Simulating the Impacts of Southern Pine Beetle and Fire on the Dynamics of Xerophytic Pine Landscapes in the Southern Appalachian Mountains

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Abstract:

Question: Can fire be used to maintain yellow pine stands disturbed by periodic outbreaks of southern pine beetle?

Location: Southern Appalachian Mountains, USA.

Methods: We used LANDIS to model vegetation disturbance and succession on four grids representative of xeric landscapes in the southern Appalachians. Forest dynamics of each landscape were simulated under three disturbance scenarios: southern pine beetle, fire, and
southern pine beetle and fire, as well as a no disturbance scenario. We compared trends in the
abundance of pine and hardwood functional types as well as individual species.

Results: Yellow pine abundance and open woodland conditions were best maintained by a
combination of fire and southern pine beetle disturbance on both low elevation sites as well as
mid elevation ridges & peaks. On mid elevation SE-W facing slopes, pine woodlands were best
maintained by fire alone.

Conclusions: Restoration of pine woodlands in xeric southern Appalachian landscapes should
incorporate prescribed burning as a maintenance strategy.

Keywords: Forest disturbance; Forest restoration; LANDIS; Landscape modeling; Southern
Appalachians; Southern pine beetle; vegetation dynamics

Abbreviations: SPB = southern pine beetle; BDA = biological disturbance agent; SV = site
vulnerability; SRD = site resource dominance; SRDm = modified site resource dominance
Disturbance events exert a strong influence on forest structure, composition, and diversity by killing trees and altering the availability of plant resources (Connell 1978; White 1979; Huston 1994). Many ecosystems are affected by multiple disturbances that create varying impacts on vegetation (Frelich 2002; Kulakowski and Veblen 2002; Platt et al. 2002; Howe and Baker 2003; Lafon and Kutac 2003). The role multiple disturbance interactions play on landscapes is not well understood, but may be fundamental in the maintenance of the vegetation structure and composition. In fact, the removal or alteration of one or more of these disturbance processes can serve as a successional catalyst, driving the change from one ecosystem or community type to another (Holling 1992).

Changes occurring on xeric slopes and ridges in the southern Appalachian Mountains of the U.S. Southeast serve as an example of the importance of multiple interacting disturbance regimes on ecosystem function. Xeric slopes and ridges in the southern Appalachians have historically been maintained as open pine woodlands through a process involving multiple interacting disturbances (Barden and Woods 1976; Kuykendall 1978; White 1987; Smith 1991; Williams 1998). These open pine woodland ecosystems are now at risk from successional pressure by hardwoods due to a change in the southern pine beetle (SPB, Dendroctonus frontalis Zimmermann (Coleoptera:Curculionidae))-fire disturbance regime that once characterized this area. In particular, fire suppression efforts have reduced the occurrence of fire, resulting in a shift toward dense forest stands with an overstory of pines and an understory of young hardwood trees that will most likely replace the pines over time (Harrod et al. 1998, 2000; Lafon and Kutac 2003). As a result, xeric slopes and ridges in the southern Appalachians are undergoing both
changes in species composition (pines to hardwoods) and changes in landscape structure (open woodlands to dense forest).

Assessing the consequences of multiple interacting disturbances on successional trajectories is challenging due to the large spatial and temporal scales involved. While empirical field observation and experimentation is not feasible, computer simulation models offer a means for exploring the long-term implications of different disturbance scenarios.

In this paper, we use LANDIS 4.0 (hereafter LANDIS), a computer model for simulating disturbance and succession on forest landscapes, to investigate the role of two types of disturbance – fire and SPB outbreaks – in xerophytic yellow pine (Pinus L., subgenus Diploxylon Koehne) forests of the southern Appalachian Mountains, USA. Understanding the relationship between fire, insect disturbance, and mesoscale (scale at which processes operate at 1s-10s of kilometers and years to decades; Holling 1992) forest landscape dynamics will not only provide insight as to the processes involved in shaping southern Appalachian ecosystems, but will also add to the general conceptual issues surrounding multiple disturbance interactions. Moreover, because land managers are increasingly using prescribed burning as a restoration tool in the southern Appalachian Mountains (Pyne 1982, SAMAB 1996, Williams 1998, Haines and Busby 2001, Palik et al. 2002, van Lear and Brose 2002) without knowing its implications on long-term forest dynamics, we demonstrate the utility of our modeling approach to forest restoration efforts.

