Forest ecosystem model intercomparison along the East Coast of the United States

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Abstract

The U.S. Department of Defense (DoD) manages 4.6 million hectares of land in the conterminous United States and an additional 32 thousand hectares in territories or overseas. DoD land managers face the challenging task of optimizing management practices to enhance the capabilities of current and future war-fighters while meeting economic, social, and environmental goals. 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 conduct a model intercomparison exercise using two popular forest biogeochemistry models, Sortie-PPA 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 for model parameterization, calibrationvalidation, and intercomparison. We assess model performance using the following temporal 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 assess static observations of soil organic C (SOC) and N (SON), and conclude 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 Sortie-PPA model indicated the best correspondence to observational data overall for the 11 temporal metrics and 2 static metrics tested (HF EMS $\overline{R^2} = 0.78, +0.07$, $\overline{RMSE} = 4.84, -1.53$; JERC RD $\overline{R^2} = 0.81, +0.02$, $\overline{RMSE} = 2.68, -0.19$. Following the successful validation of both models, our plan is to apply Sortie-PPA and/or LANDIS-II at the largest military installation in the world, Fort Bragg, NC, USA.

1 Introduction

A vast array of gap [49], forest landscape [19, 26, 14, 57, 45], and terrestrial biosphere models 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 applying truncated log-normal growth equations to cohorts defined by a theoretical growing space to mechanistic 'big-leaf' models comprised of single or many canopy layers. Belowground process models similarly vary in design, from simple stoichiometric relations to carbon and nitrogen cycling with microbial dynamics to a fully mechanistic representation of energetic and biogeochemical processes. Most recent belowground models still rely on a variant of the classical CENTURY model [33, 34].

Overall, forest ecosystem models vary in specialization and generalization, ranging from pure research in narrowly defined regions to simulating multiple landscape processes in an effort to inform land management to simulating biogeochemical dynamics across all 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 [53] and Comparison of Forest Landscape Model (CoFoLaMo) intercomparison projects [23], 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. There is a critical need to conduct similar forest ecosystem models comparisons in other regions of the world in order to establish the groundwork 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 models; (5) hybrid models combining design principles from each [49, 21, 20]. Terrestrial biosphere models similarly trace their roots back to early one-dimensional physiological models, with land surface models currently in their third generation. 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 [1]. This inspired the aforementioned forest ecosystem model intercomparisons as well as new terrestrial biosphere model designs based on gap models, bypassing 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 [46], ED/ED2 [29, 24], and LM3-PPA [54], the latter based on the Perfect Plasticity Approximation [48]. Each based on a gap model, these models represent the current state-of-the-art for modeling global vegetation dynamics. While individual-based and global models have finally begun to merge, forest landscape models have remained somewhere in the middle, focused on spatial processes of fire, harvest, and biological disturbance. While classical forest landscape models do not represent individual trees, recent models focused on computational efficiency improvements may allow up-scaling gap dynamics [44, 48], as in recent terrestrial biosphere models. For example, one recent forest landscape model participating in the CoFoLaMo model intercomparisons scales from individual trees to stands by pre-computing light tables for individual trees within forest stands [44]. Regardless of model formulation, it is clear that gap, forest landscape, and terrestrial biosphere models are finally beginning to merge. This is further attributable to improvements in computational efficiency with new processor designs and cluster or cloud computing infrastructure.

We focus our forest ecosystem model intercomparison on two sites on the East Coast of the United States. Harvard Forest (HF), MA, 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 Site (EMS) flux tower site within the Little Prospect Hill tract - the longest-running eddy covariance flux tower in the world. The site is also known as HFR1 within the AmeriFlux network. Importantly, research at the EMS tower found unusually high rates of ecosystem respiration in winter and lows in mid-to-late summer for a temperate forest [11]. The mechanism behind these observed patterns is poorly understood. Between 1992 and 2004, the site acted as a carbon sink, with a mean uptake rate of 2.5 Mg C ha-1 year-1. Aging dominated the site characteristics, with with a 101-115 Mg C ha-1 increase in biomass, comprised predominantly of the growth of red oak (*Quercus rubra*). The year 1998 showed a sharp decline in NEE and other metrics, recovering thereafter [50]. As Urbanski et al. [50] 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 presented herein, Sortie-PPA [48, 37] and LANDIS-II with NECN succession [42, 43], are intended to directly address these shortcomings of previous models.

