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 Dr. Erin M. Simons-Legaard
 School of Forest Resources
 University of Maine
 5755 Nutting Hall
 Orono, Maine 04469, USA
 Phone: 207/581.2839; Fax: 207/581.2875
 erin.simons@maine.edu

Predicting aboveground biomass with LANDIS-II: A global and temporal analysis of parameter sensitivity

Erin Simons-Legaard, School of Forest Resources, University of Maine, Orono, ME, 04469, USA

Kasey Legaard, School of Forest Resources, University of Maine, Orono, ME, 04469, USA

Aaron Weiskittel, School of Forest Resources, University of Maine, Orono, ME, 04469, USA

Abstract

Forest landscape models (FLMs) have become a valuable tool for projecting broad-scale forest dynamics, but incomplete knowledge about model behavior can make parameterization challenging and outcomes unreliable. FLMs generally model forest growth as a set of interacting processes, and, consequently, predictions can be influenced by process or parameter uncertainty. A sensitivity analysis can potentially help identify sources of uncertainty, but if it does not use global measures of sensitivity nor consider that sensitivity in a process-based model is likely time-dependent, results could be misleading. Our aim was to evaluate the sensitivity of nine key parameters when predicting live aboveground biomass (AGB) with the widely-used FLM, LANDIS-II. To fully explore parameter interactions and nonlinear model behavior, we selected a range of parameter values based on LANDIS-II applications in North America that was considerably wider than in previous local sensitivity analyses. Our results showed commonalities with previous studies, which concluded the maximum allowable biomass and maximum annual

net primary productivity specified for a species were most influential when predicting AGB. In contrast to earlier work, we also clearly demonstrated how relative importance was time-dependent for all but the least important parameters. Interactions between parameters and with simulation duration generated substantial variability in AGB and number of cohorts established. Results will improve future calibration efforts and may offer insight into opportunities for possible model refinements. This study also suggests, however, that parameters which cannot be calibrated based on empirical data will continue to be a major source of model uncertainty.

Keywords: Aboveground biomass, Forest landscape model, Global sensitivity analysis, Time-dependence, Regression trees

1. Introduction

Forest landscape models (FLMs) have become a valuable tool for projecting broad-scale forest dynamics. Like forest gap models, FLMs are founded on ecological concepts of tree growth, competition, and survival, but they are distinguished by their focus on modeling large areas and on explicitly representing landscape heterogeneity introduced by variations in abiotic, biotic, and disturbance processes (Mladenoff, 2004; Xi et al., 2009). A FLM can also be dynamic in the sense that, not only will it provide spatially-explicit predictions, but those predictions will incorporate some degree of spatial interaction between modeled entities (Mladenoff, 2004). Because of the increased computational demands that come from modeling dynamic processes at broad scales, the structure of FLMs tend to be less mechanistic and more phenomenological; thus, the finer-scale details of forest succession at the site level are simplified based on empirical relationships representing successional pathways or species life histories (He, 2008).

Although FLMs are not generally intended for developing tactical or operational plans for landscape management, they are designed to allow researchers to compare the future outcomes of alternative scenarios, which can provide valuable information and decision support for land

and resource managers (Gustafson et al., 2011). FLMs can allow explorations of the spatial and temporal variation in live aboveground biomass (AGB) resulting from anthropogenic disturbances such as timber harvesting (e.g., Duveneck et al., 2014) or natural disturbances such as fire (e.g., Sturtevant et al., 2009). AGB is a commonly modeled property of the landscape because it provides a record of previous disturbance events that can also influence the likelihood of future disturbance (Scheller & Mladenoff, 2004). Before drawing conclusions, however, it is important to understand how model predictions are influenced by different sources of uncertainty (Lexer & Hönninger, 2004). One possible source of uncertainty is lack of knowledge or consensus about how a particular ecological process operates (e.g., how trees allocate carbon to aboveground vs. belowground pools) and, thus, how that process should be structured in a model. Another is incomplete understanding of boundary conditions or model behavior in response to uncertainty or variability in parameter values, given a particular model structure. In ecological systems and the models that attempt to simulate them, nonlinear interactions among variables can create effects that are substantially different from the effect of changing one variable, and those effects are hard to predict without testing the model as a whole (Harper et al., 2011).

Performing a sensitivity analysis (SA) is a critical step in the development of any ecological model, providing information both about model structure and the effects of inputs on model outputs. Essentially two approaches are possible; a local SA (LSA) in which each parameter is varied one at a time, or a global SA (GSA) in which all parameters are varied simultaneously. Use of LSA is relatively common in ecology and results can provide generalized information about model behavior that can be helpful for informing model development and calibration. As model complexity and uncertainty increase, however, the efficacy of varying one variable at a time for understanding model behavior and parameter sensitivity may be limited

(Harper et al., 2011; Song et al., 2013). GSA, which is more computationally intensive, has been comparatively underutilized, particularly in ecology (Harper et al., 2011). Until relatively recently, statistical methods proposed to analyze the output of a GSA generally required the assumption of linear relationships between input parameters and model outputs (Saltelli et al., 1999). Even if the assumption of linearity for a complex model is valid for a narrow range of parameter values as is often used in sensitivity analyses (e.g., $\pm 10\%$ of a reference value), application and parameterization of a publically-available model to new areas may generate novel combinations of parameter values that will have unknown effects on model behavior and output.

