Article

A forest biogeochemistry model intercomparison on the East Coast of the United States

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Abstract: Recent advances in forest ecosystem modeling allow the simulation of a suite of dynamics relevant to management at the landscape scale. Yet, there is no single scale perfectly suited to the multitude of management-related questions. Here, we conducted a model intercomparison exercise using two forest biogeochemistry models, PPA-BGC and LANDIS-II. We simulated past-decade conditions at flux tower sites in Harvard Forest, MA and Jones Ecological Research Center, GA. We mined the wealth of field data available for both sites to perform model parameterization, validation, and intercomparison. We assessed model performance using the following time-series metrics: NEE, ANPP, aboveground biomass (B_{AG}), C (C_{AG}), and N (N_{AG}), belowground biomass (B_{BG}), C (C_{BG}), and N (N_{BG}), soil respiration (r_{soil}), and, species total biomass (B_{Sp}) and relative abundance (n_{Sp}). We also assessed static observations of soil organic C (SOC) and N (SON), and concluded with an assessment of general model usability, performance, and transferability. Despite substantial differences in design, both models achieved a high level of accuracy across the full range of metrics. While each model displayed strengths and weaknesses, the PPA-BGC model indicated the best overall correspondence to observational data for both sites across the 11 temporal and 2 static metrics tested (HF EMS $\overline{R^2} = 0.73, +0.07, \overline{RMSE} = 4.84, -0.39$; JERC RD $\overline{R^2} = 0.76, +0.04, \overline{RMSE} = 2.69, -0.17$).

Keywords: Perfect Plasticity Approximation; SORTIE-PPA; LANDIS-II; forest ecosystem simulation; forest biogeochemistry model; forest landscape model; model intercomparison; Harvard Forest; Jones Ecological Research Center

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1. Introduction

A vast array of gap [1], forest landscape [2–6], and terrestrial biosphere models [7,8] have been developed in the past two decades. Models of forest ecosystems vary substantially in their representation of forest dynamics and biogeochemical processes. Models of aboveground processes range from explicitly representation of three-dimensional crown geometry for individual trees (e.g., gap models) to truncated log-normal growth equations applied to cohorts defined by a theoretical growing space to mechanistic 'big-leaf' models comprised of single to many canopy layers. Belowground process models similarly vary in architecture, from simple stoichiometric relations to carbon and nitrogen cycling with microbial dynamics to a fully mechanistic representation of energetic and biogeochemical processes based on thermodynamics. These models vary considerably in their process representation and accuracy [9]. Yet, most recent belowground models still rely on a variant of the classical CENTURY model [10,11].

Forest ecosystem models vary considerably in geometric and process-related structure. Model specialization and generalization ranges from pure research applications in narrowly defined areas to simulating multiple landscape processes in an effort to inform land management to simulating biogeochemical dynamics across the world's forested biomes. To date, little is known about the net effects of variation in the design of these models on the precision and accuracy of predictions across temporal and spatial scales. While such model intercomparisons are common with terrestrial biosphere models, they are seldom applied to gap or forest landscape models. Existing efforts in

Europe include the ISI-MIP forest stand model [12] and Comparison of Forest Landscape Model (CoFoLaMo) intercomparison projects [13], the latter conducted under the European Union COST FP1304 PROFOUND action. Accordingly, existing model intercomparison frameworks are focused on robust projections for only the European continent. Previous efforts in the United States include the Throughfall Displacement Experiment (TDE) Ecosystem Model Intercomparison Project at Walker Branch Watershed in Oak Ridge, Tennessee [14]. There is a critical need to conduct ongoing forest ecosystem models comparisons in this and other regions of the world in order to establish a foundation for robust global forest projections.

Modern forest landscape models are the result of five key model development phases, listed in chronological order: (1) growth-and-yield equations; (2) fire models; (3) gap models; (4) physiological/biogeochemistry models; (5) hybrid models combining design principles from each [1,15,16]. Terrestrial biosphere models similarly trace their roots back to early one-dimensional physiological models, with land surface models currently in their third generation and dynamic global vegetation models in their second generation [17]. This latest generation of models was intended to address the lack of explicit representation of vegetation dynamics - a critical source of model uncertainty under future climate scenarios [18]. This inspired the aforementioned forest ecosystem model intercomparisons as well as new terrestrial biosphere model designs based on gap models, bypassing the trade-offs of medium-resolution forest landscape models.

Collectively, these efforts yielded a number of new terrestrial biosphere models based on the classical gap model, including LPJ-GUESS [19], ED/ED2 [20,21], and LM3-PPA [22], the latter based on the Perfect Plasticity Approximation [23,24]. These models represent the current state-of-the-art in modeling vegetation dynamics globally. While individual-based global models have begun to merge, forest landscape models have remained in between, focused on spatial processes of fire, harvest, and biological disturbance. Yet, previous research has shown that these models are often insensitive to landscape configuration and therefore aspatial [25]. While classical forest landscape models do not represent individual trees, recent models focused on computational efficiency improvements may facilitate the efficient up-scaling of gap dynamics [23,26–28], as in recent terrestrial biosphere models. For example, one recent forest landscape model participating in the CoFoLaMo model intercomparison scales from individual trees to stands by pre-computing light tables within forest stands [26]. Regardless of model formulation, it is clear that gap, forest landscape, and terrestrial biosphere models are beginning to merge into new models of the terrestrial biosphere. This trend is also attributable to improvements in computational efficiency with new processor designs and cluster or cloud computing infrastructure. As few existing models are designed for highly parallel architectures (e.g., GPGPUs), there exists strong potential for future model efficiency gains.

This forest ecosystem model intercomparison focuses on two sites on the East Coast of the United States. Harvard Forest (HF), Massachusetts, USA is one of the most-studied forests in the world, with Google Scholar returning 12,700 results for the site. We focus on results for the Environmental Measurement Station (EMS) flux tower site within the Little Prospect Hill tract - the longest-running eddy covariance flux tower in the world. This site is designated as HFR1 in the AmeriFlux network. Previous research at the EMS tower found unusually high rates of ecosystem respiration in winter and low rates in mid-to-late summer compared to other temperate forests [29]. The mechanisms behind these observed patterns is poorly understood. Between 1992 and 2004, the site acted as a net carbon sink, with a mean annual uptake rate of 2.5 Mg C ha-1 year-1. Aging dominated the site characteristics, with a 101-115 Mg C ha-1 increase in biomass, comprised predominantly of growth of red oak (*Quercus rubra*). The year 1998 showed a sharp decline in NEE and other metrics, recovering thereafter [30]. As Urbanski *et al.* [30] note of IBIS2 and similar models at the time, "the drivers of interannual and decadal changes in NEE are long-term increases in tree biomass, successional change in forest composition, and disturbance events, processes not well represented in current models." The two models used in the intercomparison study, PPA-BGC [23,24] and LANDIS-II with NECN succession [31,32], are intended to directly address these shortcomings of previous models.

While there have been fewer studies at Jones Ecological Research Center (JERC), Georgia, USA, Google Scholar returns 1,370 results for the site, reflecting its growing importance in forest sciences research. Our study focuses on the Red Dirt eddy covariance flux tower site within the mesic sector, for which a handful of relevant studies exist. All reviewed studies showed that this subtropical pine savanna functions as a moderate carbon sink (NEE = $-2.48\ Mg\ C\ ha^{-1}\ year^{-1}$; $-1.58 \pm 0.25\ Mg\ C\ ha^{-1}\ year^{-1}$), reduced to near-neutral uptake during the 2011 drought ($-0.165\ Mg\ C\ ha^{-1} year^{-1}$) and acting as a carbon source when prescribed burning is taken into account. NEE typically recovered to pre-fire rates within 30-60 days. The mechanisms behind soil respiration rates here appear to be complex and site-specific [33]. Overall, existing research highlights the importance of fire and drought to carbon exchange in these long-leaf pine (*Pinus palustris*) and oak (*Quercus spp.*) savanna systems [33–35]. This is in contrast to the secondary growth-dominated deciduous broadleaf characteristics of Harvard Forest. Species diversity at Harvard Forest EMS tower is 350% greater, with 14 species from a variety of genera compared to four species from only two genera, *Pinus* and *Quercus*.

2. Materials and Methods

LANDIS-II and PPA-BGC were parameterized for two forested sites in the eastern United States, Harvard Forest (HF), Massachusetts and Jones Ecological Research Center (JERC), Georgia. At the HF site, we focus on Little Prospect Hill and the Environmental Measurement Station (EMS) eddy covariance flux tower. At the JERC site, we focus on the mesic zone and Red Dirt eddy covariance flux tower. The two sites were selected for their representativeness of the United States Eastern Seaboard and for the availability of data needed to parameterize and calibrate/validate the models. Both sites provided local eddy covariance and meteorological measurements to conduct this study. The two models were parameterized using the best available data for each site, which included non-local information sources (e.g., species compendiums). All model parameters are provided in the Supplementary Materials. We close the methodology section with descriptions of the metrics, models, and criteria used in the intercomparisons.

2.1. Model Descriptions

In the following sections, we provide a brief overview of the two forest ecosystem models used in this intercomparison study. For detailed information on each model, readers are encouraged to refer to the original publications.

2.1.1. LANDIS-II

The LANDIS-II model is an extension of the original LANdscape DIsturbance and Succession (LANDIS) model [36–38] to an open-source modular software framework [31]. Specifically, LANDIS-II is a model core containing basic state information that can interface or communicate with external models. This design makes LANDIS-II more of a modeling framework than a model. The LANDIS family of models, which also includes LANDIS PRO [39] and Fin-LANDIS [40,41], are stochastic models based on the vital attributes/fuzzy systems approach of the LANDSIM model genre [42]. This genre borrows from cellular automata [43] by applying simple heuristic rule-based systems, in the form of vital attributes, across two-dimensional grids. Models of the LANDSIM genre focus on landscape-scale processes and assume game-theoretic vital attribute controls over successional trajectories following disturbance [44]. The LANDSIM model genre is thus a reasonable fit for the classical forest fire model of statistical physics [45] given the local cellular interaction basis. In contrast to the original LANDIS model, LANDIS-II is designed to be modular and implemented in Microsoft C# rather than ISO C++98 [46], easing model development in exchange for a single-vendor software stack [31].

While LANDIS-II was historically limited to the Microsoft Windows operating system, it may soon see native Linux support through the Microsoft .NET Core cross-platform development framework

per advice of the lead author of this study. The modularity of LANDIS-II is intended to simplify the authorship and interaction of user-provided libraries for succession and disturbance. A centralized model core stores basic state information about the landscape and acts as an interface between succession and disturbance models. While there have been numerous forest landscape models over the years [2–6], the LANDIS family of models has enjoyed notable longevity and is currently united under the LANDIS-II Foundation. Part of its success is attributable to the prioritization of functional variety over mechanistic detail in order to appeal to managers.

