cf. Fettig et al. 2007) is not simulated. Rather, BDA simply calculates the ultimate size of each infested spot that is generated during the decade. Our interest here is only in the total area infested, and therefore we do not need BDA to simulate seasonal patterns in the spread of infestations. Although insect dispersal is an important factor in structuring outbreaks, it is not included in this study. The assumption of synchronous outbreaks is acceptable for our study because SPB is capable of relatively long-range dispersal (>1 km within a few days) (Turchin and Thoeny 1993) and SPB outbreaks typically exhibit spatial synchrony at the scale of the landscapes we simulate (Coulson et al. 1999). Although the LANDIS-BDA is not capable of simulating every aspect of insect disturbances, its balance of detail with parsimony makes it a powerful tool for investigating the interaction of pattern and process in insect outbreaks.

Model parameterization

Our simulations represent a pulsed outbreak with a mean recurrence interval of 25 years and a standard

deviation of 5 years. The minimum ROS = 0 and the maximum ROS = 3. The product of SV and (ROS/3) produces the final SV. A minimum ROS of 0 ensured that some iterations in our simulations do not experience an SPB outbreak. BDA calculates the probability of an outbreak for the entire landscape based on the outbreak type selected. The pulsed outbreak type ensures that outbreaks do not occur every year. Because the determination of the outbreak status is probabilistic, there is the potential for multiple outbreaks to occur within 25 years of each other, but if the simulation were run for a long enough time, the average return interval for outbreaks would be 25 years.

The neighborhood characteristics are particularly important in this study because without including them each cell would be independent with regard to the determination of SPB infestation probability and severity. We used a neighborhood radius of 30 meters (3 cells) to calculate the neighborhood effect (i.e. mean Site Resource Dominance). We did not employ any distance decay in the calculation of the neighborhood modifier (i.e. all cells within the 30 meter radius have equal effects on the mean).

We included 11 tree species: 10 deciduous hardwood species and 1 pine (*Pinus pungens*). *P. pungens* was the only species susceptible to SPB attack. The species life history parameters (Table 1) are the same as those used previously for the southern Appalachian region (Waldron et al. 2007). We defined the ages at which *P. pungens* is a minor host, secondary host and primary host (sensu Sturtevant et al. 2004) to be 20, 40 and 50 years. Minor hosts have a relative resource value equal to 0.33. Values for secondary and primary hosts are 0.66 and 1.0. These values are calculated for each cohort of trees on a cell and averaged across all cohorts to determine the SRD value for the cell. The same ages were used to distinguish among the resistant, tolerant and vulnerable host categories for *P. pungens*. The differences among resistant, tolerant and vulnerable host categories lie in the amount of damage caused by an SPB infestation occurring on a cell. Low-severity outbreaks (Category 1) occur when $SV < 0.33$, and kill all vulnerable cohorts. Medium-severity outbreaks (Category 2) have SV between 0.33 and 0.67, and kill all tolerant and vulnerable cohorts. High-severity outbreaks (Category 3) with $SV > 0.67$ kill all resistant, tolerant and vulnerable cohorts on a cell.

Table 1 Life history parameters for species in LANDIS

| Species | Lng ^a | Mat | Shd | Fire | Resprout | Estab |
|---------------------------------|------------------|-----|-----|------|----------|-------|
| <i>Acer rubrum</i> | 150 | 25 | 4 | 1 | 0.9 | 0.152 |
| <i>Carya glabra</i> | 300 | 40 | 2 | 2 | 0.5 | 0.211 |
| <i>Nyssa sylvatica</i> | 200 | 25 | 4 | 2 | 0.3 | 0.229 |
| <i>Oxydendrum arboreum</i> | 100 | 50 | 3 | 2 | 0.9 | 0.229 |
| <i>Pinus pungens</i> | 250 | 20 | 1 | 5 | 0.3 | 0.083 |
| <i>Quercus alba</i> | 450 | 30 | 3 | 3 | 0.5 | 0.08 |
| <i>Quercus rubra</i> | 300 | 25 | 2 | 3 | 0.4 | 0.211 |
| <i>Quercus coccinea</i> | 130 | 25 | 1 | 3 | 0.4 | 0.041 |
| <i>Quercus prinus</i> | 350 | 25 | 3 | 3 | 0.9 | 0.115 |
| <i>Quercus velutina</i> | 150 | 25 | 2 | 3 | 0.7 | 0.106 |
| <i>Robinia pseudoacacia</i> | 100 | 15 | 1 | 1 | 0.9 | 0.375 |