LANDIS (Landscape Disturbance and Succession) and its updated version LANDIS-II are arguably the most well-established FLMs. First released in the mid-1990s, LANDIS was designed to stochastically simulate the spatiotemporal effects of repeated interactions between forest disturbance and succession based on a moderate number of user-specified parameters (Mladenoff & He, 1999; Mladenoff et al., 1996). Since the first release, LANDIS or LANDIS-II have been used in more than 100 peer-reviewed publications to simulate the impacts of a wide variety of disturbances for which model extensions have been developed, including wildfire, insect outbreaks, and drought. LANDIS has also served as the basis for the development of other FLMs including LANDCLIM (Schumacher et al., 2004) and QLAND (Pennanen et al., 2004).

Landscapes are represented by a grid of cells in LANDIS, and in its original design forest conditions within each cell were characterized simply by tree species and age. Developers later expanded the model output, with the release of the Biomass Succession Extension, to include predictions of AGB with an additional set of processes governing tree growth, competition, and mortality (Scheller & Mladenoff, 2004). Evaluation of parameter sensitivity in the Biomass Succession Extension has so far been limited to local analyses over a narrow range of parameter

values. Scheller & Mladenoff (2004) and Thompson et al. (2011) both varied a subset of model parameters one at a time by $\pm 10\%$ and calculated the corresponding percent change in AGB. Results were similar between the two studies; the same variables were identified as high ranking in terms of importance and each had a proportionally small effect on AGB (i.e., 4-7% change). Sensitivity was, however, only evaluated at the endpoint of their simulations, which was 300 and 50 years, respectively. Growth and the accumulation of AGB are time-dependent processes in the Biomass Succession Extension, and the model includes parameters that were designed to be more or less influential depending on stage of development (Scheller & Mladenoff, 2004). Consequently, parameter sensitivity is also likely to change with time, and a sensitivity analysis that is not global and does not explicitly consider time as a factor could be misleading for calibration (Song et al., 2013).

In the present study, we evaluated output variability and the relative influence of parameters on predicted AGB modeled with the LANDIS-II Biomass Succession Extension across a wide parameter space. We used a nonparametric GSA framework (Harper et al., 2011) that combines a Monte Carlo approach (Sobol, 2001) with analyses based on regression trees. This method has previously been applied to ecological models developed to describe coral reef ecosystem dynamics (Edmunds et al., 2014) and seabird foraging behavior (Langton et al., 2014). We selected it rather than a variance-based method (e.g., extended Fourier amplitude sensitivity test) that can quantify the variance contribution of all interactions with a certain parameter because we were interested identifying which specific sets of parameters were interacting. We also evaluated parameter importance as a function of the duration of the simulation. Although we expected that parameters identified as influential in previous analyses would also rank relatively high in our study (Scheller & Mladenoff, 2004; Thompson et al., 2011), we also expected the relative ranking of some or all parameters to change over time with

stand age and as biomass accumulated (Song et al., 2012). Our goals were 1) to better understand time-dependent sensitivity of parameters in the context of a widely-used FLM and 2) to provide end-users of LANDIS-II with a better understanding of parameter importance, parameter interactions, and nonlinear relationships between parameters and output.

2. Methods

2.1 Model description

The Biomass Succession Extension of LANDIS-II simulates forest growth annually and predicts AGB for each cell based on simplified representations of key ecosystem processes, including growth, competition, senescence, and mortality of cohorts (Scheller & Mladenoff, 2004). In the absence of disturbance, the annual change in AGB for species-age cohort ij is a product of annual net primary productivity (ANPP) and mortality (M). Adopting the notation of Scheller & Mladenoff (2004): $B_{ijt+1} = B_{ijt} + ANPP_{ijt+1} - M_{ijt+1}$; where B_{ij} is the AGB of species-age cohort ij and t is year. $ANPP_{ij}$ is the realized or actual ANPP, which is assumed to increase logarithmically and asymptotically approach the maximum ANPP for species i ($ANPP_{MAXi}$) as B_{ij} approaches the maximum for species i (B_{MAXi}). Mortality includes age-related mortality (M_{AGEij}), which increases exponentially with age, and partial cohort mortality (M_{BIOij}) that increases logistically as a function of AGB and accounts for within-cohort loss of biomass resulting from tree competition during stand development. In addition to $ANPP_{MAXi}$ and B_{MAXi} , users are required to specify values for two subjective shape parameters (r and d) related to species life history. The growth shape parameter (r) modifies the calculation of M_{BIOij} , with larger values resulting in higher rates of mortality during early stand development. The mortality shape parameter (d) modifies the calculation of M_{AGEij} , with larger values resulting in later onset of age-related mortality. Both M_{AGEij} and M_{BIOij} influence the total B_{ij} achieved over the course

of a cohort's lifespan because together they determine the number of years a cohort is able to maximize its productivity.

Growth and mortality are also influenced by the number of cohorts present in a cell, and the recruitment of new cohorts occurs via a series of stochastic processes (Mladenoff & He, 1999). Any cell with a cohort that has reached the user-specified age of sexual maturity for that species can potentially act as a seed source. The probability that seed successfully disperses from one cell to another declines with distance from seed source. The probability is modeled with two negative exponential probability distributions parameterized by the effective and maximum seed dispersal distances specified by a user for a species (Ward et al., 2005). Before seed dispersal, light and abiotic conditions are evaluated for suitability for germination and establishment. Light conditions are compared to the species shade tolerance to determine if there is sufficient light. Shade is treated as categorical variable, following the typical 1 (intolerant) to 5 (tolerant) ranking system, and users set thresholds that are used to assign a shade class to each cell. Thresholds represent the ratio between the total cell biomass at time t and B_{MAX} , and one threshold representing part of the range between 0-100% is assigned to each shade tolerance class. If light is sufficient (i.e., the species' shade tolerance class is 5 or greater than the cell's shade class), a new cohort can establish. Suitability of abiotic conditions are then evaluated based on the species' probability of establishment (P_{est}). P_{est} , which represents the relative response of each species to factors such as soil moisture, site quality, or climate, ranges from 0.01-1. If P_{est} is greater than a random number, a new cohort can establish. $ANPP_{ij}$ is down-regulated proportionally as a function of total cell AGB for each additional cohort to account for growth reduction and increased mortality resulting from inter-cohort competition (Scheller & Mladenoff, 2004).

