

Modelling for forest management synergies and trade-offs: Northern hardwood tree regeneration, timber and deer

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ABSTRACT

In many managed forests, tree regeneration density and composition following timber harvest are highly variable. This variability is due to multiple environmental drivers – including browsing by herbivores such as deer, seed availability and physical characteristics of forest gaps and stands – many of which can be influenced by forest management. Identifying management actions that produce regeneration abundance and composition appropriate for the long-term sustainability of multiple forest values (e.g., timber, wildlife) is a difficult task. However, this task can be aided by simulation tools that improve understanding and enable evaluation of synergies and trade-offs between management actions for different resources. We present a forest tree regeneration, growth, and harvest simulation model developed with the express purpose of assisting managers to evaluate the impacts of timber and deer management on tree regeneration and forest dynamics in northern hardwood forests over long time periods under different scenarios. The model couples regeneration and deer density sub-models developed from empirical data with the Ontario variant of the US Forest Service individual-based forest growth model, Forest Vegetation Simulator. Our error analyses show that model output is robust given uncertainty in the sub-models. We investigate scenarios for timber and deer management actions in northern hardwood stands for 200 years. Results indicate that higher levels of mature ironwood (*Ostrya virginiana*) removal and lower deer densities significantly increase sugar maple (*Acer saccharum*) regeneration success rates. Furthermore, our results show that although deer densities have an immediate and consistent negative impact on forest regeneration and timber through time, the non-removal of mature ironwood trees has cumulative negative impacts due to feedbacks on competition between ironwood and sugar maple. These results demonstrate the utility of the simulation model to managers for examining long-term impacts, synergies and trade-offs of multiple forest management actions.

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1. Introduction

Integrated natural resource management demands that managers balance multiple competing resource uses in a given area (Loomis, 1993). For example, in mixed upland hardwood–lowland conifer forests of the Great Lakes region of North America, managers are required to maintain timber productivity whilst ensuring habitat provision for wildlife such as economically valuable white-tailed deer (*Odocoileus virginianus* Zimm.) and bird species of conservation concern (such as the black-throated green warbler, *Contopus virens* L., Matteson et al., 2009). Interactions between ecological processes and human activities produce uncertainties in the identification of appropriate management actions for long-term

sustainability of multiple natural resources and values (Liu et al., 2012). Natural resource managers are increasingly being aided in their understanding of these uncertainties by simulation tools that allow evaluation of synergies and trade-offs between management actions for different resources over the long-term, including between timber and wildlife in forest landscapes (e.g., Larson et al., 2004; Shifley et al., 2006; Zollner et al., 2008; Millington et al., 2011; Rittenhouse et al., 2011). Here we present one such tool – a forest tree regeneration, growth and harvest model developed with the express purpose of assisting managers to evaluate the impacts of scenarios of timber and wildlife (deer) management on tree regeneration and forest dynamics in northern hardwood forests over long time periods.

Most stands of northern hardwood trees in the Great Lakes region are managed under an uneven-aged selection silviculture regime, in which juvenile trees of shade-tolerant species are expected to regenerate naturally beneath forest-canopy gaps

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created by periodic harvesting of single to small groups of overstorey trees (Arbogast, 1957; Nyland, 1998). However, variable or low densities of regeneration can lead to important changes in forest stand composition and structure over long time periods (Seagle and Liang, 2001; Pedersen and Wallis, 2004), changing habitat for wildlife (Millington et al., 2011), and presenting economic concerns for timber producers (Donovan, 2005; Racevskis and Lupi, 2006). Regeneration density and composition are known to be highly variable in forests managed using selection harvesting in this region, and northern hardwood stands have been observed to have low juvenile tree densities of species such as sugar maple (*Acer saccharum* Marsh.), despite their dominance in the overstorey (Stoekeler et al., 1957; Marquis and Brenneman, 1981; Jenkins, 1997; Miller, 2004; Donovan, 2005; Matonis et al., 2011). Among other influences, intense browsing by high densities of white-tailed deer has frequently been cited as a major cause of this regeneration failure and a driver of shifts in regeneration composition from commercially valuable and palatable species such as sugar maple towards commercially undesirable and unpalatable species such as ironwood (*Ostrya virginiana* (Mill.) K. Koch; Haugen and Davenport, 1950; Stoekeler et al., 1957; Shafer et al., 1961; Marquis and Brenneman, 1981; Rooney et al., 2000; Horsley et al., 2003; Côté et al., 2004). For simulation tools to be useful for management, models must appropriately represent impacts of the multiple drivers of regeneration and produce output readily interpretable by managers. One way to achieve this is to incorporate sub-models of drivers of regeneration dynamics into existing forest management simulation tools.

Many simulation models have been developed for improving ecological understanding of forest dynamics via the representation of the establishment, growth and senescence of individual trees in forest gaps (e.g., Botkin et al., 1972; Shugart, 1984; Urban, 1990; Bugmann et al., 1996; Liu and Ashton, 1999; Larocque et al., 2011). These models have focused on questions of fundamental ecological importance and their use and output has been of limited utility for forest managers, who have consequently relied more on growth-yield models for applied forest planning and management (Liu and Ashton, 1995; Weiskittel et al., 2011). However, because growth-yield models focus on the production of merchantable timber (i.e., the growth of overstorey trees) they lack detailed (or any) representation of regeneration of juvenile trees. For example, the US Forest Service Forest Vegetation Simulator (FVS) is a distance-independent, individual-tree forest growth-yield model that has a long history of development and use to support forest management decision-making (Crookston and Dixon, 2005) but which has limited representation of tree establishment and regeneration. Users of FVS must specify the species, density, and size of expected new trees at each simulated cycle themselves (beyond the Rocky Mountains for which a regeneration module has been developed, Ferguson and Carlson, 1993). This approach assumes that users (managers) have accurate knowledge of previous regeneration abundance and composition (or assumes new trees will be planted). This assumption is problematic in forests like the northern hardwood of the Great Lakes region where uncertainty is great because of high variability in regeneration and its multiple drivers. Furthermore, assuming observed regeneration patterns will continue into the future is also problematic as factors driving regeneration may change over the long term, including in response to previous forest management actions (such as removal of seed sources of different tree species and changes in deer populations). There is therefore a need to develop and incorporate external regeneration models into growth-yield models like FVS (Robinson, 2008). Incorporating external models that represent other drivers of regeneration which might be manipulated by management actions, such as deer, will further increase the utility of these tools.

The integrated simulation model we present here, which couples regeneration and deer sub-models with the Ontario variant of FVS (Sharma et al., 2008), was developed with the aim of contributing to efforts to improve existing simulation tools for integrated natural resource management. We first provide an overview of the sub-models and their coupling before presenting error analyses and results from using the integrated model to examine scenarios of alternative timber and deer management actions.

2. Methods

2.1. Study area

The data used in the development of the simulation model presented here were collected from stands in the forested region of the Upper Peninsula of Michigan, USA (see Millington et al., 2010, submitted for publication; Matonis et al., 2011). In this region, upland northern hardwood, lowland conifer, aspen and mixed upland forest types are juxtaposed in a mosaic across the rolling topography of the Menominee drumlin field. The primary land use in the study area is forest management for timber products, but a large deer herd supports hunting as an important part of the local economy (Shi et al., 2006). Forest managers in this area must account for these competing demands when considering management actions for the future, as well as ensuring sustainability of habitat for wildlife such as neotropical migrant songbirds (Laurent et al., 2005; Millington et al., 2011). These management issues are particularly acute given the threat to sustainability caused by variation in upland northern hardwood tree regeneration across the region (Donovan, 2005; Matonis et al., 2011). Consequently, our focus here is on the regeneration, growth and harvest of trees in northern hardwood stands. Overstorey canopies of northern hardwood stands are dominated by commercially valuable sugar maple but include other species such as American basswood (*Tilia americana* L.), black cherry (*Prunus serotina* Ehrh.), paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and yellow birch (*Betula alleghaniensis* Britton) (Matonis et al., 2011). Ironwood is the second most common tree in these forests. Compared to canopy dominant sugar maple, its relatively small maximum size relegates it to subcanopy status and low economic value. In testing our simulation model here we simulate 29 hardwood stands in the ~20 km² study area sub-section examined by Millington et al. (2010).

2.2. Forest stand regeneration, growth and harvest simulation model

Our simulation model couples regeneration and deer density sub-models developed from our empirical data with a variant of the US Forest Service individual-based forest growth model, Forest Vegetation Simulator (FVS; Ontario variant, Lacerte et al., 2006; Sharma et al., 2008). The Ontario variant of FVS (FVS-On) is a metric re-calibration of existing US variants, developed through a network of growth and yield plots (Sharma et al., 2008). The tree species represented in FVS-On (Lacerte et al., 2008) make this variant very suitable for our upper Michigan study area. The regeneration sub-model and its coupling with FVS-On is described in Millington et al. (2011, submitted for publication), and was developed in consultation with managers of public and private forest lands (see “Acknowledgements”) so that appropriate management questions could be asked and so that output was of a format readily useable by managers. The model has a temporal resolution (timestep) of 10 years and is coded in C++, utilizing the FVS database extension (Crookston et al., 2003) and R statistical functions (R Development Core Team, 2009).

Table 1

Parameter estimates for the regeneration sub-model. Environmental variables for which the 95% credible interval of a parameter estimate does not encompass 0.0 are shown in bold, and for the 90% credible interval in *italics*. Variable 'HT' is habitat type, with its corresponding category following the colon (see text). For full details of the regeneration sub-model structure, including standard deviations of the estimate distributions which were sampled from in error analyses, see Millington et al. (submitted for publication).

Variable	SM	IW	ET	OT
Intercept	0.467	0.057	0.304	0.177
HT:ATD	0.081	0.174	-0.341	0.086
HT:ATD-Hp	-0.067	-0.089	0.100	0.053
HT:ATM	0.231	0.239	-0.437	-0.03
HT:TMC	0.314	-0.244	-0.271	0.196
Deer density	-0.005	0.005	0.000	-0.001
Canopy openness	-0.012	-0.005	0.016	0.001
Ironwood BA	0.002	0.400	-0.181	-0.216

2.3. Regeneration sub-model

Our regeneration sub-model takes a stochastic, regression-based compositional approach to estimate proportions of the available growing space in forest gaps created by timber harvest (Millington et al., 2011, submitted for publication). Following a simulated timber harvest, the number and area of gaps created in a stand is estimated (Eq. 5 in Millington et al., 2011). Using this gap area, the number of growing spaces available for 7 m tall trees is calculated (Eq. 2 in Millington et al., submitted for publication). Each gap space can take one of four states: Sugar Maple, Ironwood, Other trees species, or Empty. The probability of spaces in a gap being in each of these states is estimated using a compositional regression model (Eq. 3 in Millington et al., submitted for publication) with environmental variables' values estimated from other sub-models. Environmental variables considered are forest habitat type (a proxy for soil moisture and nutrient regimes; see Burger and Kotar, 2003), deer density, canopy openness and basal area of mature ironwood trees (Table 1). The predicted state of a gap space is then established by comparing a random value in the interval [0,1] to the cumulative probability for all gap space states for a given gap. If a gap space is deemed to be non-empty, the height of the occupying tree is estimated (Eq. 2 in Millington et al., 2011). Tree growth is then estimated through time (Eq. 3 in Millington et al., 2011) until the tree is at least 7 m tall, when it passed to FVS-On for continued growth and harvest/mortality. Full description and testing of this sub-model is presented in Millington et al., 2011, submitted for publication.

Table 2

Sampling scheme for error analyses. Values for parameter estimates and initial conditions were either: the mean value of parameter estimate (for regeneration sub-model see Table 1; for deer sub-model see Table 3 of Millington et al., 2010); the empirical initial conditions ('Empirical'); sampled from the parameter estimate probability distribution (for regeneration sub-model see Table 3 of Millington et al., submitted for publication; for deer sub-model see Table 3 of Millington et al., 2010); or observed initial conditions frequency distribution ('Sampled', see Online supplemental material). We do not have accurate data for initial deer population numbers for the stands we simulate so we assume fixed values (as shown).

Set name	Regeneration sub-model	Deer sub-model	Initial stand structure	Initial deer population (deer km ⁻²)
Baseline	Means	Means	Empirical	20
R-Model	Sampled	Means	Empirical	20
D-Model	Means	Sampled	Empirical	20
SS-Initial	Means	Means	Sampled	20
DL-Initial	Means	Means	Empirical	10
DH-Initial	Means	Means	Empirical	40
R-SS	Sampled	Means	Sampled	20
D-low	Means	Sampled	Empirical	10
D-high	Means	Sampled	Empirical	40
ALL-low	Sampled	Sampled	Sampled	10
ALL-med	Sampled	Sampled	Sampled	20
ALL-high	Sampled	Sampled	Sampled	40

2.4. Deer density sub-model

The deer density sub-model is composed of two components: deer population and deer distribution. To simulate total deer population within our study area we use the deer management options model (DeerMOM, Xie et al., 1999). DeerMOM was parameterized and tested for the deer population in Michigan's Upper Peninsula. The model predicts deer population through time by taking a systems approach to represent the interactions of sex ratios, reproductive rates, mortality rates, and harvest rates. The original model has been re-coded and implemented directly in our simulation model code. At each time-step the total deer population predicted by DeerMOM is assigned to stands using the relationships between deer density and forest landscape characteristics quantified by Millington et al. (2010). These relationships are quantified by a multi-variate linear regression model with the distance of the stand to the nearest lowland conifer stand and area-weighted mean northern hardwood stand diameter-at-breast height (dbh) as the predictors (i.e., 'Best' model, Table 3 of Millington et al., 2010). As both of these sub-model components have been tested previously (see Xie et al., 1999; Millington et al., 2010) we do not test them again here.

2.5. Simulation model error analyses

To evaluate uncertainty in our simulation model parameterization and initialization, we conduct error analyses. We examine uncertainty due to our regeneration sub-model, deer density sub-model, initial stand structure conditions and initial deer population (Table 2). Error analyses use the probability distribution of model parameter estimates and initial conditions to statistically assess the effects of uncertainty about them on model output. Bayesian methods for parameter estimation implicitly consider parameters to be random variables that can take a range of values, each with a given probability. Consequently, Bayesian methods provide not only a parameter estimate, but also a posterior probability distribution for that estimate which can be used for error analyses. Because our tree regeneration and deer density sub-model parameter estimates were produced using Bayesian methods, we can conduct rigorous uncertainty analyses for these model components. For our uncertainty analyses we take a Monte Carlo approach, comparing model output for sets of parameter estimates and initial conditions that sample similar model components simultaneously (Table 2).

To investigate the importance of initial stand structure on model dynamics and results we generate initial stand structure stochastically based on empirical stand characteristics (e.g., normal distribution of stand basal area with mean 28.5 m² ha⁻¹ and

standard deviation 7.9, two different gamma distributions of tree dbh dependent on tree species composition, etc.) and from the literature (e.g., distributions for tree height and canopy cover from Pacala et al., 1994 and Canham et al., 1994 respectively). Full details of the methods used to generate initial stand structure are presented in the [Online supporting material](#).

For all simulation runs in the error analyses we use the same uneven-aged timber harvest prescription rules. This prescription specifies a target residual stand basal area of $16 \text{ m}^2 \text{ ha}^{-1}$, target harvest cycle of 10 years, maximum residual tree dbh of 55 cm, and a target q -factor of 1.4 (i.e., identical to Prescription B in Millington et al., 2011). The q -factor specifies the ratio of tree densities in each dbh size-class to its neighboring, larger, size-class with the result that larger q -factor values produce in dbh distributions with greater proportions of smaller size-class trees and lower proportions of larger size-class trees (Meyer, 1952). Other rules of the prescription are that only non-ironwood trees with dbh > 20 cm are harvested, 90% of all ironwood trees with dbh > 12.5 cm are removed, the minimum harvested basal area is $5 \text{ m}^2 \text{ ha}^{-1}$, the minimum standing basal area at time of harvest is $25 \text{ m}^2 \text{ ha}^{-1}$, and at least one legacy (seed) tree with dbh greater than 55 cm is allowed to remain (per ha). If the minimum standing basal area or harvested basal area criteria are not met in a timestep, harvest does not occur until the first subsequent timestep in which the criteria are met. The values for these criteria were established by consulting with state, provincial and private industrial foresters working in the northern hardwood forests of upper Michigan, USA and Ontario, Canada (see “Acknowledgements”).

We examine 100 simulation model runs for each set of parameters. State variables in model output we examine are those describing regeneration, deer density, and timber (see Table 3 for state variable acronyms and descriptions). Note that ironwood does not contribute to merchantable timber volumes as it does not grow sufficiently large. We assess timber variables both from trees initially in a stand (SAW and CSAW) and from those simulated as regenerating during a simulation run (SAWR and CSAWR) to identify the long-term effects of uncertainty in initial conditions and parameter estimates on standing and harvested timber via regeneration. Regeneration success (RS) is the total number of trees that regenerated in a stand during a given timestep expressed as a proportion of the maximum number of trees that could have regenerated given the space available for regenerating trees in forest gaps (Millington et al., 2011). We also assess the proportion of the total number of possible regenerating trees that are sugar maple (SM). For each of the seven state variables we examine the final mean stand value of the variable after 20 timesteps (i.e., 200 years) along with coefficients of variation for the set of 100 simulation runs for the first and second centuries.

2.6. Simulation model scenario analysis

To illustrate potential use of this model by forest and wildlife managers, we examine management scenarios for ironwood basal area removed and deer density. We examine these variables as they

are readily treatable on the ground and because parameter estimates for these regeneration model variables have been found to be most sensitive (Millington et al., submitted for publication). For example, the removal of ironwood from stands is a practice that can be easily controlled by forest managers but comes with associated costs because of its low economic value. A second action managers might be able to pursue is modification of the density of deer across sections of the forest landscape. Using our simulation model for different scenarios of ironwood removal and deer density will allow managers to identify the benefits of different levels of control given the ecological relationships represented in our model.

We examine three different scenarios for different levels of ironwood removal: removal of no ironwood in each timber harvest; removal of 50% of ironwood trees with dbh > 12.5 cm; and removal of 100% of ironwood trees with dbh > 12.5 cm. We examine four scenarios of deer density: the three values used in error analyses (10, 20 and 40 deer km^{-2}) with a fourth scenario of total deer exclusion (0 deer km^{-2}). We also examine scenarios which combine the maximum and minimum values for each of the ironwood removal and deer density scenarios (i.e., 0% and 100% removal each with 0 and 40 deer km^{-2}). For each scenario we ran the model 20 times (results show similar levels of variation to 100 runs – compare Fig. 1 with Figs. 2–4).

3. Results

3.1. Error analyses

The seven state variables respond through time with different levels of variation (Fig. 1). Regeneration success of SM decreases slightly through time (from 0.34 to 0.28; Fig. 1a) for baseline parameter values, while RS (all species) increases through time (from 0.76 to 0.92; Fig. 1c). The increase in RS (driven by an increase in ironwood regeneration) occurs because the harvest prescription we use in these analyses results in a slight increase in ironwood basal area through time which has strong positive effects on ironwood regeneration and negative effects on empty gap spaces in the regeneration sub-model (Table 1). Variation between timesteps and between simulation runs is limited (Table 4). For both RS and SM, variation in the scheduling of harvest through time is an influence, although not with the same magnitude of impact as for the timber variables. Deer density varies little for baseline conditions (Fig. 1e), but greater variation between simulation runs is observed when initial conditions are sampled (Fig. 1f), because uncertainty in initial conditions is additional to uncertainty in parameter estimates.

For baseline parameter values, greatest variation across all state variables is in CSAW and CSAWR (Fig. 1i and m, also see Table 4). Mean stand CSAW varies greatly between timesteps in the first 60 years of simulation but then settles to generally constant mean ($\sim 35 \text{ m}^3 \text{ ha}^{-1} \text{ decade}^{-1}$) but with greater variation between simulation runs (Fig. 1i). This asymptotic pattern occurs because it takes some time for the harvest prescription we use to bring the range of initial stand conditions into consistency across all stands. Variation

Table 3

Summary of state variables. Acronyms, units and descriptions of state variables examined in error analyses and referred to in the text.

State variable	Unit	Characteristic	Description
SM	Proportion	Regeneration	Mean stand regeneration success of sugar maple trees (during timestep)
RS	Proportion	Regeneration	Mean stand regeneration success of all trees (during timestep)
DD	deer km^{-2}	Deer	Mean stand deer density (at end of timestep)
SAW	$\text{m}^3 \text{ ha}^{-1}$	Timber	Mean stand merchantable standing timber (at end of timestep)
CSAW	$\text{m}^3 \text{ ha}^{-1} \text{ decade}^{-1}$	Timber	Mean stand merchantable harvested timber (during timestep)
SAWR	$\text{m}^3 \text{ ha}^{-1}$	Regeneration, Timber	Mean stand merchantable standing timber of simulated regenerated trees (at end of timestep)
CSAWR	$\text{m}^3 \text{ ha}^{-1} \text{ decade}^{-1}$	Regeneration, Timber	Mean stand merchantable harvested timber of simulated regenerated trees (during timestep)

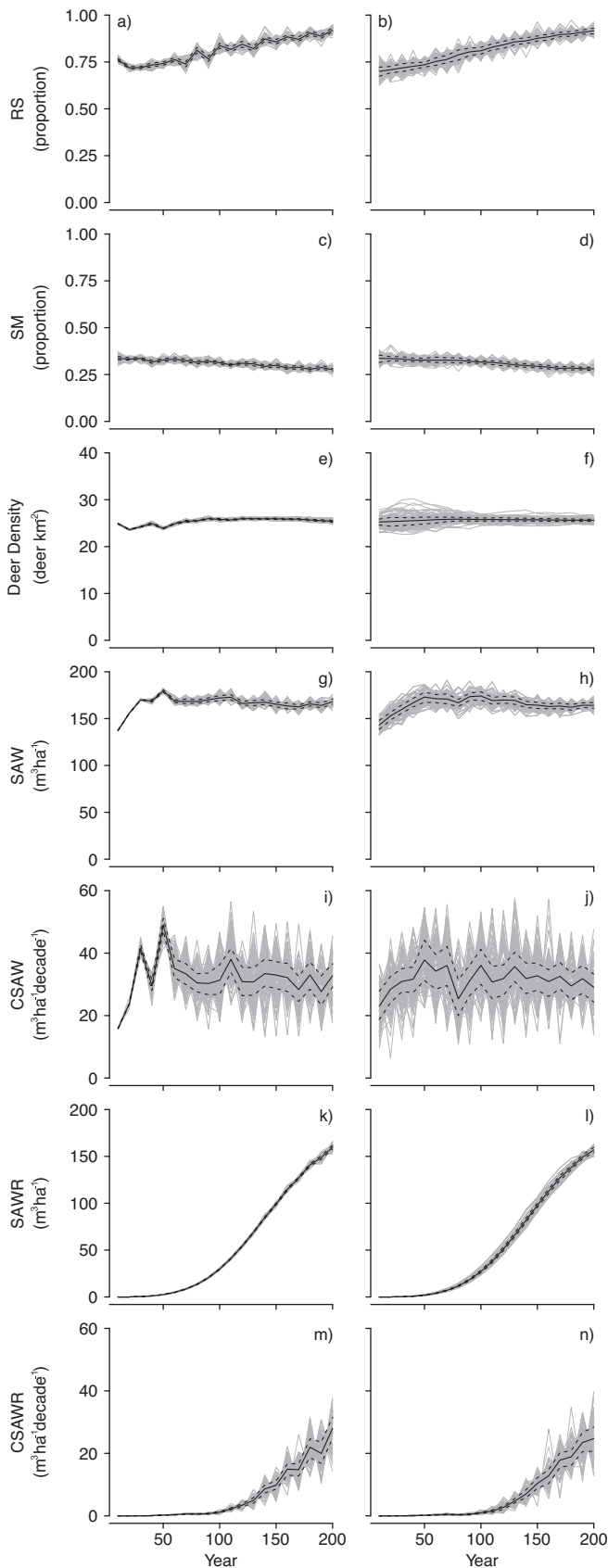


Fig. 1. Time series of state variables for baseline (a, c, e, g, i, k, m) and SS-Initial (b, d, f, h, j, l, n) parameter sets. Grey lines are for individual simulation runs, solid black line is mean and dotted black lines are 25th and 75th percentiles of all simulation runs.

between simulations runs increases because model stochasticity means that rules for harvest (e.g., minimum standing basal area) will be met in different time steps in different runs (hence the high and low peaks from timestep to timestep). For the first 60 years of simulation there is little variation between simulation runs for empirical initial stand conditions (Fig. 1i), but when sampled initial stand conditions are used (Fig. 1j) variation between runs is similar in this initial period as for the subsequent 140 years (as uncertainty in initial conditions is very low for the first 100 years of simulations (as would be expected because young regenerating trees contribute little to harvested stand volume) but increases in time during the second century of simulation (as does variation between simulation runs; Fig. 1m).

Similar to CSAWR, SAWR increases through time as regenerating trees contribute more to total stand volume (Fig. 1k). For mean stand standing volume (SAW, Fig. 1g) there is limited variation between simulation runs in the first 50 years, but values increase (from 137 to around 180 m³ ha⁻¹) before settling to constant small fluctuations around 165 m³ ha⁻¹. Variation between simulation runs is greater for cut timber state variables (CSAW, CSAWR) than standing timber variables (SAW, SAWR; Table 4). The distinct increases in SAW and CSAW in the first five decades (with minimal variation around the mean) before reaching a relatively constant mean (although with variation around the mean between simulation runs) is a response to the harvest prescription we specify in our analyses. The initial (empirical) state of the northern hardwood stands we use for our analysis is a result of (the unknown) previous harvest history. The timeseries for SAW and CSAW (Fig. 1g–j) show the shift in response to the new harvest prescription which is applied uniformly across all stands. A similar response is observed for stands with initial conditions generated stochastically but based on empirical conditions (Fig. 1h and j). The harvest prescription we use in these analyses decreases the proportion of basal area in trees with dbh < 20 cm but increases it in size classes with dbh > 20 cm (relative to empirical conditions). Consequently, although stand basal areas are similar between empirical and simulated stands, the simulated stands have greater standing and cut timber volumes because merchantable timber comes from these larger size classes. The general trends in state variable values through simulated time for all other parameter sets (Table 2) are similar to those presented in Fig. 1.

When variations between simulation runs for each parameter set are compared (Table 4), we see that the majority of variation in state variables is caused by uncertainty in regeneration model parameters. For all parameter sets in which regeneration parameters are sampled (R-Model, R-SS, ALL-low, ALL-med and ALL-high), coefficients of variation for the means of simulation runs are greater than for other parameter sets. The one exception is SS-Initial, which causes increased variation in the first century for timber state variables. However, when both regeneration sub-model parameters and initial stand conditions are sampled (R-SS), there is greater variation in the second century than when stand structure alone is varied. This indicates the influence of variation in regeneration throughout the entire run (both centuries), whereas variation in initial stand structure only influences initial variation (i.e., compare second century variation between R-Model and SS-Initial for the timber variables).

3.2. Scenario analysis

Results for the three ironwood scenarios indicate that lower ironwood removal results in significantly higher total regeneration success rates (confidence envelopes do not overlap, Fig. 2a) as ironwood saplings dominate regeneration (and SM regeneration success rate decreases, Fig. 2b). Greater ironwood removal results in

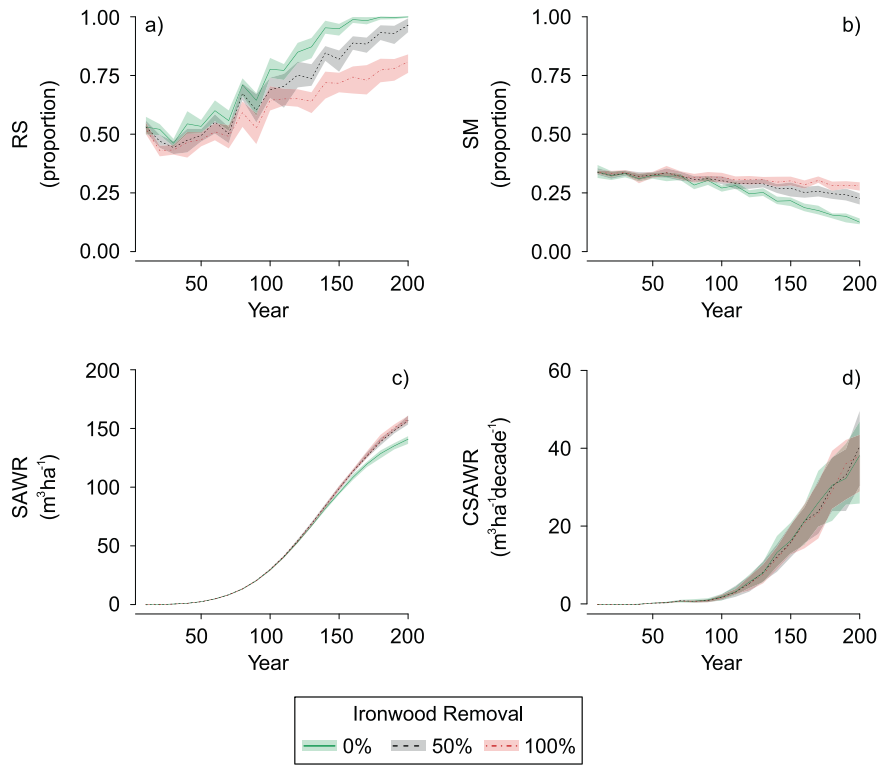


Fig. 2. Example time series from ironwood scenarios for (a) total regeneration success, (b) sugar maple regeneration success, (c) standing merchantable timber from regenerated trees, and (d) harvested merchantable timber from regenerated trees. Results are for 0% (grey, dashed line) 50% (green, solid line) and 100% (red, dotted line) ironwood removal. In each case the line is the mean and shaded area is 95% confidence envelope. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

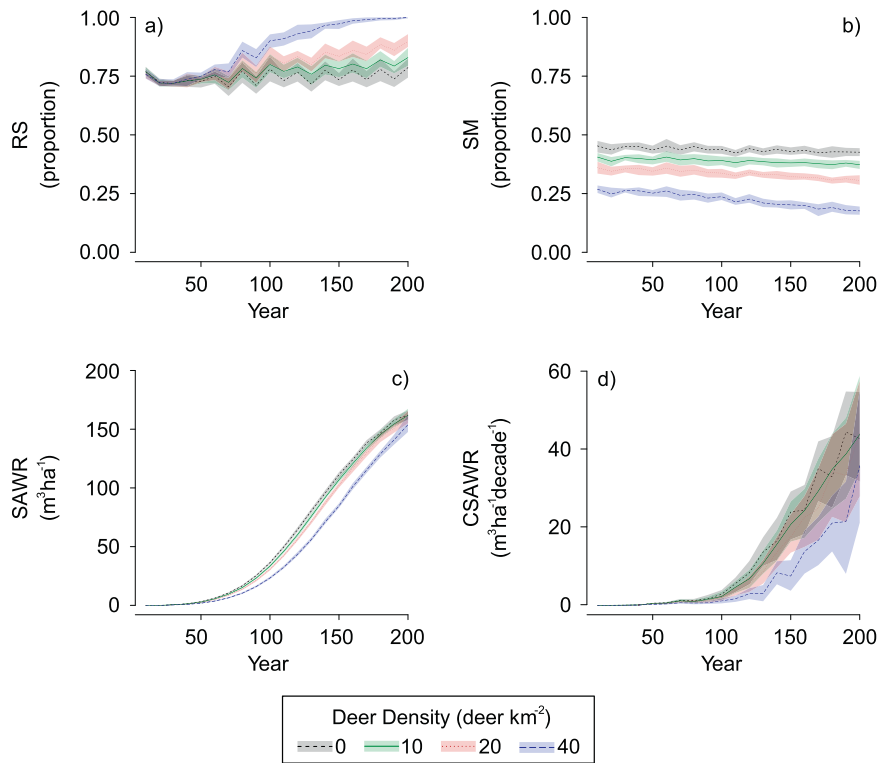


Fig. 3. Example time series from deer density scenarios for (a) total regeneration success, (b) sugar maple regeneration success, (c) standing merchantable timber from regenerated trees, and (d) harvested merchantable timber from regenerated trees. Results are for 0 (grey, dashed line), 10 (green, solid line), 20 (red, dotted line) and 40 (blue, long dashed line) deer km⁻². In each case the line is the mean and shaded area is 95% confidence envelope. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

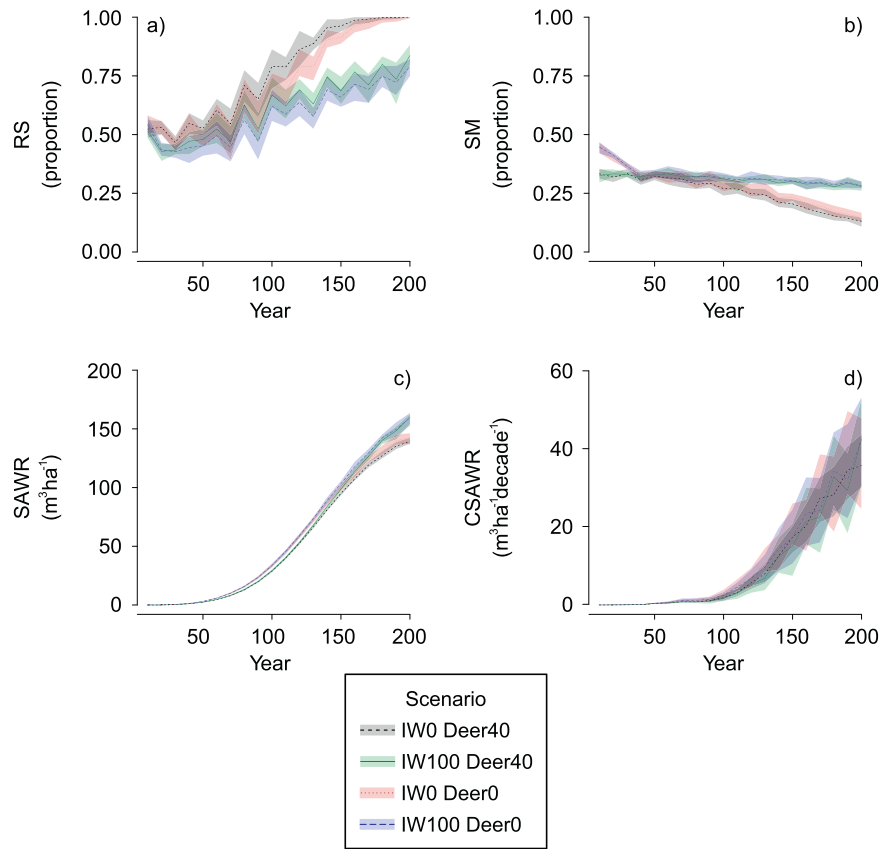


Fig. 4. Example time series from scenarios combining extreme values of ironwood removal (IR, %) and deer density (DD, deer km⁻²) for (a) total regeneration success, (b) sugar maple regeneration success, (c) standing merchantable timber from regenerated trees, and (d) harvested merchantable timber from regenerated trees. Results are for 0 IR with 40 DD (grey, dashed line), 100 IR with 40 DD (green, solid line), 0 IR with 0 DD (red, dotted line) and 100 IR with 0 DD (blue, long dashed line). In each case the line is the mean and shaded area is 95% confidence envelope. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

significantly higher sugar maple success rates (Fig. 2b), resulting in a regeneration success rate for 100% ironwood removed more than double that for 0% (mean of 0.28 compared to a mean of 0.13). Less ironwood removal results in lower standing regenerated timber volumes by the end of simulation runs, with volumes for no ironwood removed 11% lower than volumes for all ironwood removed in the final decade (141 m³ ha⁻¹ compared to 158 m³ ha⁻¹; Fig. 2c). Harvested volumes of timber from regenerated trees are not significantly different between ironwood removal levels (Fig. 2d), although the divergence in standing regenerated harvestable

timber towards the end of simulations suggests that differences may be observed even farther into the future.

Results for the deer density scenarios show that greater deer densities produce greater total regeneration success of all species (Fig. 3a), but the contribution of sugar maple to that regeneration is lower (Fig. 3b). Total regeneration increases with greater deer densities because the proportion of less-valuable (for both commercial and conservation purposes) ironwood increases as browse pressure puts it at a competitive advantage over more valuable sugar maple. When deer are totally excluded, after 200 years sugar maple

Table 4

Error analyses results. Values are for final timestep (year 200). The first value in parentheses is the mean of coefficients of variation between simulation runs for first century, second value is for second century. Coefficient of variation values in bold are significantly different (95% confidence) to the baseline value. 'Sets' are defined in Table 2 and variables are defined in Table 3.

Set	Regeneration		Deer DD	Timber			
	RS	SM		SAW	CSAW	SAWR	CSAWR
Baseline	0.92 (0.02, 0.02)	0.28 (0.04, 0.04)	25.4 (0.01, 0.01)	168.1 (0.01, 0.02)	32.8 (0.10, 0.20)	159.8 (0.03, 0.01)	28.0 (0.24, 0.21)
R-Model	0.89 (0.14, 0.13)	0.26 (0.31, 0.47)	25.5 (0.01, 0.01)	163.9 (0.01, 0.07)	28.6 (0.10, 0.22)	153.0 (0.19, 0.17)	23.2 (0.39, 0.44)
D-Model	0.92 (0.02, 0.02)	0.28 (0.04, 0.04)	25.4 (0.02, 0.02)	167.0 (0.01, 0.02)	31.4 (0.10, 0.20)	159.0 (0.04, 0.02)	26.9 (0.24, 0.20)
SS-Initial	0.92 (0.04, 0.03)	0.28 (0.05, 0.05)	25.6 (0.04, 0.02)	164.1 (0.04, 0.03)	29.1 (0.24, 0.23)	156.7 (0.11, 0.04)	24.7 (0.38, 0.26)
DL-Initial	0.91 (0.02, 0.02)	0.28 (0.03, 0.04)	25.4 (0.01, 0.01)	166.8 (0.01, 0.02)	31.7 (0.10, 0.18)	160.5 (0.04, 0.01)	28.1 (0.26, 0.19)
DH-Initial	0.92 (0.02, 0.02)	0.28 (0.03, 0.04)	25.4 (0.01, 0.01)	167.0 (0.01, 0.02)	31.3 (0.10, 0.19)	160.4 (0.04, 0.02)	27.5 (0.26, 0.20)
R-SS	0.89 (0.15, 0.14)	0.27 (0.32, 0.41)	25.6 (0.03, 0.02)	160.1 (0.04, 0.08)	30.2 (0.22, 0.26)	151.1 (0.23, 0.19)	25.0 (0.50, 0.50)
D-low	0.92 (0.02, 0.02)	0.28 (0.04, 0.04)	25.9 (0.02, 0.02)	165.8 (0.01, 0.02)	30.9 (0.08, 0.19)	158.1 (0.04, 0.02)	26.2 (0.24, 0.20)
D-high	0.92 (0.02, 0.02)	0.28 (0.04, 0.05)	25.8 (0.02, 0.02)	165.9 (0.01, 0.02)	30.7 (0.08, 0.19)	158.1 (0.05, 0.02)	26.1 (0.25, 0.20)
ALL-low	0.86 (0.16, 0.14)	0.24 (0.39, 0.48)	25.7 (0.05, 0.03)	156.1 (0.04, 0.10)	28.7 (0.24, 0.27)	143.4 (0.29, 0.27)	22.4 (0.56, 0.57)
ALL-med	0.87 (0.16, 0.15)	0.26 (0.37, 0.46)	25.6 (0.04, 0.03)	156.3 (0.04, 0.09)	28.4 (0.24, 0.26)	144.1 (0.27, 0.25)	22.6 (0.57, 0.55)
ALL-high	0.87 (0.16, 0.15)	0.27 (0.39, 0.49)	25.8 (0.04, 0.03)	157.0 (0.04, 0.09)	28.5 (0.24, 0.27)	145.0 (0.31, 0.27)	23.0 (0.57, 0.56)

regeneration success is 39% greater than for 20 deer km⁻² (mean of 0.43 compared to mean of 0.31) and 59% than for 40 deer km⁻² (mean of 0.18). These changes in composition are reflected in significantly lower standing regenerated timber volumes throughout much of simulated time (lower volumes for greater deer densities; Fig. 3c). The subsequent effect of changes in regeneration on harvested regenerated timber volumes is not influenced as significantly, but greater deer densities do generally result in lower harvested timber volumes (Fig. 3d).

When extremes of ironwood removal and deer density are combined, we can observe the relative influence of each environmental driver on state variables through time (Fig. 4). Generally, impacts on state variables by the end of two centuries are influenced more by ironwood removal than by changes in deer density. For example, total regeneration success (Fig. 4a) and standing regenerated timber volumes (Fig. 4c) are similar between ironwood and deer treatments initially (i.e., year 0), but have diverged by the conclusion of the simulation with 0% ironwood removal treatments resulting in greater total regeneration success and lesser standing regenerated timber (compared to treatments with 100% of ironwood removed). However, the importance of deer density initially and throughout simulations can be observed in the influence on sugar maple regeneration success, where low deer densities mean greater regeneration initially (Fig. 4b). Through time the importance of ironwood means that the treatment with no deer and no ironwood removal ends with much lower regeneration success than the treatment with no deer and 100% ironwood removed. A similar effect can also be observed for standing regenerated timber (Fig. 4c): volumes at year 100 are similar for the no deer with no ironwood removed scenario and the no deer with 100% ironwood removed scenario, but are lower in year 200 for the former scenario than the latter (this reversal through time for different ironwood treatments can also be seen for the scenarios with 40 deer km⁻²).

4. Discussion

4.1. Model assessment

Results from our error and scenario analyses highlight the capacity of our simulation model for identifying synergies and trade-offs between timber and wildlife management to ensure desired regeneration composition and stand structure over the long term. Results from error analyses indicate that of the tree regeneration sub-model, the deer density sub-model, initial stand structure conditions and initial deer population, the regeneration sub-model is the source of greatest uncertainty for six of the seven state variables we examined. These state variables concern regeneration and timber; the seventh state variable, deer density, showed little variation to any of the sub-models and initial conditions we examined. It was expected that deer density would show the least variation, as carrying capacity in the deer population sub-model does not respond to changes in vegetation structure (although note that this not a biologically realistic assumption). Sampling parameter estimates for the regeneration sub-model influences regeneration state variables (total regeneration success rate, RS, and sugar maple regeneration success rate, SM) throughout model runs. The consequences for timber state variables are apparent by comparing those which account for all timber (standing and removed, i.e., SAW and CSAW) with those that only account for timber from simulated regeneration (i.e., SAWR and CSAWR); for the latter, impacts are greater in later simulation timesteps than earlier (as evidenced by greater coefficients of variation across runs in the second century of simulation, Table 4). Sampling initial stand conditions results in greater variation between simulation runs in initial decades than for the use of empirical conditions for all state variables

except regeneration timber variables (i.e., SAWR and CSAWR, see Fig. 1). This is as would be expected, but importantly the initial variation is similar in magnitude to variation later in simulation runs. This suggests that the approach and use of stochastically generated stand structure (see [Online supplementary material](#)) is appropriate and that the model can be used both for stands where managers have stand inventory data and those for which they do not.

4.2. Management implications

Our scenario analyses indicate that ironwood removal has a cumulative impact on forest regeneration and timber through time, whereas deer densities have an immediate and consistent impact through time. For example, the 'no ironwood removal' scenario (with empirical deer densities) results in differences from other ironwood removal scenarios only in the later stages of simulation (Fig. 2). Standing regenerated timber is reduced relative to other scenarios from 150 years onwards as it takes this length of time for the competitive advantage of greater ironwood seed availability to manifest itself (via changes in regeneration composition) as increased abundance of mature ironwood at the expense of merchantable sugar maple. This positive feedback – of increased ironwood regeneration resulting in greater abundance of mature (seed producing) ironwood which in turn results in a greater competitive advantage and more ironwood regeneration – suggests the observed differences will likely continue to increase over longer time periods than simulated here. Furthermore, results from the scenarios that combined extremes of ironwood and deer management showed that through time the importance of ironwood could surpass that of deer (Fig. 4). For sugar maple regeneration, although managing for deer should be a shorter term (i.e., decadal) priority, over the longer term (i.e., centuries) the importance of managing ironwood is apparent (Fig. 4c). We should highlight, however, that our regeneration sub-model assumes that a regenerating sugar maple tree will be completely displaced by a taller regenerating ironwood tree. This assumption may not be entirely valid as sugar maple, with similar shade tolerance (Niinemets and Valladares, 2006) but greater maximum height (Burns and Honkala, 1990), may be able to outcompete shorter-statured ironwood in the understory. It is likely that regenerating sugar maple will have higher mortality rates and slower growth beneath taller regeneration, but in some cases may be able to ultimately displace the shorter-statured ironwood. Thus, the growing space approach we take in our regeneration model (Millington et al., [submitted for publication](#)) should be considered a maximum possible negative effect of ironwood on sugar maple. We should also highlight that the influence of interactions between ironwood and deer are not represented by our regeneration model which may further influence browse on sugar maple.

Results for using the model with scenarios of different deer density indicate that although regeneration success varies for deer densities ≤ 20 deer km⁻², standing and removed timber volumes vary little (Fig. 4). Variation in regeneration due to deer density only translate into compromises in harvested volume over 200 years for densities >20 deer km⁻² (i.e., 40 deer km⁻²). This suggests that, given other conditions are suitable, sugar maple regeneration is adequate for future timber production even at intermediate deer densities (i.e., around or just below 20 deer km⁻²). Consequently, although the current cultural climate in North America would indicate that reducing deer numbers to very low levels may be untenable, our model indicates that drastic reduction may not be necessary and that reduction in areas with high deer densities (i.e., $\gg 20$ deer km⁻²) to intermediate levels would reap benefits.

4.3. Model development

Our results show how temporal feedbacks mean that managers need to consider impacts of their actions through time. However, benefits may also be accrued by coordinating wildlife and timber management across space and time (e.g., Zollner et al., 2008). The current model operates at the stand-level and spatial interactions between stands are not considered, but the capacity to consider spatial patterns would increase utility to managers. For example, regenerating trees are most vulnerable to deer browse soon after canopy gap creation (by selective timber harvest) when trees are small. Forest and wildlife managers might take this into account by coordinating management plans to try to ensure that deer densities are lower in northern hardwood stands in the years immediately following timber harvest, thereby reducing pressure on sugar maple regeneration and potentially increasing regeneration success rates of this species (i.e., creating “windows of opportunity”, Sage et al., 2003). A spatially explicit version of our simulation model would allow managers to investigate the potential benefits of such coordinated management. Similarly, given that the juxtaposition of lowland conifer stands with northern hardwood stands is a key determinant of winter deer densities in hardwood stands (Millington et al., 2010), managers might consider removing judiciously chosen conifer stands to reduce winter deer densities. The advantage of using a spatially explicit simulation model that considers time is that it would enable an investigation of the benefits of synergistic timber harvest in neighboring conifer and hardwood stands.

The explicit consideration of space would also allow us to investigate some of the spatial patterns in our data that remain unexplainable from the factors we considered in construction of this model (Matonis et al., 2011). For example, the data presented in Matonis et al. (2011) indicates that regeneration of sugar maple, a species that prefers mesic soil conditions, was consistently greater in areas with deep winter snow near Lake Superior and nearly non-existent at sites previously classified as being more mesic and nutrient rich farther from the lake. These spatial patterns may be due to variation in winter deer density, but covariance among deer density, snow depth, and habitat types limited confidence in making that conclusion (Matonis et al., 2011). A further contributing factor to these patterns might be the influence of snow melt on soil moisture (e.g., Henne et al., 2007), thereby influencing regeneration success rates and consequent stand dynamics. Including representation of these mechanisms into our model spatially will enable managers to examine the potential combined impacts of their activities with a changing climate that alters seasonal moisture regimes.

5. Conclusions

Long-term consequences of variation in forest tree regeneration are often uncertain because multiple factors, including those constrained by management, drive dynamics. Here, we presented and tested an integrated simulation model that couples forest tree regeneration, tree growth and harvest, and deer sub-models for evaluating the long-term impacts of different management scenarios and for identifying potential synergies and trade-offs between timber and wildlife management. Our error analyses, which exploited the posterior model parameter probabilities of sub-model Bayesian parameter estimates, show that model output is robust given uncertainty in the sub-models. Results from our scenario analyses show that although deer densities have an immediate and consistent impact on forest regeneration and timber through time, ironwood removal has a cumulative impact due to feedbacks on competition between ironwood and sugar

maple. While currently this simulation model can aid the understanding of combinations of management actions through time, further development will allow examination of the importance of spatio-temporal feedbacks for management actions and guide future empirical work on the drivers of tree regeneration in upland hardwood-lowland conifer forests.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2012.09.019>.

References

- Arbogast Jr., C., 1957. Marking Guides for Northern Hardwoods Under the Selection System. USDA Forest Service Station Paper LS-SP-56, St. Paul, MN, USA.
- Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60 (3), 849–872.
- Bugmann, H.K.M., Yan, X., Sykes, M.T., Martin, P., Lindner, M., Desanker, P.V., Cumming, S.G., 1996. A comparison of forest gap models: model structure and behaviour. *Climatic Change* 34, 289–313.
- Burger, T.L., Kotar, J., 2003. A Guide to Forest Communities and Habitat Types of Michigan. The Department of Forest Ecology and Management, University of Wisconsin-Madison, WI, USA.
- Burns, R.M., Honkala, B.H., 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agricultural Handbook 654, 2. U.S. Department of Agriculture, Forest Service, Washington, DC, 877.
- Canham, C.D., Finizi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* 24, 337–349.
- Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution and Systematics* 35, 113–147.
- Crookston, N.L., Dixon, G.E., 2005. The forest vegetation simulator: a review of its structure, content, and applications. *Computers and Electronics in Agriculture* 49, 60–80.
- Crookston, N.L., Gammel, D.L., Rebain, S., Robinson, D., Keyser, C.E., 2003. Users Guide to the Database Extension of the Forest Vegetation Simulator Version 2.0. Internal Rep. U.S. Department of Agriculture, Forest Service, Forest Management Service Center, Fort Collins, CO.
- Donovan, G., 2005. Chronic regeneration failure in northern hardwood stands: a liability to certified forest landowners. In: Cook, B. (Ed.), *Proceedings of the Forests & Wildlife-striving for Balance Michigan Society of American Foresters Conference*. St. Ignace, MI, pp. 125–130.
- Ferguson, D.E., Carlson, C.E., 1993. Predicting Regeneration Establishment with the Prognosis Model. Res. Paper INT-467. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.
- Haugen, A.O., Davenport, L.A., 1950. Breeding records of whitetail deer in the Upper Peninsula of Michigan. *Journal of Wildlife Management* 14, 290–295.
- Henne, P.D., Hu, F.S., Cleland, D.T., 2007. Lake-effect snow as the dominant control of mesic-forest distribution in Michigan, USA. *Journal of Ecology* 95, 517–529.
- Horsley, S.B., Stout, S.L., deCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13, 98–118.
- Jenkins, J., 1997. *Hardwood Regeneration Failure in the Adirondacks: Preliminary Studies of Incidence and Severity*. The Wildlife Conservation Society Working Paper No. 9. White Creek, NY, USA.

- Lacerte, V., Larocque, G.R., Woods, M., Parton, W.J., 2008. Validating FVS Individual Model Components Using Independent Datasets Based on Permanent Sample Plots Located in Quebec, Information Report LAU-X-133, Natural Resources Canada.
- Lacerte, V., Larocque, G.R., Woods, M., Parton, W.J., Penner, M., 2006. Calibration of the forest vegetation simulator (FVS) model for the main forest species of Ontario, Canada. *Ecological Modelling* 199, 336–349.
- Larocque, G.R., Archambault, L., Delisle, C., 2011. Development of the gap model ZELIG-CFS to predict the dynamics of North American mixed forest types with complex structures. *Ecological Modelling* 222, 2570–2583.
- Larson, M.A., Thompson, F.R., Millsbaugh, J.J., Dijak, W.D., Shifley, S.R., 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecological Modelling* 180, 103–118.
- Laurent, E.J., Shi, H.J., Gatzliolis, D., LeBouton, J.P., Walters, M.B., Liu, J., 2005. Using the spatial and spectral precision of satellite imagery to predict wildlife occurrence patterns. *Remote Sensing of Environment* 97, 249–262.
- Liu, J., Ashton, P.S., 1995. Individual-based simulation models for forest succession and management. *Forest Ecology and Management* 73, 157–175.
- Liu, J., Ashton, P.S., 1999. Simulating effects of landscape context and timber harvest on tree species diversity. *Ecological Applications* 9, 186–201.
- Liu, J., Hull, V., Morzillo, A.T., Wiens, J., 2012. Sources, Sinks, and Sustainability. Cambridge University Press, Cambridge, UK.
- Loomis, J.B., 1993. Integrated Public Lands Management. Columbia University Press, New York.
- Marquis, D.A., Brenneman, R., 1981. The Impact of Deer on Forest Vegetation in Pennsylvania. USDA Forest Service General Technical Report NE-GTR-65. Broomall, PA, USA.
- Matonis, M.S., Walters, M.B., Millington, J.D.A., 2011. Gap-, stand-, and landscape-scale factors contribute to poor sugar maple regeneration after timber harvest. *Forest Ecology and Management* 262 (2), 286–298.
- Matteson, S., Kreitinger, K., Bartelt, G., Butcher, G., Sample, D., Will, T., 2009. Partners in Flight Bird Conservation Plan for The Boreal Hardwood Transition (Bird Conservation Region 12–US Portion). Version 1.0. Partners in Flight. <http://www.partnersinflight.org>
- Meyer, H.A., 1952. Structure, growth and drain in balanced uneven-aged forests. *Journal of Forestry* 50, 85–92.
- Miller, R.O., 2004. Regeneration in a Heavily Browsed Northern Hardwood Stand Twelve Years After Scarification and Fencing. Upper Peninsula Tree Improvement Center Research Report. Michigan State University, Escanaba, MI, USA.
- Millington, J.D.A., Walters, M.B., Matonis, M.S., Laurent, E.J., Hall, K.R., Liu, J., 2011. Combined long-term effects of variable tree regeneration and timber management on forest songbirds and timber production. *Forest Ecology and Management* 262, 718–729.
- Millington, J.D.A., Walters, M.B., Matonis, M.S., Liu, J., 2010. Effects of local and regional landscape characteristics on wildlife distribution across managed forests. *Forest Ecology and Management* 259, 1102–1110.
- Millington, J.D.A., Walters, M.B., Matonis, M.S., Liu, J. Filling the gap: a compositional gap regeneration model for managed northern hardwood forests. *Ecological Modelling*, submitted for publication.
- Niinemetts, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. *Ecological Monographs* 76, 521–547.
- Nyland, R.D., 1998. Selection system in northern hardwoods. *Journal of Forestry* 96, 18–21.
- Pacala, S.W., Canham, C.D., Silander, J.A., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Canadian Journal of Forest Research* 24, 2172–2183.
- Pedersen, B.S., Wallis, A.M., 2004. Effects of white-tailed deer herbivory on forest gap dynamics in a wildlife preserve, Pennsylvania, USA. *Natural Areas Journal* 24, 82–94.
- R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, <http://www.r-project.org> (accessed 29.11.11).
- Racevskis, L.A., Lupi, F., 2006. Comparing urban and rural perceptions of and familiarity with the management of forest ecosystems. *Society and Natural Resources* 19, 479–495.
- Rittenhouse, C.D., Shifley, S.R., Dijak, W.D., Fan, Z., Thompson, F.R., Millsbaugh, J.J., Perez, J.A., Sandeno, C.M., 2011. Application of landscape and habitat suitability models to conservation: the Hoosier national forest land-management plan. In: Li, C., Laforteza, R., Chen, J. (Eds.), *Landscape Ecology in Forest Management and Conservation*. Springer-Verlag, Berlin.
- Robinson, D.C.E., 2008. Development of external regeneration models for FVS: another Wrench in the Toolkit. In: Havis, R.N., Crookston, N.L. (Eds.), *Third Forest Vegetation Simulator Conference*. 2007 February 13–15, Fort Collins, CO, Proceedings RMRS-P-54. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Rooney, T.P., McCormick, R.J., Solheim, S.L., Waller, D.M., 2000. Regional variation in recruitment of hemlock seedlings and saplings in the upper Great Lakes, USA. *Ecological Application* 10, 1119–1132.
- Sage, R.W., Porter, W.F., Underwood, H.B., 2003. Windows of opportunity: white-tailed deer and the dynamics of northern hardwood forests of the Northeastern US. *Journal for Nature Conservation* 10, 213–220.
- Seagle, S.W., Liang, S., 2001. Application of a forest gap model for prediction of browsing effects on riparian forest succession. *Ecological Modelling* 144, 213–229.
- Shafer, E.L., Grisez, T.J., Sowa, E., 1961. Results of Deer Exclusion Studies in Northeastern Pennsylvania. USDA Forest Service Forest Research Note NE-RN-121. Upper Darby, PA, USA.
- Sharma, M., Parton, J., Woods, M., Newton, P., Penner, M., Wang, J., Stinson, A., Bell, F.W., 2008. Ontario's forest growth and yield modelling program: advances resulting from the Forestry Research Partnership. *Forestry Chronicle* 84, 694–703.
- Shi, H.J., Laurent, E.J., LeBouton, J.P., Racevskis, L., Donovan, M., Doepker, R.V., Walters, M.B., Lupi, F., Liu, J., 2006. Local spatial modeling of white-tailed deer distribution. *Ecological Modelling* 190, 171–189.
- Shifley, S.R., Thompson III, F.R., Dijak, W.D., Larson, M.A., Millsbaugh, J.J., 2006. Simulated effects of forest management alternatives on landscape structure and habitat suitability in the Midwestern United States. *Forest Ecology and Management* 229, 361–377.
- Shugart, H.H., 1984. *A Theory of Forest Dynamics*. Springer-Verlag, New York.
- Stoekeler, J.H., Strothmann, R.O., Krefting, L.W., 1957. Effect of deer browsing on reproduction in the northern hardwood-hemlock type in northeastern Wisconsin. *Journal of Wildlife Management* 21, 75–80.
- Urban, D.L., 1990. *A Versatile Model to Simulate Forest Pattern: A User's Guide to ZELIG Version 1.0*. University of Virginia, Charlottesville, VA.
- Weiskittel, A.R., Hann, D.W., Kershaw, J.A., Vanclay, J.K., 2011. *Forest Growth and Yield Modeling*. Wiley-Blackwell, Chichester.
- Xie, J., Hill, H.R., Winterstein, S.R., Campa, H., Doepker, R.V., Van Deelen, T.R., Liu, J., 1999. White-tailed deer management options model (Deer-MOM): design, quantification, and application. *Ecological Modelling* 124, 121–130.
- Zollner, P.A., Roberts, L.J., Gustafso, E.J., He, H.S., Radeloff, V., 2008. Influence of forest planning alternatives on landscape pattern and ecosystem processes in northern Wisconsin, USA. *Forest Ecology and Management* 254, 429–444.