^a Parameter abbreviations: Lng = Longevity; Mat = Maturity; Shd = Shade tolerance; Fire = Fire tolerance, Resprout = Resprouting probability; Estab = Establishment coefficient

Experimental design

Landscape creation

The neutral landscapes were created using RULE (Gardner 1999). Twelve sets of landscapes were created, each with a different structure in terms of the spatial distribution of pines versus hardwoods. The twelve sets represent different combinations of the proportion (p) of cells occupied by pine (two levels) and the fractal dimension (h) of the landscape (six levels). The two values of p are 25% and 40%, corresponding to maximum levels of pine likely to be found on the hardwood-dominated Appalachian landscapes. Values of h are 0, 0.1, 0.2, 0.3, 0.4, and 0.5. Higher values of h indicate less landscape fragmentation (Fig. 1). For each of the 12 combinations of p and h , 10 different landscapes were created. Each landscape has dimensions 512×512 cells, and each cell is 10×10 m (corresponding to the footprint of a single tree). Each landscape is 2,621.44 hectares.

The landscapes created by RULE are necessarily artificial. However, the objectives of this study require that we vary the proportion of pines on the landscape along with the spatial configuration of those pines to evaluate the effect of pattern on process. Because the creation of replicate landscapes based on real-world locations would be nearly

impossible, the use of these neutral landscapes is preferred. Li et al. (2004) tested the effectiveness of RULE-generated landscapes for representing real ones, and found that the neutral landscapes are satisfactory surrogates for real landscapes. There are cases when RULE-produced neutral landscapes are not adequate, for example when particular landscape elements, such as streams, necessarily must be grouped in particular ways (Li et al. 2004). However, these conditions are not present in our landscapes and therefore we are confident that the algorithm used to create the neutral landscapes is not overly influencing our results.

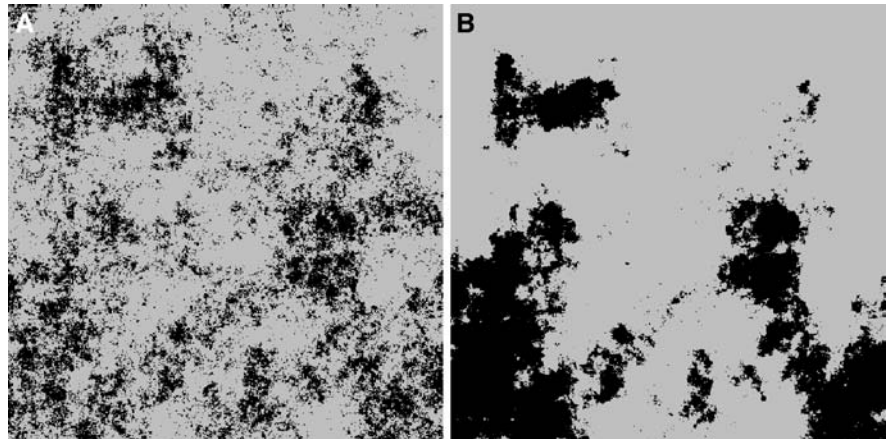
Populating the landscapes

Each neutral landscape is an example of a dry mid-elevation slope within the southern Appalachian Mountains. The choice to restrict the simulations to a single landtype is a simplification that allows us to concentrate on the importance of pattern without the confounding effects of different establishment coefficients among landtypes. We chose the southern Appalachian Mountains as the general landscape type for this study due to recent severe SPB outbreaks in old pine stands there that are the legacy of land use history, and because of the presence of *P. pungens*, which is a conservation and restoration priority. At the outset of each simulation, cells were populated with a single species. Host cells contain only *P. pungens*. Non-host cells may contain any of the non-host species in the proportions equal to those used for mid-elevation southeast—west facing slopes by Waldron et al. (2007). All *P. pungens* cohorts placed on the initial landscape are the same age (10 years).

