DESIGNING A LANDIS PRO HARVEST MODULE AND EXAMINING THE EFFECTS OF TEMPORAL RESOLUTION ON SIMULATION OUTCOMES

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by
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The undersigned, appointed by the Dean of the Graduate School, have examined the thesis entitled

DESIGNING A LANDIS PRO HARVEST MODULE AND EXAMINING THE EFFECTS OF TEMPORAL RESOLUTION ON SIMULATION OUTCOMES

Presented by Jacob Sapp Fraser

A candidate for the degree of Master of Sciences

And hereby certify that in their opinion it is worthy of acceptance.

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INTRODUCTION

Forest landscape models have been developed as tools for researching the effects of natural or anthropogenic factors on a landscape that could not be easily examined due to temporal or spatial limitations (Mlandenoff & He, 1999). Early stand dynamics models, known as gap models, were able to simulate forest succession and disturbance on small plots that were then scaled up to represent an entire landscape, but lacked spatial interaction between plots (Shugart & West, 1980). Spatially explicit forest landscape models were developed that also simulated succession and disturbance for each site but additionally allowed interaction between sites during these processes. The evolution of computational resources has allowed these models to increase the size of simulated landscapes at finer temporal resolutions while maintaining, or increasing, the site-level detail.

For this thesis I will be looking at two aspects of the LANDIS spatially explicit forest landscape model (Mlandenoff & He, 1999), specifically LANDIS PRO 7.0 (Wang, et al., 2012). The first chapter of my research will examine the theoretical design and testing of a harvest simulation module for LANDIS PRO 7.0 that utilizes quantitative tree data stored for each species in order to control harvest events. The purpose of the second chapter is to investigate the effect of time-step on model simulation outcomes by qualitatively and statistically comparing simulation results from three different time-steps using the same landscape under two separate scenarios.

CHAPTER 1. DESIGNING A LANDIS PRO HARVEST MODULE

INTRODUCTION

Spatially explicit forest landscape models have become important tools for understanding large-scale and long-term landscape (spatial) processes such as climate change, fire, windthrow, seed dispersal, insect outbreak, disease propagation, forest harvest, and fuel treatment, because controlled field experiments designed to study the effects of these processes are often not possible (Shifley, et al., 2006). In forest landscape models one of the most influential factors is disturbance. This can be simulated on a landscape as several different events such as fire, wind, disease and human activities. All the effects of these events combine to alter the heterogeneity of the landscape, from the species and age structure at the stand level to the spatial pattern at the landscape level. Harvest events are unique, in that they are completely dependent on humans and therefore can be precise about the species, size, spatial pattern and timing with regards to the harvest.

Early model types, such as gap models and ecosystem process models, were able to simulate succession and disturbance using individuals at a site level, but these processes were unable to interact with adjacent sites, limiting the model's ability to simulate landscape level processes. Eventually forest landscape models were developed to simulate disturbance and seeding across a landscape while still simulating succession at the site level (He, 2008). These new models were better suited to examine the long-term ecological effects of a scenario across a landscape (Scheller & Mladenoff, 2007). With the advancement of personal computer technology, these models have been developed to simulate fine spatial and temporal resolutions as well as an increase in site-level detail.

Traditionally forest landscape models must sacrifice many quantitative site-level details, such as number and size of individuals for each species, if a large spatial scale is to be simulated (Gustafson, et al., 2000). Without these quantitative metrics the minimum size of any disturbance occurring on a site is limited to the spatial resolution.

To date, forest landscape models have contributed relatively little to guide forest management planning and operation because of the two bottlenecks. First, they have been unable to simulate sufficiently large landscapes to demonstrate the effects of the spatial interactions between forest landscape processess and site-scale dynamics (He, et al., 2011). Second, the predicted outcomes of forest landscape models are largely incompatible to forest inventory data. Numerous approaches have been attempted to simplify site-level processes to achieve the capability of simulating forest landscape processes at landscape scales (Keane, et al., 2004) (Scheller & Mladenoff, 2007) (He, 2008). In forest landscape models, site-level processes can be divided into two distinct, hierarchical processes: species level processes and stand-level processes. Species-level processes simulate tree species birth (germination and establishment), vegetative reproduction, growth, and mortality. Stand-level processes simulate competition for resources (such as light and nutrients), which regulates species-level process, such as mortality caused by self-thinning (Oliver & Larson, 1990) (Pacala, et al., 1996) (Deutschman, et al., 1999). Most current FLMs do not explicitly simulate stand level processes. They either use rules defined through species vital attributes (e.g., higher shade tolerance species outcompete lower shade tolerance species) or predefined succession pathways to simulate stand-level processes. Consequently such an approach sacrifices the population information (e.g., density, tree number, and basal area) with results in primarily qualitative forms such as species absence/presence in LANDIS (Mladenoff, et al., 1996) (He & Mladenoff, 1999a) (He & Mladenoff, 1999b) or forest types in LANDSUM (Keane, et al., 2002) and SIMPPLLE (Chew, et al., 2004). The qualitative simulation results from FLMs are largely incompatible with and unable to be rigorously validated against tree density and size that are readily available from standard forest inventories (Jenkins, et al., 2001). Nor can contemporary FLMs be applied to guide on-the-ground forest management due to the lack of quantitative detail (Shifley, et al., 2009). The LANDIS family of models are spatially explicit and able to simulate larger landscapes with disturbance and succession occurring at the site level. Using the vital attributes method individual species interact within a site based on user-defined values for shade tolerance, longevity, reproduction age and seeding (He, 2008). In previous versions of LANDIS each species was represented on a site by the presence or absence of age classes. Any disturbance operating on a species could only remove entire age classes. LANDIS harvest module (Gustafson, et al., 2000) has spatial, temporal, and species age-cohort removal components. The spatial component controls how harvest activity is affected by stand and management unit boundaries and adjacency constraints, while the temporal component allows simulation of iterative harvesting rotations and multiple-entry silvicultural treatments (e.g., shelterwood or periodic group selection harvests within stands). The species age-cohort component allows specification of the species and age cohorts that will be removed by each harvest activity (e.g., clearcutting, selection cutting, and shelterwood cutting). Most harvest prescriptions can be simulated by various combinations of these three components (Gustafson, et al., 2000). However, due to the binary presence/absence age cohort structure, the above silvercultural treatments can be only approximated using age classes. Such a design may be useful in evaluating the dynamics forest landscape pattern as a result of harvest. However, the information such as the number of age cohorts removed is not compatible to actual forest silvercultural treatment that is often specified as target basal area and density.

Recently, LANDIS PRO forest landscape model has been developed. LANDIS PRO is a new model based on over a decade of development and testing of the original LANDIS model (He & Mladenoff, 1999a) (Mladenoff, 2004). In LANDIS PRO 7.0 the model has been modified to track numbers of individuals in each age class. This adds the ability to track quantitative site metrics such as number of individuals and, using an age to size conversion, basal area. In addition, this allows the succession and disturbance processes to operate on individuals rather than entire age cohorts.

In the LANDIS PRO 7.0 harvest module there are some elements of stochasticity, but unlike other disturbance events the user has a large amount of control over the location and severity of their occurrence. Since the model tracks individuals at the site level, the harvest module is able to select sites based on stocking level criteria set by the user,then apply harvest prescriptions that may remove all or part of individual age cohorts. The purpose of the harvest module is to allow users to simulate real or proposed management scenarios over a large landscape.

Objectives

The objectives of this study are: (1) to design a harvest module for LANDIS PRO 7.0 that uses the more detailed site data structure, allowing the user to target specific forest conditions for treatment and define harvest events that produce a predictable result on those areas; (2) to test the model's ability to realistically simulate the effects of common harvest practices on forest stands; (3) to test the effect of the harvest module on forest composition across a landscape.

APPROACH AND METHODS

Study Area

To demonstrate the design of LANDIS PRO harvest module, we selected a large forest landscape with mixed landownerships in southern Missouri. The study area that will be simulated is comprised of 6,800 square miles of forested area in the Ozark Highlands ecological section in Missouri (Figure 1). This area is designated by the US Forest Service FIA manual as unit 1 in Missouri. The Ozark Highlands cover most of the southern half of Missouri and parts of Arkansas, Oklahoma, Illinois and Kansas. Erosion and weathering of the limestone, chert and dolomite parent material has created a rugged, hilly ecosystem interspersed with sections of plateaus and rolling prairies. The karst topography found in this region is caused by the weathering of parent material and creates a landscape with many caves, springs and sinkholes. The soil formed in the ecological section is generally gravelly, shallow and acidic. The boundaries of the study area roughly coincide with ecological subsection boundaries. The five ecological subsections represented in the study area are Central Plateau, Meramec River Hills, Current River Hills, St. Francois Knobs and Basins, and Black River Ozark Border (Nigh & Schroeder, 2002). Average annual precipitation for the area ranges from 40 to 49 inches and average annual snowfall ranges from 10 to 18 inches. The mean minimum daily temperature in January is 20^{o} and the average maximum daily temperature in July is 90^{o}. The varying terrain and geology in this region cause a variety of microclimates that can create unique habitats for plant and animal species.

The study area contains 1,600 square miles that are designated as Mark Twain National Forest, including the Potosi, Salem, Fredricktown, Poplar Bluff and Eleven Point districts. Common tree species in this area include white oak (*Quercus alba*), post oak (*Quercus stellata*), black oak (*Quercus velutina*), hickory (*Carya spp*.), sugar maple (*Acer saccharum*) and shortleaf pine (*Pinus echinata*).

LANDIS 7.0 PRO Model Description

LANDIS 7.0 PRO is a new model developed that is based on previous LANDIS versions (e.g., LANDIS 2.0-6.0) (He, et al., 2009). It preserves the functionalities of LANDIS (3.0-6.0) and introduces a new succession module that is based on quantitative stand attributes. LANDIS 7.0 PRO is a raster based, spatial model that can simulate forest landscape changes over time. In addition to normal forest succession as a factor for change, LANDIS can simulate stochastic disturbances such as wind, fire, disease and insect damage as well as user defined disturbances such as harvest and controlled burning. The user provides initial condition information in the form of GIS based map files and text files that define species and event characteristics. Using these files, LANDIS 7.0 PRO creates an initial landscape where each cell is populated with individual trees. In order to simulate succession, the model calculates tree density on the plot as well as establishment and mortality (Wang, et al., 2012).

Individual tree growth is controlled by a either a default function or a user specified value for each species. The default function has two separate curves that apply to softwood or hardwood species. This function uses the fraction of species longevity plotted against the fraction of species maximum diameter that is set in the species attribute file. If the user decides to provide their own growth rate, this is done for each species up until its maximum longevity at intervals equal to the time-step of the model.

Seed dispersal is regulated by a negative exponential function by default. The user may define a custom seed dispersal for each species that is calculated by a defined probability over distance intervals equal to the cell size of the model. Once growth and seed dispersal has been calculated, the model calculates the growing space occupied (GSO), or current percent of the site that is covered by trees. The value for GSO measures the current growing space for species. The maximum GSO can exceed 1.0 when there are multiple vertical canopy structures present on the site. Each land type has a specified maximum GSO in order to simulate the effect of land type on species composition.

Next the number of potential established seedlings (NPES) is calculated for the site. This takes the GSO for the site into account and calculates a potential growing space (PGS). There are five PGS values for each site to correspond with the five shade tolerance classes that all species may fall under. A species with higher shade tolerance will have a higher PGS value. The PGS value for each species is multiplied by that species' establishment coefficient on the current land type which is specified in the land type attribute file. This determines the number of seedlings for each species that successfully establish on the site.

Mortality on the site is controlled by a probability function based on the age of a tree and the total basal area of the site. Just like other functions, the user can provide default probabilities of mortality for each species at an interval equal to the time-step of the model.

Once all these factors are calculated, LANDIS 7.0 outputs a series of GIS maps for each time-step that show the number of trees, basal area, and ages for each pixel.

LANDIS 7.0 PRO MODEL PARAMETERIZATION

Data Preparation

Both spatial and forest inventory data was required in order to simulate the identified study area in LANDIS. To begin, a digital elevation model (DEM) and the 2005 land use/land cover (LULC) classification maps were downloaded from the Missouri Spatial Data Information Service (http://msdis.missouri.edu. Both of these layers were available at 30 meters resolution and covered the entire study area. A land type map was created using Jenness Enterprises Land Facet Corridor Designer (Jenness, et al., 2010) on the DEM layer. The Land Facet Corridor Designer extension uses a small and large moving window to compare a cell's elevation to its surroundings. The output of this process was a map showing each cell's topographic position index (TPI) using the small moving window and a map showing the TPI using the large moving window. If a cell had a negative TPI, it was lower than the average of all the cells within the moving window and a positive TPI meant it was higher than the average. Decision rules were developed using the two TPI maps that categorized the landscape into four topographic classes; ridge, slope, upland drain and bottomland. The decision rules were calibrated by overlaying the results on a topographic map of the study area and examining how well the land type classes matched. The DEM layer was also run through the aspect tool available in the spatial analyst toolbox of ESRI's ArcMap 10, which created a map layer displaying each pixel's aspect. Using the aspect layer the slope topographic class in the land type map was divided into southwest and northeast facing slopes. The LULC map's 14 classes were combined to create five classes; deciduous forest, evergreen forest, mixed forest, non-forest, grassland and water.

Species life attributes

All species in the model have life history traits that are controlled by a species attribute file. For each species, this file contains parameters that define species longevity, maturity, shade tolerance, fire tolerance, seeding distance, biomass amount, maximum diameter, maximum stand density and vegetative propagation. Longevity and maturity are defined in years, shade and fire tolerance are rated on a scale of one to five and vegetative propagation is both a probability and maximum age. Seeding distance is made up of two distances; the mean seeding distance and the maximum seeding distance in meters. The species used in this study are shortleaf pine *(Pinus echinata)*, eastern redcedar *(Juniperus virginiana)*, white oaks group *(Quercus spp.)*, red oaks group *(Quercus spp.)*, hickory group *(Carya spp.)*. Parameters for species attributes were taken from the North American Silvics Manuals (Burns & Honkala, 1990) (Burns & Honkala, 1990).

Land type

The land type attribute file contains parameters that define understory shade tolerant regeneration, time since last wind disturbance and the probability of establishment or reproduction for each species for each unique land type. Each of these land type classes correspond with a class shown on the land type map. The land type map is an 8 or 16 bit GIS that defines the land type class for every pixel in the study area. For this study there are five active forested land types: southwest slope, northeast slope, ridge, upland drainage and bottoms.

Forest composition

Species distribution is defined in the species composition GIS map file where each integer on the map corresponds to a record in the map attribute text file. Each individual record in the map attribute file identifies the number of trees in each age cohorts of the individual species that are present in the cell. Species composition map and the map attribute files were generated using the software Landscape Builder, developed by William D. Dijak of the US Forest Service Northern Research Station. Landscape Builder generates species age cohorts and the number of trees per age cohort from the Forest Inventory and Analysis (FIA) data surveyed by the U.S. Forest Service (Woodall, et al., 2010). All age cohorts are in multiples of the simulation time step to be used. FIA plots that fall within the same FIA regions contained in the study area were identified and extracted. Each plot was then placed in a land type category according to slope, aspect, forest type and physiographic type. These records were further divided by forest type and size class. Each tree recorded in the FIA data was assigned an approximate age by using a linear regression derived from the diameter and species of trees with age recorded in the

FIA database. The number of trees in each plot was adjusted using the plot's expansion factor (Woodall, et al., 2010) to match the pixel size. These adjusted figures represented the individual entries in the map attribute parameter file that specifies the number and age of each tree present on the pixel. The first step to populate the species map with trees uses an FIA unit map, a land cover map obtained from the Missouri Spatial Data Information Service and the land type map created earlier to create patches on the landscape. Each patch was then randomly assigned a forest type and size class to match those within the pool created from FIA data. Each pixel within a patch was assigned a value by randomly drawing from the pool with a matching forest type, size class and age class (Landscape Builder Documentation).

Stand and management area maps

The harvest module management unit map was created by combining a county map and a Mark Twain National Forest map that identifies management units specified in the Mark Twain National Forest 2005 Land and Resource Management Plan (Figure 4) (USDA, 2005).

A stand map for the harvest module was created by populating a map of the study area with rectangles of varying size and aspect ratios to simulate ownership boundaries. The mean size of the privately owned stands was 35 HA (Ko, et al., 2006). This map was combined with a Mark Twain National Forest forest-type map to identify stands within the boundaries of the National Forest. The mean stand size of the National Forest stands was 7.3 HA.

HARVEST MODULE DESIGN

Overview

In this module harvest is conducted using similar inputs as previous versions of LANDIS (Gustafson, et al., 2000). The user provides two maps in addition to those needed for the succession module. The first is a management area raster map. Each management area is designated by an integer value within the raster and need not be contiguous. These areas provide a boundary which certain specified harvest events can occur within. Multiple harvest events can be set to occur within a management area during the same time-step. All harvest prescriptions can be set to occur at any time step and have the option of reoccurring at a specified interval. The second map is also an integer-based raster that details stand boundaries. Stands are smaller contiguous units within a management area. When a harvest event is triggered within a management area, stands are chosen using a ranking algorithm and then the harvest prescription is applied to all forested cells in the stand, one stand at a time, until the harvest amount set by the user is satisfied. Stands that are eligible for harvest are identified based on a user defined minimum basal area that is calculated using the equation:

$$BA_s = \frac{\sum BA_c}{(N*CS^2)/10000}$$

Where BA_c is the basal area in square meters of each cell within a stand, N is the number of cells within a stand and CS is the cell size in meters. If this value is higher than the one set by the user, the stand is eligible to harvest.

Currently the harvest module has two ranking algorithms to determine the order in which stands are harvested. The first is a random function where all eligible stands are placed in a pool and drawn from at random until the desired amount is reached. The second is basal area ranking where eligible stands are harvested in the descending order starting with the stand that has the greatest average basal area as calculated in the formula above.

Harvest events are applied to a stand using two treatment types. The first is a basal area thinning where the user sets a target basal area that the stand will be harvested to. This can be set to cut trees in ascending order of size starting with the smallest size classes or in descending order starting with the largest size classes. To determine the amount of cutting that needs to occur on each cell the program takes the difference between the current stand basal area (BA_s) and the target stand basal area. This difference is multiplied by each cell's relative density, $\left(\frac{BA_c}{\sum BA_c}\right)$, to calculate the harvest amount for that cell.

At the cell level the program tracks the number of individual trees in each age class. Using either a default curve or user defined values, the age of each species is converted to a diameter (Loewenstein, et al., 2000). This diameter is used to calculate a basal area for each age class for each species. The program then divides the list of age classes in to four groups based on percentage of longevity. The basal area per age group is calculated and the group is harvested until the target amount for the cell is exceeded. The program will then enter the age group that exceeded the amount and harvest individual age classes for each species until the target amount is met.

The second treatment type is the group selection method which is designed to create canopy openings within a stand based on user specifications. Starting in the specified entry year the program will choose stands from within a management area using the same ranking algorithms as the basal area harvesting to treat. Group opening treatments within a stand are clusters of cells where all tree species that are flagged eligible for harvest are removed. The size of these clusters is determined by drawing from a normal distribution with a mean number of cells and standard deviation defined by the user. The minimum group opening size is one cell so the spatial resolution should be considered when parameterizing the model for harvest. Group openings will be randomly placed within a stand until a proportion of the stand area specified by the user is reached. The program will then move on to the next stand determined by the ranking algorithm until the specified management area proportion is fulfilled (Figure 5). If a stand is treated with the group selection method the entire area of the stand is used to calculate the proportion of the management area treated, not just the cells where the groups occur (Figure 6).

In both ranking algorithms stands will be harvested until the target stand proportion is met. This is calculated using a processing loop where the total forested area of the management area is calculated. After the first stand selected by the ranking algorithm is treated the total forested area of the stand is added to a value containing the total treated area. The program will continue to treat stands until the total treated area value is greater than total stand forested area multiplied by the target proportion value.

Harvest Prescription Parameters

The harvest module uses a text based parameter file to create harvest events. Each event has a separate entry where the user sets the harvest type, management area, ranking method, entry year, return interval, proportion of management area to be treated, species to be harvested, planting amount and either basal area amount to be removed or group opening size. There is no limit to the number of harvest events that can be applied to a management area during a single year, although events are processed in the order listed within the parameter file which could affect the ranking algorithm of subsequent events if they occur within the same management area.

Harvest prescriptions for the Mark Twain National Forest portion of the landscape were designed to approximately simulate management prescriptions adopted by the US Forest Service (**Error! Reference source not found.**) (USDA, 2005). For the privately owned area we simulated a heavy thinning from above at a rate of 1% of the landscape per year (Ko, 2005).

EXPERIMENTAL DESIGN

In order to demonstrate the effects of the harvest module we applied the management prescriptions to the landscape and ran the simulation for 150 years. The harvest output results for each management unit were analyzed to check the target proportion amounts and group opening sizes against those specified in the parameter file. For the management areas that were treated with a basal area thinning the cells where harvest events occurred were identified at 10-year intervals during the entire simulation. The number of cells was divided by the total number of forested cells within the management area to determine the proportion treated. These proportions were then averaged for each management area. For management areas treated with group opening methods the groups were identified by running a region-grouping function on the harvest maps using a four-cell neighbor rule. The average opening size and average number of openings was calculated for each year that the treatment occurred.

In addition, 9 stands were chosen at random from the landscape to examine different harvest prescriptions at a stand level. Simulations were run using several different harvest methods to simulate the common management practices; clearcutting, thinning from above, thinning from below, shelterwood, and group selection. The model was set to output basal area and tree number maps that excluded the youngest age cohort. Since the model simulates seed dispersal and vegetative propagation after harvest during each time-step the values for this youngest age cohort could skew the values on the stocking chart, especially the number of trees. The results from the each individual stand were examined and plotted on a Gingrich stocking diagram to illustrate the effects of each management prescription.

Data Analysis

To generate the statistics for percentage of management units and group selection opening sizes the harvest type maps output by LANDIS were used. Each year of the simulation the model outputs and integer GIS map that contains values corresponding to the harvest records in the harvest parameter file. In order to calculate the percentage of management area, the maps were run using a batch Python script through a zonal function in ArcGIS that calculated the number of cells harvested in each management area. This was then divided by the total forested area for the management unit to get the actual treated percentage. The region grouping function to identify group selection openings was applied to the same maps using another Python looping script. The four-cell neighbor rule identified openings by examining each pixel for adjacent pixels to the north, south, east, and west of the same value. Each contiguous group that the function identified was assigned a new unique value. The pixel count of each unique group ID was analyzed in Excel to determine the mean, minimum and maximum size in each management area where group selection was used.

To build the Gingrich stocking diagrams the stands were chosen at random and a GIS mask layer was created for their boundaries. After all scenarios were simulated, the stands were examined by running a zonal statistics function in ArcGIS on the basal area and tree number maps output by the model. This returned the total basal area and number of trees present in the stands before and after the harvest. These values were then converted to square feet per acre and number of trees per acre and plotted using a Gingrich stocking chart Excel template provided by Dr. David Larsen of the University of Missouri Forestry Department.

RESULTS

For the basal area thinning method, the average proportion treated of each management area was greater than or equal to the target proportion for all management areas (Figure 7). In some cases, such as management units 2 and 6, the treated proportion was within 0.001 of the target proportion. In the cases of the private land, management areas 11 through 23, the treated proportion was on average 32% higher than the target proportion of 0.025, with a minimum difference of zero and a maximum difference of 40% higher.

For the two group-opening methods management area 5 had a target opening of 7 pixels and management area 3 had a target opening of 1 pixel. Both scenarios had a value of 1 for the standard deviation of the mean opening size. The 7-pixel target opening scenario had an average opening size of almost 8 pixels, while the 1-pixel target scenario had an average opening size of around 1.3 pixels (Table 7). The target management unit proportion for management area 5 was 0.04. The average of the actual percentage treated was 5% lower than the target and the minimum and maximum were within 1% of the average. Management unit 3's prescription had a target management unit percentage of 0.05. The actual treated percentage had an average that was 4% higher than the target. The minimum was 5% lower than the target and the maximum was 14% higher than the target.

The clearcut simulation shows each stand starting at a stocking level between 80% and 95% and then being reduced down to a level just above zero (Figure 8). In the thinning from above scenario each stand dropped approximately 30% stocking after the treatment with the quadratic mean diameter decreasing (Figure 9). The thinning from below scenario chart shows each stand decreasing in stocking by between 30% and 50% while the quadratic mean diameter increased and the trees per acre in each stand decreased sharply (Figure 10). Examining the results from the shelterwood treatment simulation shows the trees per acre decreasing in each stand and the stocking dropping to around 40% (Figure 11). The group selection simulation results showed in most stands the stocking dropping by about 20%, while the quadratic mean diameter in most cases remained the same (Figure 12).

DISCUSSION

The new design for the LANDIS 7.0 PRO harvest module takes advantage of the quantitative data structure allowing users to specify precise parameters for how the model operates at the landscape and stand level. This quantitative information about each species can be used by the module to identify and operate on stands and provide detailed spatial results of the harvest simulation.

The design of the harvest module basal area controlled cutting uses the stand as the smallest unit. Once a stand is identified, the specified action is distributed amongst all forested cells within the stand. When going through the process loop of treating stands and checking against the proportion of the management area treated, the last stand processed can cause the treated proportion of the management unit to surpass the target proportion. This effect seemed to be more pronounced as the average stand size within a management area increased. In management units 2 and 6, which had some of the lowest average stand area values, the treated proportion was the closest to the target proportion. The management areas where the difference between treated and target proportions was highest had the largest average stand areas (Table 3). In these cases some of the larger stands in the management area could contribute as much as 0.006 to the treated proportion amount, which is slightly smaller than the average difference between treated and target proportions.

Since the opening size for the group selection is drawn from a normal distribution defined by the user, the average size of each opening is very close to that amount. Unless a large opening size is chosen, the resulting sizes will be heavily skewed toward openings less than or equal in size to the mean size chosen. In cases where the stand size is small or the shape is highly dissected, the openings can end up being clumped together, causing the average group opening size to increase. Since the group selection method counts the entire forested area of the stand toward the treated proportion, the actual treated area is less than in the basal area harvest method.

When examining the individual stands using different harvest methods all behaved in a realistic manner. The clearcut method reduced the stands to the specified basal area amount and since the removal began with the largest trees the quadratic mean diameter of the stands decreased. The comparison between the thinning from below versus the thinning from above produced predictable results. Both prescriptions had the same target basal area value but one started removal with the smallest trees and the other with the largest trees. Where the removal was from above the number of trees in the stand did not decrease as much as the removal from below since fewer trees would need to be cut to reach the target basal area. The quadratic mean diameter of the stands decreased when thinned from above and increased when thinned from below. The shelterwood method performed in a similar manner to thinning from below but the amount removed was higher and the prescription planted a number of shortleaf pine seedlings on the sites which do not show up on the stocking charts. The group selection method had little effect on the quadratic mean diameters of the stands and had varying amounts of removal since the cells within each stand were chosen at random.

Some of the behavior shown in these results highlights the need for further testing and development of the model. One feature that will be added later is an option to reenter stands after the initial treatment and perform another action. This is normally used in shelterwood applications. Currently the only way to accomplish this is to create a unique management unit for this method and treat 100% of the stands. Another area that requires further research is the refinement of the ranking algorithms that select stands for harvest. Often time management plans specify minimum intervals between harvests for a stand or adjacent stands in order to create a diverse landscape. This option would be useful but early testing showed it required more processing resources and added to simulation times.

The design of this harvest module can benefit forest management research and planning by providing a tool that is able to simulate forest harvest treatments based on parameters that are commonly used in management plans. This allows stakeholders a way to assess the potential effects of harvest prescriptions spatially on a landscape as well as quantitatively at a variety of scales. This design improves on previous versions by allowing partial treatment of individual age-classes within a cell and reporting results in units commonly used in Forestry research, while performing these complex using a low amount of computing resources and processing time.

Table 1. Description of management scenarios within Mark Twain National Forest.

Management Area	Type	Entry Year	Repeat Interval	Proportion Treated	Group Size (HA)	Target BA M^2 / HA	Planting
1	Group opening	2	100	0.2	24.0	-	-
2	Basal area cutting, from above	2	2	0.025	-	0.0	-
3	Group opening	2	10	0.06	0.8	-	-
5	Group opening	10	20	0.05	5.7	-	-
6	Basal area cutting, from below	2	2	0.025	-	5.0	Shortleaf pine
8	Basal area cutting, from above	2	2	0.04	-	2.0	-
10 – 23	Basal area cutting , from above	2	2	0.02	-	2.0	-

Table 2. Statistics for group opening sizes and percentage of management area treated.

Target opening size	Average opening size	Average number of openings	Target management percentage	Average management percentage
7	7.9575	228	0.04	0.038
1	1.3307	1841	0.05	0.052

Table 3. Average stand size and ratio of average stand size to total forested area per management unit.

Management Unit	Average Stand Area (HA)	Total Forested Area (HA)	Average Stand Ratio
1	7.3	115457.4	0.00006
2	8.7	9420.3	0.00092
3	7.2	155579.9	0.00005
4	12.8	12162.2	0.00105
5	8.0	19865.3	0.00040
6	6.8	65380.0	0.00010
7	8.5	2345.8	0.00361
8	8.5	905.6	0.00943
9	13.1	10913.9	0.00120
10	34.4	164394.4	0.00021
11	33.2	172943.1	0.00019
12	36.0	118246.2	0.00030
13	35.4	165935.8	0.00021
14	31.7	103716.5	0.00031

Management Unit	Average Stand Area (HA)	Total Forested Area (HA)	Average Stand Ratio
15	30.9	107476.5	0.00029
16	39.4	151396.3	0.00026
17	30.3	174930.0	0.00017
18	33.4	226445.2	0.00015
19	30.8	163388.3	0.00019
20	29.1	94990.3	0.00031
21	61.4	162063.2	0.00038
22	38.4	162366.1	0.00024
23	34.1	123359.8	0.00028

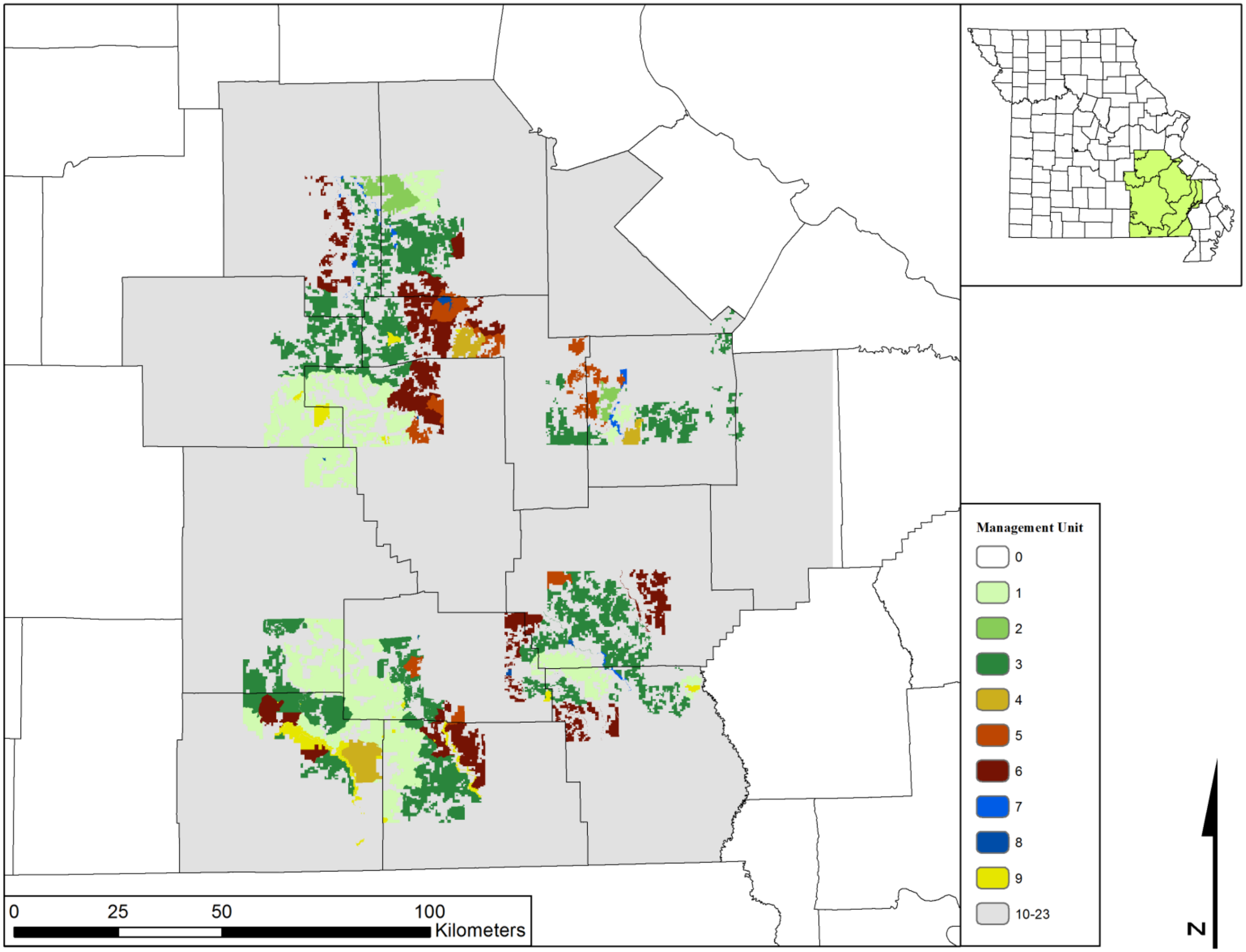

Figure 1. Management area boundaries used for simulations.

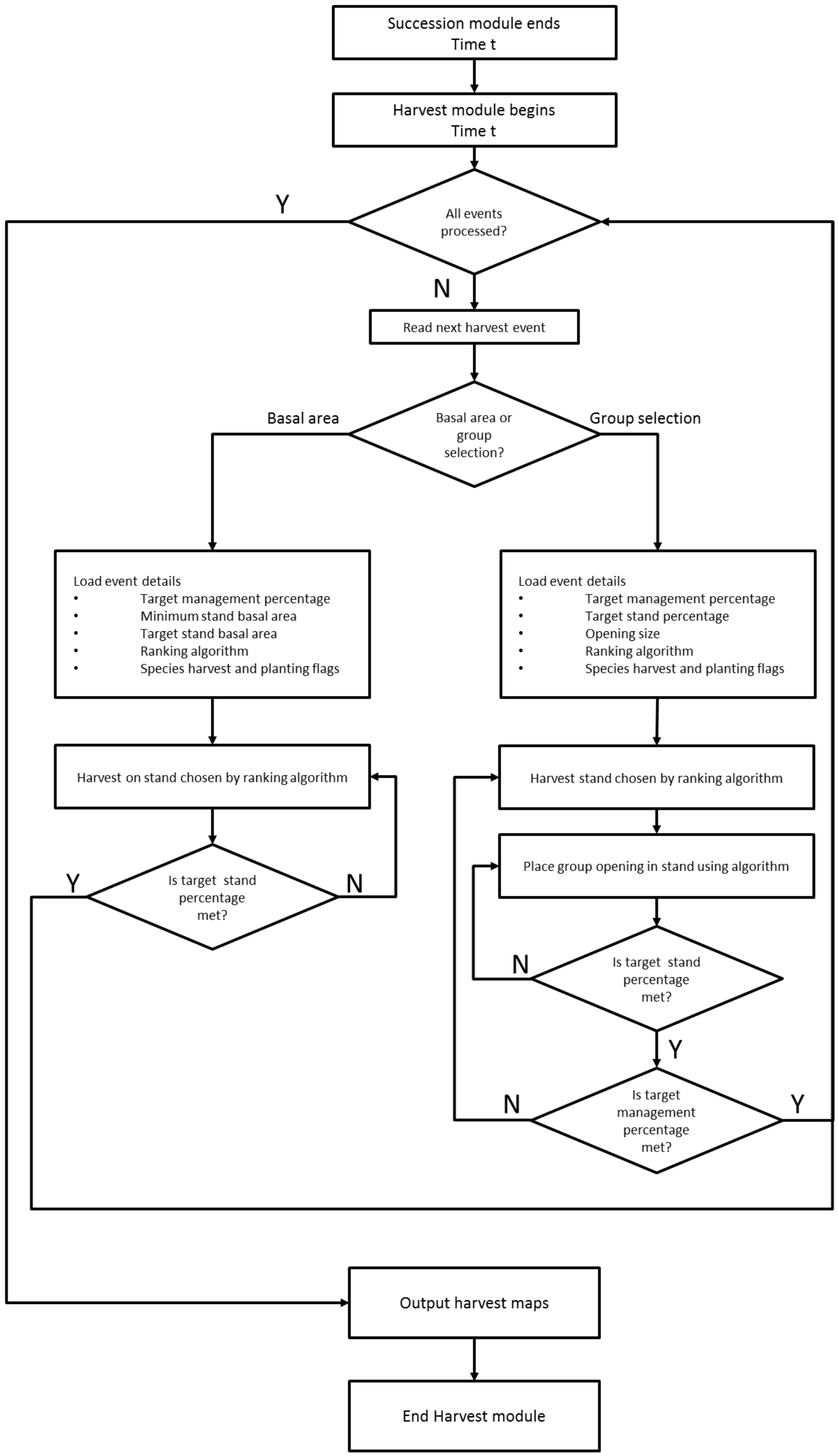

Figure 2. Process flow-chart of the LANDIS PRO 7.0 Harvest module.

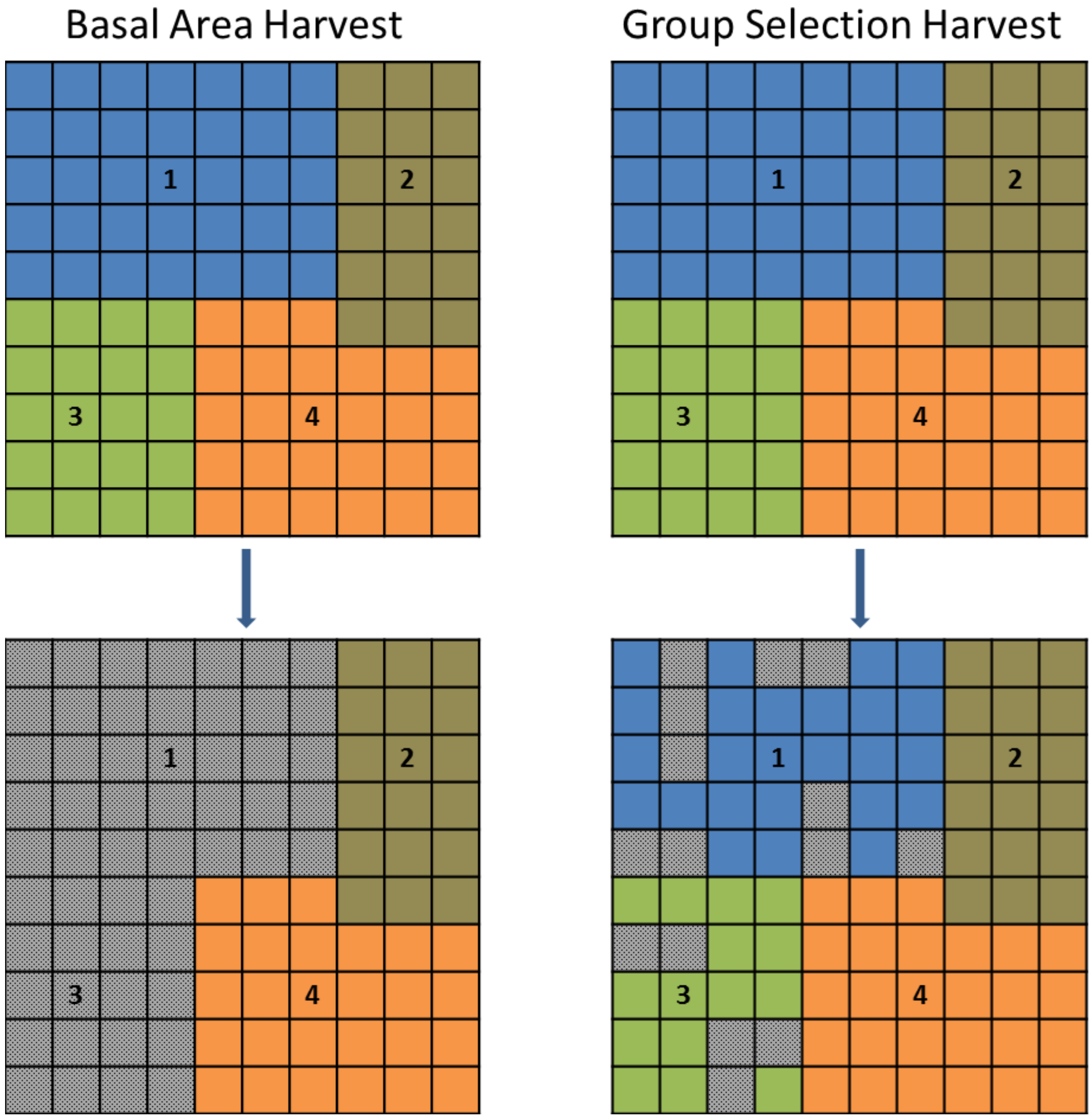

Figure 3. Illustration of the difference in harvest methods.

Stands are shown in different colors, harvested cells are shown in grey. If the entire 10x10 grid is one management area that has a harvest event that specifies 50% of the management area is to be cut using random stand selection. In the basal area method if the first stand randomly selected is stand 1, the amount to be harvested will be distributed among all cells weighted by the cells' basal area prior to harvest. Since stand 1 is 35 cells this would account for treating 35% of the management area. Since the 50% threshold is not met, the module will randomly choose another stand. If stand 3 is chosen and harvested in the same manner it will raise the treated percentage to 55%, surpassing the threshold and ending the harvest event.

For the group selection harvest method example the target percentage of the management area is again 50%, and the target stand proportion is 25%. The mean group size is 2 with a standard deviation of 1. Stand 1 is chosen and the module randomly creates openings using the size and placement algorithm until at least 9 cells are cut, then moves on. Once again this counts as treating 35% so the module chooses a new stand. In stand 3, two groups are created totaling five cells, reaching the stand proportion threshold of 25%. Stand 3 raises the management unit treated percentage to 55%, ending the harvest event.

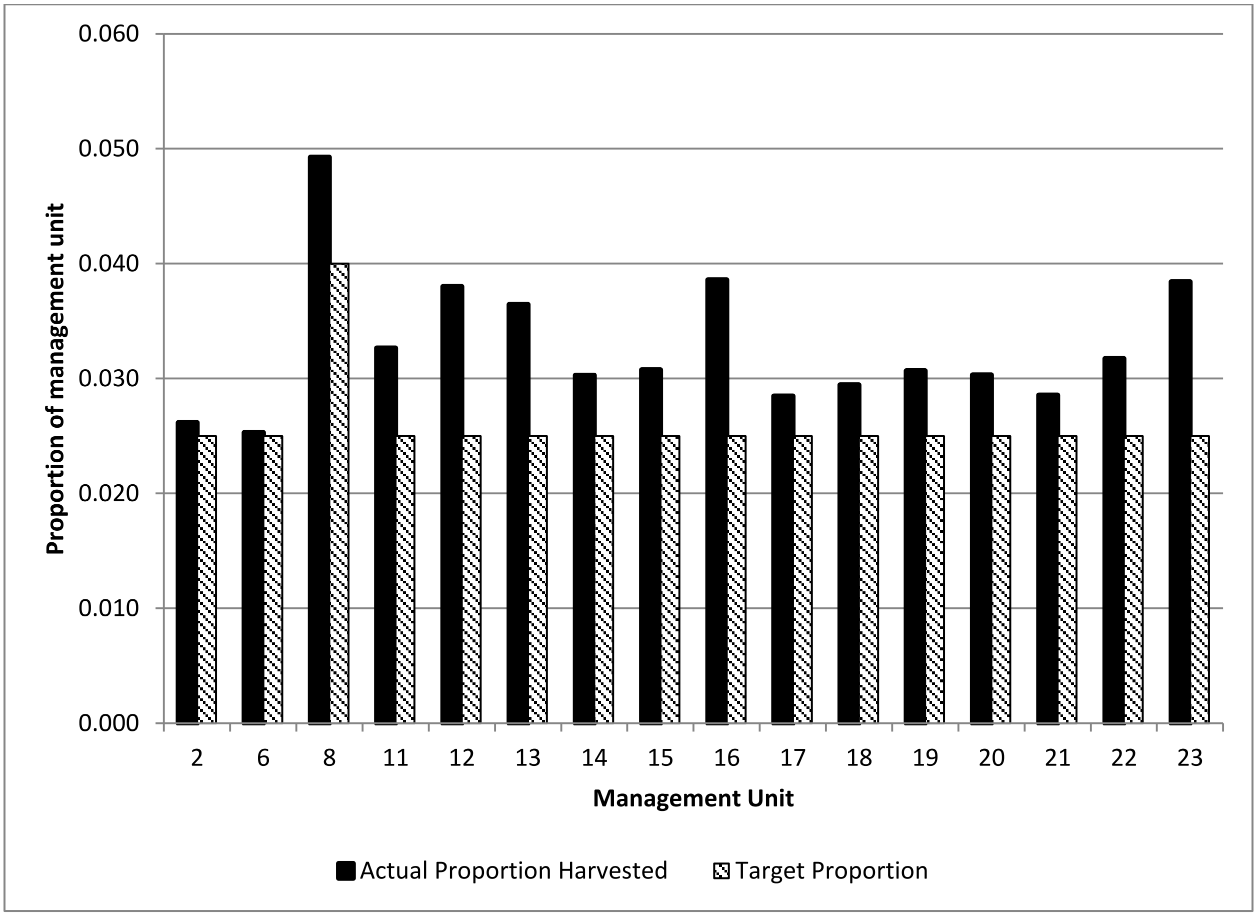

Figure 4. Comparison of actual proportion of management area treated against target proportion for management areas using basal area cutting method.

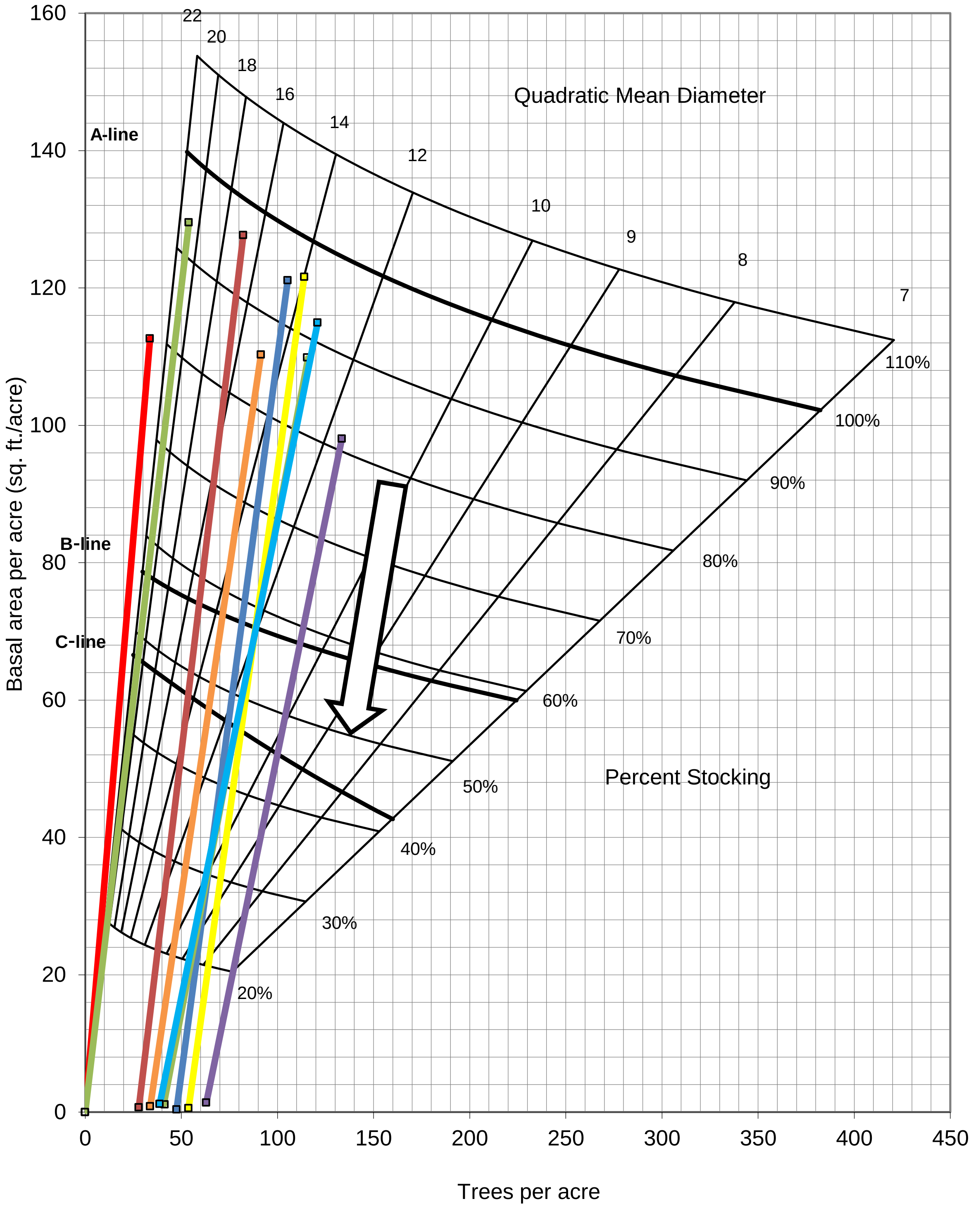

Figure 5. Gingrich stocking chart showing clearcut treatment simulation results for nine different stands.

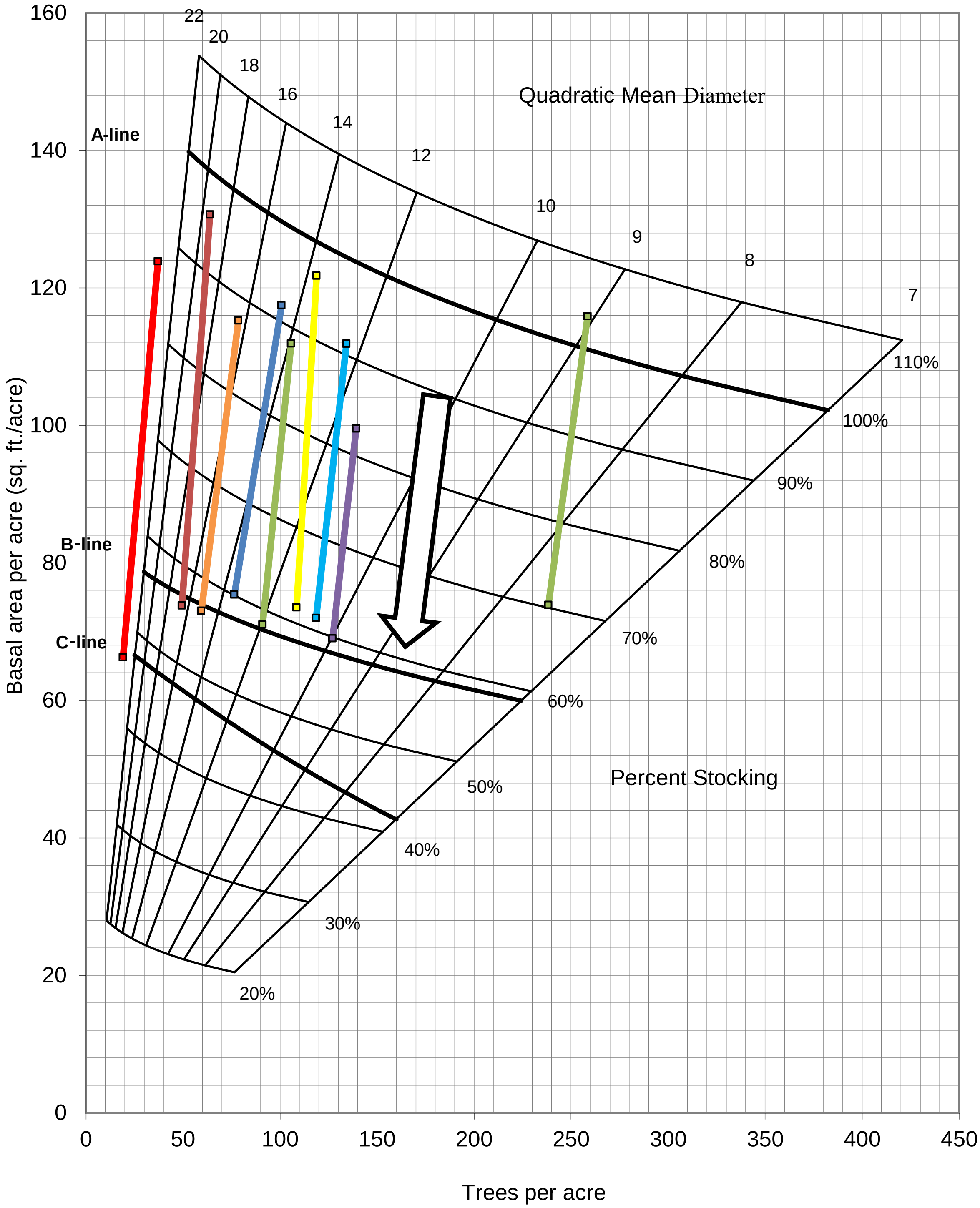

Figure 6. Stocking chart showing thinning from above treatment simulation results for nine different stands.

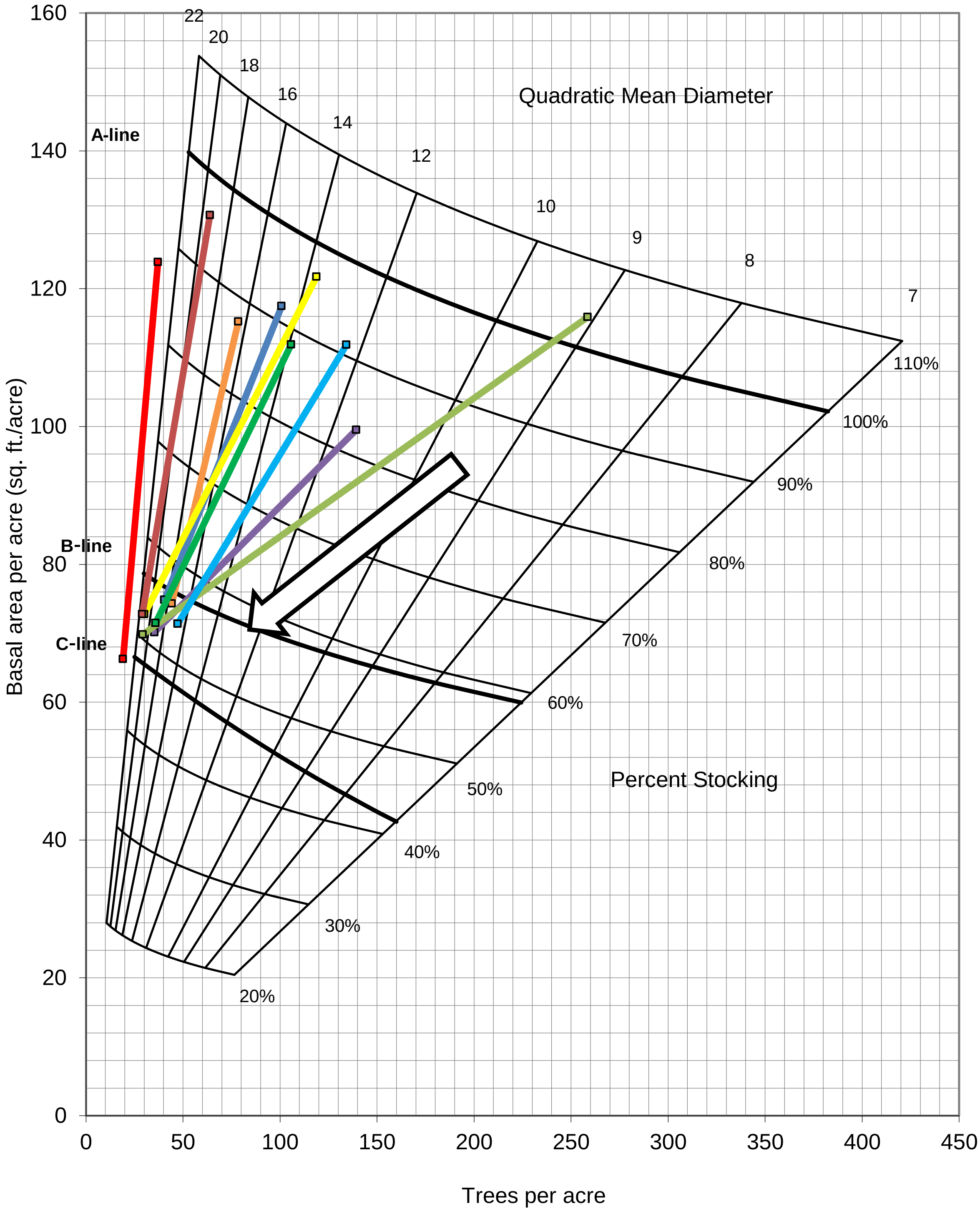

Figure 7. Stocking chart showing thinning from below treatment simulation results for nine stands.

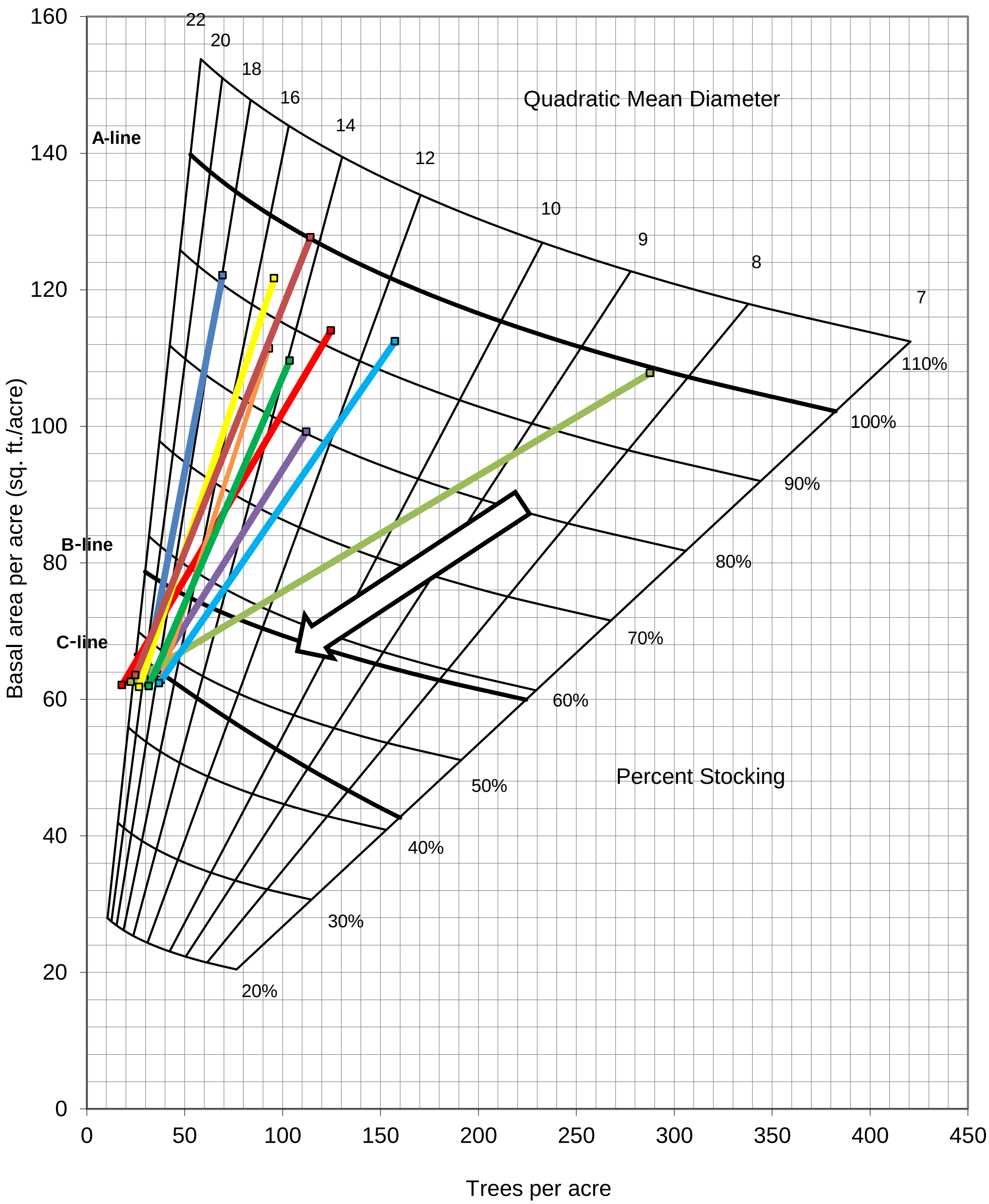

Figure 8. Stocking chart showing shelterwood treatment simulation results for nine stands.

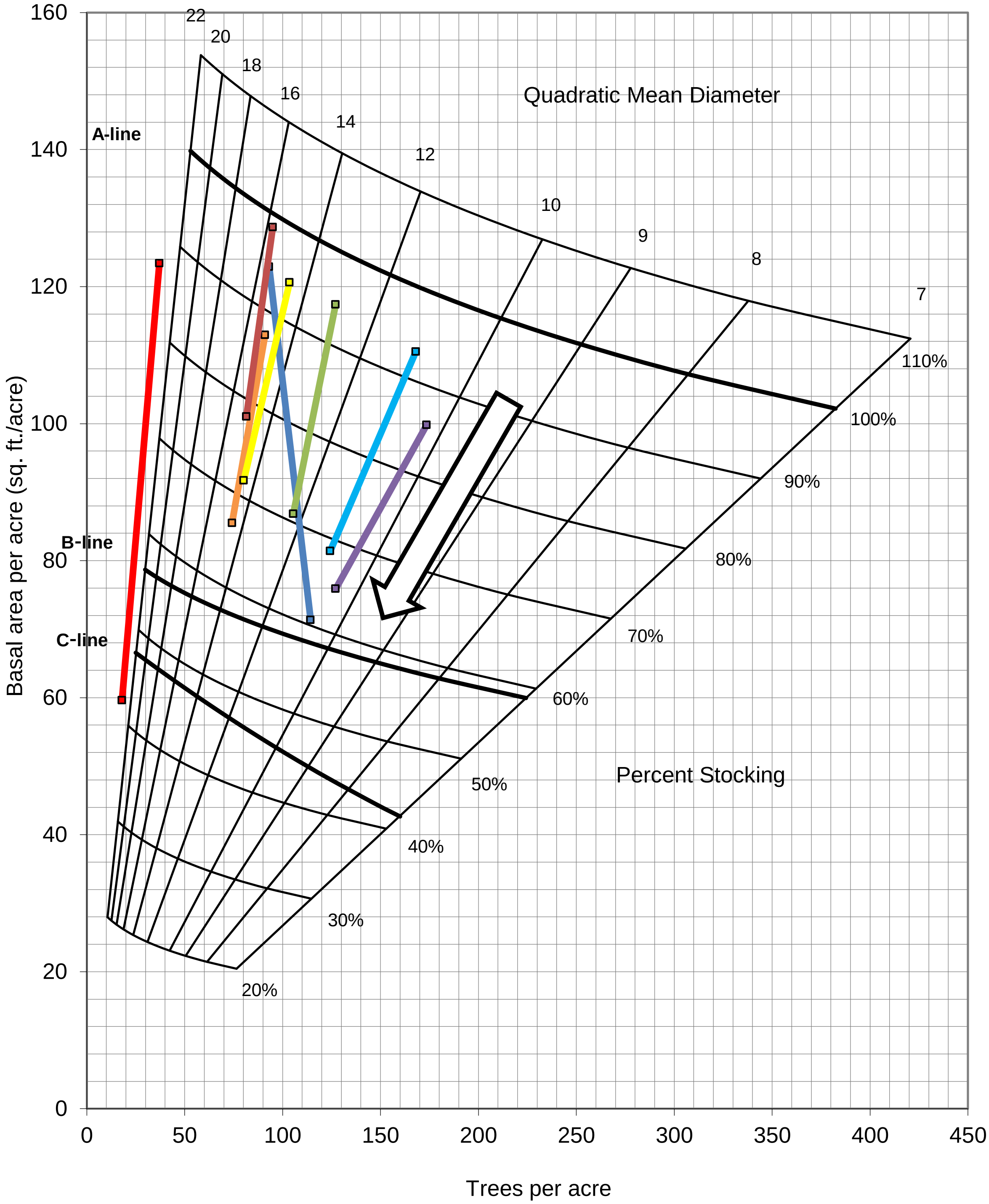

Figure 9. Stocking chart showing group selection treatment simulation results from nine stands.

APPENDIX

Basal Area Harvest Event

```
9       #Harvest Regime ID#
1       #Harvest Regime Label3
2       #Management Area#
1       #Unused#
1       #Ranking Algorithm#
10      #Entry Year#
10      #Reapplication Interval#
15.0    #Minimum Stand Basal Area#
0       #Tree Removal Method#
0.1     #Management Area Treatment Proportion#
0.1     #Target Stand Basal Area#
#Species  List#
1 1 0 0         #Species 1#
2 1 1 50        #Species 2#
3 0 0 0         #Species 3#
4 0 1 40        #Species 4#
```

Line 1 – Specifies the harvest type, 9 selects the basal area removal method.
Line 2 – Integer value that will be displayed on the harvest type maps where event occurs.
Line 3 – Integer value corresponding with management area map to set management area to be treated.
Line 4 – This value is not used in the current version of LANDIS.
Line 5 – Ranking algorithm selection. Value 1 is random stand selection and value 6 is highest average basal area.
Line 6 – Actual year the harvest event begins. Should be a multiple of the time-step being used.
Line 7 – Actual year interval which the harvest event will be repeated. Should be a multiple of the time-step being used.
Line 8 – Floating point value setting the minimum average stand basal area (see equation above) a stand must have to be eligible for harvest.
Line 9 – Value 0 will harvest starting with smallest trees and increase in size until target amount is met. Value 1 will start with largest trees and decrease in size.
Line 10 – Floating point value setting the proportion of the management area to be treated.
Line 11 – Floating point value setting the target average stand basal area.
Lines 13-X – Each species being simulated will have its own line. Species should be arranged in the same order as the species parameter file. The first number is the species' priority in the harvest order. The second number is the flag for harvest. If set to 0 the species will not be harvested, Set to 1 to harvest. The third number is the flag for planting of the species. If set to 0 there will be no planting, if set to 1 planting is enabled. The fourth number is the number of trees of the species that will be planted (added to the youngest age class) on any cell where harvest occurs as a result of the event.

Group Selection Harvest Event

```
10      #Harvest Regime ID#
2       #Harvest Regime Label3
3       #Management Area#
1       #Unused#
6       #Ranking Algorithm#
10      #Entry Year#
10      #Reapplication Interval#
0.4     #Target Proportion#
5       #Stand Proportion Denominator#
6       #Mean Group Size#
2       #Standard Deviation#
#Species  List#
1 0 0           #Species 1#
1 1 50          #Species 2#
1 0 0           #Species 3#
1 1 40          #Species 4#
```

Line 1 – Specifies the harvest event type, 10 selects the group selection removal method.
Line 2 – Integer value that will be displayed on the harvest type maps where event occurs.
Line 3 – Integer value corresponding with management area map to set management area to be treated.
Line 4 – This value is not used in the current version of LANDIS.
Line 5 – Ranking algorithm selection. Value 1 is random stand selection and value 6 is highest average basal area.
Line 6 – Actual year the harvest event begins. Should be a multiple of the time-step being used.
Line 7 – Actual year interval which the harvest event will be repeated. Should be a multiple of the time-step being used.
Line 8 – Floating point value setting the proportion of the management area to be treated.
Line 9 – Integer value that is the denominator used to determine the proportion of a stand area that will be cut. For example if 5 is used, 1/5 or 0.2 of the stand area will be cut.
Line 10 – The mean of the normal distribution that will be randomly drawn from to determine the number of cells each group will consist of.
Line 11 – The standard deviation of the normal distribution that will be randomly drawn from to determine the number of cells each group will consist of.
Lines 12-X – Each species being simulated will have its own line. Species should be arranged in the same order as the species parameter file. The first number is the flag for harvest. If set to 0 the species will not be harvested, Set to 1 to harvest. The second number is the flag for planting of the species. If set to 0 there will be no planting, if set to 1 planting is enabled. The third number is the number of trees of the species that will be planted (added to the youngest age class) on any cell where harvest occurs as a result of the event.

CHAPTER 2. EXAMINING THE EFFECTS OF TEMPORAL RESOLUTION ON LANDIS MODEL SIMULATION OUTCOMES.

INTRODUCTION

The primary goal of forest management is for the forest in question to arrive at desired state as the result of the application of management techniques. These techniques must take into account many forces that play a role in the ongoing development of a forest including tree growth, mortality, harvest, species succession, wildfire, insects, and disease. It is often difficult to assess the exact nature and intensity of events that are the result of these many influences, especially over a large forest landscape (Shifley, et al., 2000). Compounding the difficulties of large spatial scales are the large temporal scales that are associated with forest management. For this reason forest landscape simulation models are an important tool to help in identifying the specific effects of natural and human influences over time in a forest (He, et al., 2008). Simulated results showing forest succession and disturbances caused by fire, wind, disease and harvest can help create more accurate management plans for large or small areas (Gustafson, et al., 2000; Zollner, et al., 2005; Zollner, et al., 2008; Sturtevant, et al., 2009). With the emphasis on using forests in a more productive and sustainable manner increasing, so too is the importance of using landscape modeling to aid land managers in this task. Simulation models that were once used to help maximize timber production are now being adapted to assess management plans for carbon sequestration and small woody biomass harvesting (Gustafson, et al., 2010). In addition to managing forests for commercial products, landscape simulation models are used to develop forest management plans that promote recreation, wildlife habitat and conservation restoration (Xi, et al., 2009).

Application of forest landscape simulation models typically begins with an initial digital landscape based on an inventory of current forest conditions. The subsequent simulation is a result of the parameters used for species and landscape characteristics. The model then simulates the continuous, dynamic process of forest succession and provides the user with snapshots of the state of the forest at intervals equal to the time-step (He, et al., 2008). The spatial extent of these simulations can range from a few hundred to several million hectares. At its core LANDIS, the model used for this study, is a raster based model that can be parameterized to simulate succession, natural disturbances and harvesting over the parameterized landscape (Mladenoff, et al., 1996) (He, 2008). Individual modules can be switched on or off to control the simulation of events such as fire, wind, harvest and disease.

When using a forest landscape simulation model the user must make decisions about parameterization and model execution based on hardware and time limitations. Developments in computer hardware and software over time have allowed models to simulate larger landscapes at finer scales (He, et al., 2009). While processing time can be reduced using better hardware, the user still must decide if the extra cost, in both time and resources, is worth any benefit gained through a finer temporal or spatial resolution.

Wiens (1989) suggests that modeling occurring over large spatial scales must also have a broader temporal scale in order to have the ability to predict the processes that have the most effect on the system being modeled. The events that influence a landscape can differ spatially and temporally from those that are acting on a site level. In a heterogeneous landscape model an individual organism has little effect on any process being simulated. At broad spatial and temporal scales validation becomes difficult due to the lack of data to be used for comparison (Scheller & Mladenoff, 2007). The processes operating on a forest occur at a variety of spatial and temporal scales (Fielding & Bell, 1997) (Shifley, et al., 2000) (He, 2008) (Scheller, et al., 2007). In order to account for these differences, landscape modeling software often give the user the ability to control the temporal and spatial resolutions of the input and output data as well as individual modules. Previous studies have shown that spatial resolution has an effect on landscape metrics (Qi & Wu, 1996) (Wu, 2004). However, there has been little research on the effect that temporal resolution plays on these same metrics. Therefore, the objective of this chapter is to examine the effect of different temporal resolutions on the simulation results from the LANDIS PRO 7.0 forest landscape model. Since management prescriptions and natural events must be aggregated to fit the time-step of the model (He, 2008), the question arises as to whether a coarse temporal resolution can accurately reflect events that occur in a finer temporal resolution. Specifically, we investigated whether the basal area, number of trees, and spatial patterns of species differ under different temporal resolutions during the span of the simulation.

MATERIAL AND METHODS

Study Area

The study area is comprised of 6,800 square miles of forested area in the Ozark Highlands ecological section in Missouri (Figure 1). This area is designated by the US

Forest Service FIA manual as unit 1 in Missouri. Erosion and weathering of the limestone, chert and dolomite parent material has created a rugged, hilly ecosystem interspersed with sections of plateaus and rolling prairies. The karst topography found in this region is caused by the weathering of parent material and creates a landscape with many caves, springs and sinkholes. The soil formed in the ecological section is generally gravelly, shallow and acidic. The boundaries of the study area roughly coincide with ecological subsection boundaries. The five ecological subsections represented in the study area are Central Plateau, Meramec River Hills, Current River Hills, St. Francois Knobs and Basins, and Black River Ozark Border (Nigh & Schroeder, 2002). Average annual precipitation for the area ranges from 40 to 49 inches and average annual snowfall ranges from 10 to 18 inches. The mean minimum daily temperature in January is 20^{o} and the average maximum daily temperature in July is 90^{o}. The varying terrain and geology in this region cause a variety of microclimates that can create unique habitats for plant and animal species.

The study area contains 1,600 square miles that are designated as Mark Twain National Forest, including the Potosi, Salem, Fredricktown, Poplar Bluff and Eleven Point districts. Common tree species in this area include white oak (*Quercus alba* L.), post oak (*Quercus stellata* Wangenh.), black oak (*Quercus velutina* Lam.), hickory (*Carya spp*.), sugar maple (*Acer saccharum* Marsh.) and shortleaf pine (*Pinus echinata* Mill.).

Data Preparation

Physiographic spatial datasets and forest inventory results were required in order to initialize the identified study area in LANDIS. To begin, a digital elevation model (DEM) and the 2005 land use/land cover (LULC) classification maps were downloaded from the

Missouri Spatial Data Information Service (MSDIS). Both of these layers were available at 30 meters resolution and covered the entire study area. A land type map was created using Jenness Enterprises Land Facet Corridor Designer (Jenness, et al., 2010) on the DEM layer. The Land Facet Corridor Designer extension uses a small and large moving window to compare a cell's elevation to its surroundings. The output of this process was a map showing each cell's topographic position index (TPI) using the small moving window and a map showing the TPI using the large moving window. If a cell had a negative TPI, it was lower than the average of all the cells within the moving window and a positive TPI meant it was higher than the average. Decision rules were developed using the two TPI maps that categorized the landscape into four topographic classes; ridge, slope, upland drain and bottomland. The decision rules were calibrated by overlaying the results on a topographic map of the study area and examining how well the land type classes matched. The DEM layer was also run through the aspect tool available in the spatial analyst toolbox of ESRI's ArcMap 10, which created a map layer displaying each pixel's aspect. Using the aspect layer the slope topographic class in the land type map was divided into southwest and northeast facing slopes. The LULC map's 14 classes were combined to create five classes; deciduous forest, evergreen forest, mixed forest, non-forest, grassland and water.

LANDIS PRO 7.0 Model Description

LANDIS 7.0 PRO is a forest landscape model that is based on previous LANDIS versions (e.g., LANDIS 2.0-6.0) (He, et al., 2009). It preserves the functionalities of LANDIS (1.0-6.0) and introduces a new succession module that simulates stand-level processes. LANDIS 7.0 PRO is a raster based, spatial model that can simulate forest landscape changes over time. In addition to normal forest succession as a factor for change, LANDIS can simulate stochastic disturbances such as wind, fire, disease and insect damage as well as user defined disturbances such as harvest and controlled burning. The user provides initial condition information in the form of GIS based map files and text files that define species and event characteristics. Using these files, LANDIS 7.0 PRO creates an initial landscape where each forest cell is populated with individual trees with species and age classes selected to ensure the initialized forest landscape composition map matches as closely as possible the data used for the initialization. Stand dynamics within LANDIS are built around four classical stand development stages: (1) stand initiation stage, (2) stem exclusion stage, (3) understory reinitiation stage, and (4) old-growth stage. These stand development stages regulate species level processes such as germination, regeneration, establishment, growth and mortality (Wang, et al., 2012).

The growing space occupied (GSO) variable reveals the degree of within-stand competition for resources, and it can be used as a factor regulating the stand-level processes. The stand initiation stage is characterized by seed germination and establishment, and self-thinning is initialized once stands reach stem exclusion stage. Four specific growing space occupied thresholds are identified corresponding to the four stages of seed germination and establishment in stand initiation stage. These are (1) open growing ($0 \sim GSO_1$), (2) partially occupied ($GSO_1 \sim GSO_2$), (3) crown closure ($GSO_2 \sim GSO_3$), (4) fully occupied ($GSO_3 \sim GSO\_thinning$). Identification of GSO regions in the context of stages of stand development provides a convenient conceptual framework for modeling stand density and natural regeneration.

Individual tree growth is controlled by either a default function or a user specified value for each species based on known age-size relationships for the study area. The default function has two separate curves that apply to softwood or hardwood species. This function uses the fraction of species longevity plotted against the fraction of species maximum diameter that is set in the species attribute file. If the user decides to provide their own growth rate, this is done for each species up until its maximum longevity at intervals equal to the time-step of the model.

Seed dispersal is regulated by a negative exponential function by default. The user may define a custom seed dispersal for each species that is calculated by a defined probability over distance intervals equal to the cell size of the model. Once growth and seed dispersal has been calculated, the model calculates the growing space occupied (GSO), or current percent of the site that is covered by trees. The value for GSO measures the current growing space for species. The maximum GSO can exceed 1.0 when there are multiple vertical canopy structures present on the site. Each land type has a specified maximum GSO in order to simulate the effect of land type on species composition.

Next the number of potential established seedlings (NPES) is calculated for the site. This takes the GSO for the site into account as well as the number of seeds that arrive on the site during the time-step. The number of potential seedlings is multiplied by that species' establishment coefficient on the current land type which is specified in the land type attribute file. This determines the number of seedlings for each species that successfully establish on the site.

Mortality on the site includes longevity-caused mortality, self-thinning-caused mortality, and random mortality. Longevity-caused mortality simulates species mortality when an individual reaches the user-defined maximum longevity. Self-thinning-caused mortality simulates species mortality caused by inter and intra species competition for resources (e.g., light and nutrients), which usually results in high mortality rate for younger trees. Random mortality is controlled by a probability function based on the age of a tree and the total basal area of the site. Just like other functions, the user can provide default probabilities of mortality for each species at an interval equal to the time-step of the model.

Once all these factors are calculated, LANDIS 7.0 outputs a series of GIS maps for each time-step that show the number of trees, basal area, and ages for each pixel. If the harvest module is activated, the model will output maps showing the basal area removed for each species and the harvest identification value for each pixel during each time-step.

LANDIS PRO 7.0 Model Parameters

All species in the model have life history traits that are controlled by a species attribute file. For each species, this file contains parameters that define species longevity, maturity, shade tolerance, fire tolerance, seeding distance, biomass amount, maximum diameter, maximum stand density and vegetative propagation (Table 1). Longevity and maturity are defined in years, shade and fire tolerance are rated on a scale of one to five and vegetative propagation is both a probability and maximum age. Seeding distance is made up of two distances; the mean seeding distance and the maximum seeding distance in meters. The species used in this study are shortleaf pine *(Pinus echinata)*, eastern redcedar *(Juniperus virginiana)*, white oaks group *(Quercus spp.)*, red oaks group *(Quercus spp.)*, hickory group *(Carya spp.)*. Parameters for species attributes were taken from the North American Silvics Manuals (Burns & Honkala, 1990) (Burns & Honkala, 1990). Maximum densities for species were found in previous literature (Reineke, 1933) (Schnur, 1937).

The land type attribute file contains parameters that define understory shade tolerant regeneration and establishment or reproduction for each species for each unique land type. Each of these land type classes correspond with a class shown on the land type map. The land type map is an 8 or 16 bit GIS that defines the land type class for every pixel in the study area. For this study there are five active forested land types: southwest slope, northeast slope, ridge, upland drainage and bottoms.

Species distribution is defined in the species composition GIS map file where each integer on the map corresponds to a record in the map attribute text file. Each individual record in the map attribute file identifies the number of trees in each age cohorts of the individual species that are present in the cell. Species composition map and the map attribute files were generated using the software Landscape Builder, developed by William D. Dijak of the US Forest Service Northern Research Station. Landscape Builder generates species age cohorts and the number of trees per age cohort from the Forest Inventory and Analysis (FIA) data surveyed by the U.S. Forest Service (Woodall, et al., 2010). All age cohorts are in multiples of the simulation time step to be used. FIA plots that fall within the same FIA regions contained in the study area were identified and extracted. Each plot was then placed in a land type category according to slope, aspect, forest type and physiographic type. These records were further divided by forest type and size class. Each tree recorded in the FIA data was assigned an approximate age by using a linear regression derived from the diameter and species of trees with age recorded in the FIA database. The number of trees in each plot was adjusted using the plot's expansion factor (Woodall, et al., 2010) to match the pixel size. These adjusted figures represented the individual entries in the map attribute parameter file that specifies the number and age of each tree present on the pixel. The first step to populate the species map with trees uses an FIA unit map, a land cover map obtained from the Missouri Spatial Data Information Service and the land type map created earlier to create patches on the landscape. Each patch was then randomly assigned a forest type and size class to match those within the pool created from FIA data. Each pixel within a patch was assigned a value by randomly drawing from the pool with a matching forest type, size class and age class.

One set of time-step simulations will be conducted using only the succession module in the model. This means that the only methods of disturbance will come from age related mortality or from a low probability of mortality at any time, known as “background” mortality. The other set of simulations will be conducted using the harvest module. Since the study area contains several regions of Mark Twain National Forest these areas will be parameterized based on the management plan created in 2005 (USDA, 2005). All private land within the study area was treated with the same management prescription using an estimation of 1% of the area harvested per year (Kittredge, et al., 2003). For all management prescriptions the percent of the area to be treated was calculated as an amount per year. These values were then scaled to match the time-step of the simulation.

EXPERIMENTAL DESIGN

In order to investigate the effect that temporal resolution has on the modeling results, three simulation treatments with time-steps of two, five and ten years were used. For each treatment, landscape change was simulated for 150 years and have five replicates to account for stochastic variation among runs. Each replication output several files for each time-step: maps showing the basal area and number of trees for each species in each cell, a map showing the dominant species on each cell, a map for each species that shows the age of the oldest group on each cell, and the location, amount and type of harvest that occurred. Once all simulations were run the results were assessed using LandStat, a program developed alongside LANDIS (He, et al., 2009), which calculated the mean values and variance for the number of trees and basal area of each species on each land type. The results from LandStat for each scenario were examined to calculate the relative mean error of prediction (e), relative mean absolute error (MAE%), relative root mean square error of prediction (RMSE%), coefficient of determination (r^2), the Nash-Sutcliffe index of model efficiency (ME), and an index of model agreement (d) (Miehle, et al., 2006) (Janssen & Heuberger, 1995) (Willmott, 1981). These indexes are normally used to assess the accuracy of a prediction model compared to observed values, but in this case they were used to measure the difference between observed results from two different time-steps. e measures the total positive or negative error between prediction sets on the average level. MAE% and RMSE% measure the relative error between each individual set of predictions. r^2 measures correlation between the two sets of predictions and ME reports the improvement of one prediction set over the 'bench-mark', which is the mean of the prediction set being compared against. A positive ME indicates an improvement, the quality of which increases as the value nears +1 (Miehle, et al., 2006). The index of model agreement measures the agreement between two sets of observations with zero indicating no agreement and 1.0 indicating perfect agreement between the sets and no prediction error (Willmott, 1981).

In addition, response variables were analyzed using a multivariate analysis of variance (MANOVA) to test the global hypothesis that different temporal resolutions did not affect each response variable within the classes of time-step and species (Zollner, et al., 2008). The response variables used were total basal area and number of trees on the landscape for each species at three times (year 50, 100, and 150) and metrics calculated by FRAGSTATS for each species' spatial distribution at year 150 that describe patch area, shape and connectivity (McGarigal, 2000).

RESULTS

The simulations were run using a dual 6-core processor machine with 96 GB of RAM. This allowed us to run at least five simulations concurrently. Each simulation for the 10-year time-step took approximately 1.5 hours to run with the harvest module adding only 30 seconds to the processing time of each time-step. The 5-year time-step completed each replication in about 5.7 hours, with the harvest module adding around 40 seconds to each time-step. The 2-year time-step simulation required almost 46 hours to complete, and the harvest process added 70 seconds to each time-step. RAM usage increased from around 5 GB per 10-year simulation to approximately 14 GB per 2-year simulation. Each replication at the 2-year time-step with only succession used around 31 GB of storage and with harvest enabled the space used increased to 53 GB. The replications for the 5-year time-step took up 13 GB and 23 GB respectively for succession and harvest. At a 10-year simulation time-step the space used was only 7 GB for succession and 11 GB for harvest.

Succession

A qualitative assessment of the graphs showing basal area and number of trees over the simulation's course suggest, that while the general trend over time is similar between the three time-steps, the behaviors exhibited are more varied as the time-step decreases. The black oak group basal area illustrates this the most with a general pattern in the 10-year time-step where the basal area starts at 21 ft^2/acre and over the next 60 years increases to its peak of 32 ft^2/acre and then declining down to 4.5 ft^2/acre (Figure 2). In the 2-year time-step simulation the black oak group starts at 17 ft^2/acre and in 70 years reaches its peak of 64 ft^2/acre before beginning to decline.

In general, the mean error of predictions for each species in the 5-year time-step was closer to zero than those in the 2-year time-step with the exception of basal area and number of trees for the hickory group, number of trees for shortleaf pine, and number of trees for cedar (Table 2). This trend continues to hold true for the MAE% and RMSE%. The r^2 values for most individual species basal area and number of tree measurements is higher for the 5-year time-step, and the total basal area and number of trees has a higher value at the 5-year time-step. In both time-steps eastern redcedar had the best overall r^2 value suggesting that it was modeled most similarly across all time-steps. The ME for some species during the 5-year time-step was above zero, and again eastern redcedar had the highest overall values for both time-steps, but many species were below zero, suggesting that they responded differently during different time-steps. Willmott's index of agreement (d) again showed eastern redcedar seemed to be the most homogenously modeled species, and in general the number of trees was more similar than basal area.

The two most dominant species groups, black oak and white oak, had very low similarity to the 10-year time-step in number of trees.

The MANOVA comparison for the succession groups showed there was a significant effect of time-step on all three spatial pattern metric groups and the species quantitative measurements (Table 4). Each individual ANOVA test showed that all response variables responded significantly different at each time-step.

Harvest

The basal area and number of tree graphs for the harvest scenarios show each species following similar trends during the simulation (Figure 3). The 10-year time-step starts with the highest basal area, declines slightly where the other two time-steps increase, and then ends with the lowest basal area. The 5-year time-step has the highest maximum and final amount for both basal area and number of trees.

Most species had lower $\bar{e}\%$, MAE%, and RMSE% values at the 5-year time-step comparison (Table 3). The r^2, ME, and d also followed the trend, suggesting that the 5-year time-step was more similar to the 10-year time-step than the 2-year time-step. The shortleaf pine, eastern redcedar, and maple species had the highest overall similarity across all time-steps.

The MANOVA analysis for the harvest scenarios showed that the time-step had a significant effect on all measurement groups at a 0.05 significance level (Table 5). Within the patch area measurement group the individual ANOVA tests showed the null hypothesis could not be rejected for number of patches, patch density, and the coefficient of variation in patch area. In the patch cohesion group the aggregation index measurement was shown to be not statistically different between time-steps. In the patch shape index the null hypothesis could not be rejected for nine different metrics. In the quantitative measurement group the null hypothesis could not be rejected for the basal area at all three points in time and for the number of trees at year 100.

DISCUSSION

The LANDIS PRO 7.0 model was able to simulate the large study area relatively quickly at a 10-year time-step. Activating the harvest module did not add any appreciable amount of time to the simulation, but had a large effect on the landscape. As the temporal resolution becomes finer several factors combine to increase the processing time and system requirements.

As the time-step decreases, the data structure becomes more complex. The number of possible age classes increases (since the number of age classes is equal to species longevity divided by time-step), requiring more memory to be allocated to the program. This was illustrated by the increase in RAM usage as the time-step decreased. This also results in the succession portion of each time-step taking longer to simulate. The number of simulation steps increases as the time-step decreases as well. Simulating using a 2-year time-step takes five times as many simulation steps as a 10-year time-step to reach 150 years. The combination of these factors accounts for the exponential increase in both time and computing resource usage. The simulation times may have been increased slightly by the fact that we ran multiple simulations at once and all were reading and writing data on the same hard drive.

Some species, generally those not very dominant on the landscape, saw little effect from the change in time-step. The dominant species, in general, saw more variation and became less similar to the 10-year time-step as temporal resolution increased. This increase in variation can likely be attributed in part to the greater number of simulation steps involved, introducing more opportunities for stochastic processes to influence the outcome. This effect seems to have been amplified by activating the harvest module which introduces more processes influencing the landscape. In addition, the processes that operate using species basal area, such as self-thinning, are enhanced by a larger time-step. At a 10-year time-step the youngest tree simulated on the landscape is 10 years old. When a self-thinning or background mortality removes a tree, younger trees are more likely to be chosen, so the effects of removing the youngest age-class has more effect. This can be seen in columns (a) and (b) of figure 2 where self-thinning begins to occur around year 30. In the 10-year time-step simulation the basal area is maintained at a lower level than the 5-year time-step while the number of trees remains higher. In lower time-step simulations when the younger age classes are thinned, more individuals must be removed, but overall there is a higher residual basal area. Compounding this behavior is the fact that lower time-steps are biased toward creating more seeds due to the exponential behavior of seed distribution on the landscape..

Changing the time-step caused a difference in the initial parameterized data as well. Although the starting number of trees on the landscape was virtually the same across all time-steps, the initial basal area decreased as the time-step decreased. This can be attributed to the way age classes for each species are structured. In a 10-year time-step the age, and therefore size, of each individual is always rounded up to the next multiple of 10. This will cause an overestimation in basal area since it is calculated as a direct relationship to age. If the equations controlling these relationships are the same, then arguably as time-step decreases the accuracy of basal area simulation increases. This effect is also a likely influence on the increased variance and decreased similarity observed in the 2-year time-step versus the 5-year time-step when compared against the 10-year time-step simulation. Many species attributes derived during the parameterization and calibration phase for a given time-step cannot be directly scaled for use at a different time-step. The change in temporal resolution necessitates the need for an independent process of parameterization, calibration, and eventually validation, that focuses on the desired time-step.

This illustrates the difficulty using vital attribute linear relationship methods in models to simulate non-linear ecological processes. Species growth rates, mortality rates, and age-size relationships all rely on either default linear function or user defined values. Species attributes such as longevity and seed dispersal are regulated by values in the attribute table, with some stochasticity introduced by the model. We know that these are complex ecological processes that cannot be completely represented using a single equation or a single value, but with proper calibration, the simulation results can be useful in predicting the way a landscape responds under different scenarios. Finer temporal resolutions can also be useful for capturing the effects of ecological and disturbance processes more accurately, at the cost of processing time and computer system requirements.

The LANDIS PRO 7.0 model is relatively new and other model developers have not examined in detail the cause of variation in simulations caused by differing time-steps. Further testing of individual processes and modules would be useful in developing a methodology for parameterizing and calibrating variable time-step models. Results from an in depth study would also aid in further development of disturbance modules and improving on the LANDIS PRO 7.0 succession model design.

Works Cited

Burns, R. M. & Honkala, B. H., 1990. *Silvics of North America: Volume 1. Conifers,* Washington (DC): US Department of Agriculture.

Burns, R. M. & Honkala, B. H., 1990. *Silvics of North America: Volume 2. Hardwoods,* Washington (DC): US Department of Agriculture.

Chew, J., Stalling, C. & Moeller, K., 2004. Integrating knowledge for simulating vegetation change at landscape scales. *West. J. Appl. Foresters,* Issue 19, pp. 102-108.

Deutschman, D., Levin, S. & Pacala, S., 1999. Error propagation in a forest succession model: the role of fine-scale heterogeneity in light. *Ecology,* Volume 80, pp. 1927-1943.

Fielding, A. H. & Bell, J. F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation,* Volume 24, pp. 38-49.

Gustafson, E. J. et al., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. *Canadian Journal of Forest Research,* Volume 30, pp. 32-43.

Gustafson, E. J. et al., 2000. Spatial simulation of forest succession and timber harvesting using LANDIS. *Canadian Journal of Forest Research,* 30(1), pp. 32-43.

Gustafson, E., Shvidenko, A. D., Sturtevant, B. R. & Scheller, R. M., 2010. Predicting global change effects on forest biomass and composition in south-central Siberia. *Ecological Applications,* Volume 20(3), pp. 700-715.

He, H. S., 2008. Forest landscape models: Definitions, characterization, and classification. *Forest Ecology and Management,* Issue 254, pp. 484-498.

He, H. S. et al., 2009. *LANDIS, a spatially explicit model of forest landscape disturbance, management, and succession - LANDIS 6.0 Pro Users Guide,* Columbia: University of Missouri School of Natural Resources.

He, H. S., Keane, R. E. & Iverson, L. R., 2008. Forest landscape models, a tool for understanding the effect of the large-scale and long-term landscape processes. *Forest Ecology and Management,* Issue 254, pp. 371-374.

He, H. S. & Mladenoff, D., 1999b. The Effects of seed dispersal on the simulation of long-term forest landscape change. *Ecosystems,* Volume 2, pp. 308-319.

He, H. S. & Mladenoff, D. J., 1999a. Spatially Explicit and Stochastic Simulation of Forest Landscape Fire Disturbance and Succession. *Ecology,* pp. 81-99.

He, H., Yang, J., Shifley, S. & Thompson III, F., 2011. Challenges of forest landscape modeling-Simulating large landscapes and validating results. *Landscape and Urban Planning,* 100(4), pp. 400-402.

Janssen, P. & Heuberger, P., 1995. Calibration of process-oriented models. *Ecological Modelling,* pp. 55-66.

Jenkins, J., Birdsey, R. & Pan, Y., 2001. Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. *Ecological Applications,* Volume 11, pp. 1174-1193.

Jenness, J., Prost, B. & Beier, P., 2010. *Land Facet Corridor Designer: Extension for ArcGIS.* [Online]

Available at: http://www.jennessent.com/arcgis/land_facets.htm

[Accessed 2010].

Keane, R. et al., 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. *Ecological Modeling,* Issue 179, pp. 3-27.

Keane, R., Parsons, R. & Hessburg, P., 2002. Estimating historical range and variation of landscape patch dynamics: limitations of simulation approach. *Ecological Modeling,* Issue 151, pp. 29-49.

Kittredge, D. B. J., Finley, A. O. & Foster, D. R., 2003. Timber harvesting as ongoing disturbance in a landscape of diverse ownership. *Forest Ecology and Management,* 180(1-3), pp. 425-442.

Ko, D. W., 2005. *Evaluation of the private forestland ownership parcelization and its effects on the forest landscape in the southeastern Missouri Ozarks,* Ph.D. Dissertation: University of Missouri.

Ko, D. W., He, H. S. & Larsen, D. R., 2006. Simulating private land ownership fragmentation in the Missouri Ozarks, USA. *Landscape Ecology,* Volume 21, pp. 671-686.

Loewenstein, E. F., Johnson, P. & Garrett, H., 2000. Age and diameter structure of a managed uneven-aged oak forest. *Canadian Journal of Forest Research,* 30(7), pp. 1060-1070.

McGarigal, K., 2000. *FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps.* [Online]
Available at:
http://www.umass.edu/landeco/research/fragstats/documents/fragstats_documents.html
[Accessed 13 October 2010].

Miehle, P. et al., 2006. Quantifying uncertainty from large-scale model predictions of forest carbon dynamics. *Global Change Biology,* 12(8), pp. 1421-1434.

Mladenoff, D. J., 2004. LANDIS and forest landscape models. *Ecological Modelling,* pp. 7-19.

Mladenoff, D. J., Host, G., Boeder, J. & Crow, T., 1996. LANDIS: a spatial model of forest landscape disturbance, succession, and management. In: M. F. Goodchild, et al. eds. *GIS and environmental modeling: progress and research issues.* New York: John Wiley & Sons, pp. 175-180.

Mlandenoff, D. & He, H., 1999. Design and behavior of LANDIS, an object-oriented model of forest landscape disturbance and succession. In: D. Mladenoff & W. Baker, eds. *Spatial Modeling of Forest Landscapes: Approaches and Applications.* Cambridge, UK: Cambridge University Press, pp. 125-162.

Nigh, T. A. & Schroeder, W. A., 2002. *Atlas of Missouri Ecoregions.* Jefferson City(MO): Missouri Department of Conservation.

Oliver, C. D. & Larson, B. C., 1990. *Forest stand dynamics.* Updated ed. New York: John Wiley and Sons Inc..

Pacala, S. et al., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs,* Issue 66, pp. 57-74.

Qi, Y. & Wu, J., 1996. Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. *Landscape Ecology,* 11(1), pp. 39-49.

Reineke, L., 1933. Perfecting a stand-density index for even-aged forests. *Journal of Agricultural Research,* 46(7), pp. 627-638.

Scheller, R. M. et al., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. *Ecological Modelling,* Issue 201, pp. 409-419.

Scheller, R. & Mladenoff, D., 2007. An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecology,* 22(4), pp. 491-505.

Schnur, G. L., 1937. Yield, stand, and volume tables for even-aged upland oak forests. *Technical Bulletin 560, U.S. Dept. of Agriculture,* pp. 1-88.

Shifley, S. R., Rittenhouse, C. D. & Millspaugh, J. J., 2009. Validation of landscape-scale decision support models that predict vegetation and wildlife dynamics. In: J. J. Millspaugh & F. R. Thompson, eds. *Models for planning wildlife conservation in large landscapes.* San Diego(California): Elsevier Science, pp. 415-448.

Shifley, S. R., Thompson, F. R. I., Dijak, W. D. & Fan, Z., 2008. Forecasting landscape-scale, cumulative effects of forest management on vegetation and wildlife habitat: A case study of issues, limitations, and opportunities. *Forest Ecology and Management,* Volume 254, pp. 474-483.

Shifley, S. R. et al., 2006. Simulated effects of forest management alternatives on landscape structure and habitat suitability in the Midwestern United States. *Forest Ecology and Management,* Volume 229, pp. 361-377.

Shifley, S. R., Thompson, F. R., Larsen, D. R. & Dijak, W. D., 2000. Modeling forest landscape change in the Missouri Ozarks under alternative management practices. *Computers and Electronics in Agriculture,* Volume 27, pp. 7-24.

Shugart, H. H. & West, D. C., 1980. Forest succession models. *Bioscience,* 30(5), pp. 308-313.

Sturtevant, B. R. et al., 2009. Studying fire mitigation strategies in multi-ownership landscapes: balancing the management of fire-dependent ecosystems and fire risk. *Ecosystems,* Volume 12, pp. 445-461.

USDA, 2005. *2005 Land and Resource Management Plan - Mark Twain National Forest,* s.l.: USDA Forest Service.

Wang, W. J. et al., 2012. *A Large-Scale Forest Landscape Model Validated With Forest Inventory Data,* s.l.: In Preparation.

Wiens, J., 1989. Spatial Scaling in Ecology. *Functional Ecology,* 3(4), pp. 385-397.

Willmott, C., 1981. On the validation of models. *Physical Geography,* 2(2), pp. 184-194.

Woodall, C. W. et al., 2010. *The Forest Inventory and Analysis Database Version 4.0: Database Description and Users Manual for Phase 3,* Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station.

Wu, J., 2004. Effects of changing scale on landscape pattern analysis: scaling relations. *Landscape Ecology,* 19(2), pp. 125-138.

Xi, W. et al., 2009. Landscape modeling for forest restoration planning and assessment: lessons from the Southern Appalachian Mountains. *Journal of Forestry,* pp. 191-198.

Zollner, P. A. et al., 2005. Modeling the Influence of Dynamic Zoning of Forest Harvesting on Ecological Succession in a Northern Hardwoods Landscape. *Environmental Management,* 35(4), pp. 410-425.

Zollner, P. A. et al., 2008. Influence of forest planning alternatives on landscape pattern and ecosystem processes in northern Wisconsin, USA. *Forest Ecology and Management,* Issue 254, pp. 429-444.

Table 4. Species attributes as specified in the simulation.

	Pinus echinata	*Juniperus virginiana*	*Quercus alba (Group)*	*Quercus velutina (Group)*	*Carya spp.*	*Acer saccharum*	*Ulmus spp.*
Longevity (years)	200	300	300	150	250	200	200
Maturity (years)	20	10	20	20	20	20	20
Shade Tolerance (class)	2	3	3	4	3	5	4
Fire Tolerance (class)	4	2	4	3	3	1	1
Effective Seed Distance (meters)	40	250	45	45	45	100	40
Maximum Seed Distance (meters)	80	500	45	45	45	200	80
Vegetative Propogation (probability)	0.5	0	0.5	0.4	0.5	0.3	0.5
Minimum Sprout Age (years)	1	0	10	10	10	10	0
Maximum Sprout Age (years)	47	0	50	70	70	70	150
Reclassification Coefficient (scale)	0.66	0.99	1	0.5	0.83	0.65	0.64
Species Type 1 (class)[a]	1	1	0	0	0	0	0
Species Type 2 (class)[b]	17	12	11	11	9	8	7
Maximum Diameter (cm)	61	64	132	111	84	94	34
Maximum Density (trees/hectare)[c]	990	900	570	570	570	570	570
Total Seed (seeds/tree)	60	60	10	15	5	40	50
Carbon Coefficient (ratio)	0.5	0.5	0.5	0.5	0.5	0.5	0.5

[a] Specifies hardwood or softwood.

[b] Specifies a class for calculation of biomass.

[c] Maximum stand density in number of 25.5cm trees per hectare.

Table 5. Comparisons of the 5-year and 2-year time-step results against the 10-year time-step simulations using only succession.

Succession Species		*e*		MAE%		RMSE%		r^2		ME		d	
		5-Year	2-Year	5-Year	2-Year	5-Year	2-Year	5-Year	2-Year	5-Year	2-Year	5-Year	2-Year
Pinus echinata	BA(ft^2/acre)	-42.71	-51.74	44.85	52.49	50.13	22.72	0.39	0.65	-1.58	-2.51	0.556	0.604
	Trees per acre	-27.31	-25.94	28.20	27.03	31.39	6.37	0.98	0.97	0.94	0.93	0.984	0.983
Juniperus virginiana	BA(ft^2/acre)	-4.09	10.51	7.69	15.55	9.06	18.95	0.99	0.89	0.96	0.83	0.991	0.959
	Trees per acre	-16.71	-0.09	16.71	44.68	22.06	62.57	0.98	0.76	0.94	0.62	0.986	0.823
Quercus velutina	BA(ft^2/acre)	-26.16	-94.02	27.74	96.46	35.78	77.64	0.88	0.42	0.32	-5.12	0.886	0.492
(Group)	Trees per acre	-13.40	-244.38	30.58	258.57	55.71	389.23	0.81	0.11	0.69	-14.83	0.934	0.156
Quercus alba	BA(ft^2/acre)	-4.79	19.45	8.48	23.62	11.10	32.18	0.93	0.70	0.86	0.18	0.971	0.719
(Group)	Trees per acre	15.32	43.42	65.61	59.03	77.33	40.09	0.01	0.11	-5.14	-4.75	0.248	0.237
Carya spp.	BA(ft^2/acre)	-43.64	-20.35	45.40	23.02	49.79	26.34	0.71	0.77	-22.07	-4.47	0.334	0.587
	Trees per acre	-25.37	-13.66	25.57	19.59	43.68	24.01	0.94	0.96	0.88	0.94	0.973	0.986
Acer saccharum	BA(ft^2/acre)	32.38	58.98	34.99	59.16	51.43	33.64	0.98	0.98	0.59	-0.10	0.834	0.592
	Trees per acre	39.09	71.80	46.52	74.57	53.86	45.38	0.71	0.04	0.27	-1.25	0.754	0.467
Ulmus spp.	BA(ft^2/acre)	2.86	37.98	98.09	67.97	129.60	37.38	0.45	0.05	-0.23	-0.15	0.028	0.295
	Trees per acre	-6.83	11.45	11.32	20.03	24.80	24.11	0.98	0.97	0.97	0.96	0.993	0.990
Total	BA(ft^2/acre)	-14.90	-16.40	18.33	19.99	19.27	8.49	0.87	0.57	-5.35	-7.87	0.606	0.516
	Trees per acre	6.82	9.93	39.08	50.63	46.29	27.77	0.13	0.01	-0.71	-1.96	0.607	0.339

Table 6. Comparisons of the 5-year and 2-year time-step results against the 10-year time-step simulations using succession and harvest.

Harvest Species		*e* 5-Year	*e* 2-Year	MAE% 5-Year	MAE% 2-Year	RMSE% 5-Year	RMSE% 2-Year	r^2 5-Year	r^2 2-Year	ME 5-Year	ME 2-Year	d 5-Year	d 2-Year
Pinus echinata	BA(ft^2/acre)	-49.28	-59.70	31.15	40.99	32.03	14.64	0.88	0.77	-0.38	-1.44	0.685	0.630
	Trees per acre	-18.31	-17.39	28.83	11.29	30.55	30.66	0.97	0.96	0.80	0.94	0.949	0.987
Juniperus virginiana	BA(ft^2/acre)	-4.76	12.23	22.05	15.06	29.09	16.16	0.92	0.91	0.53	0.82	0.921	0.963
	Trees per acre	-5.32	-0.03	39.48	45.23	47.67	15.31	0.81	0.64	-1.14	-1.75	0.728	0.685
Quercus velutina	BA(ft^2/acre)	-35.23	-126.61	16.89	45.06	20.72	30.63	0.70	0.26	0.02	-4.13	0.825	0.446
(Group)	Trees per acre	-7.94	-144.72	28.55	51.66	35.99	50.63	0.77	0.04	-0.20	-3.10	0.801	0.474
Quercus alba	BA(ft^2/acre)	-7.81	31.70	18.93	9.28	20.25	25.00	0.60	0.08	-5.36	-0.65	0.506	0.131
(Group)	Trees per acre	10.25	29.07	18.36	30.81	21.30	39.99	0.32	0.28	-0.69	-3.27	0.686	0.446
Carya spp.	BA(ft^2/acre)	-62.42	-29.10	39.87	25.17	42.24	17.49	0.00	0.06	-9.44	-3.07	0.319	0.461
	Trees per acre	-10.65	-5.73	29.93	17.50	31.24	18.71	0.96	0.91	0.32	0.72	0.841	0.917
Acer saccharum	BA(ft^2/acre)	84.62	154.11	7.31	24.12	9.38	26.08	0.93	0.87	0.92	0.26	0.977	0.783
	Trees per acre	59.62	109.50	20.13	16.28	23.32	14.62	0.69	0.92	-0.26	0.25	0.744	0.861
Ulmus spp.	BA(ft^2/acre)	1.54	20.49	64.20	72.32	77.29	8.39	0.01	0.12	-2.18	-2.70	0.423	0.418
	Trees per acre	-3.90	6.53	20.97	23.94	23.09	42.79	0.98	0.98	0.88	0.86	0.970	0.970
Total	BA(ft^2/acre)	-20.77	-22.86	15.76	12.92	16.79	6.16	0.25	0.02	-4.08	-2.74	0.141	0.248
	Trees per acre	3.95	5.75	21.03	15.73	25.50	22.45	0.12	0.01	-5.48	-2.44	0.367	0.444[1]

[1] *e* - Relative mean error of prediction
MAE% - Relative mean absolute error
RMSE% - Relative root mean square error of prediction
r^2 – Coefficient of determination
ME – Nash-Sutcliffe index of model efficiency
d – Index of model agreement

Table 7. MANOVA test results of landscape spatial patterns and species responses to time-step using succession.

Succession MANOVA global test of hypothesis	Patch area	Patch cohesion	Patch shape	Basal area / number of trees
d.f. (n, d)	18, 152	10, 162	34, 138	12, 184
Pillai's trace	2.00	1.99	2.00	2.00
F	103731	5997	6233	1.287×10^7
Prob > F	< .0001	< .0001	< .0001	< .0001

Individual ANOVA tests of hypotheses	d.f.	Type III SS	F	Prob > F
Number of patches				
Time-Step	2	2531825747	327900	< .0001
Error	84	324296		
Patch density				
Time-Step	2	2.363	326437	< .0001
Error	84	0.0003		
Largest patch index				
Time-Step	2	4782.31	3398.06	< .0001
Error	84	59.11		
Patch area mean				
Time-Step	2	153704.5	4712541	< .0001
Error	84	13.7		
Patch area-weighted mean				
Time-Step	2	4.36	2684.53	< .0001
Error	84	68148026391		
Median patch area				
Time-Step	2	8.26	661	< .0001
Error	84	0.52		
Range in patch area				
Time-Step	2	5.12	3398.75	< .0001
Error	84	63327482093		
Standard deviation in patch area				
Time-Step	2	777749567.1	8431.68	< .0001
Error	84	3874139		

Individual ANOVA tests of hypotheses	d.f.	Type III SS	F	Prob > F
Coefficient of variation in patch area				
Time-Step	2	149371828.5	609.62	< .0001
Error	84	10291086.3		
Patch cohesion index				
Time-Step	2	895.25	57046.1	< .0001
Error	84	0.66		
Landscape division index				
Time-Step	2	0.086	4474.76	< .0001
Error	84	0.0008		
Aggregation index				
Time-Step	2	3162.5	4805888	< .0001
Error	84	0.028		
Mean shape index distribution				
Time-Step	2	0.00216	146.87	< .0001
Error	84	0.00062		
Area-weighted mean shape index distribution				
Time-Step	2	63046.71	628.21	< .0001
Error	84	4215.11		
Range in shape index distribution				
Time-Step	2	46004.41	392.46	< .0001
Error	84	4923.26		
Standard deviation in shape index distribution				
Time-Step	2	2.663	127788	< .0001
Error	84	0.00088		
Coefficient of variation of shape index distribution				
Time-Step	2	15552.09	43999.1	< .0001
Error	84	14.845		
Mean perimeter-area ratio distribution				
Time-Step	2	8399.533	54130.5	< .0001
Error	84	6.517		

Individual ANOVA tests of hypotheses	d.f.	Type III SS	F	Prob > F
Area-weighted mean perimeter-area ratio distribution				
Time-Step	2	62563.34	4827172	< .0001
Error	84	0.54435		
Median of perimeter-area ratio distribution				
Time-Step	2	41080.41	1572.25	< .0001
Error	84	1097.39		
Range in perimeter-area ratio distribution				
Time-Step	2	1858.29	295.17	< .0001
Error	84	264.42		
Standard deviation in perimeter-area ratio distribution				
Time-Step	2	592.84	8680.09	< .0001
Error	84	2.869		
Coefficient of variation of perimeter-area ratio distribution				
Time-Step	2	305.419	38884.5	< .0001
Error	84	0.33		
Mean contiguity index distribution				
Time-Step	2	0.0332	46930.2	< .0001
Error	84	0.00003		
Area-weighted mean contiguity index distribution				
Time-Step	2	0.3377	6342864	< .0001
Error	84	0.000002		
Median of contiguity index distribution				
Time-Step	2	0.05946	1558.33	< .0001
Error	84	0.0016		
Range in contiguity index distribution				
Time-Step	2	0.0172	359.08	< .0001
Error	84	0.002		
Standard deviation incontiguity index distribution				
Time-Step	2	0.00365	12934.5	< .0001
Error	84	0.000012		
Coefficient of variation of contiguity index distribution				
Time-Step	2	2814.06	24544.6	< .0001
Error	84	4.82		

Individual ANOVA tests of hypotheses	d.f.	Type III SS	F	Prob > F
Basal area, year 50				
Time-Step	2	1.441550E+14	Infty	< .0001
Error	96	0		
Basal area, year 100				
Time-Step	2	7.770876E+13	50720000	< .0001
Error	96	73547013.11		
Basal area, year 150				
Time-Step	2	5.175414E+13	1045000	< .0001
Error	96	237650651.3		
Number of trees, year 50				
Time-Step	2	1.371520E+18	3.346000E+07	< .0001
Error	96	1.967292E+12		
Number of trees, year 100				
Time-Step	2	4.492492E+17	1794748	< .0001
Error	96	1.201504E+13		
Number of trees, year 150				
Time-Step	2	5.221058E+16	653431	< 0.0001
Error	96	3.835307E+12		

Table 8. MANOVA test results of landscape spatial patterns and species responses to time-step using succession and harvest.

Harvest MANOVA global test of hypothesis	Patch area	Patch cohesion	Patch shape	Basal area / number of trees
d.f. (n, d)	14, 158	10, 162	34, 138	12, 184
Pillai's trace	0.32	0.34	1.05	0.40036837
F	2.18	3.3	4.48	3.84
Prob > F	0.0107	0.0006	< .0001	< .0001

Individual ANOVA tests of hypotheses	d.f.	Type III SS	F	Prob > F
Number of patches				
Time-Step	2	281684212	0.53	0.5907
Error	84	22334416892		
Patch density				
Time-Step	2	0.2629	0.53	0.5908
Error	84	20.844		
Largest patch index				
Time-Step	2	375.83	3.97	0.0224
Error	84	3972.305		
Patch area mean				
Time-Step	2	4302.33817	3.98	0.0223
Error	84	45397.877		
Patch area-weighted mean				
Time-Step	2	3.64783E+11	4.45	0.0132
Error	84	3.36E+12		
Median patch area				
Time-Step	2	0.91229	6.64	0.0021
Error	84	5.7737		
Range in patch area				
Time-Step	2	4.0269E+11	3.97	0.0224
Error	84	4.26E+12		
Standard deviation in patch area				
Time-Step	2	38450051.5	4.1	0.02
Error	84	393684655.9		
Coefficient of variation in patch area				
Time-Step	2	16861992.4	2.26	0.1103
Error	84	312935681.7		

Individual ANOVA tests of hypotheses	d.f.	Type III SS	F	Prob > F
Patch cohesion index				
Time-Step	2	61.188	0.92	0.403
Error	84	2797.254		
Landscape division index				
Time-Step	2	0.00636	4.8	0.0106
Error	84	0.05561		
Aggregation index				
Time-Step	2	66.866	0.46	0.6299
Error	84	6043.13		
Mean shape index distribution				
Time-Step	2	0.03415	8.38	0.0005
Error	84	0.1712		
Area-weighted mean shape index distribution				
Time-Step	2	8980.1578	2.78	0.0679
Error	84	135769.9918		
Range in shape index distribution				
Time-Step	2	12926.5833	2.6	0.0805
Error	84	209048.3005		
Standard deviation in shape index distribution				
Time-Step	2	1.4004	6.47	0.0024
Error	84	9.0968		
Coefficient of variation of shape index distribution				
Time-Step	2	6771.3985	6	0.0037
Error	84	47394.852		
Mean perimeter-area ratio distribution				
Time-Step	2	1728.066	8.71	0.0004
Error	84	8329.953		

Individual ANOVA tests of hypotheses	d.f.	Type III SS	F	Prob > F
Area-weighted mean perimeter-area ratio distribution				
Time-Step	2	1326.8782	0.47	0.6285
Error	84	119327.6131		
Median of perimeter-area ratio distribution				
Time-Step	2	13203.909	5.89	0.004
Error	84	94184.32		
Range in perimeter-area ratio distribution				
Time-Step	2	538.8236	5.19	0.0075
Error	84	4364.256		
Standard deviation in perimeter-area ratio distribution				
Time-Step	2	224.3242	2.51	0.0872
Error	84	3751.2795		
Coefficient of variation of perimeter-area ratio distribution				
Time-Step	2	51.7956	3.84	0.0253
Error	84	565.8684		
Mean contiguity index distribution				
Time-Step	2	0.006957	8.5	0.0004
Error	84	0.03436		
Area-weighted mean contiguity index distribution				
Time-Step	2	0.008056	0.54	0.582
Error	84	0.621086		
Median of contiguity index distribution				
Time-Step	2	0.01702	5.67	0.0049
Error	84	0.126		
Range in contiguity index distribution				
Time-Step	2	0.00362	4.76	0.011
Error	84	0.032		

Individual ANOVA tests of hypotheses	d.f.	Type III SS	F	Prob > F
Standard deviation incontiguity index distribution				
Time-Step	2	0.00125	2.45	0.0922
Error	84	0.02146		
Coefficient of variation of contiguity index distribution				
Time-Step	2	1727.323	10.83	< .0001
Error	84	6698.5886		
Basal area, year 50				
Time-Step	2	1.392688E+13	1.66	0.1962
Error	96	4.03E+14		
Basal area, year 100				
Time-Step	2	3.032554E+13	2.81	0.0652
Error	96	5.18E+14		
Basal area, year 150				
Time-Step	2	1.240615E+13	1.13	0.3258
Error	96	5.25E+14		
Number of trees, year 50				
Time-Step	2	4.802716E+17	4.61	0.0122
Error	96	4.998735E+18		
Number of trees, year 100				
Time-Step	2	7.570666E+17	3.02	0.0535
Error	96	1.203790E+19		
Number of trees, year 150				
Time-Step	2	8.942124E+17	4.08	0.02
Error	96	1.052684E+19		

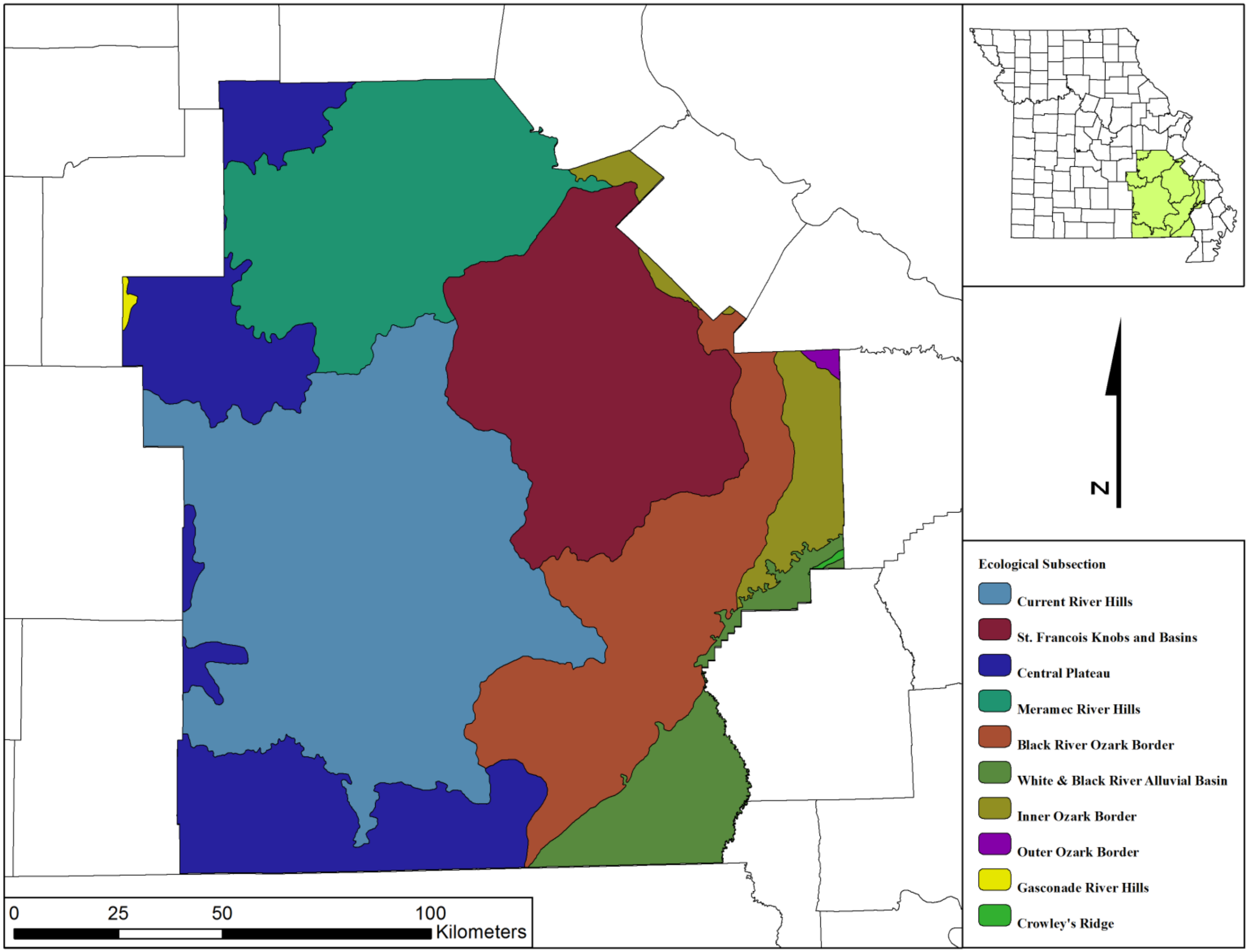

Figure 10. Map of study area used in simulations with ecological subsections shown.

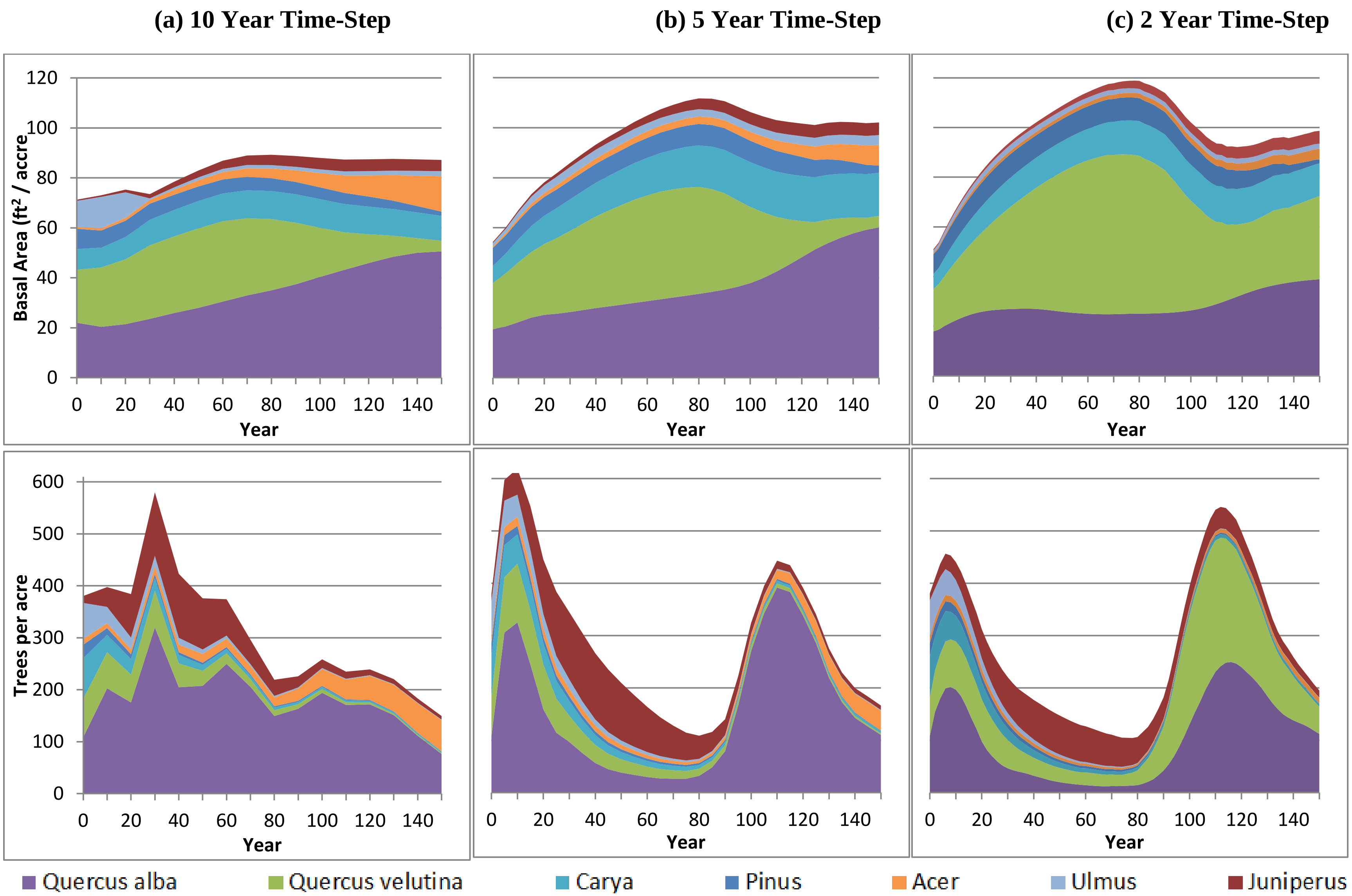

Figure 11. Graphs showing basal area and number of tree trajectories over the span of the 150 year simulation using succession.

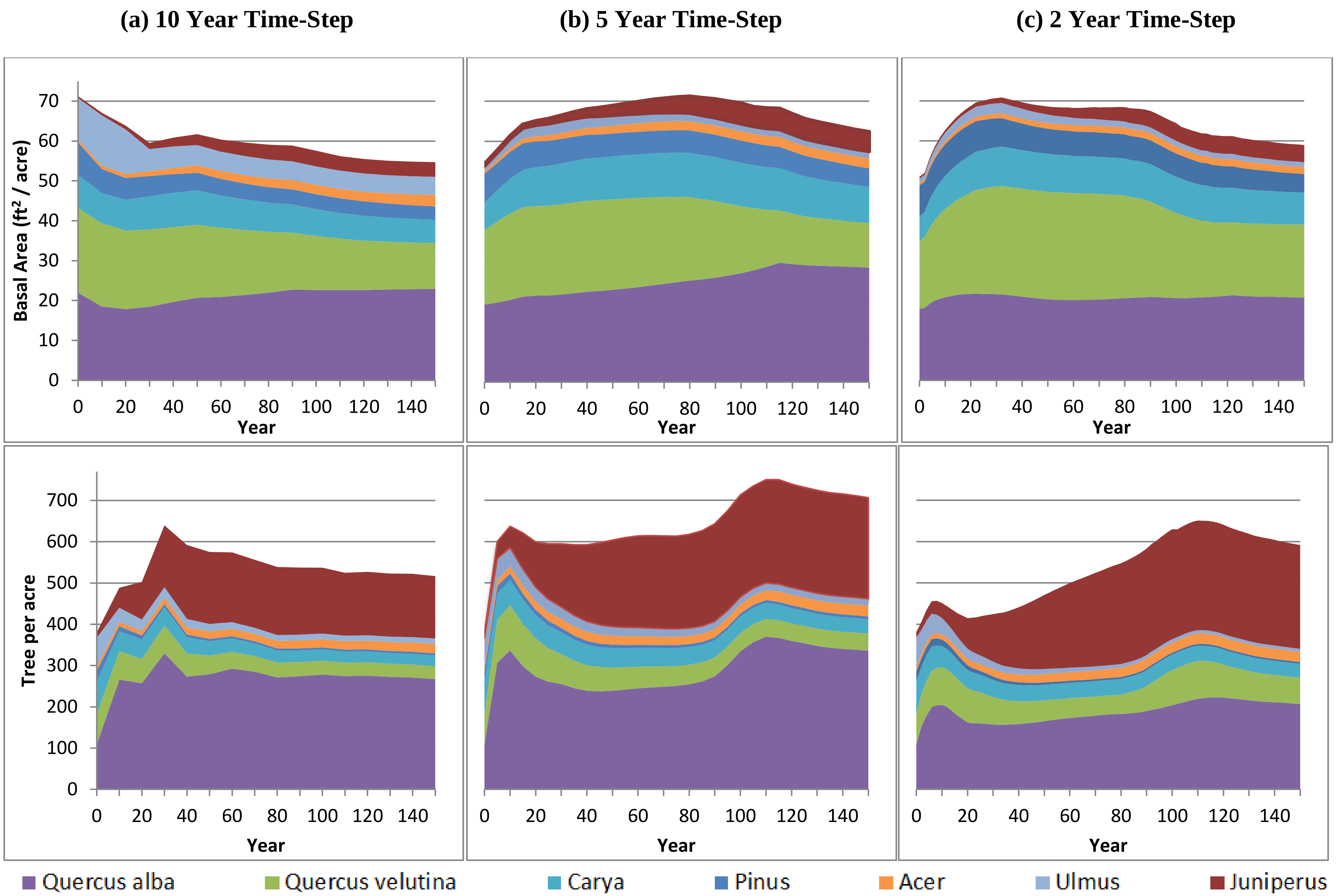

Figure 12. Graphs showing basal area and number of tree trajectories over the span of the 150 year simulation using succession and harvest.