Similar to the original CENTURY succession model [32], the Net Ecosystem Carbon and Nitrogen (NECN) model is derived from the classical CENTURY model [10,11]. The NECN succession model is therefore a process-based model that simulates C and N dynamics along the plant-soil continuum. Atmospheric effects are included through monthly climate (i.e., temperature maxima, minima, means, and standard deviations, and precipitation means and standard deviations). Explicit geometric representation of tree canopies is forgone in favor of bounded statistical growth models based theoretically on Liebig's law of the minimum. The LANDIS-II variant of the CENTURY model found in NECN succession also incorporates functionality from the biomass succession extension and other model core logic (i.e., rule-based controls). For a detailed description of the model, readers may refer to the original CENTURY publication [32]. Parameterization of the LANDIS-II model for both sites was based on updating parameters used in recent [47–50] and ongoing (Flanagan et al., *in review*) work.

2.1.2. PPA-BGC

The PPA-BGC model [27] is a model of the SORTIE-PPA family, it based on a simple and analytically tractable model approximation of the classical SORTIE gap model [51,52]. The Perfect Plasticity Approximation, or PPA [23,24], was derived from the dual assumptions of perfect crown plasticity (e.g., space-filling) and phototropism (e.g., stem-leaning), both of which are well-supported in empirical and modeling studies [27]. The discovery of the PPA was rooted in extensive empirical and simulation-based research [23]. The PPA was designed to overcome the most computationally challenging aspects of gap models in order to facilitate model scaling from landscape to global levels. Accordingly, the PPA and its predecessor, the size-and-age structured (SAS) equations [20,53], are popular model reduction techniques employed in current state-of-the-art terrestrial biosphere models [8]. The PPA model may be thought of metaphorically as Navier-Stokes equations of forest dynamics, capable of modeling individual tree population dynamics with a one-dimensional von Foerster partial differential equation [23]. The simple mathematical foundation of the PPA model is provided in Equation 1.

$$1 = \sum_{j=1}^{k} \int_{z^*}^{\infty} N_j(z) A_j(z^*, z) dz \tag{1}$$

where k is the number of species, j is the species index, $N_j(z)$ is the density of species j at height z, $A_j(a^*, z)$ is the projected crown area of species j at height z, and dz is the derivative of height. In other words, we discard the spatial location of individual trees and calculate the height at which the integral of tree crown area is equal to the ground area of the stand. This height is known as the theoretical z^* height, which segments trees into overstory and understory classes [23]. The segmentation of the forest canopy into understory and overstory layers allows for separate coefficients or models of growth, mortality, and fecundity to be applied across strata, whose first moment accurately approximates the dynamics of individual-based forest models. Supporting model validation performed in the original publications [23,24], recent studies has shown that the PPA model also reduces the dynamics of the Sortie-ND gap model [54] and accurately and precisely capture forest dynamics [55,56].

In this work, we apply a biogeochemistry variant of the SORTIE-PPA model, PPA-BGC model. In this model, empirical measurements are relied upon for the C and N content of tree species compartments. Stoichiometric relations were used to estimate N from C, based on empirical

measurements provided for both sites. Previously published equations were used to model crown allometry [57], using parameters published in another study [58]. Together with inventory data, general biomass equations were used to estimated dry weight mass (*kg*) for tree stems, branches, leaves, and, fine and coarse roots [59]. Carbon content is assumed to be 50% of dry mass, as is commonly used. Monthly soil respiration is modeled using the classical approach of Raich *et al.* [60], while soil organic C is modeled using the simple generalized approach of Domke *et al.* [61]. Model parameters were calculated from empirical data available for both sites, including understory and overstory species parameters for growth and mortality, as well as fecundity.

2.2. Site Descriptions

In the following sections, we describe the two forested sites on the East Coast of the United States: Harvard Forest (HF) Environmental Measurement Site (EMS) flux tower site within the Little Prospect Hill tract and the Jones Ecological Research Center (JERC) Red Dirt (RD) flux tower site within the mesic tract. A critical factor in the selection of the sites was the availability of eddy covariance flux tower data needed to validate net ecosystem exchange (NEE) in the models.

2.2.1. Harvard Forest EMS Flux Tower

The EMS flux tower is located within the Little Prospect Hill tract of Harvard Forest (42.538°N, 72.171°W, 340 m elevation) in Petersham, Massachusetts (Figure 1), approximately 100 km from the city of Boston [30]. The tower has been recording net ecosystem exchange (NEE), heat, and meteorological measurements since 1989, with continuous measurements since 1991, making it the longest-running eddy covariance measurement system in the world. The site is predominantly deciduous broadleaf second-growth forests approximately 75-95 years in age, based on previous estimates [62]. Soils at Harvard Forest originate from sandy loam glacial till and are reported to be mildly acidic [30].

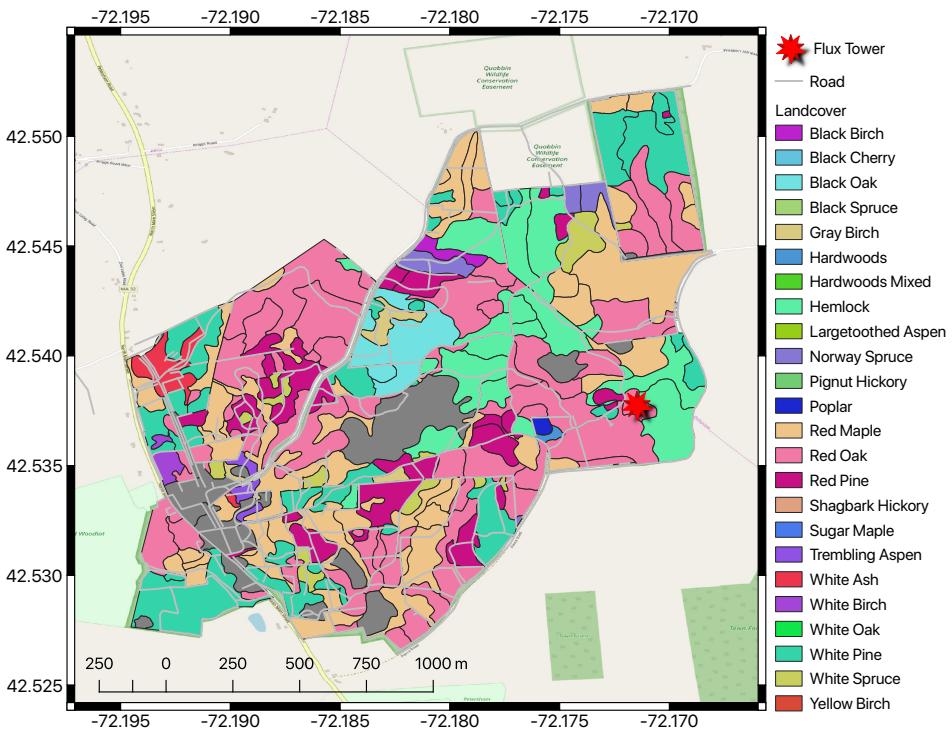

Figure 1. Harvard Forest EMS flux tower and landcover classes

The site is dominated by red oak (*Quercus rubra*) and red maple (*Acer rubrum*) stands, with sporadic stands of Eastern hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), and red pine (*Pinus resinosa*). When the site was established, it contained 100 Mg C ha-1 in live aboveground woody biomass [62]. As noted by Urbanski *et al.* [30], approximately 33% of red oak stands were established prior to 1895, 33% prior to 1930, and 33% before 1940. A relatively hilly and undisturbed forest (since the 1930s) extends continuously for several km^2 around the tower. In 2000, harvest operations removed 22.5 Mg C ha-1 of live aboveground woody biomass about 300 m S-SE from the tower, with little known effect on the flux tower measurements. The 40 biometric plots were designated via stratified random sampling within eight 500 m transects Urbanski *et al.* [30]. The EMS tower site currently contains 34 biometric plots at 10 m radius each, covering 10,681 m^2, or approximately one hectare, in area.

Recent historical mean daily fluxes of temperature ($^\circ C$), ecosystem respiration ($\mu mol\ CO_2\ m^{-2}$), and NEE ($\mu mol\ C\ m^{-2}$) for the EMS flux tower are shown in Figure 2.

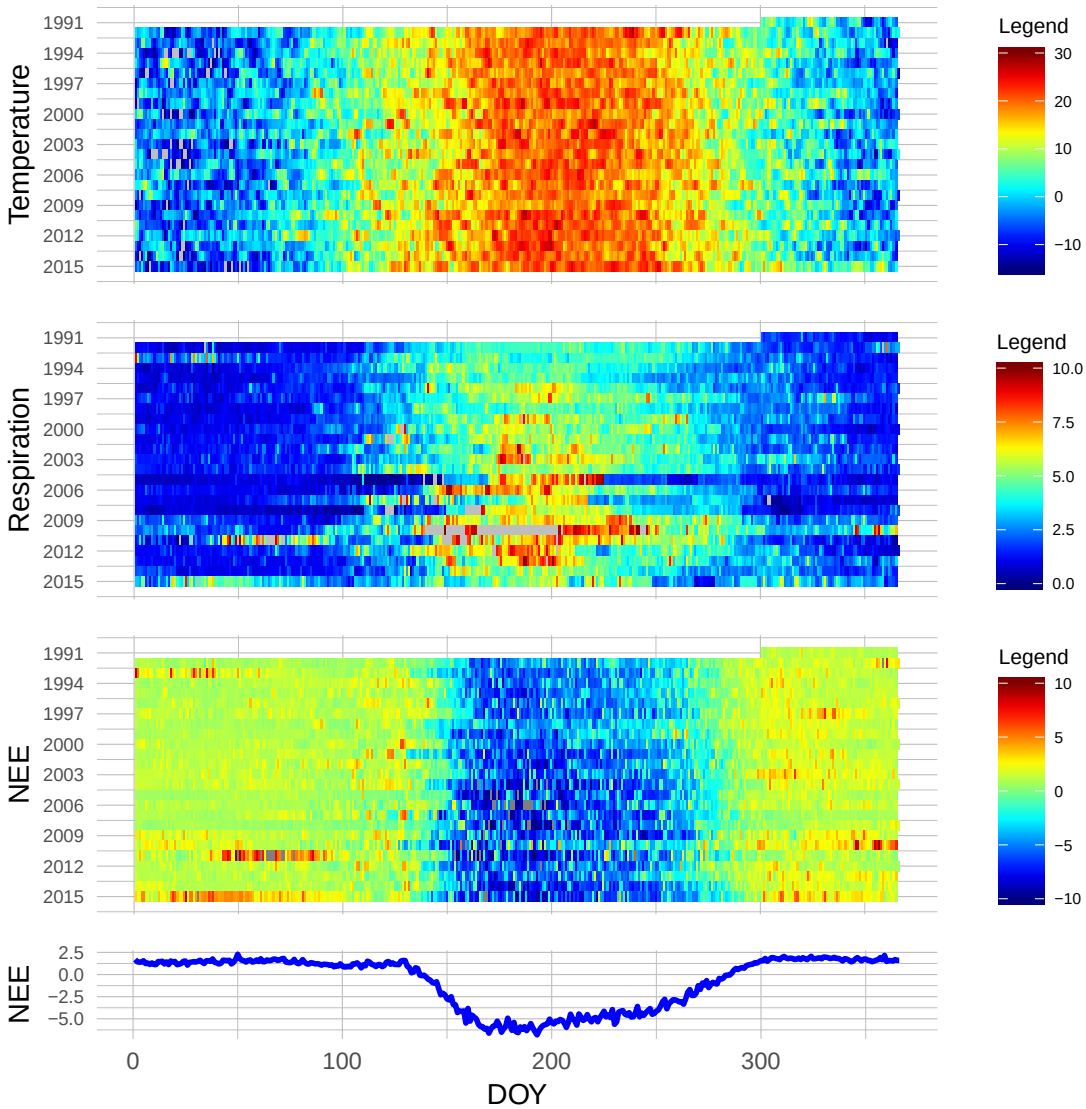

Figure 2. Harvard Forest EMS tower daily averages

Patterns in daytime and nighttime NEE are shown in Figure 3. This was calculated by taking daily mean NEE values for three-hour windows surrounding noon and midnight, respectively (1100-1300

and 2300-0100 hours). These patterns are important to diagnose, as they demonstrate responses to a gradient of light and temperature conditions.