Simulations

Simulations were run for 150 years to permit multiple SPB outbreaks to occur, but without having *Pinus pungens* approach its maximum lifespan. Hence the relationships of SPB-caused pine mortality to landscape structure were not obscured by age-related mortality. At 10-year intervals LANDIS produced maps of species/cohort presence/absence and outbreak intensity. The proportion of the landscape

Fig. 1 Sample of simulated landscapes that represent the least aggregated conditions (a) $h = 0$, and the most aggregated case (b) $h = 0.5$. Both landscapes have 25% of the cells as host cells (black)



occupied by pine was calculated for each year in each simulation. Because LANDIS is a spatial model incorporating important spatial processes, the landscape structure will change over time. Cells that previously did not contain pines were considered non-host cells. If a pine cohort invaded a non-host cell it became a host cell.

Spatial metrics

Landscape and class metrics were calculated for each landscape in each output year using Fragstats (McGarigal and Marks 1995). We used the clumpiness metric to represent the aggregation of pines for every output landscape (10 years apart). Although the initial landscapes were created in RULE using h values to specify the amount of aggregation, h cannot be calculated for an existing landscape. Therefore, we used the clumpiness metric as a proxy for h . We found good correspondence between h and clumpiness for the initial landscapes (data not shown). Higher values of clumpiness correspond to more aggregated landscapes.

Results

Outbreak timing and area

Outbreaks did not occur before year 40 in any of the simulations. At year 40, the first year with vulnerable hosts present, outbreaks began to appear, and continued every decade (Fig. 2). These results are

aggregated across all realizations for each set of initial conditions. Therefore, although the figures show outbreaks every decade, this is only true for the collection of realizations and not for an individual landscape. Although the return interval of outbreaks is the same for all of our simulated landscapes, the realizations are not synchronized in regard to outbreak timing.

The initial infestations were dominated by Category 2. Category 1 infestations did not appear until year 50. Landscapes with higher initial values of h had a higher frequency of Category 3 outbreaks than did landscapes that were initially more patchy (i.e. low h values). This was true at both levels of p (Fig. 2).

Changes in landscape structure

Landscapes became less fragmented over time as large contiguous patches of pine fragmented into smaller ones (Fig. 3). The impact of the early SPB outbreaks in years 40 and 50 appeared as dramatic reductions in the clumpiness metric. These trends in landscape structure were robust across the simulations and were not dependent on either p or h . However, there was an enduring effect of the initial landscape aggregation throughout the simulation. Landscapes that were more highly aggregated initially retained higher clumpiness values throughout the simulations (Fig. 3).

Although clumpiness changed over time, the general pattern of the landscapes in terms of the location of pine stands did not change dramatically.

Fig. 2 Patch area distributions (as proportions of total potential host area) for outbreak categories 1, 2 and 3. Category 0 (no outbreak) is not included because it is so much greater than the other categories. Panels represent values of $h = 0$ (fragmented) and 0.5 (aggregated), and p (proportion of landscape initially populated with pine) = 25 and 40. All results are the average of 10 landscapes per year. (a) $h = 0, p = 40\%$; (b) $h = 0.5, p = 40\%$; (c) $h = 0, p = 25\%$; (d) $h = 0.5, p = 25\%$

