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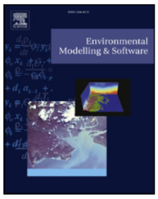

Local and global parameter sensitivity within an ecophysiologically based forest landscape model

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ABSTRACT

Forest landscape models (FLM) are widely used for simulating forest ecosystems. As FLMs have become more mechanistic, more input parameters are required, which increases model parameter uncertainty. To better understand the increased mechanistic detail provided by LANDIS-II/PnET-Succession, we studied the effects of parameter uncertainty on model outputs based on three different approaches. Global sensitivity analyses summarized the influence of each parameter, a local sensitivity analysis determined the magnitude of and degree of nonlinearity of variation in model outputs alongside variation in individual parameters, and a regression tree analysis identified hierarchical relationships among and interaction effects between parameters. Foliar nitrogen, maintenance respiration, and atmospheric carbon dioxide concentration were the most influential parameters in the global analysis. Knowing where parameter influence is concentrated will help model users interpret results from LANDIS-II/PnET-Succession to address ecological questions and should guide priorities for data acquisition.

1. Introduction

Forest Landscape Models (FLMs) are a class of spatially interactive, stochastic simulation models that are widely used by researchers and natural resource managers to project long-term and broad-scale changes to forested landscapes (Shifley et al., 2017). FLMs are increasingly used to simulate the effects of global change drivers, such as climate and land-use change, on future forest composition and function (Duveneck and Thompson, 2017; Liang et al., 2017). Because global change scenarios are complex and often without observed precedent, FLMs have become more mechanistic regarding the major drivers of forest change, with steps toward inclusion of the physiological responses to changing temperature, moisture, atmospheric conditions, fire and defoliation (Gustafson, 2013). While mechanistic approaches for simulating global change offer a strong foundation for simulating emergent and novel conditions, they require many more input parameters than did their statistically-based predecessors. The presumed increase in conceptual robustness gained by using a mechanistic model could potentially be undermined by increased parameter uncertainty associated with a lack of empirical data and/or mechanistic understanding of each of the model coefficients (Cuddington et al., 2013; Dietze, 2017).

A sensitivity analysis (SA) can be used to quantify the impact of model input parameters on model outputs (Saltelli et al., 2000). By systematically varying input parameters and quantifying the relationship of this variation to the resulting variation in model outputs, a SA identifies the parameters that are most influential over model outcomes, as well as the "critical regions" in which parameter values have a disproportionate effect on the model output (Saltelli et al., 2006). Thus, while guiding model use, a sensitivity analysis can also prioritize future research by suggesting which ecological parameters require more accurate estimation. From an ecological perspective, sensitivity analyses may also be useful for identifying dominant mechanisms in the behavior of the model, and thus can improve our understanding of how the modeled system functions (Reusser et al., 2011). Additionally, sensitivity analyses can reveal parameter interactions and correlations, and they can simplify models by suggesting which input parameters are less relevant (Saltelli et al., 2006).

There are two broad approaches for conducting sensitivity analyses: local sensitivity analysis (LSA) and global sensitivity analysis (GSA). Each approach has strengths and weaknesses. LSA, also called one-at-a-time sensitivity analysis, is relatively simple to implement and has been widely used to evaluate FLMs (Sturtevant et al., 2009; Thompson et al., 2011; Xu et al., 2009). In a LSA, all parameters are kept constant at

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their mean or another predefined reference value, while a single parameter is varied within a specified range. This process is repeated for all of the parameters of interest, and the absolute and/or relative influences on a given response variable are compared. The strength of LSA is that it is easy to perform and straightforward to interpret, because just one input parameter is varied for each test. However, interpretations from LSA are limited when several parameters might interact dynamically through the range of individual values (Campolongo et al., 2007; Saltelli and Annoni, 2010). To capture model sensitivity throughout all of input parameter space, GSAs are required.

In GSA, all parameters are varied simultaneously. GSA is more robust than LSA for summarizing parameter effects in complex models because it determines parameter sensitivities across large regions of parameter space (Reusser et al., 2011). There are many types of GSA, including variance-based tests like the Fourier Amplitude Sensitivity Test (FAST), Sobol's method, the derivatives-based Morris method, and various regression-based approaches. Sobol's method is an extensive global sensitivity analysis; it calculates total sensitivity indices for each parameter, including influence due to interaction effects (Sobol, 1993). However, Sobol's method relies on a search function that requires many model runs and is therefore not computationally feasible for highly complex models. FAST, like Sobol's method, is a variance-based global sensitivity analysis summarizing the effect of each parameter on model outputs (Cukier et al., 1975, 1973; McRae et al., 1982). FAST varies all tested input parameters simultaneously through the full input parameter space and then uses Fourier transforms to identify the degree to which each parameter is responsible for variation in model outputs. FAST relies on a characteristic frequency of variation assigned to each input parameter to estimate sensitivity indices. This allows FAST to be much more efficient for calculating main effects than comparable methods, such as Sobol's Method (Saltelli and Bolado, 1998). A variation of FAST known as "extended FAST" (eFAST) also exists for calculating total effect (i.e., including interactions) indices for each parameter (Saltelli et al., 1999). However, the total effect index for each parameter comes at the cost of many more simulations.

Another type of sensitivity analysis, similar to FAST, is the Method of Morris (MoM) which randomizes one-at-a-time testing in a structured framework for global parameter screening (Morris, 1991). Like FAST, MoM assigns indices to parameters indicating their global influence. Additionally, MoM indicates the directionality of each parameter's influence, and it returns an index for each parameter that corresponds to the combination of its non-linear effects on model outputs and its interactions with all other parameters (Wainwright et al., 2014). However, the numeric values of MoM indices are specific to the units of the model outputs; this is a contrast with FAST, whose indices represent the proportion of variance explained. Additionally, while MoM returns an index corresponding to the combined interactions and nonlinear effects of each parameter, it cannot distinguish between interactions and nonlinearities or determine where they occur in parameter space (Brevault et al., 2013).

Beyond FAST and MoM, classification and regression trees have been used in predictive modeling and, more recently, as methods of global sensitivity analysis (Almeida et al., 2017; Breiman et al., 1984; Cutler et al., 2007; Iverson and Prasad, 1998; Pappenberger et al., 2006). Because classification and regression tree models are defined by a hierarchy of split input parameters, fitted regression trees can identify regions in the ranges of individual input parameters where they interact with other input parameters. In this way, classification and regression trees can supplement global sensitivity analyses that either exclude interaction effects (e.g., FAST) or return a single value per parameter that corresponds to the summed interactive and nonlinear effects of that parameter (e.g., MoM, Sobol's Method, and eFAST). Regression tree models are relatively robust to various sampling schemes, especially when compared with FAST, which requires very specific sampling. This allows classification or regression tree analysis to be performed directly on the same data used for a separate global sensitivity analysis. Until recently, the use of tree-based approaches has been uncommon in sensitivity analyses, and what little work has been done was mostly limited to slope stability and hydrological models (Almeida et al., 2017; Singh et al., 2014). However, a regression tree was used in a study of the LANDIS-II Biomass-Succession extension FLM (Simons-Legaard et al., 2015).

LANDIS-II (Scheller et al., 2007) is an FLM modeling platform that has been used extensively to simulate landscape-scale temperate and boreal forest dynamics (Duveneck and Scheller, 2015; Duveneck and Thompson, 2017; Kretchun et al., 2014; Loudermilk et al., 2013). LANDIS-II simulates the establishment, growth, competition, and mortality of tree species-by-age cohorts as they are affected by climate and disturbance. Seed dispersal and various disturbances are simulated across a landscape as spatially interactive processes (Scheller et al., 2007). LANDIS-II requires users to select a succession extension based on their specific research question. Previous sensitivity analyses have been completed for the Biomass-Succession extension (Scheller and Mladenoff, 2004; Thompson et al., 2011). Scheller and Mladenoff (2004) and Thompson et al. (2011) assessed the sensitivity of six and nine key parameters, respectively, with LSAs varying each parameter by 10%. They found that Biomass-Succession was not overly sensitive to any one of the parameters tested, but that the model outputs were most sensitive to the parameters specifying the maximum allowable biomass and maximum annual net primary productivity (NPP). Xu et al. (2009) completed a FAST global sensitivity analysis with Biomass-Succession using different climate variables including temperature (Temp), precipitation (Precip), atmospheric CO_2 (CO_2), and photosynthetically active radiation (PAR). Of the climate variables, they found forest composition to be most sensitive to Temp, followed by PAR, CO_2, and Precip. Simons-Legaard et al. (2015) conducted a global and temporal sensitivity analysis of nine key parameters of Biomass-Succession and also found that maximum allowable biomass and maximum annual NPP were most influential on predicted biomass. In addition, they found that temporal variation and interactions between parameters influenced the biomass output.