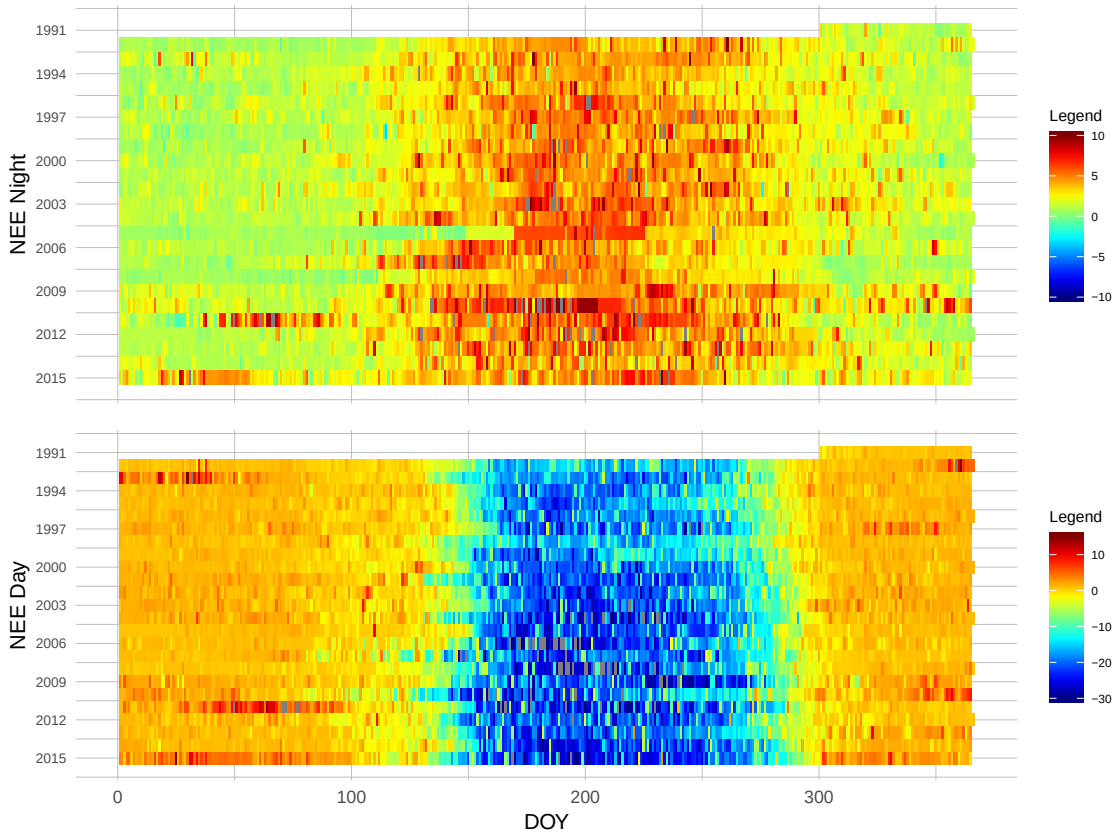

Figure 3. Harvard Forest EMS tower daily diurnal averages

2.2.2. Jones Ecological Research Center RD Flux Tower

Jones Ecological Research Center (JERC) at Ichauway (Figure 4) is located near Newton, Georgina, USA (31°N, 84°W, 25-200 m elevation). The site is located in the East Gulf Coastal Plain and consists of flat to rolling land sloping to the southwest. The region is characterized by a humid subtropical climate with temperatures ranging from 5-34 °C and precipitation averaging 132 cm year-1. The overall site is 12,000 ha in area, 7,500 ha of which are forested [63]. The site also exists within a tributary drainage basin that eventually empties into the Flint River. Soils here are underlain by karst Ocala limestone and mostly Typic Quartzipsamments, with sporadic Grossarenic and Aquic Arenic Paleudults [64]. Soils here often lack well-developed organic horizons [63–65].

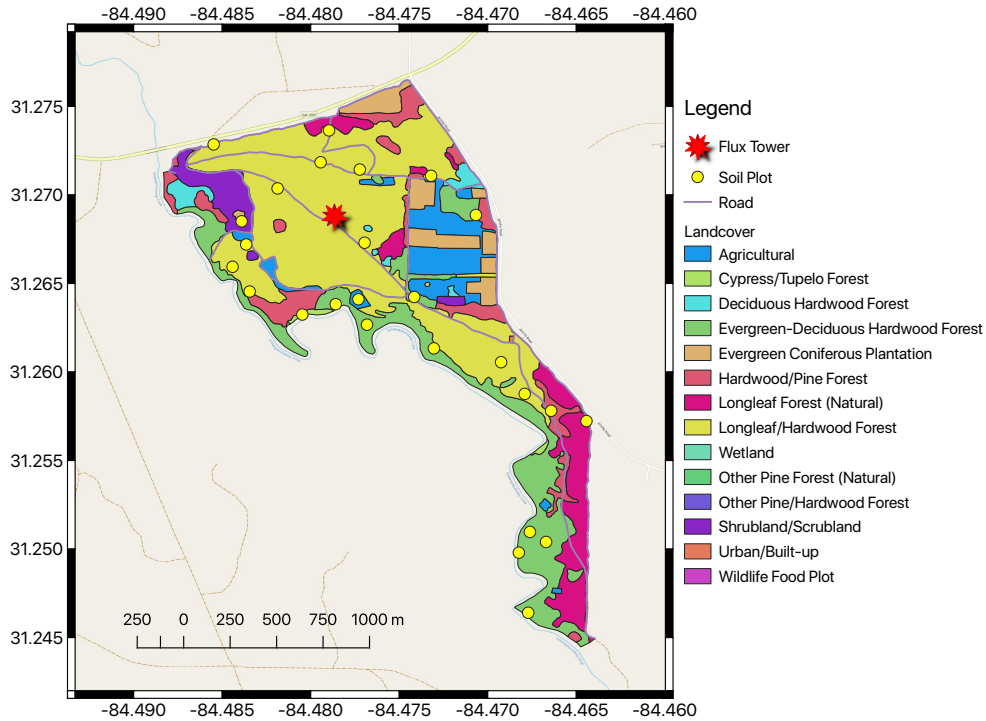

Figure 4. Jones Ecological Research Center Red Dirt flux tower and landcover classes

Forests here are mostly second-growth, approximately 65-95 years in age. Long-leaf pine (*Pinus palustris*) dominates the overstory, while the understory is comprised primarily of wiregrass (*Aristida stricta*) and secondarily of shrubs, legumes, forbs, immature hardwoods, and regenerating long-leaf pine forests [66]. Prescribed fire is a regular component of management here, with stands often burned at regular 1-5 year intervals [63]. This has promoted wiregrass and legumes in the understory, while reducing the number of hardwoods [63]. The Red Dirt (RD) tower is contained within the mesic/intermediate sector of JERC. This site consists of only four primary tree species from two genera: long-leaf pine (*Pinus palustris*), water oak (*Quercus nigra*), southern live oak (*Quercus virginiana*), and bluejack oak (*Quercus incana*). Flux tower measurements for the Red Dirt tower are available for the 2008-2013 time period.

Recent historical mean daily fluxes of latent heat flux (LE) ($W\ m^{-2}$), ecosystem respiration ($\mu mol\ CO_2\ m^{-2}$), and NEE ($\mu mol\ C\ m^{-2}$) for the RD flux tower are shown in Figure 5.

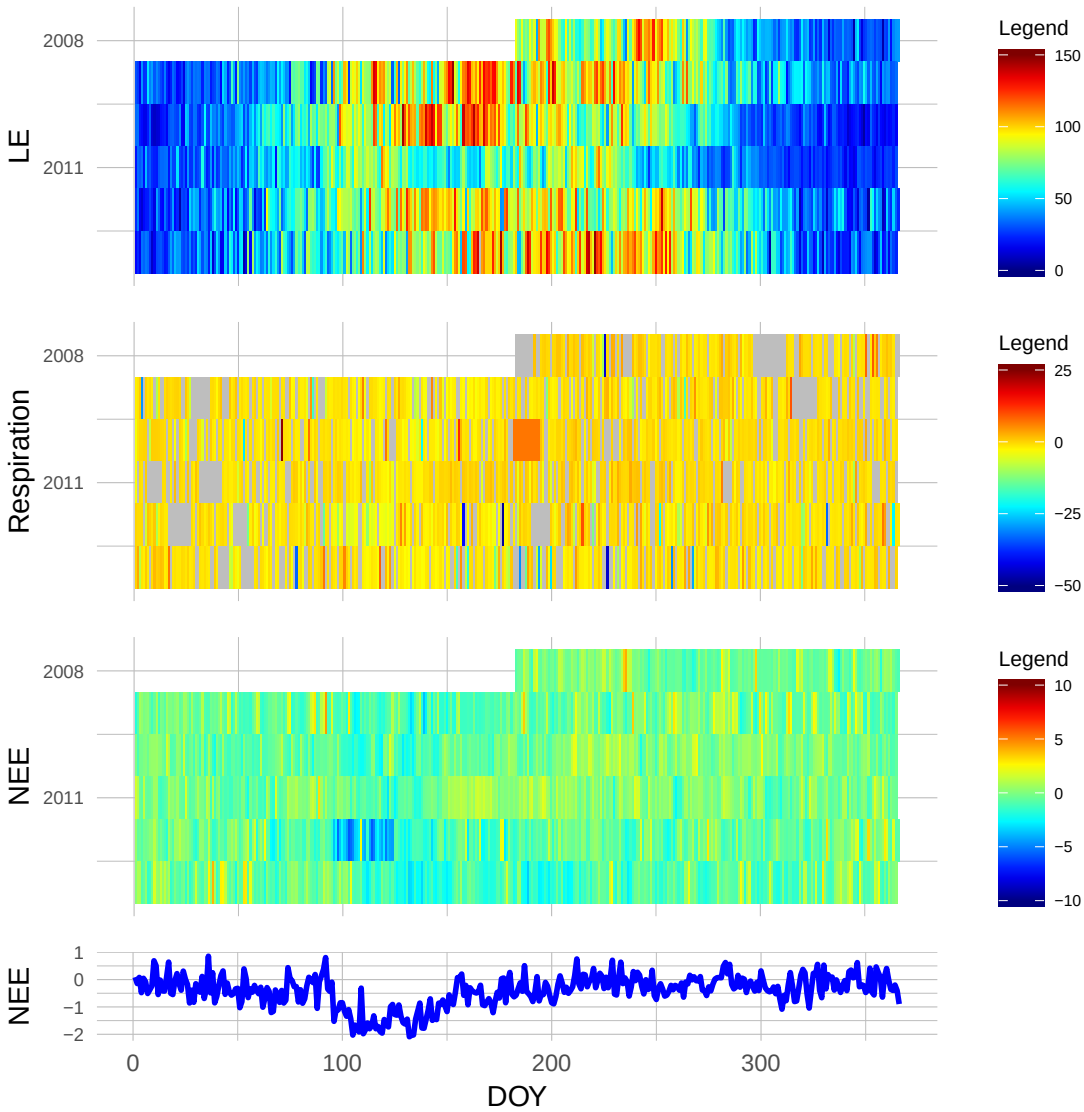

Figure 5. Jones Ecological Research Center RD tower daily averages

Patterns of daytime and nighttime NEE are shown in Figure 3. Again, this was calculated by taking daily mean NEE values for three-hour windows surrounding noon and midnight, respectively (1100-1300 and 2300-0100 hours).