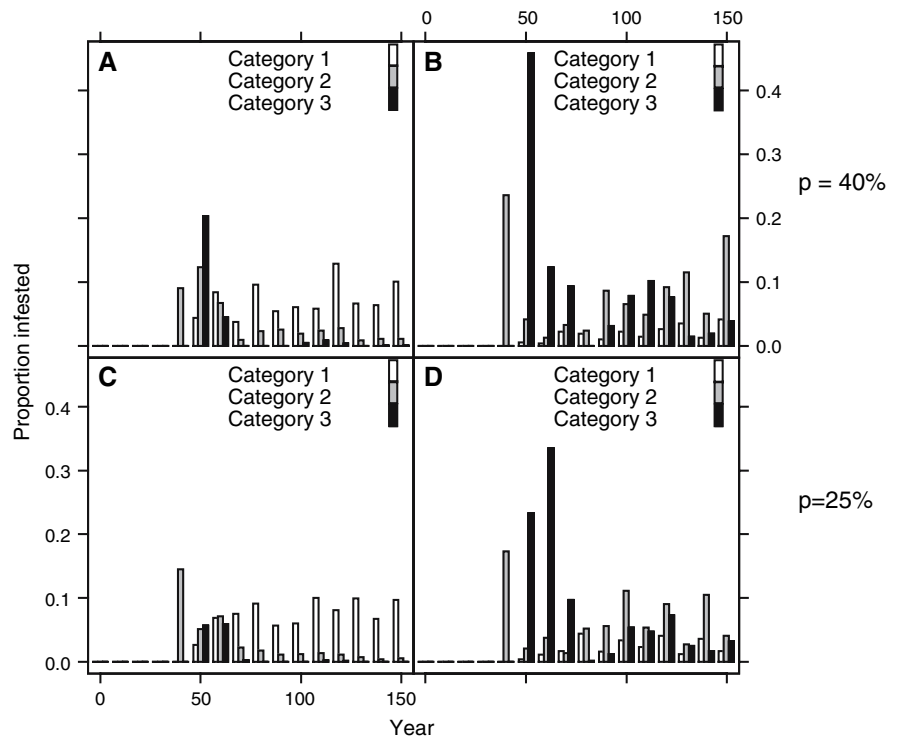
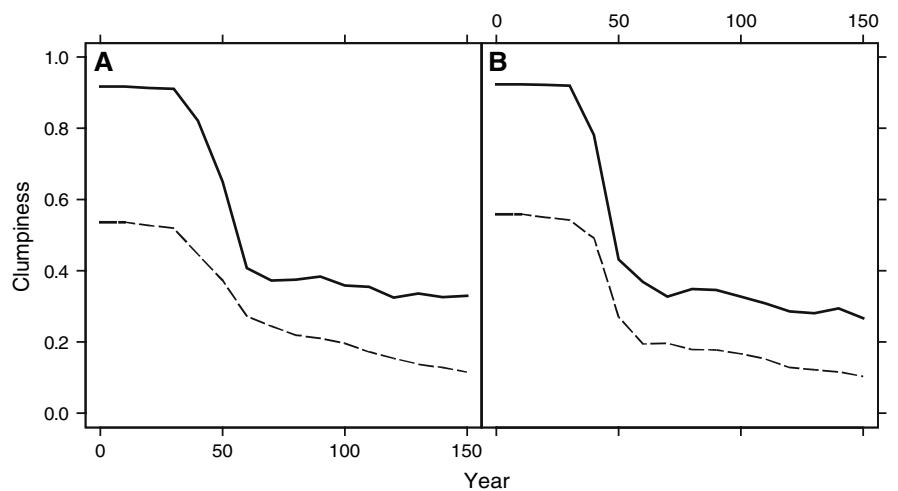


Fig. 3 Changes in patch aggregation over time. Solid line represents aggregated landscapes ($h = 0.5$), dashed line represents fragmented landscapes ($h = 0$). Clumpiness values for each year are the average of 10 replicate landscapes. (a) Landscapes with 25% pine initially; (b) landscapes with 40% pine initially



At the end of the simulations, the outlines of the large patches still existed, but they had been perforated by the SPB disturbances (Fig. 4).

Landscape pattern and process

The effects of landscape structure on the size of infested area depended on the aggregation of the

susceptible species on the landscape, and the proportion of the landscape occupied by old pines. Old pines here corresponded to the vulnerable host category (>40 years) in the BDA parameterization. The results of the 25% and 40% simulations were qualitatively similar; therefore, only the 25% simulations are discussed here.