While there have been fewer studies at Jones Ecological Research Center (JERC), GA, USA, Google Scholar still 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 $=$ $-2.48\, Mg\, C\, ha^{-1}\, year^{-1}$; $-1.58 \pm 0.25\, Mg\, C\, ha^{-1}\, year^{-1}$ ($10\, Mg\, ha^{-1} = 1\, kg\, m^{-2}$)), reduced to near-neutral uptake during a 2011 drought ($-0.165\, Mg\ C\ ha^{-1} year^{-1}$) and acting as a carbon source when prescribed burns are taken into account. Meanwhile, NEE typically returned to pre-fire rates within 30-60 days. The mechanisms behind soil respiration here appear to be complex and site-specific [56]. Overall, existing recent research highlights the importance of fire and drought to carbon exchange in these long-leaf pine (*Pinus palustris*) and oak (*Quercus spp.*) savanna systems [55, 47, 56]. 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 Sortie-PPA were parameterized for two forested sites in the eastern United States, Harvard Forest (HF), MA and Jones Ecological Research Center (JERC), GA. At the HF site, we focus on Little Prospect Hill and the Environmental Measurement Site (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 positions along the United States Eastern Seaboard and for their availability of data needed to parameterize, calibrate, and validate both models. This model intercomparison work is intended as a calibration/validation study before application of one or both models at Fort Bragg, NC, USA. 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 from sources such as species compendiums. Our model parameters are provided in the Supplementary Materials 4. We close the methodology section with descriptions of the metrics, models, and criteria used in the intercomparisons.

2.1 Site Descriptions

In the following sections, we describe the two forested sites on the east coast of the United States where we conducted our model intercomparison exercise. The two sites are within Harvard Forest, MA and Jones Ecological Research Center, GA. Both sites were chosen for their representativeness of eastern seaboard forests and exceptional quantity of quality of field data. A critical factor in the selection of sites was the availability of eddy covariance flux tower data needed to validate net ecosystem exchange (NEE) in the models. The two sites selected are the 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.

2.1.1 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, approximately 100 km from the city of Boston [50]. 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 and is comprised of second-growth forests approximately 75-95 years in age, based on previous estimates [3]. Soils at Harvard Forest originate from sandy loam glacial till and are mildly acidic [50].

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 [3]. As noted by Urbanski et al. [50], approximately 33% of red oak stands were established prior to 1895, 33% prior to 1930, and 33% before 1940. A mildly hilly and relatively undisturbed forest (since the 1930s) extends continuously for several km^2 around the tower. In 2000, harvest operations were conducted removing 22.5 Mg C ha-1 of live aboveground woody biomass about 300 m S-SE from the tower, with little effect on measurements. The 40 biometric plots were designated via stratified random sampling within eight 500 m transects Urbanski et al. [50]. The EMS tower site currently contains 34 biometric plots at 10 m radius each, covering 10,681 m^2, or just over one hectare, in area.

Recent 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 1.