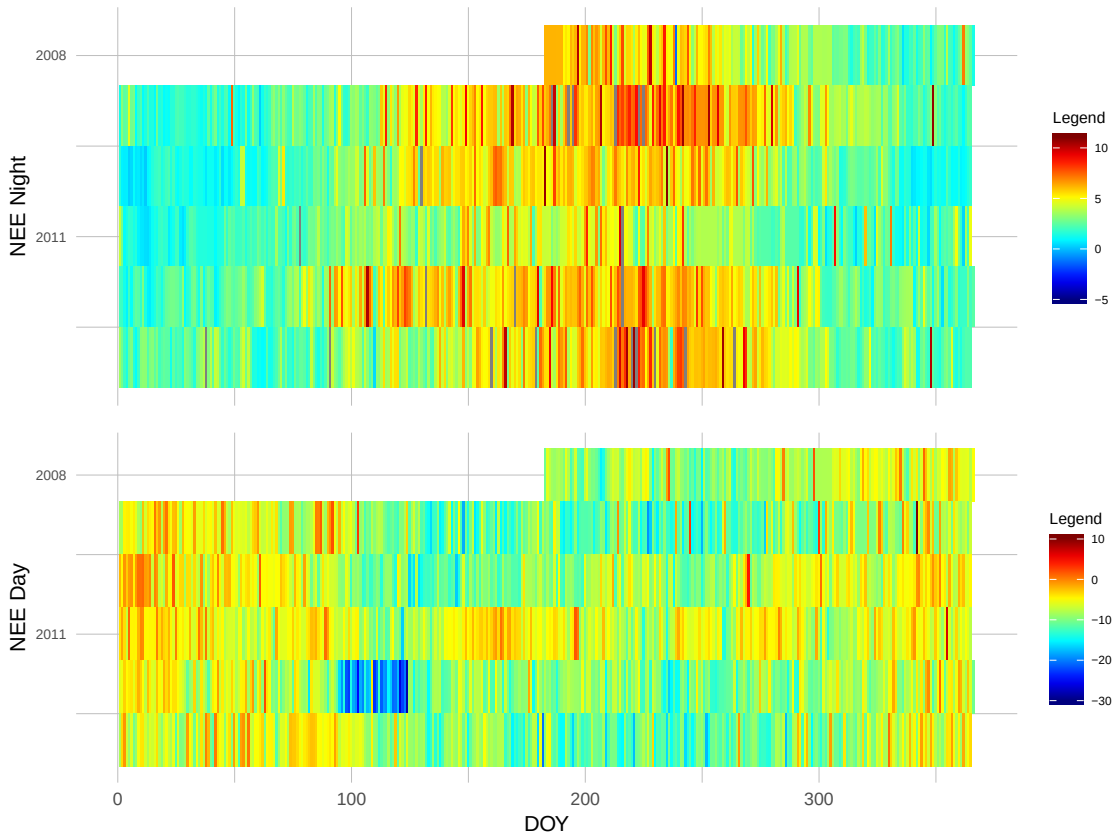

Figure 6. Jones Ecological Research Center RD tower daily diurnal averages

2.3. Site Data

To conduct this model intercomparison exercise, we leveraged the large amount of data available for Harvard Forest. All Harvard Forest data used in this study is openly available to the public through the Harvard Forest Data Archive:

http://harvardforest.fas.harvard.edu/harvard-forest-data-archive

Jones Ecological Research Center has hosted multiple research efforts over the years, collectively resulting in the collection of a large data library. However, JERC data are not made openly available to the public and are thus only available by request. One may find contact information located within their website:

http://www.jonesctr.org

2.4. Metrics and Units

The areal extent of the single-cell model intercomparison were designed to correspond to available field measurements. At both sites, tree inventories were conducted within 10,000 m^2, or one-hectare, areas. All target metrics were converted to an areal basis to ease interpretation, comparison, and transferability of results. Importantly, an areal conversion will allow comparison to other sites around the world. While flux tower measurements for both sites were already provided on an areal (m^{-2}) basis, many other variables were converted to harmonize metrics between models and study sites. For example, moles CO_2 measurements were converted to moles C through well-described molecular weights, all other measures of mass were converted to kg, and all areal and flux measurements were harmonized to m^{-2}. A table of metrics and units used in the intercomparison of LANDIS-II and PPA-BGC is provided in Table 1.

Table 1. Model intercomparison abbreviations, metrics, and units

Abbreviation	Metric	Units
NEE	Net ecosystem exchange	$kg\ C\ m^{-2}\ year^{-1}$
B_{AG}	Aboveground biomass	$kg\ mass\ m^{-2}$
C_{AG}	Aboveground C	$kg\ C\ m^{-2}$
N_{AG}	Aboveground N	$kg\ N\ m^{-2}$
B_{BG}	Belowground biomass	$kg\ mass\ m^{-2}$
C_{BG}	Belowground C	$kg\ C\ m^{-2}$
N_{BG}	Belowground N	$kg\ N\ m^{-2}$
C_{SO}	Soil organic C	$kg\ C\ m^{-2}$
N_{SO}	Soil organic N	$kg\ N\ m^{-2}$
r_{soil}	Soil respiration (C)	$kg\ C\ m^{-2}\ year^{-1}$
ANPP	Aboveground net primary production	$kg\ mass\ m^{-2}\ year^{-1}$
B_{Sp}	Species aboveground biomass	$kg\ mass\ m^{-2}$
n_{Sp}	Species relative abundance	%

In the subsequent section, we describe the model intercomparison methodology.

2.5. Model Intercomparison

Intercomparison of the PPA-BGC and LANDIS-II models at Harvard Forest (HF) EMS and Jones Ecological Research Center (JERC) RD flux tower sites was conducted using a collection of object-oriented functional programming scripts written in the R language for statistical computing [67]. The scripts were designed to simplify model configuration, parameterization, operation, calibration/validation, plotting, and error calculation. These scripts and our parameters are available on GitHub (https://github.com/adam-erickson/ecosystem-model-comparison), making our results fully and efficiently reproducible. The R scripts are designed to automatically load and parse the results from previous model simulations, in order to avoid reproducibility issues stemming from model stochasticity. We use standard regression metrics applied to the time-series of observation and simulation data to assess model fitness. The metrics used include the coefficient of determination (R^2), root mean squared error (RMSE), and mean absolute error (MAE), calculated using simulated and observed values. Our implementation of R^2 follows the Bravais-Pearson interpretation as the squared correlation coefficient between observed and predicted values [68]. Our implementation of R^2 is provided in Equation 2.

$$R^2 = r^2 = \left(\frac{\sum_{i=1}^{n}(y_i - \overline{y})(\hat{y}_i - \overline{\hat{y}})}{\sqrt{\sum_{i=1}^{n}(y_i - \overline{y})^2(\hat{y}_i - \overline{\hat{y}})^2}} \right)^2 \tag{2}$$

Meanwhile, calculation of RMSE follows the standard formulation, as shown in Equation 3.

$$RMSE = \sqrt{\frac{1}{n}\sum_{t=1}^{n} e_t^2} \tag{3}$$

The calculation of MAE is similarly unexceptional, per Equation 4.

$$MAE = \frac{1}{n}\sum_{t=1}^{n} |e_t| \tag{4}$$

While Nash-Sutcliffe efficiency (NSE) is often used in a simulation model context, we selected the Bravais-Pearson interpretation of R^2 over NSE to simplify the interpretation of results. The NSE metric replaces $1 - (SS_{predictions}/SS_{observations})$ with $(SS_{observations} - SS_{predictions})/SS_{observations}$, where SS is the sum of squares. Thus, NSE is analogous to the standard R^2 coefficient of determination used in regression analysis [69]. The implementation of R^2 that we selected is important to note, as its

results are purely correlative and quantify only dispersion, ranging in value between 0 and 1. This has some desirable properties in that no negative or large values are produced, and that it is insensitive to differences in scale. Regardless of the correlation metric used, complementary metrics are needed to quantify the direction (e.g., bias) and/or magnitude of error. We rely on RMSE and MAE to provide information on error or residual magnitude. We utilize a visual analysis to assess error directionality over time, as this can be poorly characterized by a single coefficient (e.g., periodicity).

We compute R^2, RMSE, and MAE for the metrics described in Table 1 on page 11. These include net ecosystem exchange (NEE), above- and below-ground biomass, C, and N, soil organic C and N, soil respiration (r_{soil}), aboveground net primary production (ANPP), and, species aboveground biomass and relative abundance. All of these metrics are pools with the exception of NEE, r_{soil}, and ANPP fluxes. Finally, we diagnose the ability of both models to meet a range of logistical criteria related to deployment: *model usability, performance, and transferability*. Model usability is assessed per four criteria:

1. Ease of installation
2. Ease of parameterization
3. Ease of program operation
4. Ease of parsing outputs

Model performance is assessed per a single metric: the speed of program execution for each site for the predefined simulation duration. The durations are 11 years and 5 years for the HF EMS and JERC RD flux tower sites, respectively. Each simulation is conducted at annual temporal resolution, the standard resolution for both models. Finally, model transferability is assessed per the following five criteria:

1. Model generalizability
2. Availability of parameterization data
3. Size of the program
4. Cross-platform support
5. Ease of training new users

Each of these logistical criteria are quantified, rescaled to 0-1, and weighted evenly. While a Likert scale is used in qualitative cases, we otherwise seek to quantify criteria using simple defensible methods. For example, given that there are three major operating systems in use on personal computers (Linux, MacOS, and Windows), supporting all three would result in a score of 1.0 while supporting only one would result in a score of $1/3 = 0.33$. Similarly, maxima are given values of 1.0 while corresponding values are rescaled by the product of the inverse ($x = x * (1/maximum)$).