Early in the simulations there was a strong linear response between host aggregation and the proportion

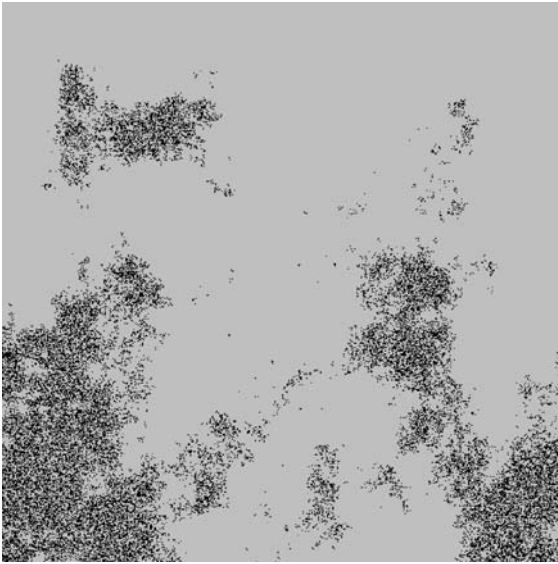


Fig. 4 A simulated landscape in year 150. Initial conditions were $h = 0.5$ (highly aggregated), $p = 25\%$ (initial amount of pine). Grey areas are cells with no pines, black areas are cells that contain pines. See Fig. 1b for conditions in year 0

of host area experiencing an SPB infestation. About half of the landscapes (29/60) experienced no outbreak at all and varied in clumpiness between 0.37 and 0.92, thereby spanning most of the range of possible aggregations (Fig. 5a). All infestations in year 50 occurred at sites where old pines account for more than 80% of the pines on the landscape.

At year 60, the importance of the age of pines on the landscape becomes clear. Prior to this year cells with only young pines were rare due to the uniform age class distributions used in the initial conditions. However, the infestations that occurred during years 40 and 50 allowed more pine to establish on sites previously cleared of pine by the SPB, thereby resulting in cells with primarily young cohorts of pine. The relationship between clumpiness and proportion of the host area infested remains strongly positive and linear (slope = 1.0631; $r^2 = 0.9922$; $F_{(1,26)} = 3320$, $P < 0.0001$). Those landscapes with less than 80% old pines, however tended to have lower proportions of infested cells (Fig. 5b).

After 50 years, the number of landscapes where old pines accounted for more than 80% of the total pines decreased dramatically. By year 70 there were no such landscapes. SPB attacks kept the pine populations fairly young (Fig. 6). Later years in the simulations continued to show the positive

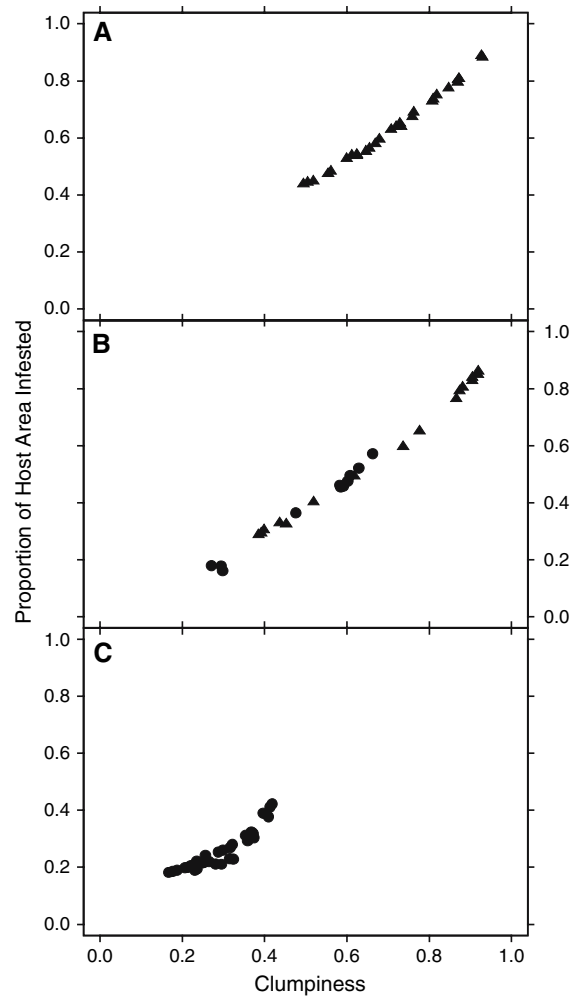


Fig. 5 Responses of area infested by southern pine beetle to changes in patch aggregation (clumpiness). Points represents the average clumpiness value for pine patches in each of the 10 replications of the model runs with the five different initial values of h . There are a total of 60 possible points in each figure. All results are for landscapes with 25% pine in year 0. Circles represent cases where there are few (<80%) old pines (>40 years) on the landscape. Triangles are cases with many old pines on the landscape. (a) Year 50, (b) Year 60, (c) Year 110