Partly in response to the influence of the "maximum allowable biomass" and "maximum annual NPP" parameters of Biomass-Succession – both of which are phenomenological and without mechanistic basis – de Bruijn et al. (2014) developed the PnET-Succession extension, replacing these parameters with a more mechanistic approach to simulating biomass accumulation (Gustafson et al., 2014). PnET-Succession (de Bruijn et al., 2014) incorporates algorithms of the PnET-II ecophysiological model (Aber et al., 1995), which uses first-principles of photosynthesis to simulate competition for resources within vertical canopy layers. Because LANDIS-II tracks biomass rather than canopy height, variation in the biomass of cohorts within a cell is used to define distinct canopy layers. Incoming radiation is allocated to the separate layers to simulate extinction and competition for light. Photosynthetic production is allocated to foliage, wood, roots, and reserves (non-structural carbon). PnET-Succession has been evaluated at several sites (de Bruijn et al., 2014; Duveneck et al., 2017; Gustafson and Sturtevant, 2013), and has been used to answer a variety of research questions (Duveneck and Thompson, 2019, 2017). A local sensitivity analysis by Gustafson et al. (2017a) explored the sensitivity of model outputs to six climate-related input parameters to demonstrate the advantage of employing first principles to predict forest responses to climate change. The analysis quantified the relative effects of climate parameters with directionality and extended the LSA by varying multiple parameters simultaneously, highlighting the interactions between parameters. However, the analysis did not directly compare the absolute effects of parameters to one another, and it excluded several PnET-Succession parameters not related to climate that which affect forest growth. To build upon the recent work by Gustafson et al. (2017a), we describe the results of a three-tiered SA that attempts to harness the strength of the SA approaches discussed above as applied to the PnET-II succession extension used within the LANDIS-II v-6.1 FLM framework.

Table 1
PnET-Succession parameters selected for use in the sensitivity analysis.

Name	Type	Description	Units
TOroot	Single value	Fraction of root biomass lost per year to damage, breakage, or death	Proportion/yr
TOwood	Single value	Fraction of wood biomass lost per year to damage, breakage, or death	Proportion/yr
DNSC	Single value	Proportion of NSC relative to total active biomass that will be maintained as long as net photosynthesis exceeds maintenance respiration	Proportion of active biomass
MaintResp	Single value	Loss of NSC due to maintenance respiration	proportion NSC lost/month
EstMoist	Single value	Tuning parameter to control the sensitivity of establishment to soil moisture.	Unitless
EstRad	Single value	Tuning parameter to control the sensitivity of establishment to light level.	Unitless
WUEcnst	Single value	Constant in equation for computing water use efficiency as a function of VPD	None
FrActWd	Single value	Shape parameter of negative exponential function that calculates the amount of woody biomass that has active xylem capable of supporting foliage	Unitless
IMAX	Single value	Number of subcanopy layers into which each major canopy layer is subdivided	Number of layers
PrecLossFrac	Single value	Proportion of precipitation that does not enter the soil	Proportion
RootingDepth	Single value	Soil depth to which roots typically penetrate	mm
WRP	Single value	Disturbance Frequency (Average time needed to disturb a cumulative area equal to the size of the landscape)	yrs
CO_2	Monthly	Atmospheric CO_2 concentration	ppm
Temp	Monthly	Maximum monthly temperature	Maximum and minimum °C
PAR	Monthly	Photosynthetically active radiation above the upper canopy layer	umol/m^2/sec
Precip	Monthly	Monthly precipitation	mm/mo
FolN	Species-specific	Foliar nitrogen content	% by weight
SLWmax	Species-specific	Maximum specific leaf weight at the top of canopy	g/m^2
PsnTOpt	Species-specific	Optimal temperature for photosynthesis	°C
FracFol	Species-specific	Fraction of the amount of active woody biomass that is allocated to foliage per year	Proportion/yr

For our initial GSA, we selected 20 parameters that had previously demonstrated influential behavior (Table 1).

The objective of this study was to identify the variables most influential in determining the outputs of LANDIS-II/PnET-Succession across time and to identify both interactive effects among parameters and nonlinear responses of model outputs to variation in individual parameters. Identifying highly influential parameters will help model users understand the drivers of model outputs, and will help prioritize areas for model refinement. Our hybrid approach employs three separate analyses – a global sensitivity analysis, a one-at-a-time local sensitivity analysis, and regression tree analysis – and leverages the strengths of each to quantify the sensitivity of two types of model response variables to variation in input parameters, offering users a more complete understanding of model responses to variation in model inputs. This approach also provides a replicable framework for assessing parameter uncertainty and for prioritizing data collection to improve the accuracy of model predictions.

2. Methods

2.1. Approach

Using LANDIS-II v-6.1 and PnET-Succession v-1.0.0, we simulated an artificial 25-by-25 pixel grid landscape totaling 625 cells, each representing 6 ha of forested land, for 200 years, with five year time steps. We populated the landscape with 50 unique initial communities (i.e., species-age cohort mixes) sampled from the FIA database (Bechtold and Patterson, 2005) in New England, USA. These initial communities were made up of 26 tree species, each of which is common among temperate forests of the northeastern United States (Table 2). Our general approach to conduct sensitivity analyses was as follows (Fig. 1): To summarize the influence of each parameter (Table 1) on selected response variables through the full parameter space of the model, we began the sensitivity analysis using the MoM and a FAST GSA (See Global Sensitivity Analysis details below). The MoM and FAST analyses each ranked parameters; and MoM indicated directionality and the combined effects of nonlinearity and interactions for each parameter. From the FAST analysis, we evaluated the total proportion of variance explained by each parameter at each five-year time step of the model. We also conducted hierarchical partitioning of biomass outputs at years 0 and 200 (chosen to capture temporal differences in parameter influence) in order to determine the break points in the influence of each interacting parameter (see regression tree analysis details, below). Finally, we identified the most influential parameters from the results of the global analyses and conducted a LSA of each of those parameters on biomass and area occupied by specific tree species to detect nonlinear relationships between input parameters and their effects on model outputs (See LSA details, below).

Our sensitivity analyses examined variation in two types of outputs: total landscape aboveground biomass and the number of landscape cells occupied by each of three dominant New England species; red maple (*Acer rubrum*), red oak (*Quercus rubra*), and white pine (*Pinus strobus*). Aboveground biomass is the forest growth currency in LANDIS-II, and cell occupancy of individual species defines forest composition spatially. Taken together, changes in aboveground biomass and forest composition are useful metrics to capture forest growth and successional responses to disturbance and are therefore appropriate response variables for our sensitivity analysis (Duveneck et al., 2017).

We limited our parameter selection to twenty based on what was computationally feasible. We selected parameters that were newly introduced with the PnET-Succession extension or were linked to the photosynthetic mechanisms targeted by the extension. Parameter selection was motivated by either a parameter's known importance to the model, or by large uncertainty about the input value for the parameter. The selected parameters were chosen to lead to a better understanding of both the model and the specific contribution of each parameter to output variance. Some parameters tested (foliar nitrogen (FolN), maximum specific leaf weight (SLWmax), optimal temperature for photosynthesis (PsnTOpt), and the fraction of the amount of active woody biomass that is allocated to foliage per year (FracFol)) were species-specific, and we jointly varied these linearly across species. The values sampled by FAST for these parameters ranged from 0 to 1, where “0” meant that each species' sampled parameter value was 90% of its default value, and “1” meant that it was 110% of its default value for each species. The FolN range for each species was set to include the middle 90% of values from the NERC foliar chemistry database (Table 2) (Northeastern Ecosystem Research Cooperative, 2016) and was also varied linearly within those bounds. Climate parameters (average monthly maximum and minimum temperature values (Temp), monthly carbon dioxide concentration (CO_2), monthly precipitation (Precip), and monthly photosynthetically active radiation (PAR)), were varied across the range predicted from 2000 to 2100 provided by the Regional Concentration Pathway 8.5 emission scenario (IPCC, 2013) as simulated by the Hadley Global Environment Model v.2-Earth System Global

Table 2
Tree species simulated and species-specific parameter minimum (min) and maximum (max) values used in the GSA, along with the default (def) values for each parameter and species. Full unit descriptions are described in Table 1.