2.2 Global sensitivity analysis

2.2.1 Parameter selection

We performed a sensitivity analysis on 9 parameters (Table 1), including 5 specifically required by the Biomass Succession Extension and 4 other species-specific parameters required by LANDIS-II that influence establishment or growth in the absence of disturbance. Following the GSA framework suggested by Harper et al. (2011), we selected three values for each parameter. Most of the parameters are continuous with a potentially wide range of values, but shade tolerance can only take on discrete values between 1 and 5. Thus, the range of variation expressible was constrained by shade tolerance. Our options were to include a range of values for shade tolerance representing a perturbation around the central value of 1) $\pm 33\%$ (e.g., 1, 2, 3 or 3, 4, 5) or 2) $\pm 67\%$ (i.e., 1, 3, 5). We chose option 2 to more fully explore parameter interactions and nonlinear model behavior, and applied the same perturbation to the medium values of the other parameters in order to match the range of variation.

When selecting medium values for the other parameters we referenced previous applications of LANDIS-II in North America when possible (Table 1). LANDIS-II researchers often report the values used in their simulations for parameters that have an empirical basis (e.g., $ANPP_{MAXi}$, B_{MAXi} , P_{est}), and we used the median of the reported values as our medium value. The values used for subjective parameters such as the two shape parameters (i.e., r and d) or the thresholds used to assign shade class, however, are rarely reported. Curve parameters such as these are not uncommon in forest growth models and expert opinion is usually the source of parameterization, which could be a major source of uncertainty, particularly if applications from developers do not report their values and rationale (Wang et al., 2013). For our analysis, we selected a medium value near the midpoint of the bounded ranges of r (0.01-1.0) and d (5-25). For seed dispersal distance, we fixed the maximum dispersal distance at 200 m, the width of our

null landscape, and varied the effective distance (SEEDeff). Values for species longevity were selected to represent shorter- (e.g., *Betula papyrifera*, *Abies balsamea*), medium- (e.g., *Betula alleghaniensis*, *Acer saccharum*), and longer-lived species (e.g., *Picea rubens*, *Tsuga canadensis*). Finally, as described above (Section 2.1) LANDIS-II requires the definition of thresholds in order to assign a shade class to a cell. We focused on the definition of shade class 1 threshold (MINth) as our parameter of interest and selected the values to maintain the 67% perturbation and a 10% difference between thresholds. For example, if the shade class 1 value was selected as 30%, the 2, 3, 4, and 5 classes were set as 40%, 50%, 60%, and 70%, respectively.

2.2.2 Implementation

We evaluated parameter sensitivity by simulating forest growth using the GSA framework suggested by Harper et al. (2011). Their method combines a Monte Carlo approach (Sobol, 2001) with nonparametric analyses based on regression trees. Parameter importance is quantified using the Random Forest method (Breiman, 2001) and a classification and regression tree (CART) (Breiman et al., 1984) is used to explore parameter interactions. For this analysis, we wrote a script in Matlab (Mathworks, 2014) to manage the three primary steps of our analysis.

First, a value for each of the 9 input parameters was randomly selected and then written into a set of text files required to initialize and run LANDIS-II. Second, we simulated forest growth for a specified number of years on a 200 x 200 null landscape (spatial resolution = 10 m). The null landscape consisted of an open focal cell with no cohorts embedded in a matrix of cells each populated by a single mature cohort of a species characterized by the combination of random values selected for the 9 parameters. We set our minimum simulation duration at 10 years, and then increased by 20-year increments up to a maximum of 210 years (i.e., 10, 30, 50,

... 210) to determine if and how parameter importance changed as a function of time. Third, at the end of each LANDIS-II simulation we recorded the final AGB and the number of cohorts at the focal cell. We completed 1000 iterations per duration length, resulting in a total of 11,000 separate iterations.

We used Matlab's TreeBagger function to calculate each parameter's "importance value" by duration length based on 500 trees. The importance value represents the change in prediction error associated with the calculation of AGB that occurs when a single parameter is changed, averaged across all trees. In addition to the temporal analysis, we calculated importance across the entire dataset, including duration length as an additional parameter along with the 11,000 random combinations of the 9 input parameters. Finally, we generated two pruned regression tree using the *rpart* package in R (R Development Core Team, 2014), one for AGB and the other for number of cohorts. Trees were pruned using a 10-fold cross-validation procedure that optimized tree size and maximized model fit on the basis of reduction in prediction error.

3. Results

Predicted live aboveground biomass (AGB) was highly variable across simulations (mean = 9,458 g/m²; range 0-45,437 g/m²) and the relative influence of the 9 input parameters included in our analyses on the accumulation of AGB varied through time (Fig. 1). At year 10 the most important parameters were the maximum annual net primary productivity, ANPP_{MAXi} (MSE = 2.2%), and the probability of establishment, P_{est} (MSE = 2.1%) (Fig. 1). Starting values of MSE for the other 6 parameters were <0.24%. Unlike ANPP_{MAXi}, the importance of which remained relatively high across durations, the importance of P_{est} quickly peaked (MSE = 3.3%) and then declined, remaining near 1.5% MSE in the second half of the simulation durations.