relationship between aggregation and proportion of host area infested (Fig. 5c). The strength of this relationship was, however, slightly less (slope = 0.87, $r^2 = 0.8496$; $F_{(1,29)} = 163.8$, $P < 0.0001$).

Persistence of pine on the landscape

In all simulations the proportion of pine on the landscape increased slightly until year 40, when the

Fig. 6 Age structure for table mountain pine (*Pinus pungens*) in year 150. The data presented here are the average of 10 realizations of LANDIS derived from 10 landscapes with initial proportion of pine on the landscape set to 25%, and high aggregation ($h = 0.5$). Proportions are of pines in each age class relative to all pines on the landscape

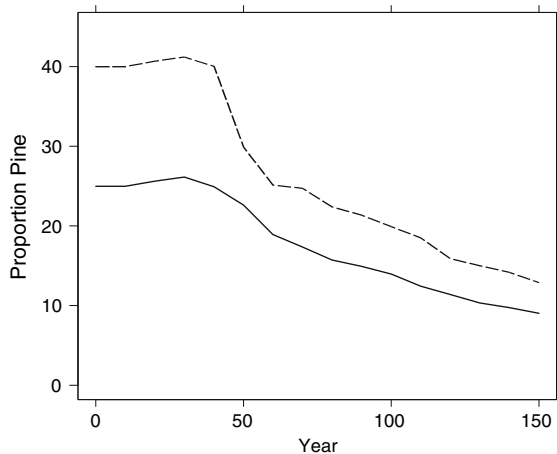
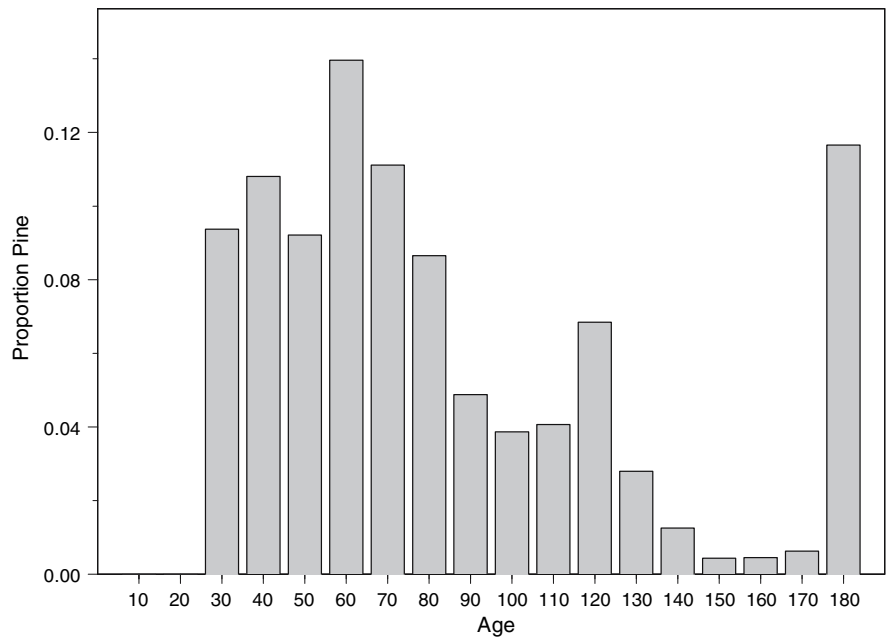


Fig. 7 Persistence of pine on the simulated landscape with initial conditions of $h = 0$ and $p = 25$ (solid line) and $p = 40$ (dashed line). Results are the average values of 10 different landscapes for each year