Species	FolN (%)			SLWmax (g/m^2)			PsnTOpt (°C)			FracFol (proportion/yr)		
	Min	*Max*	*Def*	*Min*	*Max*	*Def*	*Min*	*Max*	*Def*	*Min*	*Max*	*Def*
Abies balsamea	0.941	2.03	1.4	194	237	215	17.1	20.9	19	0.108	0.0132	0.12
Acer rubrum	1.02	2.54	2.6	72.0	88.0	80	23.4	28.6	26	0.0270	0.0330	0.03
Acer saccharum	1.25	2.63	2.1	63.0	77.0	70	20.7	25.3	23	0.0270	0.0330	0.03
Betula alleghaniensis	1.65	3.22	2.2	72.0	88.0	80	18.9	23.1	21	0.0270	0.0330	0.03
Betula lenta	2.05	3.19	2.26	72.0	88.0	80	18.9	23.1	21	0.0270	0.0330	0.03
Betula papyrifera	1.33	3.19	2.3	72.0	88.0	80	18.9	23.1	21	0.0270	0.0330	0.03
Carya glabra	1.53	2.65	2.6	81.0	99.0	90	20.7	25.3	23	0.0270	0.0330	0.03
Fagus grandifolia	1.49	2.98	1.8	72.0	88.0	80	20.7	25.3	23	0.0270	0.0330	0.03
Fraxinus americana	1.52	2.93	2.5	76.5	93.5	85	22.5	27.5	25	0.0270	0.0330	0.03
Ostrya virginiana	1.24	2.12	2.02	90.0	110	100	20.7	25.3	23	0.027	0.0330	0.03
Picea glauca	0.875	1.24	1.4	225	275	250	18.0	22.0	20	0.108	0.132	0.12
Picea mariana	0.630	1.04	1.2	225	275	250	18.0	22.0	20	0.108	0.132	0.12
Picea rubens	0.680	1.47	1.2	225	275	250	18.0	22.0	20	0.0270	0.0330	0.03
Picea resinosa	0.810	1.39	1.7	225	275	250	18.9	23.1	21	0.108	0.132	0.12
Pinus strobus	0.960	1.70	2.0	212	259	235	18.9	23.1	21	0.108	0.132	0.12
Populus grandidentata	1.79	3.05	2.5	104	127	115	19.8	24.2	22	0.0270	0.0330	0.03
Populus tremuloides	1.40	3.37	2.5	104	127	115	19.8	24.2	22	0.0270	0.0330	0.03
Prunus serotina	1.67	4.15	2.8	81.0	99.0	90	22.5	27.5	25	0.0270	0.0330	0.03
Quercus alba	1.85	2.27	2.5	90.0	110	100	23.4	28.6	26	0.0270	0.0330	0.03
Quercus prinus	1.99	2.04	2.39	81.0	99.0	90	23.4	28.6	26	0.0270	0.0330	0.03
Quercus rubra	0.780	2.87	2.5	76.5	93.5	85	21.6	26.4	24	0.0270	0.0330	0.03
Quercus velutina	1.90	3.13	2.7	76.5	93.5	85	21.6	26.4	24	0.0270	0.0330	0.03
Thuja occidentalis	0.830	1.43	1.3	221	270	245	18.0	22.0	20	0.117	0.143	0.13
Tilia americana	1.90	3.13	2.6	67.5	82.5	75	20.7	25.3	23	0.0270	0.0330	0.03
Tsuga canadensis	0.830	1.66	1.1	176	215	195	18.9	23.1	21	0.0720	0.0880	0.08
Ulmus americana	2.29	3.43	2.3	76.5	93.5	85	20.7	25.3	23	0.0270	0.0330	0.03

Circulation Model downscaled for New England, obtained from the USGS Geo Data Portal (Stoner et al., 2013). For these parameters, we sampled from within the range of average annual climate values – a single value per parameter. After sampling this average annual parameter value (e.g. the average temperature for the year), we then parameterized the model using the monthly values corresponding to the year from the data with the closest average annual value (e.g., the year with the closest average temperature to the sampled value was chosen, and then the monthly values were extracted from that year's data) (Table 3). For Temp, an overall average for each year was used for sampling. Then, the monthly maximum and minimum temperature values (Tmax and Tmin) required by PnET-LANDIS-II were selected

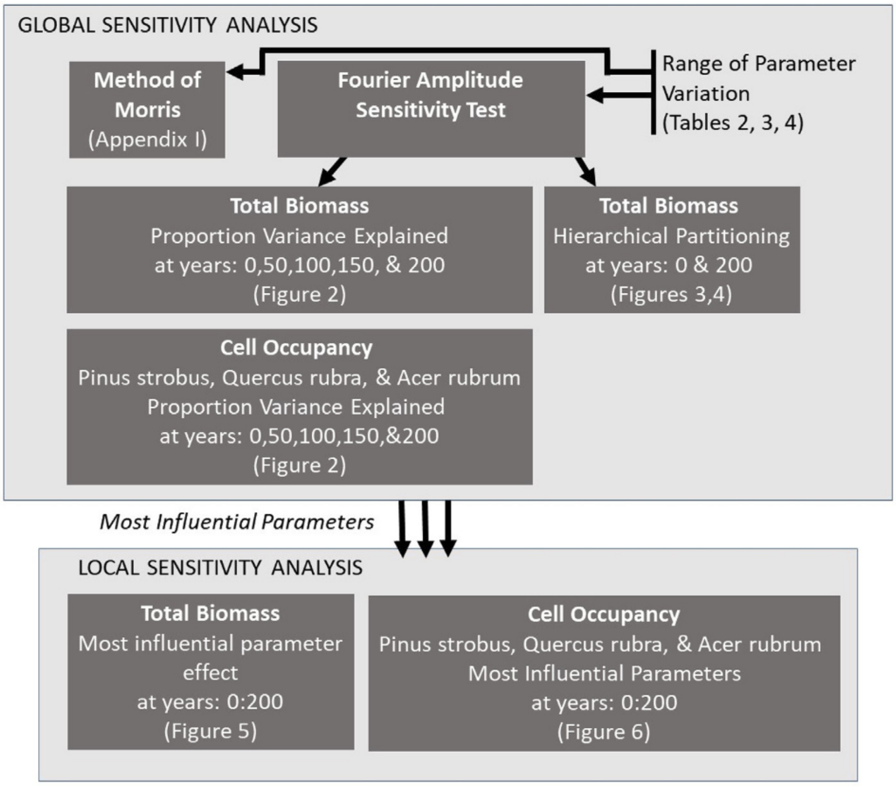

Fig. 1. Conceptual flow diagram of our sensitivity analysis methods combining global and local sensitivity analyses. Using the range of parameter variation, we started by completing a Fourier Amplitude Sensitivity Test and a Method of Morris analysis. These two methods summarized the influence of each parameter (which corroborated each other). Next, we evaluated the proportion of variance in total biomass and cell occupancy of dominant species at multiple timesteps. Then, we conducted hierarchical partitioning in order to identify hierarchical relationships among and interaction effects between parameters. Finally, using the most influential parameters identified from above, we conducted local sensitivity analyses to determine the magnitude and degree of nonlinearity of the variation in total biomass and cell occupancy of dominant species.

Table 3
Scenario specific parameter minimum and maximum values used in the GSA. Full unit descriptions are described in Table 1. Note that the climate parameters (bottom four rows) were filled with monthly values from the year with the closest average value from predicted data from 2000 to 2100 provided by the Regional Concentration Pathway 8.5 emission scenario (IPCC, 2013) as simulated by to the Hadley Global Environment Model v.2-Earth System Global Circulation Model downscaled for New England obtained from the USGS Geo Data Portal (Stoner et al., 2013).

	Min	*Max*
TOroot (Proportion/yr)	0.0100	0.0300
TOwood (Proportion/yr)	0.00100	0.0200
DNSC (Proportion)	0.0100	0.500
MaintResp (proportion NSC lost/month)	0.00100	0.00500
EstMoist (Unitless)	2.00	20.0
EstRad (Unitless)	2.00	20.0
WUEcnst (None)	8.00	13.0
FrActWd (Proportion/yr)	3.00e-5	1.00e-4
IMAX (Number of layers)	3.00	10.0
PrecLossFrac (Proportion)	0.0500	0.600
RootingDepth (mm)	600	1000
WRP (yrs)	50.0	500
CO_2 (ppm)	400	927
Temp (°C)	8.16	17.33
PAR (umol/m^2/s)	289	353
Precip (mm)	57.8	158

together from the data for the year whose average temperature was closest to the sampled value. The sampled climate parameters were held constant across years in each simulation. Other parameters were not species nor temporally specific and were composed of a single value for a given scenario, (e.g., maintenance respiration (MaintResp) and the proportion of non-structural carbon to be maintained when net photosynthesis exceeds MaintResp (DNSC)). These values were varied within their limits as defined by the PnET-Succession user manual or expert knowledge of the model (Table 3) (Gustafson et al., 2017b).