3. Results and Discussion

Both PPA-BGC and LANDIS-II showed strong performance at the two model intercomparison sites, frequently achieving R^2 values approaching unity. The R^2 values for both models and sites are visualized in Figure 7.

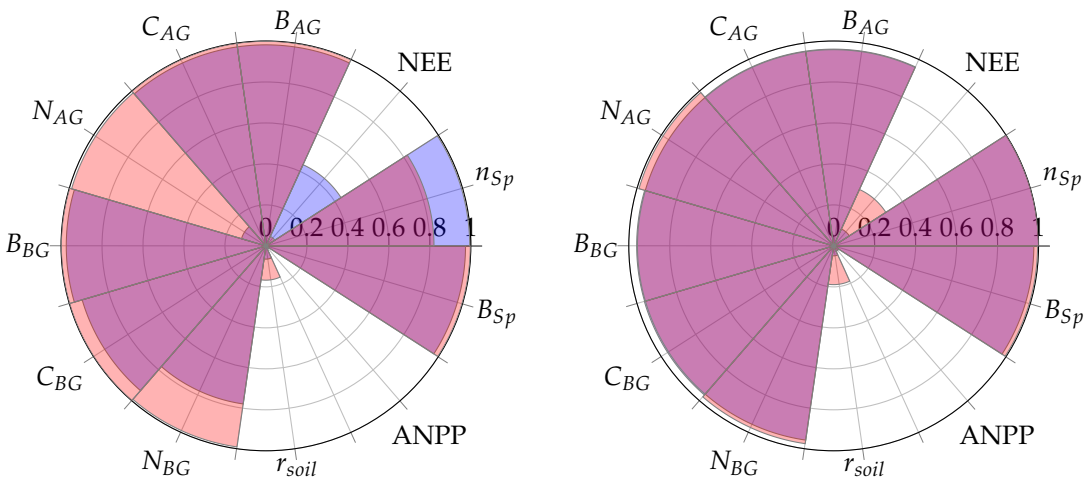

Figure 7. Overall model performance (R^2) for both models and sites; *left = Harvard Forest EMS tower; right = Jones Ecological Research Center RD tower; pink = PPA-BGC; periwinkle = LANDIS-II; violet = intersection*

Both models showed strong time-series correlations between predictions and observations across the range of metrics. On average, PPA-BGC outperformed LANDIS-II across all sites and metrics tested (HF EMS $\overline{R^2} = 0.73, +0.07$, $\overline{RMSE} = 4.84, -0.39$; JERC RD $\overline{R^2} = 0.76, +0.04$, $\overline{RMSE} = 2.69, -0.17$). This result is based on calculating mean values for R^2, RMSE, and MAE in order to clearly translate the overall results. The two models produced the following mean values for each of the three statistical metrics and two sites:

Table 2. Overall mean values across each of the sites and metrics tested

	PPA-BGC			LANDIS-II		
Metric	R^2	RMSE	MAE	R^2	RMSE	MAE
Mean	0.80	3.76	3.57	0.75	4.62	4.46

As shown in Table 2, PPA-BGC yielded higher R^2 values and lower RMSE and MAE values in comparison to LANDIS-II, on average, across all sites and metrics tested. Below, we provide model intercomparison results individually for the two sites, Harvard Forest EMS and Jones Ecological Research Center RD.

3.1. Harvard Forest EMS Tower

For the Harvard Forest EMS flux tower site, PPA-BGC showed higher R^2 values and lower RMSE and MAE values compared to LANDIS-II across the range of metrics. While PPA-BGC predicted NEE and species relative abundance showed weaker correlations with observed values compared the LANDIS-II, the magnitude of error was lower, as evidenced by lower RMSE and MAE values. While LANDIS-II showed a lower magnitude of error for belowground N, this is the only metric where this is the case, while the correlation of this metric to observed values was also lower than that of PPA-BGC. Overall results for the Harvard Forest EMS flux tower site model intercomparison are shown in Table 3.

Table 3. Model fitness for Harvard Forest EMS tower

	PPA-BGC			LANDIS-II		
Metric	R^2	RMSE	MAE	R^2	RMSE	MAE
NEE	0.05	0.19	0.16	0.44	0.49	0.44
B_{AG}	1.00	10.12	10.11	0.98	2.48	2.48
C_{AG}	1.00	0.03	0.03	0.98	1.24	1.24
N_{AG}	0.99	1.44	1.44	0.12	1.99	1.99
B_{BG}	1.00	9.09	9.08	0.94	17.30	17.29
C_{BG}	1.00	7.82	7.81	0.93	9.87	9.86
N_{BG}	0.99	0.56	0.56	0.78	0.12	0.12
r_{soil}	0.17	0.63	0.62	0.06	1.10	1.10
ANPP	0.02	0.16	0.15	0.0002	1.14	1.08
C_{SO}	...	26.49	26.49	...	36.63	36.63
N_{SO}	...	1.33	1.33	...	1.60	1.60
B_{Sp}	1.00	5.02	2.89	0.97	8.54	7.80
n_{Sp}	0.81	0.05	0.03	0.98	0.30	0.23
Mean	0.73	4.84	4.67	0.66	5.23	5.16

Analyzing figures for the Harvard Forest EMS flux tower site shows the temporal dynamics between observed and predicted values for both models. In Figure 8, the temporal differences in modeled NEE and aboveground C are shown for the two models in comparison to observations for Harvard Forest EMS flux tower. Both models effectively captured temporal dynamics in biomass, C, and, species biomass and abundance. While LANDIS-II predictions showed a higher correlation with observations, the magnitude of error was higher. Meanwhile, PPA-BGC outperformed LANDIS-II in aboveground C per both criteria. While LANDIS-II tended to underpredict aboveground metrics, PPA-BGC tended to overpredict these metrics.

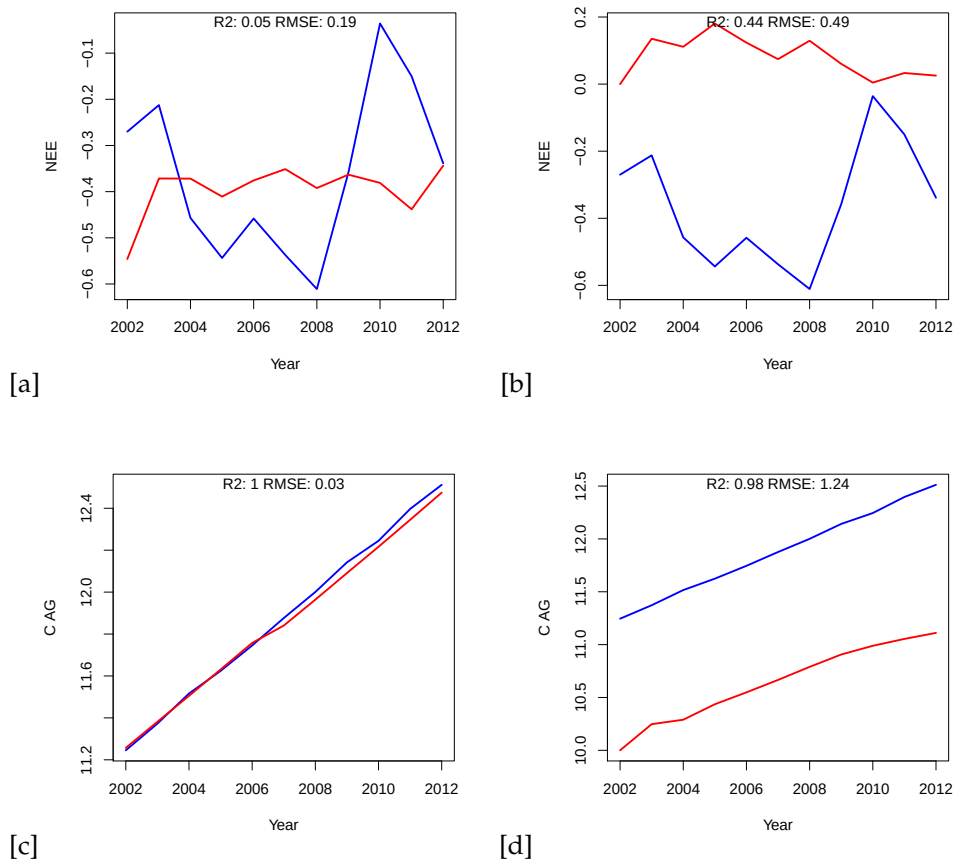

Figure 8. Simulated and observed NEE and aboveground C; observations = blue; simulations = red; a = PPA-BGC NEE; b = LANDIS-II NEE; c = PPA-BGC C_{AG}; d = LANDIS-II C_{AG}

An analysis of simulated species biomass and abundance also shows greater fidelity of the PPA-BGC model to data, as shown in Figure 9. As LANDIS-II does not contain data on individual trees, species relative abundance is calculated based on the number of cohorts of each species. Results for PPA-BGC indicate that species relative abundance may be improved by optimizing mortality and fecundity rates. Meanwhile, species biomass predictions output by LANDIS-II were inverted from those of the observations.

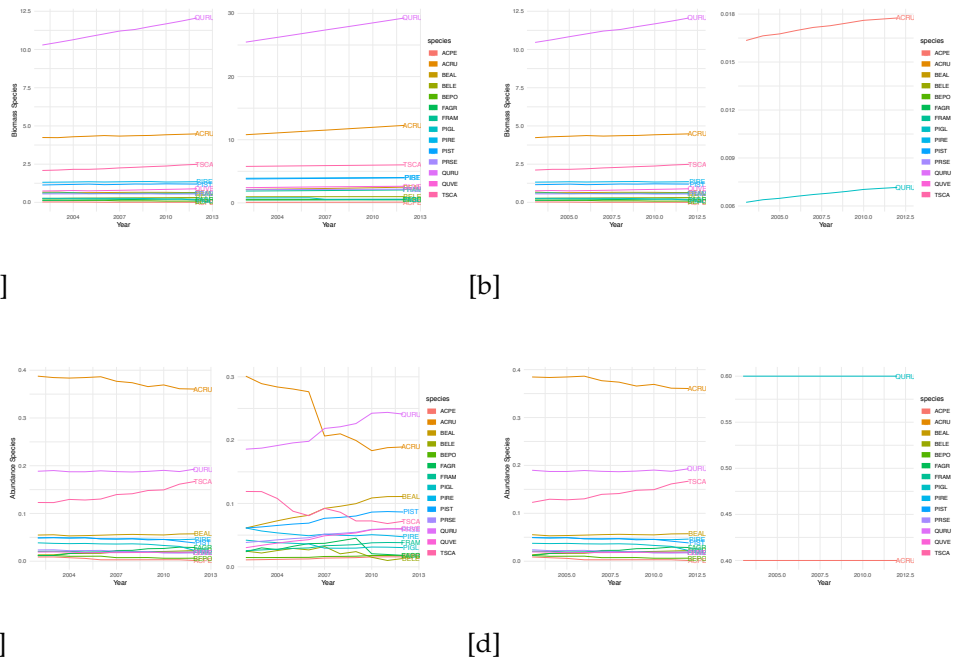

Figure 9. HF EMS: Simulated and observed species biomass and abundance; left = observations, right = predictions; a = PPA-BGC B_{Sp}; b = LANDIS-II B_{Sp}; c = PPA-BGC n_{Sp}; d = LANDIS-II n_{Sp}

3.2. Jones Ecological Research Center, Red Dirt Flux Tower

For the Jones Ecological Research Center (JERC) RD flux tower site, both models showed stronger fidelity to data than for the Harvard Forest EMS tower site. Again, PPA-BGC showed higher R^2 values and lower RMSE and MAE values compared to LANDIS-II across the range of metrics tested. Yet, the margin between models was smaller for the JERC RD site. While PPA-BGC demonstrated higher correlations and lower errors for most metrics tested, LANDIS-II outperformed PPA-BGC in a few cases. This includes lower error magnitude for NEE, aboveground N, belowground biomass, SOC, and SON. However, PPA-BGC showed correlations equal or higher for all metrics tested, and lower errors for all other metrics. Overall results for the JERC RD flux tower site model intercomparison are shown in Table 4.