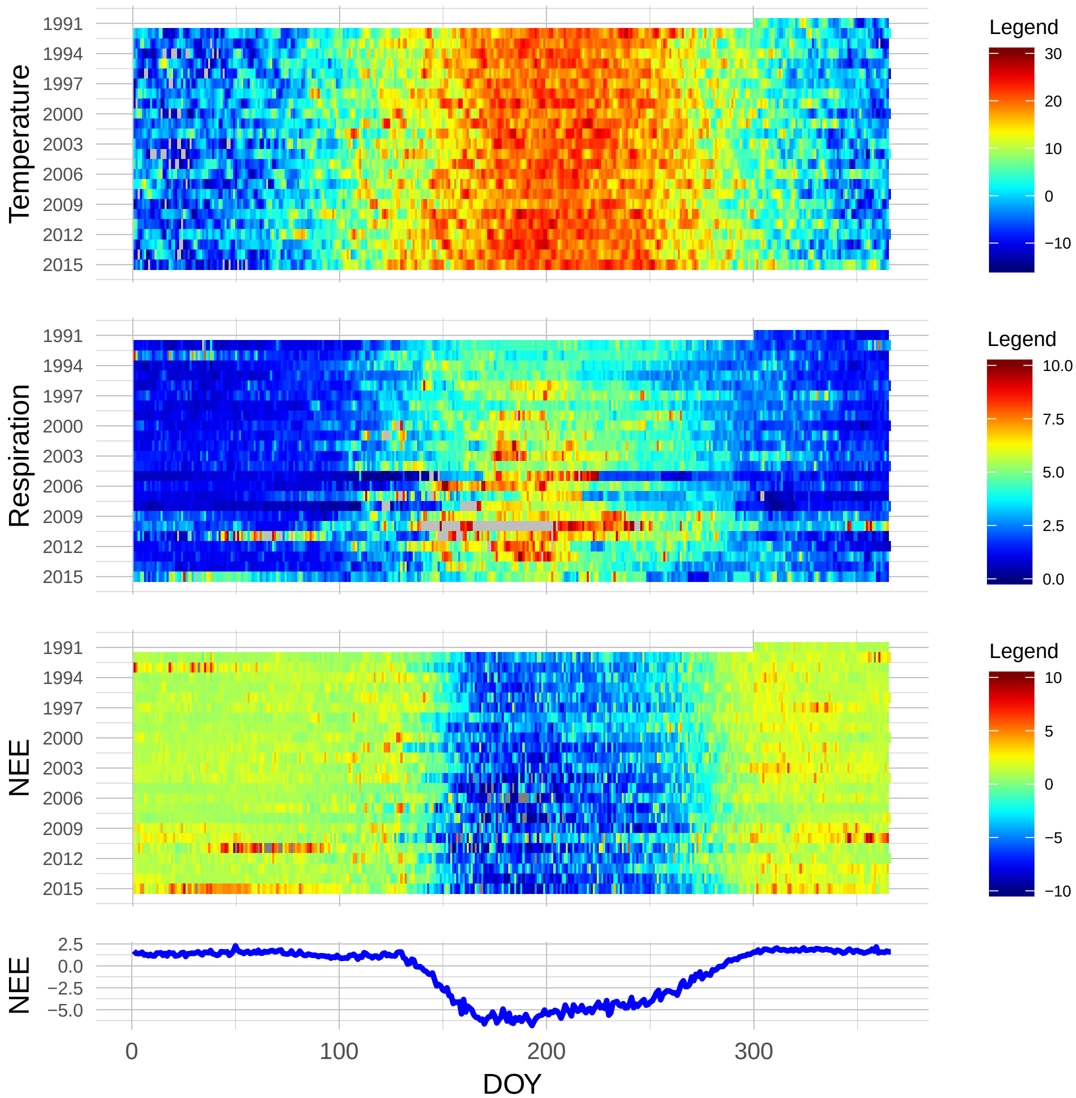


Figure 1: Harvard Forest EMS tower daily averages

Patterns in daytime and nighttime NEE are shown below in Figure 2. 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.