2.2. Global sensitivity analyses

We performed the FAST analysis using the R package *fast* (R Development Core Team, 2006; Reusser et al., 2011). FAST is a variance-based sensitivity analysis that calculates the main effect (i.e., excluding interactions with other parameters), of each parameter on variation in model outputs. FAST generates parameter samples to be used as simulation inputs within the bounds of a user-defined minimum and maximum value for each parameter by assigning each parameter a characteristic frequency. Each parameter is systematically varied at this frequency within the bounds defined by the maximum and minimum values across all of the parameter samples, and the model is then run on each set of parameter samples. Afterward, a fast Fourier transform is applied to observed variation in model outputs to produce a power spectrum. The values from the first four multiples of the characteristic frequencies for each parameter are summed and divided by the total summed power spectrum across all frequencies to calculate the main effect sensitivity indices (Cukier et al., 1975). We generated 8378 samples, four times the minimum number required by the Nyquist criterion (i.e., the function frequency limits and the corresponding discrete sampling rate required to describe a continuous function; see (Jerri, 1977)), to ensure convergence (McRae et al., 1982; Saltelli and Bolado, 1998). We then used each parameter sample to conduct a LANDIS-II simulation. To capture variation in behavior through the successional trajectories experienced over time, we calculated FAST sensitivity indices at each 5-year time-step of the simulations.

We performed MoM using the R package *sensitivity* to rank parameters in order of importance, to determine directionality of parameters, and to estimate the extent to which each parameter interacts with other parameters or affects outputs nonlinearly (Iooss et al., 2015; R Development Core Team, 2006). In contrast to FAST, which calculates "main effect" indices, MoM estimates total effect indices for the model parameters, which include influence over model outputs due to interactions with other parameters. We designed our MoM analysis to sample 40 one-at-a-time paths (r) for the 20 parameters (k), for a total of $(r)^*(k+1) = (40)^*(20 + 1) = 840$ model runs in addition to those by FAST. The minimum and maximum values constraining parameter sampling were the same as those used in FAST (described above and listed in Tables 2 and 3). MoM returns a single "elementary effect" for each parameter for each path, which summarizes the influence of that parameter through the individual path. The mean of the elementary effects (μ) is used to calculate the total effect index for each parameter. The sign of the mean of the elementary effects then corresponds to directionality of the parameter's influence, with the exception of when the parameter has both positive and negative effects on model outputs, in which case the sign of the individual elementary effects would have to be analyzed (Campolongo et al., 2007; King and Perera, 2013). The mean of the absolute values of the elementary effects for each parameter (μ*) has also been used to summarize the parameter's global influence over a particular output while incorporating non-monotonic behavior (Campolongo et al., 2007). Finally, the standard deviation of the elementary effects (σ) around the mean (μ) corresponds to the combined nonlinearity and interactions associated with each parameter.

2.3. Regression tree analysis

We performed a regression tree analysis (RTA) using the *PARTY* package in R (Hothorn et al., 2006). RTA is a non-parametric technique for recursively partitioning a continuous variable into increasingly homogeneous subsets, where the partitions are identified by testing all potential partitions across all values of all the predictor variables then selecting the partition that maximizes the difference between groups (De'ath and Fabricius, 2000). RTA results in a dendrogram that shows the hierarchical relationships among predictors and between predictors and the response. The same samples developed for the FAST analysis were reused, with biomass outputs from years 0 and 200 as the response variables. The specific RTA implementation within the *PARTY* package is called "conditional inference trees", which requires a significant difference (p-value < 0.05, as determined from a Monte Carlo randomization test) in order to create a partition in the regression tree. This technique minimizes bias and prevents over-fitting and the need for regression tree pruning (De'ath and Fabricius, 2000; Hothorn et al., 2006; Hothorn and Zeileis, 2015).

2.4. Local sensitivity analysis

Finally, we conducted a LSA to detect the magnitude of each parameter's influence at a point in parameter space in model output units (rather than relative to variance in outputs from other parameters), and to determine whether LANDIS-II outputs respond nonlinearly to linear variation across each parameter's range. Like the MoM, the LSA results also indicate directionality and magnitude of parameter influence. We performed an LSA on the top four influential parameters identified in the FAST analysis for each type of output (biomass and landscape composition). We performed 24 total simulations for the local sensitivity testing on each output type: simulations were performed at six evenly spaced values across the parameter's possible range while all other input parameters were held at their calibrated values, for each of the four parameters tested. In order to assess variation over time, output values were assessed at each five-year time step for each simulation.

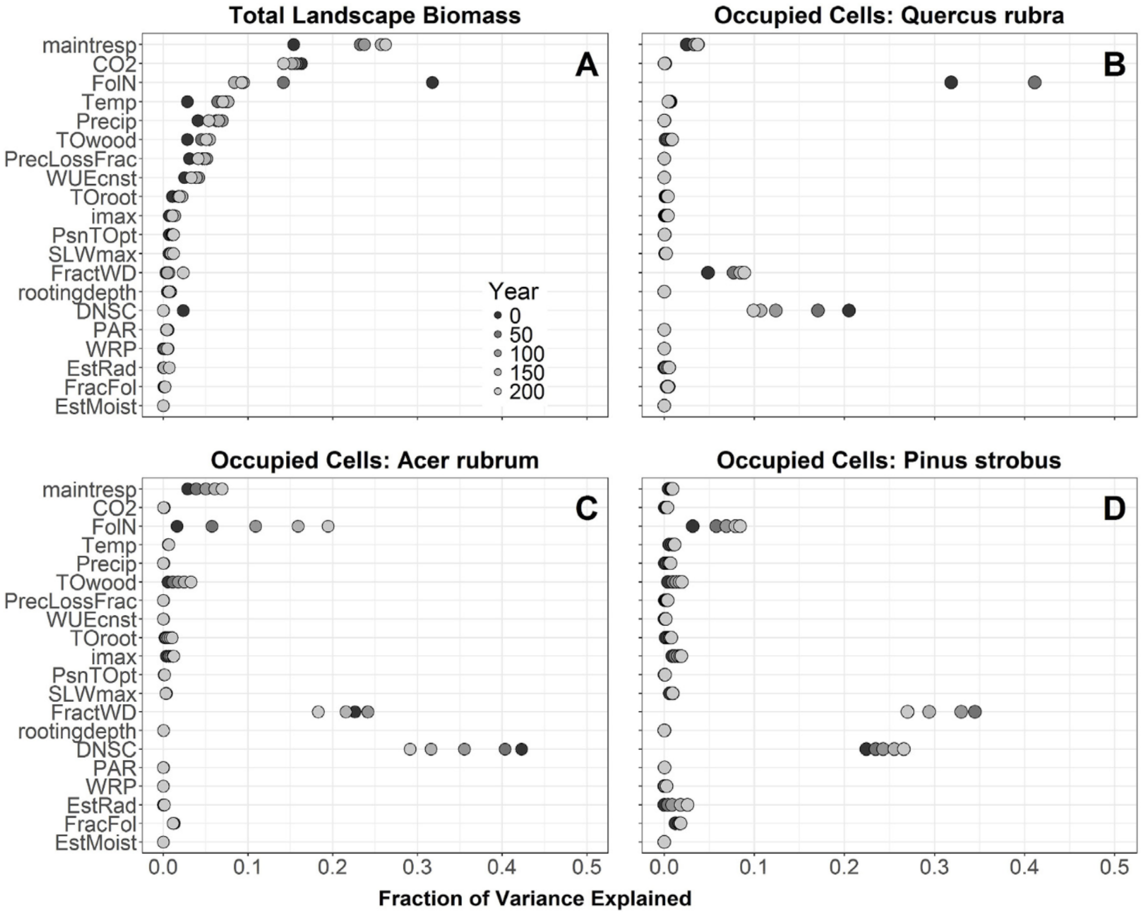

Fig. 2. Sensitivity results from the FAST analysis showing the fraction of variance explained for each input parameter for A) total landscape biomass, B) occupied cells of *Quercus rubra*, C) occupied cells of *Acer rubrum*, and D) occupied cells of *Pinus strobus*. Increasingly lighter points indicates later simulation time steps.