Table 4. Model fitness for Jones Ecological Research Center RD tower

	PPA-BGC			LANDIS-II		
Metric	R^2	RMSE	MAE	R^2	RMSE	MAE
NEE	0.30	1.68	1.64	0.09	0.13	0.11
B_{AG}	0.96	1.48	1.47	0.96	9.77	9.76
C_{AG}	0.96	1.63	1.63	0.96	4.88	4.88
N_{AG}	0.99	0.29	0.29	0.96	0.05	0.05
B_{BG}	0.96	10.84	10.83	0.96	1.37	1.20
C_{BG}	0.96	5.26	5.26	0.96	6.46	6.46
N_{BG}	0.98	1.44	1.44	0.96	1.60	1.60
r_{soil}	0.19	0.78	0.71	0.05	2.40	2.40
ANPP	0.03	0.39	0.37	0.03	0.48	0.46
C_{SO}	...	4.30	4.30	...	0.17	0.17
N_{SO}	...	0.38	0.38	...	0.12	0.12
B_{Sp}	1.00	6.47	3.90	0.98	9.71	6.87
n_{Sp}	1.00	0.02	0.01	1.00	0.09	0.09
Mean	0.76	2.69	2.48	0.72	2.86	2.63

While both models showed higher performance at the JERC RD site, an analysis of simulated species biomass and abundance again indicates greater fidelity of the PPA-BGC model to data, as shown in Figure 10. While LANDIS-II overpredicts the rate of longleaf pine growth, PPA-BGC nearly perfectly matches observed species abundance and biomass trajectories for all species present. While the correlations are high, PPA-BGC overpredicts the magnitude of biomass here.

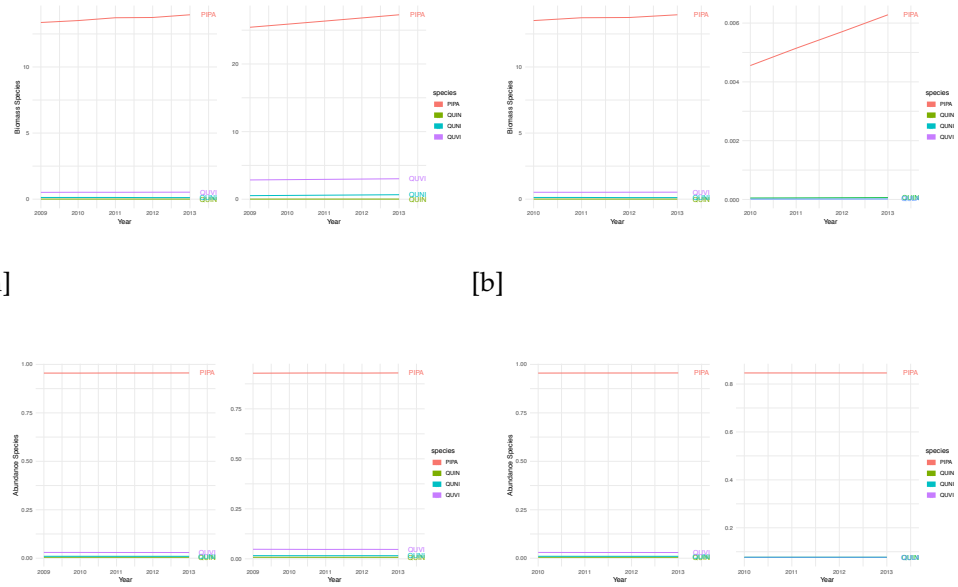

Figure 10. JERC RD: Simulated and observed species biomass and abundance; left = observations, right = predictions; a = PPA-BGC; B_{Sp}; b = LANDIS-II B_{Sp}; c = PPA-BGC n_{Sp}; d = LANDIS-II n_{Sp}

Our results for the Harvard Forest EMS tower and Jones Ecological Research Center RD tower model intercomparison exercise clearly indicate strong performance for both models and both sites. Results for the JERC RD tower are particularly close between the two models. On average, PPA-BGC demonstrated better fidelity to observational data across the full range of metrics. Next, we assess results related to the logistics of model deployment to new computers, users, and modeling sites.

3.3. Model Usability, Performance, and Transferability

While the two models share a somewhat similar basis in forest dynamics and biogeochemistry modeling, they differ in important practical and conceptual terms. The command-line version of the PPA-BGC model used in this work, version 5.0, consists of approximately 500 lines of R code and is thus readily cross-platform, including cloud providers. Meanwhile, the LANDIS-II model core and Net Ecosystem Carbon and Nitrogen (NECN) succession extension are an estimated 2,000 and 0.5 million lines of code, respectively. While this version of PPA-BGC fuses an explicit tree canopy geometry model with empirical data on fecundity, growth, mortality, and stoichiometry, the NECN extension of LANDIS-II borrows heavily from the process-based CENTURY model [11], similar to the MC1 model [70]. This carries important implications for model parameterization needs. While PPA-BGC relies on typical forest inventory data including tree species, age/size, and densities, LANDIS-II relies on species age/size, and species traits in the form of vital attributes. Below, we summarize our findings regarding the logistics of model deployment.

3.3.1. Model Usability

Below, we provide an assessment of model usability based on four criteria.

1. *Ease of installation*
   While LANDIS-II requires the installation of one or more Windows executable files, depending on the options desired, PPA-BGC is contained in a single R script and requires only a working R installation.
2. *Ease of parameterization*
   While both models can be difficult to parameterize for regions with little to no observational data, the simple biogeochemistry variant of PPA-BGC requires an order of magnitude fewer parameters than LANDIS-II with NECN. In addition, PPA-BGC requires commonly available forest inventory data while NECN requires a number of parameters seldom seen in the literature, let alone forest inventories.
3. *Ease of program operation*
   Both models use a command-line interface and are thus equally easy to operate. However, PPA-BGC is cross-platform and uses comma-separated-value (CSV) files for input tables, which are easier to work with than multiple tables nested within an unstructured text files. This additionally allows for simplification in designing model application programming interfaces (APIs), or model wrappers, a layer of abstraction above the models. These abstractions are important for simplifying model operation and reproducibility, and enable a number of research applications.
4. *Ease of parsing outputs*
   All PPA-BGC outputs are provided in CSV files in a single folder while LANDIS-II generates outputs in multiple formats in multiple folders. While the PPA-BGC format is simpler and easier to parse, the image output formats used by LANDIS-II carry considerable benefit for spatial applications. Both models may benefit by transitioning spatial data to the NetCDF scientific file format used by most general circulation and terrestrial biosphere models.

3.3.2. Model Performance

Next, we assess model performance in terms of the speed of operation on a consumer-off-the-shelf (COTS) laptop computer with a dual-core 2.8 GHz Intel Core i7-7600U CPU and 16 GB of DDR4-2400 RAM. We focus on a single performance metric, the timing of simulations. Other aspects of model performance in the form of precision and accuracy are described in previous sections. As shown in Table 5, PPA-BGC was between 1,200 and 2,800% faster than LANDIS-II in our timing tests. This was surprising given that PPA-BGC models true cohorts (i.e., individual trees) in an interpreted language while LANDIS-II models abstract cohorts (i.e., cohorts without trees) in a compiled language. The difference in speed is likely attributable to the simplicity of the PPA-BGC model.

Table 5. Simulation timing results

Site	Model	Duration (years)	Elapsed (sec)
HF EMS	PPA-BGC	11	8.51
HF EMS	LANDIS-II	11	101.15
JERC RD	PPA-BGC	5	2.25
JERC RD	LANDIS-II	5	61.51

3.3.3. Model Transferability

Here, we discuss model transferability. In this section, we assess the effort required to transfer the models to new locations, new computer systems, or new users. All three are important logistical criteria for effective model deployment.

1. *Model generalization*
   Both models appear to generalize effectively to different forested regions of the world, as both have shown strong performance in this study and others. No clear winner is evident in this regard.
2. *Availability of parameterization data*
   While LANDIS-II with NECN requires substantially greater parameterization data compared to PPA-BGC, it may often be possible to rely on previously published parameters. Meanwhile, the growth, mortality, and fecundity parameters used by PPA-BGC are easy to calculate using common field inventory data. PPA-BGC is simpler to transfer in this regard given the wide availability of this data.
3. *Size of the program*
   PPA-BGC is approximately 500 lines of R code, while LANDIS-II with NECN is estimated at half a million lines of C# code.
4. *Cross-platform support*
   While Linux support may soon be supported with Microsoft .NET Core, LANDIS-II is written in C# and is thus Microsoft Windows-based. PPA-BGC is written in standard R code and has full cross-platform support.
5. *Ease of training new users*
   While both models have a learning curve, the practical simplicity of PPA-BGC makes it easier to train new users. While LANDIS-II contains more features, these come at the cost of training new users. The model wrapper library we developed as part of work vastly eases this process for both models. Future studies should measure the time required for new users to fully operate both models.

The results of our experiments for Harvard Forest and Jones Ecological Research Center demonstrate stronger performance for PPA-BGC than LANDIS-II, despite the smaller size and shorter execution time of the former model. The result fits our hypothesis that vegetation dynamics drive biogeochemistry pools and fluxes to a higher degree than simple 1-D processes. Our results suggest that improving the representation of forest dynamics in models may yield accurate biogeochemistry predictions, even when allometric and stoichiometry biogeochemistry models are used. This finding supports the current focus of work on improving the representation of vegetation dynamics in global terrestrial biosphere models [17,18,71].

Future studies should combine the Perfect Plasticity Approximation, or PPA, with a first-principles representation of biogeochemical processes. This work should fuse the new state-of-the-art forest biogeochemistry model with an application programming interface (API) written in R or Python, in order to expand native model functions to include Monte Carlo methods, model emulation, parameter optimization, and sampling from empirical or modeled priors.