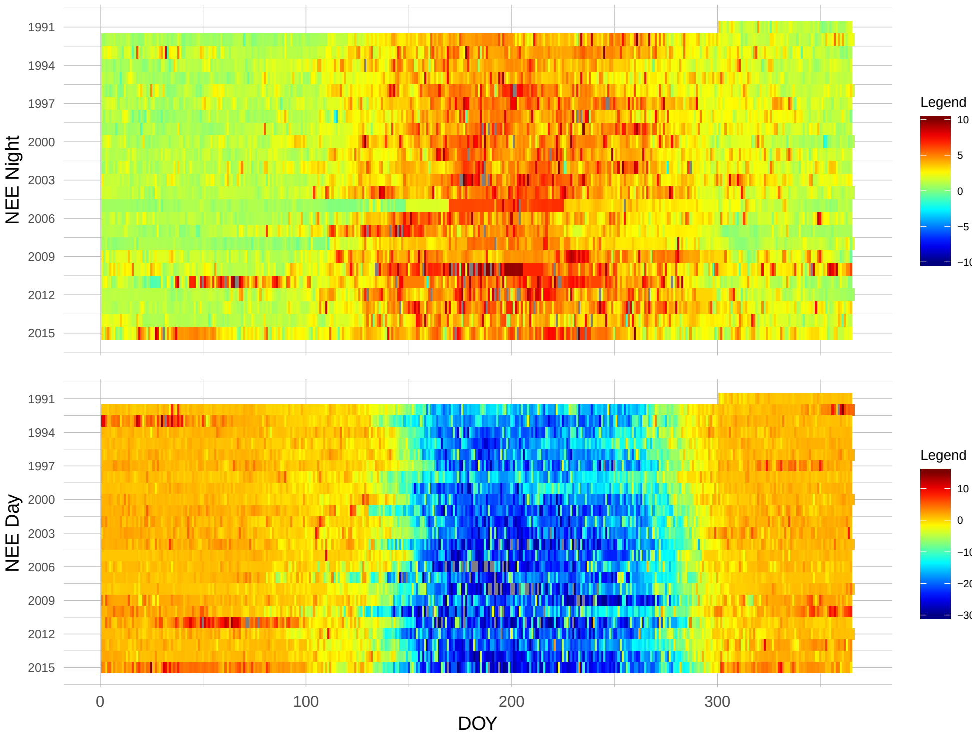


Figure 2: Harvard Forest EMS tower daily diurnal averages

2.1.2 Jones Ecological Research Center RD Flux Tower

Jones Ecological Research Center (JERC) at Ichauway is located near Newton, GA, 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 southwestward. 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 [16]. 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 [8]. Soils here often lack well-developed organic horizons [16, 8, 12].

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 [25]. Prescribed fire is a regular component of management here. Stands were often burned at regular 1-5 year intervals [16]. This has promoted wiregrass and legumes in the understory, while reducing the number of hardwoods [16]. The Red Dirt (RD) tower is contained within the mesic/intermediate sector of JERC. The 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 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 3.