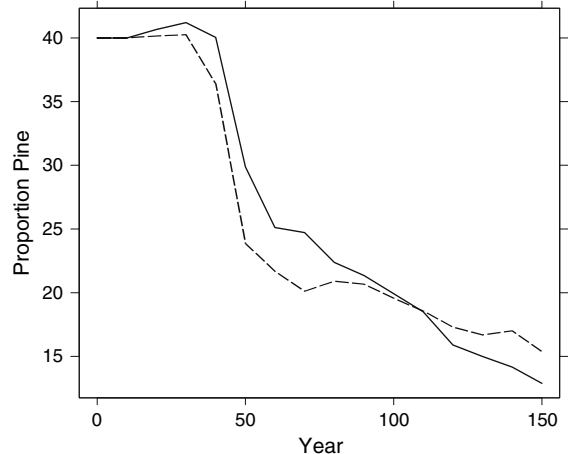


Fig. 8 Comparison of changes in pine proportion between two initial levels of h . Results are the average of 10 simulations for each year and are for when 40% of the initial landscape is covered in pines. The solid line represents less aggregated landscapes ($h = 0$); the dashed line represents more aggregated landscapes ($h = 0.5$)

pinus were considered to be extremely susceptible to SPB infestation. After year 40, the proportion of pines decreased markedly (Fig. 7). When h was high, the initial reduction in pine proportion was greater than when h was low (Fig. 8). However, by the end of the simulation pine had declined further in the landscapes with low h than those with high h values.

Discussion

Our simulations suggest that landscape structure can influence the severity and extent of insect outbreaks. A considerable body of empirical research has developed regarding the response of insect herbivory to finer-scale spatial heterogeneity, i.e., the interspersed

of host and non-host trees within a stand (e.g., Jactel and Brockerhoff 2007). These studies indicate that insect herbivory is greater in pure stands than in those containing a mix of host and non-host tree species, a pattern that has been found for SPB-affected stands (Schowalter and Turchin 1993; Zhang and Zeide 1999). Several mechanisms have been proposed to explain why herbivory is lower in mixed stands: lower host availability, physical and chemical barriers to host location, and a greater abundance of predators and parasites (Jactel and Brockerhoff 2007).

In contrast, few studies have been conducted to investigate the implications of such neighborhood-scale forest heterogeneity for broader patterns of insect disturbance across a landscape. Jactel et al. (2002) found less insect infestation in pine stands in France that were located near mixed-species hardwood stands than in pine stands distant from hardwood stands, a broader pattern consistent with the finer-scale studies. Similarly, Powers et al. (1999) discovered that landscape “windows” with large patches of mature Douglas-fir (*Pseudotsuga menziesii*) were more vulnerable to bark beetle infestation than were windows with smaller patches or lower host abundance. A study of SPB infestations in Alabama (Ylioja et al. 2005) implied that a landscape containing small pine patches may be affected less severely by SPB than would a landscape with larger aggregations of pine. Our LANDIS simulations strongly suggest that the degree of forest aggregation that characterizes a landscape influences the severity and extent of insect infestations on that landscape. LANDIS modeling by Sturtevant et al. (2004), who used BDA to simulate spruce budworm infestations, projected that greater landscape aggregation would lead to more highly aggregated outbreaks. Together, these simulations and empirical studies imply that highly aggregated forest landscapes will be characterized by more extensive insect infestations, greater outbreak severity, and larger disturbed patches than less aggregated forests.

The spatial resolution of our simulated landscapes is particularly appropriate for investigating such patterns. Whereas most previous LANDIS applications, including (Sturtevant et al. (2004), use larger cell sizes (e.g. 1 ha), the use of 0.01 ha cells in this study represents the size of individual mature trees and thereby incorporates the tree-by-tree

neighborhood interactions important for the development of insect infestations (Jactel and Brockerhoff 2007). Although there is debate about the specific mechanisms by which these fine-scale tree distribution patterns affect infestations (Jactel and Brockerhoff 2007), LANDIS incorporates their influence via the neighborhood modifier. Hence our simulations predict the emergence of landscape-level disturbance patterns as a consequence of the characteristic arrangement of tree neighborhoods across a landscape.