4. Conclusions

In conclusion, both PPA-BGC and LANDIS-II effectively captured vegetation dynamics previously absent in modeling studies at these sites. This includes "...long-term increases in tree biomass, successional change in forest composition, and disturbance events, processes not well represented in current models," which drive interannual and decadal variation in NEE [30]. While PPA-BGC showed stronger performance across the range of metrics tested, including the logistics of model deployment, LANDIS-II also performed well across the tested metrics. Further studies are needed to compare more aspects of the two models in a structured manner. Ultimately, we hope that this study serves as the foundation for future forest ecosystem model intercomparisons in the North American continent, similar in spirit to the former TDE Ecosystem Model Intercomparison project [14]. The aims of this work were not to determine which model is 'best' for diagnosis and prognosis at two locations, but to improve the capabilities of existing models across a range of locations in order to advance earth system

models. In this regard, there are beneficial aspects to both modeling approaches and the trade-offs presented largely depend on the desired application.

Supplementary Materials: Parameter tables for both models and sites are provided in Appendix A. All model, parameter, script files used in this model intercomparison exercise are available for download at the following public GitHub repository:

https://github.com/adam-erickson/ecosystem-model-comparison

The repository provides tables containing parameter values and climate drivers used in the PPA-BGC and LANDIS-II model simulations for the two model intercomparison sites. Tree species codes are adopted from the USDA PLANTS database, accessible at the following URL:

https://plants.sc.egov.usda.gov

Scripts provided include a simple object-oriented forest biogeochemistry model wrapper library implemented in the R language [67]. The model wrapper library includes a number of features for simplifying the operation of this class of models, including functions for cleaning up and parsing model outputs into memory in a common format for comparison. Importantly, the wrapper library enables full reproducibility of results through the *hf_ems.r* and *jerc_rd.r* scripts. Using these scripts with the object-oriented *classes.r* model wrapper, it is possible to load pre-computed model results and calculate all intercomparison metrics for verification. The directory structure of the repository is shown in Figure 11.

```
ecosystem-model-comparison
├── figures
├── models
│   ├── landis_2
│   │   ├── hf_ems
│   │   │   ├── extensions
│   │   │   │   └── succession
│   │   │   │       └── necn
│   │   │   │           ├── climate
│   │   │   │           └── maps
│   │   │   └── outputs
│   │   │       └── succession
│   │   │           └── necn
│   │   │               ├── logs
│   │   │               └── metadata
│   │   └── jerc_rd
│   │       ├── extensions
│   │       │   └── succession
│   │       │       └── necn
│   │       │           ├── climate
│   │       │           └── maps
│   │       └── outputs
│   │           └── succession
│   │               └── necn
│   │                   ├── logs
│   │                   └── metadata
│   └── ppa_bgc
│       ├── hf_ems
│       │   ├── lut
│       │   └── outputs
│       └── jerc_rd
│           ├── lut
│           └── outputs
└── scripts
```

Figure 11. Directory structure of the GitHub repository

Author Contributions: Individual contributions provided to complete this work include the following: conceptualization, N.S.; methodology, A.E. and N.S.; software, A.E.; validation, A.E.; formal analysis, A.E.; investigation, A.E.; resources, N.S.; data curation, A.E.; writing—original draft preparation, A.E.; writing—review and editing, A.E. and N.S.; visualization, A.E.; supervision, N.S.; project administration, N.S.; funding acquisition, N.S.

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Abbreviations

The following abbreviations are used in this manuscript:

ANPP	Aboveground net primary production
API	Application programming interface
BGC	Biogeochemistry
CPU	Central processing unit
CSV	Comma-separated values
DoD	Department of Defense
ED	Ecosystem Demography model
EMS	Environmental Measurement Station
GPGPU	General-purpose graphics processing unit
HF	Harvard Forest
JERC	Jones Ecological Research Center
L-systems	Lindenmayer systems
LANDIS	Landscape Disturbance and Succession model
MAE	Mean absolute error
NECN	Net Ecosystem Carbon and Nitrogen model
NEE	Net ecosystem exchange
NSE	Nash-Sutcliffe efficiency
PPA	Perfect Plasticity Approximation model
RAM	Random access memory
RD	Red Dirt
RMSE	Root mean squared error
SOC	Soil organic carbon
SON	Soil organic nitrogen
TDE	Throughfall Displacement Experiment

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Appendix Model Parameters

Appendix A.1 Harvard Forest EMS Flux Tower

Appendix A.1.1 PPA-BGC

Table A1. Species crown allometry parameters

Species	Type	h_{coeff}	cr_1	cr_2	cd
ACPE	adult	0.063	0.108	1	0.490
ACRU	adult	0.063	0.108	1	0.490
BEAL	adult	0.063	0.109	1	0.540
BELE	adult	0.024	0.109	1	0.540
BEPO	adult	0.063	0.109	1	0.540
FAGR	adult	0.035	0.152	1	0.664
FRAM	adult	0.056	0.095	1	0.319
PIGL	adult	0.033	0.087	1	0.413
PIRE	adult	0.033	0.087	1	0.413
PIST	adult	0.033	0.087	1	0.413
PRSE	adult	0.045	0.116	1	0.370
QURU	adult	0.042	0.119	1	0.413
QUVE	adult	0.042	0.119	1	0.413
TSCA	adult	0.024	0.100	1	0.846
ACPE	sapling	0.062	0.107	1	0.580
ACRU	sapling	0.063	0.108	1	0.490
BEAL	sapling	0.063	0.109	1	0.540
BELE	sapling	0.024	0.109	1	0.540
BEPO	sapling	0.063	0.109	1	0.540
FAGR	sapling	0.035	0.152	1	0.664
FRAM	sapling	0.056	0.095	1	0.319
PIGL	sapling	0.033	0.087	1	0.413
PIRE	sapling	0.033	0.087	1	0.413
PIST	sapling	0.033	0.087	1	0.413
PRSE	sapling	0.045	0.116	1	0.370
QURU	sapling	0.042	0.119	1	0.413
QUVE	sapling	0.042	0.119	1	0.413
TSCA	sapling	0.024	0.100	1	0.846

Table A2. Species biomass equation parameters

Species	$b0$	$b1$	f_{stem}	f_{branch}	f_{leaf}	f_{root}	f_{soil}
ACPE	−2.047	2.385	0.700	0.230	0.070	0.240	0.680
ACRU	−2.047	2.385	0.700	0.230	0.070	0.240	0.680
BEAL	−1.810	2.348	0.700	0.230	0.070	0.240	0.680
BELE	−1.810	2.348	0.700	0.230	0.070	0.240	0.680
BEPO	−2.227	2.451	0.700	0.230	0.070	0.240	0.680
FAGR	−2.070	2.441	0.700	0.230	0.070	0.240	0.680
FRAM	−1.838	2.352	0.700	0.230	0.070	0.240	0.680
PIGL	−2.136	2.323	0.700	0.230	0.070	0.240	0.680
PIRE	−2.618	2.464	0.700	0.230	0.070	0.240	0.680
PIST	−2.618	2.464	0.700	0.230	0.070	0.240	0.680
PRSE	−2.212	2.413	0.700	0.230	0.070	0.240	0.680
QURU	−2.070	2.441	0.700	0.230	0.070	0.240	0.680
QUVE	−2.070	2.441	0.700	0.230	0.070	0.240	0.680
TSCA	−2.348	2.388	0.700	0.230	0.070	0.240	0.680

Table A3. Biomass carbon fraction parameters

f_{stem}	f_{branch}	f_{leaf}	f_{root}	f_{soil}
0.500	0.500	0.500	0.500	0.143

Table A4. Species DBH increment parameters

Species	Type	I_{DBH}
ACPE	adult	0.277
ACRU	adult	0.312
BEAL	adult	0.280
BELE	adult	0.198
BEPO	adult	0.103
FAGR	adult	0.303
FRAM	adult	0.149
PIGL	adult	0.274
PIRE	adult	0.390
PIST	adult	0.277
PRSE	adult	0.120
QURU	adult	0.420
QUVE	adult	0.322
TSCA	adult	0.563
ACPE	sapling	0.895
ACRU	sapling	0.269
BEAL	sapling	0.520
BELE	sapling	0.201
BEPO	sapling	0.300
FAGR	sapling	0.530
FRAM	sapling	0.500
PIGL	sapling	0.353
PIRE	sapling	0.350
PIST	sapling	0.350
PRSE	sapling	0.200
QURU	sapling	0.098
QUVE	sapling	0.100
TSCA	sapling	0.509

Table A5. Species mortality parameters

Species	Type	$p_{mortality}$
ACPE	adult	0.115
ACRU	adult	0.030
BEAL	adult	0.035
BELE	adult	0.009
BEPO	adult	0.032
FAGR	adult	0.015
FRAM	adult	0.004
PIGL	adult	0.074
PIRE	adult	0.023
PIST	adult	0.010
PRSE	adult	0.009
QURU	adult	0.007
QUVE	adult	0.001
TSCA	adult	0.022
ACPE	sapling	0.001
ACRU	sapling	0.873
BEAL	sapling	0.001
BELE	sapling	0.667
BEPO	sapling	0.001
FAGR	sapling	0.354
FRAM	sapling	0.001
PIGL	sapling	0.001
PIRE	sapling	0.001
PIST	sapling	0.001
PRSE	sapling	0.001
QURU	sapling	0.001
QUVE	sapling	0.001
TSCA	sapling	0.821

Table A6. Species fecundity parameters

Species	Fecundity
ACPE	2
ACRU	29
BEAL	16
BELE	8
BEPO	2
FAGR	11
FRAM	5
PIGL	3
PIRE	3
PIST	11
PRSE	8
QURU	29
QUVE	9
TSCA	17

Table A7. Species C:N ratio parameters

Species	CN_{stem}	CN_{branch}	CN_{leaf}	CN_{litter}	CN_{root}	CN_{soil}
ACPE	548.590	71.460	30.460	58.800	68.548	23.087
ACRU	548.590	71.460	30.460	58.800	68.548	23.087
BEAL	548.590	71.460	22.420	58.800	68.548	23.087
BELE	548.590	71.460	21.200	58.800	68.548	23.087
BEPO	548.590	71.460	21.560	58.800	68.548	23.087
FAGR	548.590	71.460	22.420	58.800	68.548	23.087
FRAM	548.590	71.460	21.910	58.800	68.548	23.087
PIGL	548.590	71.460	38	58.800	68.548	23.087
PIRE	548.590	71.460	33	58.800	68.548	23.087
PIST	548.590	71.460	38	58.800	68.548	23.087
PRSE	548.590	71.460	21.500	58.800	68.548	23.087
QURU	548.590	71.460	21.920	58.800	68.548	23.087
QUVE	548.590	71.460	21.920	58.800	68.548	23.087
TSCA	548.590	71.460	42.520	58.800	68.548	23.087

Appendix A.1.2 LANDIS-II

Table A8. NECN adjustment parameters

Parameter	Value
p_{est} modifier	0.1
$N_{mineral}$ initial	3.0
$Fuels_{fine}$ initial	0.1
N_{atmos} slope	0.007
N_{atmos} intercept	0.011
$Latitude_{deg}$	43.3
$r_{denitrification}$	0.001
r_{decay} surface	0.65
r_{decay} SOM1	1.0
r_{decay} SOM2	0.125
r_{decay} SOM3	0.0002