Two primary patterns of increasing importance with simulation duration emerged amongst the parameters. Along with $ANPP_{MAXi}$, the importance of maximum allowable AGB (B_{MAXi}) and the growth shape parameter (r) increased rapidly between years 10 and 50 (Fig. 1). After year 50, importance fluctuated but remained relatively high. Importance of $ANPP_{MAXi}$ and r both declined slightly after year 90. The importance of the mortality shape parameter (d) and longevity (LONG) also demonstrated a generally increasing trend with simulation duration, but this pattern developed later, after year 50 (Fig. 1). By year 210, $ANPP_{MAXi}$ and LONG were ranked similarly at 3.3% and 3.9% MSE, respectively. The importance of shade tolerance (SHtol) steadily increased with duration, but at a low rate compared to the other parameters that increased in importance. In contrast to all the other parameters, the importance of the minimum threshold used to assign shade class 1 (MINth) and effective seed dispersal distance (SEEDeff) were consistently low ranking, demonstrating no effect of simulation duration.

The analysis of importance from the pooled dataset across all random combinations of values and duration lengths indicated that the parameters with the most influence on predicted AGB were B_{MAXi} (20.9% MSE) and $ANPP_{MAXi}$ (20.0% MSE) (Fig. 2). The duration of the simulation ranked third in term of importance (17.4% MSE), followed by the two shape parameters, r and d , which were approximately equal in importance (15.4% and 15.2% MSE, respectively). LONG, P_{est} , and SHtol, in decreasing rank order, were intermediate in importance. As was apparent in the temporal analysis (Fig. 1), MINth and SEEDeff had relatively little influence on predicted AGB.

The tree that resulted from the CART analysis of AGB explained 74% of the variance and revealed complex interactions between parameters, and between parameters and simulation duration length (Fig. 3). B_{MAXi} and $ANPP_{MAXi}$ acted as primary constraints on the system, such that if either was low, AGB was generally low. If $ANPP_{MAXi}$ was low, the only pathway by

which an intermediate level of AGB was achieved was if d and LONG were both high. Even if B_{MAXi} and $ANPP_{MAXi}$ were not low, however, interactions between other parameters acted as limiting factors on the percentage of B_{MAXi} that was achieved for a given simulation duration. If, for example, r was high (i.e., mortality was high in early stages of development) and P_{est} was low, estimated AGB was low even if the values of B_{MAXi} and $ANPP_{MAXi}$ were intermediate or high. High r or low d , the latter of which corresponds to early onset of age-related mortality (i.e., M_{AGEij}), constrained AGB to intermediate values. When B_{MAXi} was high, AGB only achieved a similar value when 1) $ANPP_{MAXi}$ was intermediate or high, 2) r was low, 3) d was high, 4) LONG was intermediate or high and 5) simulation duration was greater than 100 years (Fig. 3).

Stochasticity modeled by LANDIS-II generated broad distributions of AGB for each duration length that were generally positively-skewed and frequently included maximum values that were greater than the selected B_{MAXi} for a given iteration (Fig. 4). The influence of initial cohort establishment on AGB was particularly limiting at year 10 (median = 0 g/m²; range = 0-1,169 g/m²); one or more cohorts were established in only 30% of the 1000 iterations. Starting at year 30, however, the percentage of iterations with successful cohort establishment was >96%. Median number of cohorts established increased from 5 at year 30 (range = 0-16) to 19 at year 210 (range = 1-116). Median AGB increased from 4,785 g/m² (range = 0-24,975 g/m²) to 8,491 g/m² (range = 1-45,437 g/m²), respectively. Predicted AGB was higher than B_{MAXi} in 8.5% of iterations, and for those iterations the median number of cohorts was 41 (range = 3-116). A large number of cohorts was not, however, always associated with a high AGB. For the 68 iterations in which greater than 100 cohorts were established, for example, predicted AGB ranged from 27% to 224% of simulation B_{MAXi} .

The tree that resulted from the CART analysis of number of cohorts explained 75% of the variance and again revealed complex interactions that included duration length (Fig. 5). P_{est} and

SHtol were identified as the model parameters having the most influence on number of cohorts. Interactions between the two generated a relatively high number of cohorts when both were medium or high in value. The largest number of cohorts occurred when high values of P_{est} and SHtol occurred with high species longevity and longer simulation duration. Large number of cohorts also occurred when P_{est} was high and SHtol was medium, if B_{MAXi} was also medium or high and $ANPP_{MAXi}$ was low.

4. Discussion

Our aim was to provide a better understanding of the sensitivity and associated uncertainty of parameters that are involved in the predictions of live aboveground biomass (AGB) in the Biomass Succession Extension of the forest landscape model LANDIS-II. LANDIS-II is a process-based ecological model that was designed to be flexible, requiring only a moderate number of parameters, but representations of recruitment, growth, and mortality processes are still relatively complex. Our results showed commonalities with previous studies that evaluated parameter sensitivity by varying a subset of parameters one-at-a-time and concluded the maximum allowable AGB (B_{MAXi}) and maximum annual net primary productivity ($ANPP_{MAXi}$) were highly important parameters. In contrast, however, we also clearly demonstrated that parameter importance was time-dependent for all but the least important parameters. By varying parameters simultaneously, we were also able to reveal how parameter interactions were influenced by time and had variable effects on different outputs. Those results suggest that simulation duration should in a sense be considered carefully as an additional factor during parameterization and calibration, particularly if disturbance is also being modeled. The decision to simulate 100 years versus 200 years with the Biomass Succession Extension has important implications both for the range of AGB values and the number of cohorts that may be

obtained, including the increasing likelihood the user-specified B_{MAXi} will be exceeded as the number of cohorts in a cell increases.