3. Results

3.1. Global sensitivity analyses

Based on the FAST results, MaintResp was the most influential parameter for determining total landscape biomass output by the model across a 200-year simulation (Fig. 2A). Although FolN was more influential for determining total biomass than MaintResp during model initialization (year 0), the influence of FolN for determining total landscape biomass declined quickly after year 0, giving FolN a slightly lower average index value than that of MaintResp. Other influential parameters included the climate parameters – CO_2, Temp, and Precip – and precipitation loss fraction (PrecLossFrac), which determines the proportion of water that does not enter the soil.

The FAST analysis also indicated that the same parameters to which biomass outputs are sensitive tend to be important in determining species composition (Fig. 2 B, C, & D). The three species differed somewhat regarding the relative influence of the most important parameters for determining species cell occupancy, with FolN explaining more variance in cell occupancy of *Quercus rubra* than in the other two species. However, the same parameters were influential for determining cell occupancy for each of the three species; FolN, MaintResp, DNSC, the amount of woody biomass capable of supporting foliage (FrActWD), and sensitivity of establishment to light (EstRad). Climate parameters were not influential in determining species composition, contrary to our results for outputs which are directly related to growth. For both total landscape biomass and species cell occupancy tests, PAR, establishment parameters, rooting depth (RootingDepth), and disturbance frequency (WRP) were not identified as being very influential.

Temporal variation in the FAST sensitivity index for each parameter indicated how the relative influences of particular variables on model outputs changed through time. As noted above, total landscape biomass was especially sensitive to FolN early in each simulation, where the parameter's variation accounted for one-third of the variation in output landscape biomass. After 200 simulation years, variation explained by FolN only accounted for ten percent of output variance. In contrast, MaintResp explained ten percent more variation in total landscape biomass by the end of simulations than at the beginning. The change in relative influence of the two variables is a result of increasing biomass in the simulations, which is associated with increases in the contribution of MaintResp. Temporal variation was observed in the FAST results for cell occupancy as well, where the influence of FolN increased with time. From year 0 to year 200, the influence of FolN on *Quercus rubra* occupancy increased from approximately thirty percent to explaining over half the variation in cell occupancy by year 200.

Building on the results from FAST, the MoM analysis estimated total effect sensitivity values for each parameter. When ordered by absolute-valued indices (μ*), the parameter rankings of MoM closely mirror the rankings of the FAST analysis (Table 4). Additionally, the sign of mean elementary effects for each parameter indicated directionality for the influence of the parameter (Figure A1). The large standard deviations (σ) of the sets of elementary effects for the input parameters also suggested a substantial amount of combined nonlinearity and/or interactions between parameters. See Appendix I for a more detailed explanation of the MoM results.

Table 4
Rankings of input parameters from average indices of FAST and MoM (μ*) across simulation years 0, 50, 100, 150 and 200 for each parameter's influence over total landscape biomass. The similarity in the parameter rankings suggests robustness of the GSA results.

Ranking	FAST	MoM
1	MaintResp	MaintResp
2	CO_2	CO_2
3	FolN	FolN
4	Temp	Precip
5	Precip	Temp
6	TOwood	PrecLossFrac
7	PrecLossFrac	TOwood
8	WUEcnst	WUEcnst
9	TOroot	TOroot
10	IMAX	PsnTOpt
11	PsnTOpt	SLWmax
12	SLWmax	FrActWd
13	FrActWd	IMAX
14	RootingDepth	RootingDepth
15	DNSC	DNSC
16	PAR	PAR
17	WRP	WRP
18	EstRad	FracFol
19	FracFol	EstRad
20	EstMoist	EstMoist

3.2. Regression tree analysis

While we performed the RTA across time-slices of the model, we found that most of the relevant information offered by the RTA was contained within the analysis at year 0 and at year 200, which are presented here (Figs. 3 and 4). The RTA of total biomass accumulated during model initialization (year 0) partitioned the simulations into 12 terminal nodes, which are shown as boxplots in Fig. 3. Each boxplot shows the distribution of year 0 biomass within the subset of simulations in that branch of the regression tree. Consistent with the findings of FAST, the RTA shows that FolN, CO_2 and MaintResp explain much of the variation in the year 0 biomass. Indeed, of the 11 partitions that the RTA identified, 10 came from those three variables. Temp entered as a significant variable only in the relatively small subset of simulations ($n = 1664$) where FolN and CO_2 were high and MaintResp was low. The first partition at the top of the RTA was based on whether FolN was greater or less than 44% of its potential range, indicating FolN as the most significant predictor variable overall. Not surprisingly, higher values of FolN were associated with greater biomass. Working down both sides of the tree for high and low values of FolN, the next splits were based on whether CO_2 concentration was greater or less than ~620 ppm. Higher values of CO_2 were associated with higher levels of biomass. At this level in the regression tree, the analysis has partitioned four groups of simulations that represent high/low FolN and high/low CO_2; the corresponding values of biomass in these simulations range from 14,449 g/m^2 with low FolN and low CO_2, to 29,661 g/m^2 with high FolN and high CO_2. Below this level on the regression tree, the predictor variables diverge. Within the branch with high FolN (the right side of the tree), MaintResp was identified as the next most predictive, for both the high and low CO_2 groups. Within the branch with low FolN (the left side of the tree), FolN was again identified as the most predictive, for both high and low CO_2 groups. Overall, by the bottom of tree and thus at the point where RTA cannot identify any additional significant partitions, the simulations with low MaintResp (< 0.003) and the highest levels of FolN (> 0.7) had the highest average year 0 biomass. The lowest levels of year 0 biomass occurred when FolN was below 0.2 and CO_2 was below 620 ppm.

By year 200 of the simulations, FolN, CO_2, and MaintResp were still

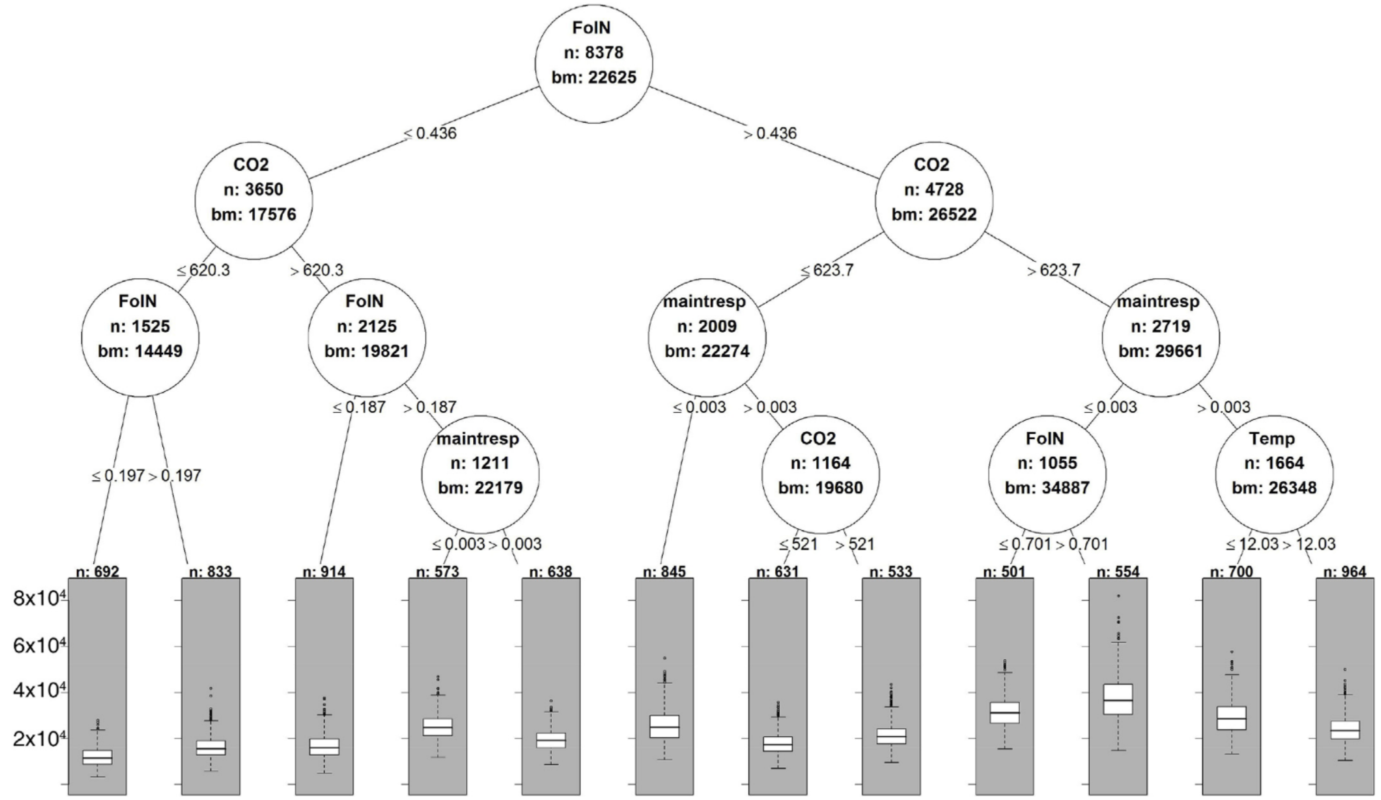

Fig. 3. Regression tree analysis for total aboveground biomass (g m^{-2}) for model initialization (year 0). Circles show the predictor variable that was selected to be partitioned, the size of the sample of runs (n) that remain at that branch in the tree, and the average value of biomass (bm) before the partition. The lines below each circle indicate the break points for that predictor that maximize the difference in the response (i.e., biomass). Box plots at the terminal nodes show the variation within the response (biomass) within that branch of the tree.