Table A9. NECN maximum LAI parameters

$Class_{shade}$	LAI_{max}
1	1
2	2.5
3	3.5
4	6
5	8

Table A10. NECN light establishment parameters

$Class_{shade}$	$Shade_0$	$Shade_1$	$Shade_2$	$Shade_3$	$Shade_4$	$Shade_5$
1	1	1	0.25	0.1	0	0
2	0.5	0.5	1	0.25	0.1	0
3	0.1	0.5	1	1	0.5	0.1
4	0.1	0.25	0.5	0.5	1	0.25
5	0	0.1	0.25	0.25	0.5	1

Table A11. NECN species parameters

Species	PFT	N_{fix}	GDD_{min}	GDD_{max}	T_{min}	D_{max}	$Long_{leaf}$	R_{epi}	L_{leaf}	L_{root_f}	L_{wood}	L_{root_c}	CN_{leaf}	CN_{root_f}	CN_{wood}	CN_{root_c}	CN_{litter}	$ANPP_{max}$	B_{max}
ACRU	3	N	1260	6600	-18	0.23	1	N	0.183	0.334	0.125	0.312	28.20	26	565	50	55	440	25000
QURU	2	N	1100	4571	-17	0.2025	1	N	0.249	0.334	0.225	0.303	18.50	58	398	113	32	380	25000

Table A12. Functional group parameters

PFT	Index	T_{mean}	T_{max}	T_{shape}	T_{shape}	f_Cf	$BTOLAI$	$kLAI$	LAI_{max}	$PPRPTS_2$	$PPRPTS_3$	$r_{decay}w$	m_{wood}	m_{shape}	$drop_{month}$	$f_{root}c$	$f_{root}f$
Oaks	2	25	40	1.5	2.5	0.6	-0.9	10000	9	0.1	0.8	0.5	0.0006	15	9	0.2	0.5
NorthHardwoods	3	25	40	1.5	2.5	0.6	-0.9	7000	10	1.5	0.96	0.7	0.0006	15	9	0.2	0.5

Table A13. Fire reduction parameters; inactive

$Class_{severity}$	$Reduction_{wood}$	$Reduction_{litter}$	$Reduction_{SOM}$
1	0.0	0.5	1.0
2	0.05	0.75	1.0
3	0.2	1.0	1.0
4	0.5	1.0	1.0
5	0.8	1.0	1.0

Table A14. Harvest reduction parameters; inactive

Class	$Reduction_{wood}$	$Reduction_{litter}$	$Reduction_{SOM}$	$Removal_{leaf}$	$Removal_{wood}$
HandThinning	0.05	1.0	1.0	1.0	1.0
MechThinning	0.05	1.0	1.0	0.85	1.0

Table A15. Species parameters; only ACRU and QURU were simulated

Species	Longevity	Maturity	T_{shade}	T_{fire}	D_{eff}	D_{max}	p_{veg}	S_{min}	S_{max}	R_{fire}
ABBA	200	25	5	1	30	160	0	0	0	none
ACRU	235	5	4	1	100	200	0.75	0	150	none
ACSA	300	40	5	1	100	200	0.1	0	60	none
BEAL	300	40	3	2	100	400	0.1	0	180	none
BELE	250	40	4	2	100	400	0.1	0	0	none
BEPA	150	40	4	2	100	600	0.75	0	150	none
BEPO	150	40	4	2	100	400	0.1	0	0	none
CAGL	200	30	3	2	50	100	0.25	0	200	resprout
FAGR	350	10	5	1	30	300	0.4	10	200	resprout
FRAM	300	30	2	1	70	140	0.1	0	70	none
FRNI	150	30	4	2	200	2000	0.8	10	140	resprout
LALA	180	35	2	2	100	400	0.2	0	0	none
OSVI	110	25	4	2	100	200	0.15	0	100	resprout
PIGL	300	25	3	2	30	200	0	0	0	none
PIMA	215	30	3	3	79	158	0	0	0	none
PIRU	350	15	5	2	80	125	0	0	0	none
PIRE	250	15	2	4	100	275	0.1	0	20	none
PIRI	200	10	2	4	90	150	0.5	10	100	resprout
PIST	400	25	3	3	60	210	0	0	0	none
POBA	150	10	1	2	100	200	0.8	10	80	resprout
POGR	110	20	1	1	1000	5000	0.9	0	100	resprout
POTR	110	20	1	1	1000	5000	0.9	0	100	resprout
PRSE	200	10	2	3	100	200	0.5	20	90	resprout
QUAL	400	25	3	2	30	800	0.1	20	200	resprout
QUCO	150	20	2	3	50	100	0.5	20	100	resprout
QUPR	300	20	3	3	50	150	0.5	10	200	resprout
QURU	250	30	3	2	30	800	0.5	20	200	resprout
QUVE	120	20	3	2	70	150	0.1	20	90	resprout
THOC	800	30	2	1	45	100	0.5	0	200	none
TIAM	250	15	4	1	75	150	0.8	10	240	resprout
TSCA	500	20	5	2	30	100	0	0	0	none
ULAM	85	20	4	2	90	400	0.3	5	70	resprout

Appendix A.2 Jones Ecological Research Center RD Flux Tower

Appendix A.2.1 PPA-BGC

Table A16. Species crown allometry parameters

Species	Type	h_{coeff}	$cr1$	$cr2$	cd
PIPA	adult	0.033	0.087	1	0.413
QUIN	adult	0.042	0.119	1	0.413
QUNI	adult	0.042	0.119	1	0.413
QUVI	adult	0.042	0.119	1	0.413
PIPA	sapling	0.033	0.087	1	0.413
QUIN	sapling	0.042	0.119	1	0.413
QUNI	sapling	0.042	0.119	1	0.413
QUVI	sapling	0.042	0.119	1	0.413

Table A17. Species biomass equation parameters

Species	$b0$	$b1$	f_{stem}	f_{branch}	f_{leaf}	f_{root}	f_{soil}
PIPA	-3.051	2.647	0.700	0.230	0.070	0.240	0.680
QUIN	-2.070	2.441	0.700	0.230	0.070	0.240	0.680
QUNI	-2.070	2.441	0.700	0.230	0.070	0.240	0.680
QUVI	-2.070	2.441	0.700	0.230	0.070	0.240	0.680

Table A18. Biomass carbon fraction parameters

f_{stem}	f_{branch}	f_{leaf}	f_{root}	f_{soil}
0.500	0.500	0.500	0.500	0.143

Table A19. Species DBH increment parameters

Species	Type	I_{DBH}
PIPA	adult	0.261
QUIN	adult	0.119
QUNI	adult	0.994
QUVI	adult	0.276
PIPA	sapling	0.197
QUIN	sapling	0.100
QUNI	sapling	0.440
QUVI	sapling	0.271

Table A20. Species mortality parameters

Species	Type	$p_{mortality}$
PIPA	adult	0.001
QUIN	adult	0.001
QUNI	adult	0.001
QUVI	adult	0.001
PIPA	sapling	0.174
QUIN	sapling	0.333
QUNI	sapling	0.143
QUVI	sapling	0.111

Table A21. Species fecundity parameters

Species	Fecundity
PIPA	2
QUIN	0
QUNI	0
QUVI	0

Table A22. Species C:N ratio parameters

Species	CN_{stem}	CN_{branch}	CN_{leaf}	CN_{litter}	CN_{root}	CN_{soil}
PIPA	133.721	133.721	255.103	255.103	133.721	23.087
QUIN	96.370	96.370	85.259	85.259	96.370	23.087
QUNI	96.370	96.370	85.259	85.259	96.370	23.087
QUVI	96.370	96.370	85.259	85.259	96.370	23.087

Appendix A.2.2 LANDIS-II

Table A23. NECN adjustment parameters

Parameter	Value
p_{est} modifier	0.4
$N_{mineral}$ initial	0.5
$Fuels_{fine}$ initial	0.1
N_{atmos} slope	0.004
N_{atmos} intercept	0.017
$Latitude_{deg}$	31.220731
$r_{denitrification}$	0.02
r_{decay} surface	0.70
r_{decay} SOM1	0.81
r_{decay} SOM2	0.05
r_{decay} SOM3	0.00006

Table A24. NECN maximum LAI parameters

$Class_{shade}$	LAI_{max}
1	1
2	2.5
3	3.5
4	6
5	8

Table A25. NECN light establishment parameters

$Class_{shade}$	$Shade_0$	$Shade_1$	$Shade_2$	$Shade_3$	$Shade_4$	$Shade_5$
1	1	1	0.25	0.1	0	0
2	0.5	0.5	1	0.25	0.1	0
3	0.1	1	1	1	0.5	0.1
4	0.1	0.25	0.5	0.5	1	0.25
5	0	0.1	0.25	0.25	0.5	1

Table A26. NECN species parameters

Species	PFT	N_{fix}	GDD_{min}	GDD_{max}	T_{min}	D_{max}	$Long_{leaf}$	R_{epi}	L_{leaf}	L_{root_f}	L_{wood}	L_{root_c}	CN_{leaf}	CN_{root_f}	CN_{wood}	CN_{root_c}	CN_{litter}	$ANPP_{max}$	B_{max}
QUIN	2	N	3915	7000	1	0.423	1	N	0.293	0.23	0.23	0.35	24	48	500	333	55	250	15000
QULA	2	N	3915	7000	1	0.423	1	N	0.293	0.23	0.23	0.35	24	48	500	333	55	250	15000
PIPA	1	N	3915	7000	1	0.423	2	N	0.2	0.2	0.35	0.35	50	50	380	170	100	500	15000

Table A27. Functional group parameters

PFT	Index	T_{mean}	T_{max}	T_{shape}	T_{shape}	f_{C_f}	$BTOLAI$	$kLAI$	LAI_{max}	$PPRPTS_2$	$PPRPTS_3$	r_{decay_w}	m_{wood}	m_{shape}	$month_{drop}$	f_{root_c}	f_{root_f}
Pine	1	28	45	3.0	2.5	0.37	-0.9	2000	10	1	0.8	0.6	0.001	15	9	0.31	0.56
Oaks	2	27	45	2.2	2.5	0.5	-0.9	2000	20	0.1	0.75	0.6	0.001	15	9	0.21	0.59

Table A28. Fire reduction parameters; inactive

$Class_{severity}$	$Reduction_{wood}$	$Reduction_{litter}$	$Reduction_{SOM}$
1	0.0	0.5	1.0
2	0.05	0.75	1.0
3	0.2	1.0	1.0
4	0.5	1.0	1.0
5	0.8	1.0	1.0

Table A29. Harvest reduction parameters; inactive

$Class_{severity}$	$Reduction_{wood}$	$Reduction_{litter}$	$Reduction_{SOM}$	$Removal_{leaf}$	$Removal_{wood}$
HandThinning	0.05	1.0	1.0	1.0	1.0
MechThinning	0.05	1.0	1.0	0.85	1.0

Table A30. Species parameters

Species	Longevity	Maturity	T_{shade}	T_{fire}	D_{eff}	D_{max}	p_{veg}	S_{min}	S_{max}	R_{fire}
QUIN	150	10	4	5	50	3000	0.75	5	40	resprout
QULA	150	20	4	3	50	3000	0.75	5	40	resprout
PIPA	400	20	1	5	20	200	0.0	0	5	none