Two patterns of increasing importance with simulation duration emerged. The first was characterized by a rapid increase in relative importance between years 10 and 50, after which importance remained relatively high with some fluctuations (Fig. 1). The parameters identified as most influential in the temporal analysis and the pooled analysis, B_{MAXi} and $ANPP_{MAXi}$, as well as the growth shape parameter (r) all followed this pattern. Interactions between these three parameters and nonlinear effects on AGB are to be expected as the realized or actual ANPP for a species-age cohort in a given time step is a function of those parameters (See Equations 3 and 4 in Scheller & Mladenoff, 2004). Previous sensitivity analyses that have also identified B_{MAXi} , $ANPP_{MAXi}$, and r as the most influential parameters in LANDIS-II's calculation of AGB have indicated that the effect size associated with a $\pm 10\%$ change in value is similar across those parameters (i.e., 4-7% in AGB) (Scheller & Mladenoff, 2004; Thompson et al., 2011). We also observed a similar effect size in median AGB with an increase from the low to the medium value of approximately $\pm 40\%$ for those three parameters across all iterations. The same was, however, not true with an increase from the medium to the high value, which resulted in a change in median AGB of 5%, 48%, and -12% for B_{MAXi} , $ANPP_{MAXi}$, and r , respectively. AGB was, thus, more responsive to changes in the value of B_{MAXi} and r at the low-to-mid range of tested values than the mid-to-high range. The relationship between AGB and $ANPP_{MAXi}$ was comparatively uniform, but still nonlinear.

The second pattern that emerged was characterized by low importance values in the first 10-50 years, followed by an increasing trend with longer simulation durations (Fig. 2). The parameters associated with modeling senescence and mortality, species longevity (LONG) and the mortality shape parameter (d), and, to a lesser degree, shade tolerance (SHtol) followed this

general pattern. Our results, while in agreement with previous work that identified LONG, d , and Shtol as low ranking in terms of importance at year 50 (Thompson et al., 2011), also highlights how a snapshot approach to evaluating parameter importance for a time-dependent process-based model could be misleading if importance not independent of simulation duration. The regression tree of AGB (Fig. 3) revealed that LONG and d interacted with B_{MAXi} , which is not surprising because the rate of biomass loss from age-related mortality (M_{AGEij}) is a function of those parameters and calculated as a fraction of cohort biomass (Scheller & Mladenoff, 2004). The influence of LONG and d on predicted AGB increased with simulation duration because of the time-dependence of M_{AGEij} . Scheller & Mladenoff (2004) concluded that the Biomass Succession Extension was not sensitive to most parameters at year 300, including d . Their analysis of sensitivity was, however, local and based on a narrow parameter space (i.e., $\pm 10\%$). Although the range of values we tested was much wider, and, thus, by design more likely to produce nonlinear behavior, our analysis should still provide a fair representation because our values were drawn from real applications whenever possible (Table 1).

In addition to growth and mortality, LANDIS-II models the establishment of new cohorts. Unlike the growth and mortality processes, which are deterministic, the success of seed dispersing to a given cell and the subsequent establishment of a new cohort are probabilistic. Establishment is controlled by a single parameter (i.e., P_{est}), that can be varied spatially and by species to reflect differential response to environmental conditions. We began each simulation with an open focal cell, thus, we expected that the importance of P_{est} to be relatively high at the outset. Our landscape was, however, not particularly limiting in terms of available seed. Cells adjacent to the focal cell were populated with cohorts capable of producing seed, which likely contributed to the consistently low importance of the effective seed dispersal distance (SEEDeff; Fig. 1). Dispersal distance may have had greater influence on AGB in a landscape populated

with competing species that varied both in colonization ability and growth potential (Xu et al. 2012).

Xu et al. (2012) discuss how the importance of P_{est} relative to $ANPP_{MAXi}$ in LANDIS-II was likely dependent on the availability of open sites. They concluded that in landscapes with high rates of disturbance, differences between species' colonization ability may become a more important driver of succession than their competitive ability. We only simulated one "species" per iteration and our longest simulation duration was 210 years, but our results suggest that both parameters are important in the first 10-20 years of a simulation, after which the importance of $ANPP_{MAXi}$ quickly exceeds that of P_{est} . Contrary to Xu et al. (2012), the importance of P_{est} and $ANPP_{MAXi}$ did not negatively co-vary over time in our analysis, and the importance of P_{est} did not increase over time as a consequence of age-related mortality. One potential reason we did not observe the latter was that cohort establishment did not appear to be a particularly limiting factor in the simulations even when P_{est} was low (Fig. 5). Rather, our results suggest that users should be conservative when calibrating P_{est} . Otherwise, high rates of cohort establishment may cause AGB to grossly exceed the user-specified B_{MAXi} and confound LANDIS-II's ability to accurately model biomass and species dynamics under certain circumstances.