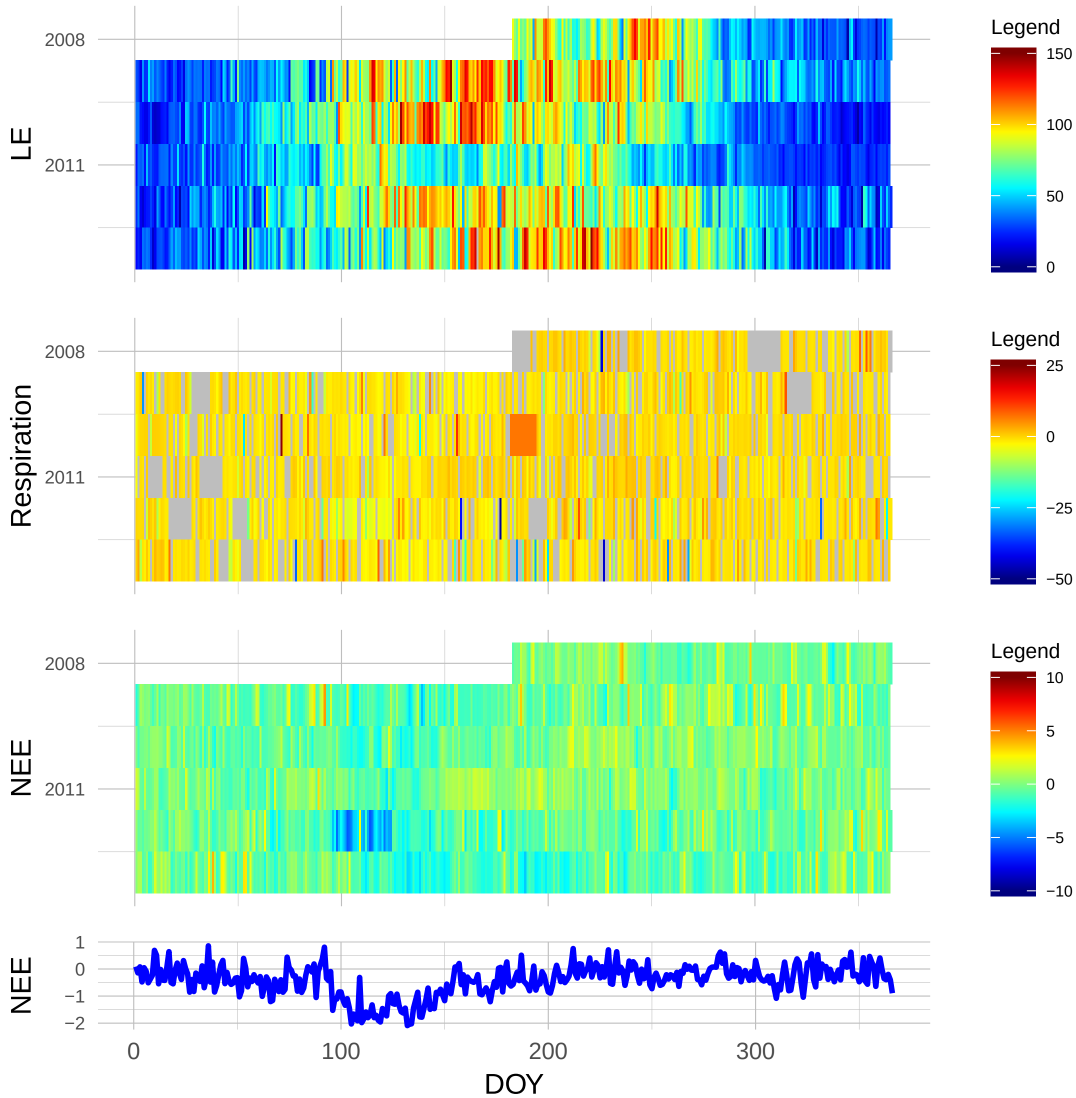


Figure 3: Jones Ecological Research Center RD tower daily averages

Patterns in daytime and nighttime NEE are shown below in Figure 2. 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).