Background

Fire and the southern Appalachian Mountains
The southern Appalachians, defined here as the portion of the Appalachian Mountains that extends from the southern terminus of the range in northeastern Alabama to the northern border of Virginia, are mountainous with a humid, continental climate (Bailey 1978). Because of the topographic variation, temperature and precipitation exhibit pronounced microscale spatial patterns. Community types range from mesophytic hemlock-hardwood forests on valley bottoms, to xeric yellow pine woodlands on ridgetops; and from low-elevation temperate deciduous forests to high-elevation spruce-fir (*Picea-Abies*) stands (Whittaker 1956; Stephenson *et al.* 1993).

Fire was historically important in shaping the vegetation communities in the southern Appalachians (Harmon 1982, Sutherland *et al.* 1995, Randles *et al.* 2002, Waldrop *et al.* 2002, Lafon *et al.* in review). Detailed records of fire history have been constructed for the past 150–400 years using dendroecological techniques (Harmon, 1982; Sutherland *et al.*, 1995; Shumway *et al.*, 2001; Armbrister, 2002; Shuler and McClain, 2003). These studies suggest that surface fires burned at intervals of about 5–15 years in pine and oak woodlands of the southern and central Appalachian Mountains. More intense stand-replacing fires are also known to have occurred (Sutherland *et al.*, 1995). These fire history analyses also reveal a marked decline in fire frequency during the mid-1900s which is associated with efforts to exclude fire from the forests.

**Southern Pine Beetle**

Indigenous to the southern U.S., SPB has been known to infest pitch pine (*Pinus rigida* Mill.), Virginia pine (*Pinus virginiana* P. Mill.), Table Mountain pine (*Pinus pungens* Lamb.), and occasionally eastern white pine (*Pinus strobus* L.) (Payne 1980, Coulson *et al.* 1999,
Coulson and Wunneburger 2000) in the southern Appalachian Mountains. Pertinent features of the natural history of the SPB were summarized by Flamm et al. (1988) and Coulson et al. (1998). The SPB is a cryptic insect that spends most of its life cycle in the inner bark of host trees. The host tree provides a protected habitat as well as food resources. Upon completion of the life cycle, adults disperse and colonize new hosts. Multiple-tree infestations often develop in stands occurring on sites with poor nutrient and/or moisture content that contain mature host species with high basal area and stagnant radial growth. Such stands are considered to be at high hazard for infestation (see Mason et al. 1985 for a discussion of hazard rating systems for the SPB). These high hazard stands are important in SPB epizootiology as they represent habitat patches suitable for enlargement of infestations. Outbreaks are centered initially in high hazard stands, but when populations of the insect become large, less preferred hosts occurring on low hazard sites are also infested.

Outbreaks of SPB occur periodically. In the Piedmont and Coastal Plain, outbreaks generally occur on a 7-10 yr cycle (Price et al. 1998). However, in the southern Appalachians the cycles are less frequent and occur on 10-25 year cycles. Causes for SPB outbreaks are poorly understood but when favorable environmental conditions coincide with optimal resource availability, populations increase in size and outbreaks often follow (Rykiel et al. 1988).

Fire-Beetle Interaction on Xeric Slopes & Ridges

The xeric slopes and ridges of the southern Appalachian Mountains are dominated by Yellow pines (Pinus) and oaks (Quercus). It has been suggested that SPB outbreaks are a key factor in driving the succession of these yellow pine woodlands (Harmon 1980; Harrod et al. 1998; Williams 1998; Harrod et al. 2000). When disturbances, such as ice storms and SPB
outbreaks, impact xeric pine-oak forests, the successional trend may be towards oak domination (Williams 1998). However, when fire is also present, the successional trend will be towards pine domination, maintained in a drought-beetle-fire cycle (Barden and Woods 1976; Kuykendall 1978; White 1987; Smith 1991; Williams 1998). For instance, Lafon and Kutac (2003) discovered that pine populations were heavily reduced and pine regeneration was absent on xeric sites disturbed by ice storms and SPB; however, abundant regeneration occurred on neighboring sites disturbed by ice, SPB, and fire. While SPB may aid in regenerating pines by adding to fuel loads under an active fire regime, they may reduce pine populations in the absence of fire (Kuykendall 1978; Williams 1998). A relationship between fire and SPB has been suggested (Showalter et al. 1981), but is not yet fully understood. Over long time periods, fire reduces tree density and creates more open woodland conditions (Delcourt and Delcourt 1998, Harrod et al. 2000). Such low-density spacing would be unfavorable to severe SPB outbreaks.