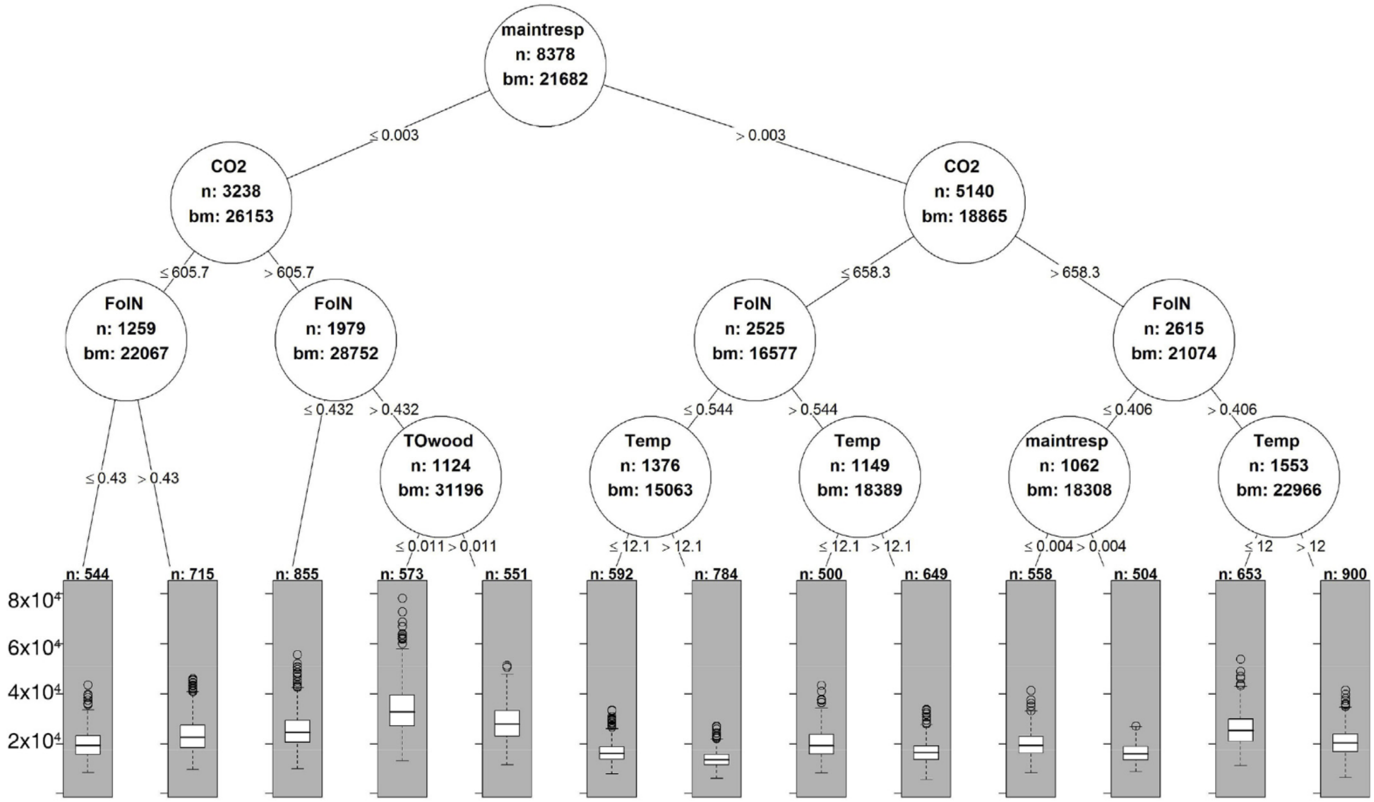

Fig. 4. Regression tree analysis for the biomass response variable at year 200. Details of each figure component are described in the caption for Fig. 3.

identified as the most influential variables, and thus they represent the most common partitions in the tree (Fig. 4). However, their relative importance had shifted. At year 200, the first partition is on MaintResp, followed by CO_2, then FolN (Fig. 4). Like time 0, the RTA partitioned CO_2 in the mid-600s. Working down the side of the tree with higher values of MaintResp, the climatic variable Temp entered as a significant predictor. Overall, after 200 years, simulations where MaintResp was < 0.003, CO_2 concentrations were > 606 ppm, FolN was > 0.43 and TOwood was < 0.01 had the highest average biomass.

3.3. Local sensitivity analysis

Results from the LSA showed that simulations at calibrated values responded to variation in selected (most influential) input parameters as expected relative to each other given the results of the GSA and RTA analyses. The local analysis supported the direction and magnitude of the influence of each parameter on total biomass (Fig. 5) and species occupancy (Fig. 6), both of which had been indicated by GSA. While increasing MaintResp and Temp inputs decreased landscape biomass, increasing FolN and CO_2 inputs increased landscape biomass. Additionally, the LSA revealed particular nonlinear effects in the range of variation for each parameter. These effects had been captured in the standard deviation of elementary effects from the MoM GSA, but MoM does not discriminate between interactions and non-linearities. In contrast, the LSA can identify regions of nonlinearity across points in parameter space but cannot identify interactions. For example, while the change in total biomass corresponded nearly linearly with change in MaintResp at year 200, the model showed much higher sensitivity to FolN in the middle of the parameter's range than near the lower and upper limits of its range.

4. Discussion

Our primary objective in this study was to identify the most influential parameters within a mechanistically based FLM—i.e., the coupled LANDIS-II-PnET-Succession framework. De Brujin et al. (2014) developed this succession module with the goal of moving away from earlier succession modules within LANDIS-II, which were largely phenomenological and whose most influential parameters were not explicitly linked to processes that govern tree growth and forest development and are essentially unknowable outside of some limited range of observations. Given that the goal of PnET-Succession was to develop a module driven by eco-physiological first principles, it is not surprising that the most influential parameters we identified were FolN, MaintResp, and CO_2. All three parameters are closely linked to the mechanisms of tree growth and survival. This contrasts with sensitivity analyses of the biomass-succession extension to LANDIS-II (Scheller and Mladenoff, 2004) which found that maximum allowable biomass and maximum annual NPP were most sensitive (Simons-Legaard et al., 2015; Thompson et al., 2011). In this context, the PnET model represents significant progress toward an FLM that can be reasonably expected to simulate forest processes under future conditions of climate and atmospheric chemistry that have not been observed in the past. Nonetheless, each of these parameters has distinct limitations for use in an FLM and present challenges for model users.