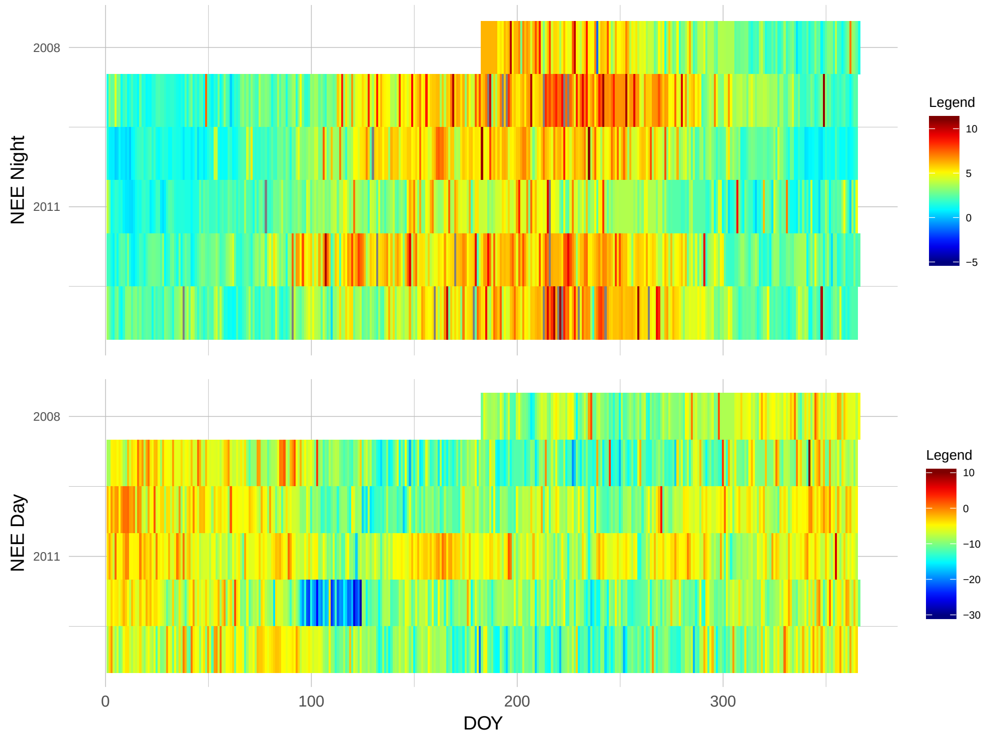


Figure 4: Jones Ecological Research Center RD tower daily diurnal averages

2.2 Site Data

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

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

Meanwhile, Jones Ecological Research Center has hosted multiple research efforts over the years, collectively resulting in a large data library. However, JERC data are not made open to the public and are thus only available upon request. One may find contact and other information at their website:

`http://www.jonesctr.org`

2.3 Metrics and Units

The areal extents of the single-cell model intercomparison were designed to correspond to 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, this 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, other conversions were necessary to harmonize metrics between the models and study sites. For example, moles CO_2 measurements were converted to moles C through 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 Sortie-PPA is provided in Table 1 below.

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 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.

2.4 LANDIS-II

The LANDIS-II model is an extension of the original LANdscape DIsturbance and Succession (LANDIS) model [28, 27, 15] into an open-source modular software framework [42]. The LANDIS family of models, which also includes LANDIS PRO [52] and Fin-LANDIS [35, 36], are stochastic models based on the vital attributes/fuzzy systems approach of the LANDSIM model genre [41]. This model genre borrows heavily from cellular automata [51] by applying simple heuristic rule-based systems, in the form of vital attributes, across two-dimensional grids. Models of this genre focuses on landscape-scale processes while assuming game-theoretic vital attribute controls over successional trajectories following disturbance [31]. The LANDSIM model genre is a natural fit for the classical forest fire model of statistical physics [9] given the cellular interaction basis of these model. In contrast to the original LANDIS model, LANDIS-II is designed to be modular, open-source, and implemented in Microsoft C# rather than ISO C++98 [18], easing model development in trade for a Microsoft software stack [42].

While LANDIS-II was historically limited the Microsoft Windows operating systems, the model may soon see native Linux support through the Microsoft .NET Core cross-platform development framework. 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 [19, 26, 14, 57, 45], the LANDIS family of models has enjoyable notable longevity and are currently united under the LANDIS-II Foundation.

Similar to the original CENTURY succession model [43], the Net Ecosystem Carbon and Nitrogen (NECN) model is heavily based on the classical CENTURY model [33, 34]. 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 only 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 in theory on Liebig's law of the minimum. The LANDIS-II variant of the CENTURY model found in NECN succession incorporates functionality from the biomass succession extension as well as other model core logic (i.e., rule-based controls). For a detailed description of the model, readers may refer to the original CENTURY publication [43]. Parameterization of LANDIS-II for both sites was based on updating parameters used in recent [10] and ongoing (Loudermilk et al., *in review*) work.

2.5 Sortie-PPA

The Sortie-PPA model [48] is based on a model reduction of the classical Sortie gap model that is simple and analytically tractable [32, 40]. The Perfect Plasticity Approximation, or PPA [48], is based on dual assumptions of perfect crown plasticity (e.g., space-filling) and phototropism (e.g., stem-leaning), both well supported in empirical and modeling studies [48, 37]. The discovery of the PPA was rooted in extensive empirical and simulation-based research [48]. 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 [17, 29], are popular model reduction techniques employed in current state-of-the-art terrestrial biosphere models. 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 partial differential equation [48]. The simple mathematical foundation of the PPA model is provided below 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 [48]. The segmentation of the forest canopy into understory and overstory 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. Following the orginal publication [48], recent work has again demonstrated that the PPA model accurately and precisely reduces the dynamics of the Sortie-ND gap model (Robbins and Strigul, *in review*).

In this work, we apply a simple biogeochemistry variant of the Sortie-PPA model. In this variant, 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 [4], using parameters based on another study [5]. Together with inventory data, general biomass equations were used to estimated dry weight biomass for tree stems, branches, leaves, and, fine and coarse roots [6]. Carbon content was assumed to be 50% of dry mass, as is commonly used. Monthly soil respiration was modeled using the classical approach of Raich et al. [39]. