



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



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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.

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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 and Mladenoff, 2004). Before drawing conclusions, however, it is important to understand how model predictions are influenced by different sources of uncertainty (Lexer and Hönninger, 2004). One possible source of uncertainty is lack of knowledge or consensus about how a particular ecological process operates (e.g., how

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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 (Scheller et al. 2007) 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 and 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 and 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 and 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 and

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 in 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 and 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 and 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 and Mladenoff (2004): $B_{ijt+1} = B_{ijt} + \text{ANPP}_{ijt+1} - M_{ijt+1}$; 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 ($\text{ANPP}_{\text{MAX}i}$) as B_{ij} approaches the maximum for species i ($B_{\text{MAX}i}$). Mortality includes age-related mortality ($M_{\text{AGE}ij}$), which increases exponentially with age, and partial cohort mortality ($M_{\text{BIO}ij}$) 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 $\text{ANPP}_{\text{MAX}i}$ and $B_{\text{MAX}i}$, 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 $M_{\text{BIO}ij}$, with larger values resulting in higher rates of mortality during early stand development. The mortality shape parameter (d) modifies the calculation of $M_{\text{AGE}ij}$, with larger values resulting in later onset of age-related mortality. Both $M_{\text{AGE}ij}$ and $M_{\text{BIO}ij}$ 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 and He, 1999). Any cell with a cohort that has reached the user-specified age of sexually maturity for that species can potentially act as a seed source. The probability that seed successfully disperses from one cell to another

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