In order for a new cohort to establish from seed in LANDIS-II there must be sufficient light. Light availability is calculated as percent shade based on the ratio between total cell biomass at time t and B_{MAXi} , and shade classes are assigned to cells from user-defined thresholds. Our analysis indicated that AGB was not sensitive to the definitions of those thresholds, but that shade tolerance (SHtol) became more important over time (Fig. 2). New cohorts can establish as long as a species' shade tolerance is greater than the percent shade or is shade tolerance class 5, which can always establish. Our analysis revealed how this model design feature was largely responsible for nonlinearity in the number of established cohorts (Fig. 4). Although P_{est} and

SHtol were low ranking in terms of overall importance with respect to AGB (Fig. 2), interactions between those parameters resulted in large numbers of cohorts in some iterations when given medium or high values (Fig 5). It is important to note, that the values that we used as high in our analysis for SHtol (i.e., class = 5) and P_{est} (probability = 50%) are routinely used in LANDIS-II applications. When P_{est} and SHtol were medium or high, the number of cohorts only appeared to be limited by LONG and the duration of the simulation. When those parameters were also both high, the resulting AGB was often well above B_{MAXi} . In contrast, other combinations of parameter values, for example 1) high SHtol, 2) high P_{est} , 3) high LONG, but 4) low d , resulted in large numbers of cohorts established, but low AGB. That combination of species characteristics could result in a large number of cohorts being established that were long-lived but that experienced very early onset of senescence relative to cohort lifespan (e.g., 50% of species longevity). Under those conditions, each cohort would lose nearly all its biomass well before it exceeded its longevity and was removed from the landscape.

In addition to identifying sensitive parameters, our GSA also provided information about parameters to which the model may be relatively insensitive. AGB predictions by LANDIS-II in our analysis were consistently insensitive to the effective seed dispersal distance (SEEDeff) and the assignment of threshold classes for shade. Neither parameter influenced the number of cohorts. Our results, thus, suggest that these are input parameters that users can safely set to a wide range of values and expect little interference with scenario comparison. As mentioned above, however, our landscape was not particularly limiting in terms of available seed sources. More testing is needed to determine if and how spatial landscape conditions influence the relative importance of seed dispersal distance in LANDIS-II, particularly considering that dispersal capability may be an important factor that needs to be considered along with a species' tolerance to changing site

conditions (e.g., drought tolerance) when modeling forest response to future climate change (Xu et al., 2012).

5. Conclusions

FLMs are generally used to compare different land management or disturbance scenarios, and applications often include interactions between two or more disturbance types. Comparisons between scenarios should be interpreted with caution, however, if the presence of parameters with high sensitivity and high uncertainty may cause the model to be more sensitive to parameterization than scenario differences. Elkin et al. (2012) demonstrated using another in the family of LANDIS models, LANDCLIM (Schumacher et al., 2004), that small changes to the formulation or parameterization of the underlying growth model could substantially alter biomass outcomes depending on the scale of evaluation. Aggregate measures (e.g., total landscape biomass) were relatively robust to parameter uncertainty, but one of the primary benefits of using a spatially-explicit FLM is the ability to evaluate outcomes based on spatial metrics that require information at a finer resolution. If the accuracy of growth model parameterization varies by species and parameterization has a disproportionately large effect on model outcomes, this has particularly important implications for applications that project the effects of, for example, climate change on species distributions (Elkin et al., 2012). Further, if nonlinear interactions involving highly sensitive parameters can create artifacts, such as the large number of cohorts generated by certain combinations of parameter values in LANDIS-II, that impair even simple representations of stand structure and biomass, this is important information for users to have during calibration.

Song et al. (2013) recently demonstrated for the well-established, stand-level forest growth model, 3-PG2, that parameter sensitivities were time dependent. Projections of stand

volume and foliage biomass were sensitive to some parameters early in the simulations and other
 parameters later. Our study indicates that that the same is true for LANDIS-II projections of
 AGB. Growth model parameterization, thus, should not be biased by *a priori* assumptions about
 dominant condition across a large, heterogeneous landscape (Elkin et al., 2012). Users should
 make every effort to model all species and stages of development with the same level of
 accuracy, particularly with respect to parameters that have an empirical basis and have been
 consistently shown to be highly influential, such as $ANPP_{MAXi}$ and B_{MAXi} (Scheller & Mladenoff,
 2004; Thompson et al., 2011; this study). Users should be especially cautious when calibrating
 parameters that are relatively important, but have no empirical basis for parameterization (i.e., r
 and d). Curve parameters such as r and d are not uncommon in forest growth models, and their
 subjectivity is likely to be a continuing source of uncertainty in model outcomes from LANDIS-
 II and other time dependent process-based models (Wang et al., 2013). Additional research over
 longer simulation durations using our framework would demonstrate if and how the patterns of
 parameter sensitivities continue to change over time. Another natural extension would be to
 integrate more spatially heterogeneous initial landscapes. If certain parameters are repeatedly
 identified as has low sensitivity, model developers should consider whether those parameters
 should be removed or the model restructured.

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458 **Literature Cited**

459 Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression
 460 Trees. Chapman and Hall, New York, New York, USA.

461 Breiman, L.E.O., 2001. Random Forests. Mach. Learn. 5–32.

462 Duveneck, M.J., Scheller, R.M., White, M.A., 2014. Effects of alternative forest management on
 463 biomass and species diversity in the face of climate change in the northern Great Lakes
 464 region (USA). Can. J. For. Res. 710, 700–710.

465 Edmunds, P.J., Adjeroud, M., Baskett, M.L., Baums, I.B., Budd, A.F., Carpenter, R.C., Fabina,
 466 N.S., Fan, T.-Y., Franklin, E.C., Gross, K., Han, X., Jacobson, L., Klaus, J.S., McClanahan,
 467 T.R., O’Leary, J.K., van Oppen, M.J.H., Pochon, X., Putnam, H.M., Smith, T.B., Stat, M.,
 468 Sweatman, H., van Woesik, R., Gates, R.D., 2014. Persistence and Change in Community
 469 Composition of Reef Corals through Present, Past, and Future Climates. PLoS One 9,
 470 e107525. doi:10.1371/journal.pone.0107525

471 Gustafson, E.J., Sturtevant, B.R., Shvidenko, A.Z., Scheller, R.M., 2011. Using Landscape
 472 Disturbance and Succession Models to Support Forest Management, in: Li, C., Laforzezza,
 473 R., Chen, J. (Eds.), Landscape Ecology in Forest Management and Conservation. Springer-
 474 Verlag, Berlin, pp. 99–118.