The importance of FolN as identified by our global SA reflects the original design of the original PnET family of models developed in the 1990s (Aber et al., 1997, 1995; Ollinger et al., 1998), all of which use FolN to represent N availability and to estimate gross photosynthesis. In the context of LANDIS-II/PnET-Succession, this is consistent with the developers' intentions to have broad-scale mechanistic underpinnings within the model and reflects the fact that foliar nitrogen concentrations are strongly linked to rates of photosynthesis and ecosystem-scale carbon assimilation across forests worldwide (Reich et al., 1997). From the perspective of the user of Landis-II/PnET-Succession, there are many published studies and public databases documenting foliar N that can aid parameterization, such as the Foliar Chemistry Database (Northeastern Ecosystem Research Cooperative, 2016) which we used

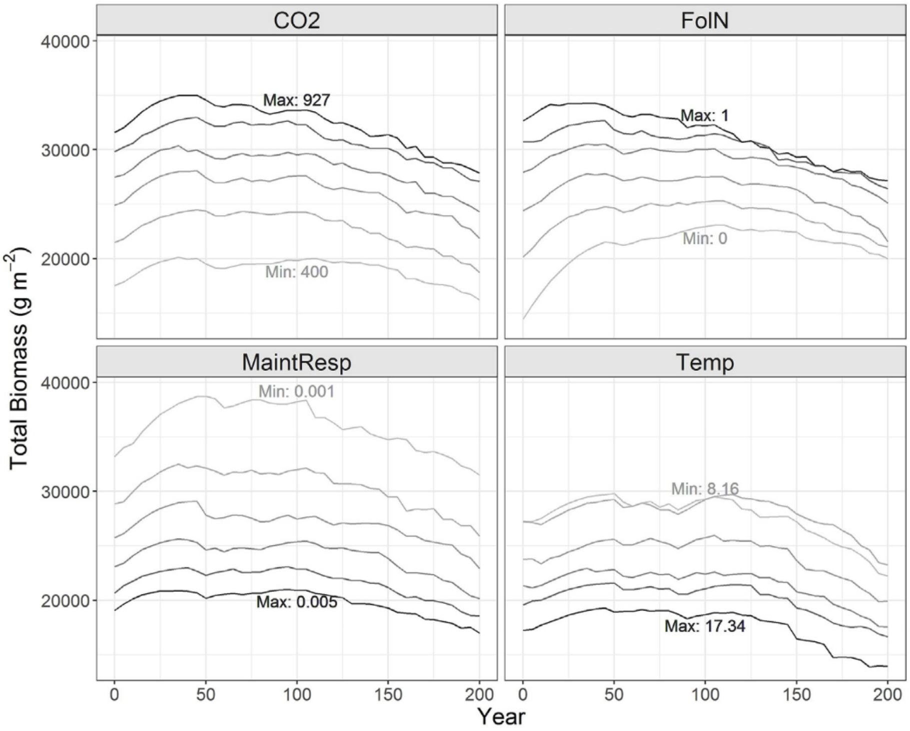

Fig. 5. Local sensitivity analysis of biomass through time of the top four most influential parameters from the FAST analysis, where all other parameters are set at calibrated values.

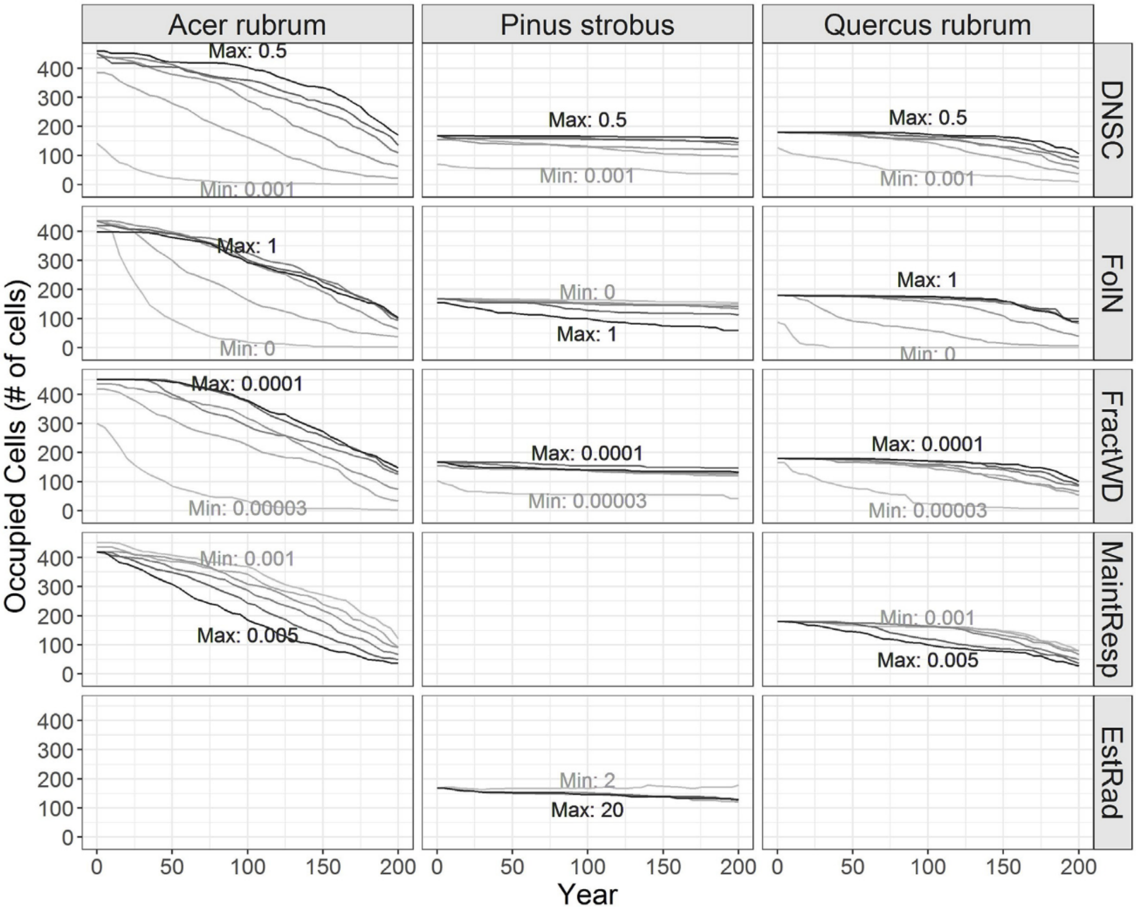

Fig. 6. Local sensitivity analysis of three species cell occupancy from the top four species-specific most influential parameters from the FAST analysis, while all other parameters are set at calibrated values. Note that seemingly missing plots occur as the top three selected parameters were different across species.

here. Within LANDIS-II/PnET-Succession, FolN is a species-specific parameter, which results in differential growth rates among species and allows users to simulate within-stand competition, which is an advancement over the earlier, lumped-parameter versions of PnET-II.

While the model allows FolN to vary by species, FolN cannot vary over space, nor through vertical layers of a canopy in the current implementation. Neglecting spatial variability in foliar N (and thus N availability) is a limitation of the model. Correlational studies using broad-scale remote sensing data, like that from the Airborne Visible/InfraRed Imaging Spectrometer (AVIRIS) and the MODerate-resolution Imaging Spectroradiometer (MODIS), have described the potential use of these datasets for mapping the spatial variation of FolN in temperate forests (Lepine et al., 2016; Ollinger et al., 2008b). And, modifications to PnET-Succession are also being tested to allow FolN to vary vertically in response to light availability (Gustafson et al., 2018). Our results suggest that developing the model's capability to make FolN more dynamic rather than as a species constant is a high priority for management and could greatly reduce uncertainty in model results.

MaintResp was also among the most influential parameters in our sensitivity analyses. MaintResp is the amount of non-structural carbon lost to maintenance respiration each month and is used in the calculation of cohort NPP and mortality. MaintResp is affected by temperature (de Bruijn et al., 2014) and is thus consistent with the model's more mechanistic underpinnings and utility for modeling forest change in future climates. However, the formulation of MaintResp is greatly simplified as compared to the respiration calculations in the original version of PnET-II (Aber et al., 1995), and it is applied universally across all species. This formulation was required to achieve computational tractability (Gustafson et al., 2017b). The consequence of these simplifications is that MaintResp is not an empirically measurable value and has a definition that does not exist outside the model. From the user's perspective, MaintResp is effectively a tuning parameter. While we see no obvious alternative, having a tuning parameter as among the most sensitive in the model is challenging from the perspective of developing an FLM based on mechanisms that are expected to perform predictably, including under conditions that have not been observed and thus not tuned to. Future improvements to the model should incorporate maintenance respiration requirements to growth that can be measured and tested, preferably at a landscape scale.

CO_2 was the other parameter that our SA analyses identified as highly influential. Greater CO_2 concentrations result in increased water use efficiency and increased rates of photosynthesis, and atmospheric CO_2 concentrations are expected to continue to rise even further to unprecedented levels (Keenan et al., 2013). Our findings support other studies using the PnET family of models, including Ollinger et al. (2008a), which found CO_2 to be more influential than temperature in predicting changes to NPP over multiple climate change scenarios throughout the 21st century. The long-term effects of increasing CO_2 on forest growth and demographics remain highly uncertain and comprise an area of rapidly developing research (Norby et al., 2010; Schimel et al., 2015). Given this, the model's high sensitivity to CO_2 should be viewed with a level of caution commensurate with the uncertainty in the broader scientific understanding. Like MaintResp and FolN, CO_2's effect on the model should continuously be evaluated as improvements are made to the understanding of the physiological effects of CO_2 on forest growth.