The simulations suggest further that insect disturbances can restructure a landscape in ways that influence the continued impact of that disturbance agent. Specifically, the simulated SPB outbreaks altered the aggregation of host cells. These vegetation changes were the consequence of SPB-related pine mortality combined with colonization of some of the disturbed cells by more shade-tolerant hardwoods, which excluded further pine establishment on those sites. The disaggregation of the host patches influenced the characteristics of subsequent SPB outbreaks—regardless of the initial aggregation of pines, the extent of subsequent outbreaks was related to the level of pine aggregation at the time step in which an outbreak occurred (Fig. 5). Therefore SPB outbreaks rendered the landscapes less susceptible to extensive outbreaks later, and pines were able to persist at low levels even on the landscapes that initially were highly susceptible to SPB outbreaks (Fig. 8). The interplay between herbivory and pine forest fragmentation is consistent with the sequence of SPB infestations and pine fragmentation observed over several years on an actual landscape (Coulson and Wunneberger 2000) and, more generally, with the landscape ecological concept of reciprocal interactions between landscape pattern and process.

Although the disaggregation of pine stands destroyed the large contiguous patches of pine, the general outlines of the patches were not erased, but simply perforated, over the course of the simulations. This ecological memory (sensu Peterson 2002) was in part the result of the limited dispersal distances of trees used. Because the effective and maximum dispersal distances for our pines were set at 1 and 4 cells (10 and 40 m), in 150 years it is unlikely that the original structure of the landscape would be completely erased. Ecological memory also was a consequence of SPB infestations creating canopy

gaps that were colonized subsequently by the shade-intolerant pines. SPB outbreaks, combined with fire, are thought to play an important role in Table Mountain pine recruitment (Williams 1998). Interaction between SPB outbreaks and pine recruitment would appear to favor a feedback that could perpetuate the spatial patterns of both pine stands and SPB outbreaks, consistent with the hypothesis (Peterson 2002) that contagious disturbances interact with the landscape to generate ecological memory.

The simulation experiments we report here point toward a broader set of modeling experiments that need to be conducted to concretely tie the results to the real world. First, successional patterns of vegetation in this environment need to be simulated in an aspatial context. We have previously shown that LANDIS is capable of simulating the successional trajectories for the southern Appalachian Mountains (Lafon et al. 2007). Next, the importance of disturbances (fire and SPB) were evaluated singly and in concert with regard to succession on these sites (Waldron et al. 2007). The current study extends the previous ones to address specifically how neutral landscapes with controlled spatial characteristics respond to and influence SPB outbreaks. A further step in establishing these reciprocal interactions is to simulate actual landscapes with varying pine configurations, and to compare the simulated patterns to empirical observations on outbreak patterns during recent SPB outbreaks. Additional simulations for an actual landscape will explore how changes in management decisions or disturbance frequencies and intensities affect it. Such a real landscape will be subjected to multiple disturbances and have a more complicated spatial structure due to the presence of multiple landtypes representative of the complex terrain of the southern Appalachians. The results presented here are, thus, one step in a larger simulation endeavor aimed at increasing understanding of the effects of SPB on the southern Appalachian landscape.

Although we do not specifically address management issues in this paper, the results presented here should have implications for forest managers in the southern Appalachians concerned with the restoration of Table Mountain pine stands. In a recent review of the state of landscape ecological research, Turner (2005a) notes that landscape ecological principles in general, and the effect of pattern on process in

particular, have become important in formulating management plans for conservation areas and harvested forests in some instances (e.g. Bruinderink et al. 2003; Dupré and Ehrlén 2002). In the southern Appalachian Mountains, landscape structure has been altered considerably since the beginning of the 20th century by extensive logging and burning, which favored pine expansion (Williams 1998), followed by fire suppression. Large tracts of land dominated by mature pines that are particularly susceptible to SPB outbreaks have become common. Recently there has been interest in restoring southern Appalachian ecosystems to a more “natural” functioning. Our results imply that restoration scenarios for Table Mountain pine should consider not only how best to implement fire or other techniques to regenerate pines in decadent stands (e.g., Williams 1998), but also how management actions influence the spatial arrangement of pine stands throughout a landscape.

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