475 Harper, E.B., Stella, J.C., Fremier, A.K., 2011. Global sensitivity analysis for complex
 476 ecological models: a case study of riparian cottonwood population dynamics. Ecol. Appl.
 477 21, 1225–40.

478 He, H.S., 2008. Forest landscape models: Definitions, characterization, and classification. For.
 479 Ecol. Manage. 254, 484–498. doi:10.1016/j.foreco.2007.08.022

480 He, H.S., Mladenoff, D.J., Crow, T.R., 1999. Linking an ecosystem model and a landscape
 481 model to study forest species response to climate warming. Ecol. Modell. 114, 213–233.

482 Langton, R., Davies, I.M., Scott, B.E., 2014. A simulation model coupling the behaviour and
 483 energetics of a breeding central place forager to assess the impact of environmental
 484 changes. Ecol. Modell. 273, 31–43. doi:10.1016/j.ecolmodel.2013.10.030

485 Lexer, M.J., Hönninger, K., 2004. Effects of error in model input: experiments with a forest
 486 patch model. Ecol. Modell. 173, 159–176. doi:10.1016/j.ecolmodel.2003.08.018

487 Mathworks, 2014. The Mathworks, Inc., Natick, Massachusetts, USA.

- 488 Mladenoff, D.J., 2004. LANDIS and forest landscape models. *Ecol. Modell.* 180, 7–19.
489 doi:10.1016/j.ecolmodel.2004.03.016
- 490 Mladenoff, D.J., He, H., 1999. Design, behavior and application of LANDIS, and object-oriented
491 model of forest landscape disturbance and succession, in: Mladenoff, D.J.; Baker, W.L.
492 (Ed.), *Spatial Modeling of Forest Landscape Change: Approaches and Applications*.
493 Cambridge University Press, Cambridge, UK, pp. 125–162.
- 494 Mladenoff, D.J., Host, G.E., Boeder, J., Crow, T.R., 1996. LANDIS: a spatial model of forest
495 landscape disturbance, succession, and management, in: Goodchild, M.F.; Steyaert, L.T.;
496 Parks, B.O. (Ed.), *GIS and Environmental Modeling: Progress and Research Issues*. GIS
497 World Books, Fort Collins, CO, USA, pp. 175–180.
- 498 Pennanen, J., Greene, D.F., Fortin, M.-J., Messier, C., 2004. Spatially explicit simulation of
499 long-term boreal forest landscape dynamics: incorporating quantitative stand attributes.
500 *Ecol. Modell.* 180, 195–209. doi:10.1016/j.ecolmodel.2004.02.023
- 501 R Development Core Team, 2014. R: A language and environment for statistical computing. R
502 Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0. URL
503 <http://www.r-project.org/>
- 504 Ravenscroft, C., Scheller, R.M., Mladenoff, D.J., White, M.A., 2010. Forest restoration in a
505 mixed-ownership landscape under climate change. *Ecol. Appl.* 20, 327–346.
- 506 Saltelli, A., Tarantola, S., Chan, K.P.-S., 1999. Method for Global Sensitivity of Model Output
507 Analysis. *Technometrics* 41, 39–56.
- 508 Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J.,
509 Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial
510 landscape simulation model with flexible temporal and spatial resolution. *Ecol. Modell.*
511 201, 409–419. doi:10.1016/j.ecolmodel.2006.10.009
- 512 Scheller, R.M., Mladenoff, D.J., 2004. A forest growth and biomass module for a landscape
513 simulation model, LANDIS: design, validation, and application. *Ecol. Modell.* 180, 211–
514 229. doi:10.1016/j.ecolmodel.2004.01.022
- 515 Scheller, R.M., Mladenoff, D.J., Crow, T.R., Sickley, T.A., 2005. Simulating the Effects of Fire
516 Reintroduction Versus Continued Fire Absence on Forest Composition and Landscape
517 Structure in the Boundary Waters Canoe Area, Northern Minnesota, USA. *Ecosystems* 8,
518 396–411. doi:10.1007/s10021-003-0087-2
- 519 Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth
520 and succession in a spatially explicit landscape model. *Ecol. Modell.* 180, 175–194.
521 doi:10.1016/j.ecolmodel.2003.12.055