Using a hybrid methodology of combining GSA, RTA, and LSA to assess output sensitivities provided unique insights about LANDIS-II/PnET-Succession (Pianosi et al., 2016). The main effect indices from the FAST analysis allowed us to understand the output variation driven by each parameter tested within the GSA. Additionally, the MoM analysis returned sensitivities corresponding to the total effects of each parameter. The rankings of parameters under the MoM results were similar to those of FAST, attesting to the robustness of our results. However, despite their similarity in this study, FAST and MoM results are not directly comparable as they are estimating different values: main effect indices for FAST, and total effect indices for MoM. Depending on the scale of interactions, though, they might often yield similar rankings as we found in this study. MoM and LSA indicated the directionality of each parameter's influence on outputs, and MoM indicated the extent to which each parameter interacted with other parameters and/or exhibited nonlinearity. For example, MoM and LSA showed that increasing FolN resulted in greater biomass, which is consistent with the known role of foliar nitrogen in determining the maximum rate of carboxylation and the maximum rate of electron transport during photosynthesis (Walker et al., 2014). Likewise, increasing MaintResp reduced total landscape biomass, because high ratios of respiration rate to photosynthetic rate are known to deplete carbon stores (Van Oijen et al., 2010). To then examine in detail how the influence identified by GSA methods is partitioned, RTA allowed us to identify parameter break points and specific parameter interactions. In part, the partitioning by RTA reflected the parameter rankings from the other analyses. Additionally, we can visually inspect the output variation in the box-plots in Figs. 3 and 4 alongside the parameter variation that produced it to identify interactions. For example, the RTA output at year 200 shows CO_2 contributing to greater variation at low values of MaintResp than at high values of MaintResp, and TOwood appears to contribute substantially to variation in outputs when FolN and CO_2 values are high, and when MaintResp is low. Finally, the LSA allowed us to examine the nonlinearity of the effects of individual parameters on model outputs at a particular part of parameter space.

5. Conclusions

While each SA method offered additional information about the influence of input parameters on model outputs, they also overlapped significantly in their conclusions. Fundamentally, all methods supported FolN, MaintResp, and CO_2 as being highly influential. This combination approach provided a more robust analysis and associated conclusions than if we had used just one of these methods alone. By using all four methods (FAST, MoM, LSA, and RTA) in consort, we were able to assemble a more complete picture about the influence of each parameter and ultimately, a greater understanding of LANDIS-II/PnET-Succession (Pianosi et al., 2016).

We have presented a thorough analysis of the sensitivity of LANDIS-II/PnET-Succession outputs to variation in twenty input parameters. Our work here builds upon that of Gustafson et al. (2017a), and where our analysis overlapped, our results were consistent. Specifically, the directionalities of the effects of Temp and Precip parameters on biomass in this study were the same as shown in their sensitivity analysis. While the magnitude of the response of biomass to variation in Temp versus Precip in Gustafson et al. (2017a) suggested that Precip was a stronger driver of biomass than Temp in their simulations, our analysis instead suggests that Temp has slightly more influence than Precip over biomass outputs. This discrepancy is likely due to differences in the sampling of parameter space. The local analysis performed by Gustafson et al. (2017a) was not designed to compare the relative influences of parameters to each other and instead aimed to capture individual parameter directionality and parameter interactions. As such, they only varied Temp and Precip values over limited ranges. On the other hand, our analysis was specifically designed to sample each parameter throughout its possible input range, allowing us to compare the overall importance of parameters for determining model output values. We selected proportional ranges of variation for climate variables and tested the influence of all input parameters through the space of variation of the other parameters, which should make comparing the relative influence of parameters more reliable.

We evaluated the area within a landscape occupied by three species, identified the parameters that contribute most to variation in model outputs, and described their effects. Our sensitivity analysis showed little similarity between the effects of input parameters on different response variables, with total landscape biomass being driven primarily by parameters directly influencing carbon assimilation, such as FolN and MaintResp, and with cell occupancy being driven more by parameters associated with carbon allocation. Strikingly, the sensitivity of cell occupancy to each of various input parameters was highly variable between species. This highlights the known danger of extrapolating the results of a sensitivity analysis on one model variable to different response variables. As demonstrated in previous studies, to understand the sensitivity of a specific model output to various input parameters, that output must be individually tested (Rosolem et al., 2012; van Werkhoven et al., 2008). Another important feature of our analysis was implementing the SA across time steps as in Reusser et al. (2011). Our analysis showed that some parameters, like FolN in the landscape biomass analysis, exert much more influence early in the simulations than in later time steps. Others, like MaintResp, may become more influential through time.

Across temperate forests, the influential parameters FolN, CO_2, Temp, and Precip are relatively well-supported by data for estimating their values. However, data supporting other important parameters MaintResp, FractWD, DNSC, and EstRad are less easily estimated, despite the ecological realism of these variables. Given that our analysis has shown a tendency of these parameters to strongly influence model outputs, this uncertainty contributes to greater uncertainty in model outputs. In the absence of additional data or model modification, the process of determining values for these parameters should then be guided by calibration, and the analysis of outputs must consider uncertainty in the high-influence, high-uncertainty parameters (Higgins et al., 2003).

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Appendix I. Method of Morris Results

We performed MoM alongside FAST in order to 1) corroborate conclusions about relative parameter influences over the total biomass output with estimates of total effects, 2) determine the direction of influence of each parameter, and 3) investigate the summed effects of parameter interactions and nonlinearities.

MoM is different from FAST in that it estimates a total effects index for each model parameter. Total effects indices differ from the main effects of FAST in that they incorporate interactions with other parameters.

Our MoM analysis sampled 40 one-at-a-time paths (r) for the 20 parameters (k) for a total of $(r)*(k+1) = (40)*(20 + 1) = 840$ model runs. The upper and lower bounds for the MoM sampling of each parameter were the same as those used in FAST (Tables 2 and 3). All analysis was done in R, using the MoM functions included in the package *sensitivity*.

The MoM analysis, like the FAST analysis, was performed at different time points through the simulations. The raw output at each time point consisted of 40 elementary effect indices for each of the 20 parameters (a 40 × 20 matrix). The mean of the elementary effects for each parameter gives the estimated total effects (μ), the sign of the mean of the elementary effects the average directional effect of each parameter, and the standard deviation of the elementary effects (σ) indicates the combined interactions and nonlinearity for the parameter. Additionally, the mean of the absolute values of the elementary effects gives an "absolute" total effects index (μ*) that better accounts for the overall influence of parameters that can have positive and negative influence on the output (Campolongo et al., 2007). Figure A1 shows each of these values from our MoM at 5 time points for each parameter.

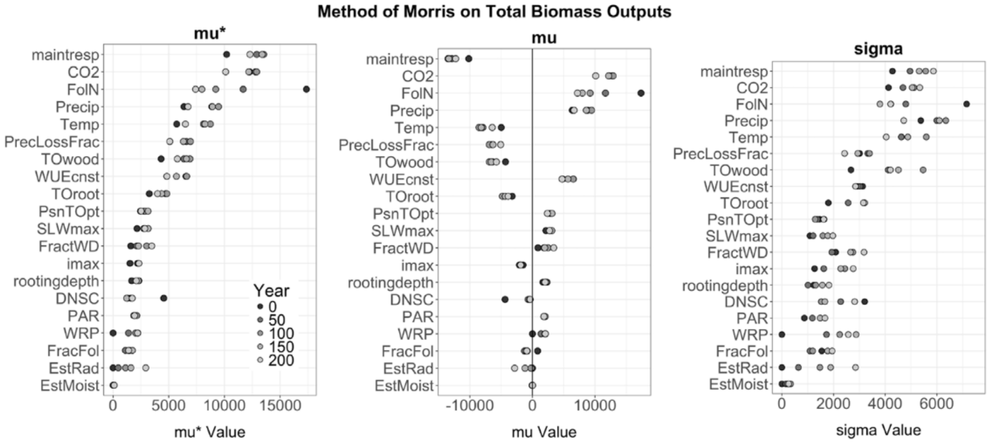

Figure A1. Sensitivity results from the MoM analysis. The parameters are ranked down the y-axis decreasing by average μ*. The leftmost panel shows μ*, the "absolute" total effects index for each parameter. The middle panel shows μ, the estimated total effects index for each parameter. Values below zero indicate that the parameter has a negative relationship with total biomass outputs, while values above zero indicate that the parameter value has a positive influence on total biomass outputs. The rightmost panel shows σ, the estimated value of combined interactions and nonlinearities associated with each parameter.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envsoft.2019.03.002.

Declaration of interest

The authors have no competing interests to declare.

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