Methods

Study Area

Great Smoky Mountains National Park (GSMNP) serves as a model for the hypothetical landscapes we simulate. GSMNP is a 2,110 km² World Heritage Site and International Biosphere Reserve straddling the border between western North Carolina and eastern Tennessee. GSMNP serves as an ideal model for this study as most major ecosystems of the southern Appalachians are represented, and the general topographic distribution of communities and tree species have previously been described (Whittaker 1956).

Model description
LANDIS (LANdscape DIsturbance and Succession) is a raster-based spatially explicit computer model designed to simulate forest succession and disturbance across broad spatial and temporal scales (Mladenoff et al. 1996, He et al. 1996, He and Mladenoff 1999a,b, He et al. 1999a,b, Mladenoff and He 1999). Originally developed to simulate succession as well as harvesting, windthrow, and fire disturbance on the glaciated plains of the upper Midwest (Mladenoff 2004), LANDIS has been successfully adapted for use in the Missouri Ozarks (Shifley et al. 1998, 2000), the southern California foothills (Franklin et al. 2001, Franklin 2002, Syphard and Franklin 2004), northeastern China (He et al. 2002, Xu et al. 2004), Fennoscandia (Pennanen and Kuuluvainen 2002), Quebec (Pennanen et al. 2004), the Dischma Valley, Switzerland (Schumacher et al. 2004), and the Georgia Piedmont (Wimberley 2004). Recently, we have demonstrated the utility of LANDIS in modeling the effects of fire on pine and oak forests in the southern Appalachians (Lafon et al. in review).

Landscapes in LANDIS are subdivided into landtypes which contain environmentally specific parameters regarding species establishment as well as disturbance behavior. These landtypes are then further subdivided into individual sites or cells. Tree species are simulated as the presence or absence of 10-yr age cohorts on each cell. At the site (cell) level, LANDIS manages user-defined species life history traits (longevity, min age at reproduction, shade tolerance, fire tolerance, min/max seed dispersal distances, and resprout probability) at 10-yr time steps. Succession is based on the species specific characteristics of dispersal, shade tolerance, and habitat suitability. Disturbance can be modeled in terms of fire, wind, harvesting, and biological agents (insects, disease) (Sturtevant et al. 2004a).

Fire is modeled in LANDIS as hierarchical stochastic processes based on fire ignition, fire initiation, and fire spread (Yang et al. 2004). The number of ignitions on a given landtype is
first determined based on a user-determined value corresponding to the average number of ignitions per decade. Fire initiation occurs if the probability of ignition, which is determined by the time since the last fire, is sufficient to generate a fire. Once fire initiation occurs, fire is spread in the cardinal directions until it reaches its maximum possible user-defined size or until it reaches a break (Yang et al. 2004). Fire severity is an integer between 1 (least severe) and 5 (most severe) and is determined by the time passed since the last fire event on each cell. Probability of mortality from fire is a function of tree age and species whereby low-intensity fires kill young/fire-intolerant species, while fires of higher intensity kill larger trees and more fire-tolerant species (He and Mladenoff 1999b).

Biological disturbances in LANDIS are modeled using the Biological Disturbance Agent (BDA) module. Biological disturbances are probabilistic at the site (cell) level. Each site is assigned a Site Vulnerability (SV) probability value that is checked against a uniform random number to ultimately determine if that site has been affected by a biological agent. Site vulnerability can either be directly equated with the Site Resource Dominance (SRD) value which ranges from 0-1 and is based on species and species age, or it can also be modified by three variables to determine the impact on a given site. The first of these variables is the Modified Site Resource Dominance (SRDm) which determines the presence of susceptible hosts based on stress from other disturbance or environmental factors. The second factor, Neighborhood Resource Dominance (NRD), determines the effect of hosts/nonhosts in neighboring cells. The third factor is the periodicity of outbreaks which can either be chronic, cyclic, or random. The functioning of these variables, and of the BDA in general, are described in detail in Sturtevant et al. (2004b) and thus will not be discussed here.
The study of forest pattern, structure, and succession is scale dependent. LANDIS is an effective tool for generalizing forest succession on mesoscale landscapes. At these scales, disturbance processes such as fire and insect outbreaks dominate the formation of vegetation pattern (Holling 1992). It is important to note, however, that these generalizations, while important, neither apply to microscale processes that may be occurring at sub-annual and sub-meter levels nor to macroscale processes that may influences forest dynamics at 100s of kilometers or centuries to millennia (Holling 1992).

Model Simulations

We used LANDIS to simulate forest dynamics over a 1000-year period on low and mid elevation xeric landscapes. For consistency, each landscape comprised and single landtype represented by a 100 x 100 cell grid with a cell size of 10 m × 10 m. To capture xerophytic landscapes, we used 4 landtypes 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).

To capture the predominant elevation and moisture gradients that influence vegetation distribution in the southern Appalachians, we used hypothetical landscapes. Hypothetical landscapes are commonly used in simulation modeling studies to facilitate model interpretation on a controlled environment (e.g., Mladenoff and He 1999; Pennanen et al. 2004; Syphard and Franklin 2004). For this study we used a simple grid environment to glean information on within-landtype successional dynamics without the influence of spatial complexities. By first understanding succession and process behavior on simple landscapes, we will later be able to better interpret subsequent modeling investigations using more complex spatial arrangements.
We used fifteen tree species in our simulations (Appendix; 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 (e.g., Lafon, 2004; Sturtevant et al., 2004b; Wimberly, 2004). These life history traits were further altered to reflect species responses specific to the southern Appalachian Mountains (David Loftis and Henry McNab, Bent Creek Experimental Forest, Asheville, NC. Unpublished Data). Because we were not investigating dispersal effects for this study, identical dispersal capabilities (0.95 within 20 m and 0.05 between 20 m and 40 m) were assigned to all species to minimize the influence of dispersal effects on model projections. Establishment coefficients were based on the abundance of tree species along the elevation and moisture gradients in the Great Smoky Mountains (Whittaker 1956). These initial abundance values were further modified by drought and shade tolerance parameters to obtain species-specific establishment coefficients for each landtype (Lafon et al. in review).

The initial abundance of species on each landtype was based on the relative abundance of the species following Whittaker (1956). Each 100 m$^2$ cell was then populated randomly with a single species based on its relative abundance in each of the landtypes (Figure 1).

We simulated three disturbance scenarios: (1) SPB, (2) Historic Fire Regime, and (3) SPB with Historic Fire Regime. A non-disturbance scenario was added for comparison. For the historic fire regime, target fire return intervals for each landtype were derived from dendroecological reconstructions of past fire return intervals in yellow pine forests of the southern Appalachian Mountains (Harmon 1982; Sutherland et al. 1995; Armbrister 2002). The return interval for each landtype was calibrated by adjusting fire parameters until the mean return interval for ten 1,000-year simulations was within 10% of the target interval of 10 years on xeric sites (cf. Wimberly 2004, Lafon et al. in review). Because fire history information is lacking to
distinguish among the fire regimes of the four landtypes we simulate, fire severity curves were identical for all four landscapes with class 2 fires occurring after 10 years, class 3 fires after 30 years, class 4 fires after 60 years, and class 5 fires after 120 years without burning.

The BDA module was parameterized to mimic SPB outbreaks in the southern Appalachians. Each of the pine species in the model (\textit{P. pungens}, \textit{P. rigida}, \textit{P. virginiana}, and \textit{P. strobus}) was assessed for its vulnerability to SPB attack. Vulnerability in LANDIS is defined by tree age. Vulnerability of southern Appalachian yellow pine species to attack by SPB is correlated to tree diameter (Coulson \textit{et al.} 1974, Leuschner \textit{et al.} 1976) (Appendix; Table 2). Growth rates were generalized for the southern Appalachians to arrive at vulnerability ages (Brian Kloeppl, Coweeta LTER Co-Lead Principal Investigator, pers. comm. November 11, 2004.) (Appendix; Table 2). These data were then rounded to the appropriate 10-yr age cohort class for LANDIS input.

For these simulations, we modified vulnerability by fire. Because of subsequent density reduction, the disturbance modifier, which can range from -1 to +1, was set equal to -1 for 20 years following fire. The radius of influence for the Neighborhood Resource Dominance was set to 30m which is consistent with the attractiveness area of pines under bark beetle attack (Turchin 1998). The weight of the Neighborhood Resource Dominance was set to be equal to that of the Site Resource Dominance (Neighborhood Weight = 1). 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, which is an integer between 0 (no activity) and 3 (severe outbreak), was set at a minimum of 1 and maximum of 3 for each 10-yr time step as SPB activity is chronic and there is a high potential for SPB outbreaks to occur each decade.
Because LANDIS is a stochastic model, we generated 10 sets of model runs for each disturbance scenario on each landtype to account for potential variability. Each of the sets was created by varying the LANDIS seed variable by increments of 1000 for replication.

**Results**

Each of the four disturbance scenarios had distinct impacts on the abundance of pines in each of the four landtypes (Figure 2). While there is some variation in results between the four landtypes, in general, SPB alone leads to the removal of pines and dominance of hardwoods, Fire alone leads to the removal of hardwoods and dominance of pines, and the combination of SPB and fire tends to stabilize both pine and hardwood populations at levels near the initial conditions. In the no disturbance scenario, hardwoods become dominant because of a combination of resprouting and shade tolerance.

The functional type results may be somewhat misleading without also interpreting the results of individual pine species trends (Figure 3). The most distinctive difference was between the behavior of white pine (*Pinus strobus*) and the three yellow pines, however, individual variations were present for all species and landtypes.

In the low elevation scenarios, *P. strobus* substantially increased in abundance in the absence of fire and in the presence of SPB but was removed from the landscape in the presence of fire and SPB/fire (Figure 3C,G). *P. rigida* increased in abundance with presence of fire and maintained abundance with SPB/fire, but was removed from the landscape with SPB alone and with no disturbance (Figure 3B,F). *P. virginiana*, which began as the most dominant species, maintained abundance with fire and SPB/fire and was removed from the landscape with SPB disturbance only as well as with no disturbance (Figure 3D,H).
On mid elevation SE-W facing slopes both *P. rigida* and *Pinus pungens* (Figure 3I,J) increased in abundance in the fire scenario. In the SPB/fire scenario, *P. rigida* declined, while *P. pungens* remained stable. *P. rigida* and *P. pungens* populations were reduced to zero in the SPB scenario and to near zero in the no disturbance scenario. On mid elevation ridges and peaks, both *P. rigida* and *P. pungens* (Figure 3M,N) increased in abundance with the presence of fire and were nearly removed with just SPB and no fire. In the SPB/fire scenario, *P. rigida* dropped in abundance while *P. pungens* maintained its abundance.

Based on the proportion of empty cells, the mixed SPB/fire scenario created and maintained open woodland conditions on ridges & peaks as well as on low elevation SE-W facing slopes (Figures 4,5). Fire alone also created such conditions, although to a somewhat lesser extent. The SPB only disturbance scenario resulted in a spatial arrangement suggestive of denser closed-canopy forests.

**Discussion**

The modeling projections presented here suggest that the regime of multiple interacting disturbances have important implications for the successional dynamics and vegetation characteristics in yellow pine woodlands of the southern Appalachian Mountains. When acting alone, fire was projected to create conditions favoring pine presence at levels higher than input, while SPB disturbance acting alone resulted in the removal of yellow pines. Additionally, our model projections suggest that a combination of fire and SPB disturbance creates sustainable yellow pine communities over the long term. This conclusion is consistent with the hypothesis that fire and SPB are part of a disturbance regime that maintains yellow pine woodlands (White 1987; Williams 1998; Harrod et al 1998, 2000; Lafon and Kutac 2003). Our results also suggest
that the combination of fire and SPB would maintain open woodland conditions more consistently and at a higher proportion than any other scenario. This vegetation configuration, which likely consisted of an understory of shrubs and/or grasses, is thought to have been typical of xeric sites in the southern Appalachians at the time of contact (Delcourt and Delcourt 1998, Harrod et al. 2000).

The only landtype that did not fit the pattern of open conditions was mid elevation SE-W facing slopes. In this scenario, fire alone created more open conditions than did the combination of fire and SPB. This is directly attributable to the rise of one species, black locust (*Robinia pseudoacacia* L.). In the simulations, *R. pseudoacacia* is present only in low- and mid-elevation SE-W facing slopes. In the low elevation simulations, *R. pseudoacacia* became dominant at year 750 and *P. virginiana* and *P. rigida* share dominance but to a lesser extent. However, in the mid-elevation simulations, *R. pseudoacacia* became dominant by year 350 and shared dominance only with *P. pungens*. The reason for this trend lies in the nature of *R. pseudoacacia* as an extremely shade-intolerant and fire-intolerant species. While fire disturbance keeps *R. pseudoacacia* populations low in the fire-only scenario, in the SPB/fire scenario gaps are created where *R. pseudoacacia* can establish following the removal of pines by SPB. Once *R. pseudoacacia* establishes under these conditions it is very difficult to remove, because although it is very intolerant of fire, it has a very high probability of resprouting. Consequently, mid-elevation sites were converted to a *R. pseudoacacia/P. pungens* forest with relatively closed canopy conditions. These results are consistent with ecological data for the southern Appalachian region (Beck and McGhee 1974, McGhee and Hooper 1975). Boring and Swank (1984) found that *R. pseudoacacia* dominated former *Q. prinus* communities and became a major component in *Q. coccinea-P. rigida* communities after clearcutting. However, they also
noted that these stands eventually decrease in abundance as a result of locust stem borer
(megacyllene robiniae Forster), which is not accounted for in these simulations.

The results of this study provide a step toward incorporating mesoscale modeling as a
decision-making aid for restoration of xerophytic vegetation in the southern Appalachian
Mountains. Our modeling results yield several conclusions that are important to forest managers
when undertaking restoration efforts. First, our projections suggest that P. pungens, more than
any other species, thrives when in a disturbance regime combining SPB and fire disturbances on
xeric sites. Because P. pungens is a southern Appalachian endemic, it is also important for
biodiversity conservation (Zobel 1969). These factors suggest that P. pungens could be a species
of particular interest for restoration efforts on low- to mid-elevation ridges and SE-W facing
open slopes in the southern Appalachians. Second, because forest stand conditions resulting from
fire and SPB herbivory would eliminate large contiguous pine forests, and therefore reduce the
likelihood of outbreaks, a management strategy that includes prescribed burning would be
beneficial. This conclusion is further supported by the fact that low basal area forests, such as
those created in the SPB and fire scenario, are not conducive to development of large individual
infestations. According to these simulations, it is therefore likely that restoring historic
disturbance regimes (i.e., fire) would result in a concomitant restoration of community
composition and structure in which the extent and severity of SPB outbreaks are within the
historic range of variability.

LANDIS has a number of limitations that must be considered when interpreting the
results of a study such as this. For example, the LANDIS model design did not permit us to
assess the contribution of SPB outbreaks to fuel loads and fire behavior. Moreover, we have
been unable to assess the impact of shrub and herbaceous species that may be important in the
functioning of these systems. Also, our results concerning open woodland conditions are contingent on the assumption that the open cells would represent the conditions of grass and shrub presence. While open cells act as fire breaks within the model, they would act as fire conduits in a real-world setting.

The work presented here is part of a larger effort to apply LANDIS as a decision-making tool for restoration of southern Appalachian forests that are influenced by multiple disturbance agents. Our modeling results imply that while SPB can play an important role in maintaining these systems, the beetle could eventually lead to the destruction of xeric pine forests in the southern Appalachians if the key disturbance process of fire is not reintroduced. As fire is an important part of the maintenance of these systems it should be considered in developing management strategies. However, because the southern Appalachian Mountains exhibit complex and interacting climatic, topographic, and biological features, any restoration efforts would require careful consideration and planning.

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Figure 1. Abundance (percentage of grid cells occupied) for each landscape at year 0; A) Low Elevation SE-W Facing Slopes, B) Low Elevation Ridges and Peaks, C) Mid Elevation SE-W Facing Slopes, D) Mid Elevation Ridges and Peaks.
Figure 2. Change in abundance (percentage of grid cells occupied) of Pine and Hardwood functional types through time. Solid lines show average values for ten model runs, dashed lines delineate the maximum and minimum values returned for each of ten model runs.
Figure 3. Change in Abundance (percentage of grid cells occupied) of pine species over time.
Figure 4. Change in abundance (percentage of grid cells occupied) of empty cells through time.
Figure 5. Distribution of empty cells (white) versus occupied cells (gray) across all scenarios and landtypes.
Appendix
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<td><em>Pinus virginiana</em></td>
<td>100</td>
<td>20</td>
<td>1</td>
<td>4</td>
<td>0.1</td>
<td>0.083</td>
<td>0.075</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td><em>Quercus alba</em></td>
<td>450</td>
<td>30</td>
<td>3</td>
<td>3</td>
<td>0.5</td>
<td>0.016</td>
<td>N/A</td>
<td>0.08</td>
<td>N/A</td>
</tr>
<tr>
<td><em>Quercus rubra</em></td>
<td>300</td>
<td>25</td>
<td>2</td>
<td>3</td>
<td>0.4</td>
<td>0.018</td>
<td>N/A</td>
<td>0.211</td>
<td>0.106</td>
</tr>
<tr>
<td><em>Quercus coccinea</em></td>
<td>130</td>
<td>25</td>
<td>1</td>
<td>3</td>
<td>0.4</td>
<td>0.083</td>
<td>0.075</td>
<td>0.041</td>
<td>0.041</td>
</tr>
<tr>
<td><em>Quercus prinus</em></td>
<td>350</td>
<td>25</td>
<td>3</td>
<td>3</td>
<td>0.9</td>
<td>0.115</td>
<td>0.053</td>
<td>0.115</td>
<td>0.057</td>
</tr>
<tr>
<td><em>Quercus velutina</em></td>
<td>150</td>
<td>25</td>
<td>2</td>
<td>3</td>
<td>0.7</td>
<td>0.106</td>
<td>N/A</td>
<td>0.106</td>
<td>N/A</td>
</tr>
<tr>
<td><em>Robinia pseudoacacia</em></td>
<td>100</td>
<td>15</td>
<td>1</td>
<td>1</td>
<td>0.9</td>
<td>0.188</td>
<td>0.094</td>
<td>0.375</td>
<td>0.188</td>
</tr>
<tr>
<td><em>Tsuga canadensis</em></td>
<td>450</td>
<td>50</td>
<td>5</td>
<td>1</td>
<td>0</td>
<td>0.008</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
</tbody>
</table>

mxAge: expected longevity; mtAge: Age at reproductive maturity; shTl: Shade Tolerance (1-5, 1 denotes least shade tolerance); frTl: Fire Tolerance (1-5, 1 denotes least tolerance to fire); prRes: Probability of resprouting; esPb: Establishment Probability (1: low elevation SE-W facing slopes, 2: low elevation ridges & peaks, 3: mid elevation SE-W facing slopes, 4: mid elevation ridges & peaks).
Table 2

SPB Host Vulnerability Ages

<table>
<thead>
<tr>
<th>Minor Host dbh</th>
<th>Minor Host Age</th>
<th>Secondary Host dbh</th>
<th>Secondary Host Age</th>
<th>Primary Host dbh</th>
<th>Primary Host Age</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pinus pungens</em></td>
<td>10.16 cm</td>
<td>20</td>
<td>10.16 – 15.24 cm</td>
<td>35</td>
<td>&gt; 15.24 cm</td>
</tr>
<tr>
<td><em>Pinus rigida</em></td>
<td>10.16 cm</td>
<td>15</td>
<td>10.16 cm</td>
<td>15</td>
<td>&gt; 10.16 cm</td>
</tr>
<tr>
<td><em>Pinus virginiana</em></td>
<td>10.16 cm</td>
<td>20</td>
<td>10.16 – 15.24 cm</td>
<td>25</td>
<td>&gt; 15.24 cm</td>
</tr>
<tr>
<td><em>Pinus strobus</em></td>
<td>10.16 cm</td>
<td>15</td>
<td>10.16 – 20.32 cm</td>
<td>25</td>
<td>N/A</td>
</tr>
</tbody>
</table>