- Shinneman, D.J., Palik, B.J., Cornett, M.W., 2012. Can landscape-level ecological restoration influence fire risk? A spatially-explicit assessment of a northern temperate-southern boreal forest landscape. *For. Ecol. Manage.* 274, 126–135. doi:10.1016/j.foreco.2012.02.030
- Sobol, I.M., 2001. Global sensitivity indices for nonlinear mathematical models and their Monte Carlo estimates. *Math. Comput. Simul.* 55, 271–280.
- Song, X., Bryan, B. a., Almeida, A.C., Paul, K.I., Zhao, G., Ren, Y., 2013. Time-dependent sensitivity of a process-based ecological model. *Ecol. Modell.* 265, 114–123. doi:10.1016/j.ecolmodel.2013.06.013
- Song, X., Bryan, B. a., Paul, K.I., Zhao, G., 2012. Variance-based sensitivity analysis of a forest growth model. *Ecol. Modell.* 247, 135–143. doi:10.1016/j.ecolmodel.2012.08.005
- Steenberg, J.W.N., Duinker, P.N., Bush, P.G., 2011. Exploring adaptation to climate change in the forests of central Nova Scotia, Canada. *For. Ecol. Manage.* 262, 2316–2327. doi:10.1016/j.foreco.2011.08.027
- Steenberg, J.W.N., Duinker, P.N., Bush, P.G., 2012. Modelling the effects of climate change and timber harvest on the forests of central Nova Scotia, Canada. *Ann. For. Sci.* 70, 61–73. doi:10.1007/s13595-012-0235-y
- Sturtevant, B.R., Scheller, R.M., Miranda, B.R., Shinneman, D., Syphard, A., 2009. Simulating dynamic and mixed-severity fire regimes: A process-based fire extension for LANDIS-II. *Ecol. Modell.* 220, 3380–3393. doi:10.1016/j.ecolmodel.2009.07.030
- Thompson, J.R., Foster, D.R., Scheller, R., Kittredge, D., 2011. The influence of land use and climate change on forest biomass and composition in Massachusetts , USA. *Ecol. Appl.* 21, 2425–2444.
- Wang, F., Mladenoff, D.J., Forrester, J. a., Keough, C., Parton, W.J., 2013. Global sensitivity analysis of a modified CENTURY model for simulating impacts of harvesting fine woody biomass for bioenergy. *Ecol. Modell.* 259, 16–23. doi:10.1016/j.ecolmodel.2013.03.008
- Ward, B.C., Mladenoff, D.J., Scheller, R.M., 2005. Simulating Landscape-Level Effects of Constraints to Public Forest Regeneration Harvests due to Adjacent Residential Development in Northern Wisconsin. *For. Sci.* 51, 616–632.
- Xi, W., Coulson, R.N., Birt, A.G., Shang, Z.-B., Waldron, J.D., Lafon, C.W., Cairns, D.M., Tchakerian, M.D., Klepzig, K.D., 2009. Review of forest landscape models: Types, methods, development and applications. *Acta Ecol. Sin.* 29, 69–78. doi:10.1016/j.chnaes.2009.01.001
- Xu, C., Gertner, G.Z., Scheller, R.M., 2009. Uncertainties in the response of a forest landscape to global climatic change. *Glob. Chang. Biol.* 15, 116–131. doi:10.1111/j.1365-2486.2008.01705.x

557 Fig.1. Temporal analysis (0-210 years) of the relative importance of nine parameters required
 558 for predicting live aboveground biomass. Relative importance is calculated as average difference
 559 in mean-squared error (MSE) before and after permutation across all trees. See Table 1 for a
 560 description of parameters.

561 Fig. 2. Pooled analysis of relative importance, including nine parameters required for predicting
 562 live aboveground biomass (See Table 1 for description) and duration of the simulation. Relative
 563 importance is calculated as average difference in mean-squared error (MSE) before and after
 564 permutation across all trees.

565 Fig.3. Regression tree illustrating the influence of and interactions between parameters when
 566 predicting live aboveground biomass. Unit at the end of each terminal node is g/m^2 . Branch
 567 lengths are proportional to the reduction in deviance associated with the splitting variable
 568 labelled at the top of each branch, along with how the variable was summarized. The selected
 569 variables were (1) maximum allowable biomass (B_{MAX}), (2) duration of simulation (Duration),
 570 (3) maximum annual net primary productivity (ANPP_{MAX}), (4) growth shape parameter (r), (5)
 571 morality shape parameter (d), (6) species longevity (LONG), and probability of establishment
 572 (P_{est}).

573 Fig. 4. Predicted AGB by duration of the simulation. Coloring coding represents the number of
 574 cohorts established in each simulation, ranging from low (blue) to high (red).

575 Fig. 5. Regression tree illustrating the influence of and interactions between parameters on the
 576 number of cohorts established in a simulation. Branch lengths are proportional to the reduction in
 577 deviance associated with the splitting variable labelled at the top of each branch, along with how
 578 the variable was summarized. The selected variables were (1) duration of simulation (Duration),
 579 (2) probability of establishment (P_{est}), (3) shade tolerance (SHtol), (4) maximum annual net
 580 primary productivity (ANPP_{MAX}), (5) maximum allowable biomass (B_{MAX}), and (6) species
 581 longevity (LONG).

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Table 1. Selected parameters and representative values¹ used in a global sensitivity analysis to evaluate importance, interactions, and output variability associated with predictions of aboveground live biomass by LANDIS-II and the Biomass Succession Extension.

	Parameter	Abbreviation	Units	Low	Medium	High
1	Shade tolerance ²	SHtol	unitless	1	3	5
2	Maximum annual net primary productivity ³	ANPP _{MAX<i>i</i>}	g/m ²	230	700	1170
3	Maximum aboveground live biomass ³	B _{MAX<i>i</i>}	g/m ²	6270	19,000	31,730
4	Probability of establishment ²	P _{est}	proportion	0.1	0.3	0.5
5	Growth shape parameter ³	<i>r</i>	unitless	0.2	0.6	1.0
6	Mortality shape parameter ³	<i>d</i>	unitless	5	15	25
7	Effective seed dispersal distance ²	SEEDeff	m	30	100	170
8	Species longevity ²	LONG	years	100	300	500
9	Minimum threshold for shade class 1 ³	MINth	percent	10	30	50

¹(He et al., 1999; Ravenscroft et al., 2010; Scheller & Mladenoff, 2004; Scheller et al., 2005; Shinneman et al., 2012; Steenberg et al., 2012, 2011; Thompson et al., 2011; Xu et al., 2009)

²Required by LANDIS-II

³Required by Biomass Succession Extension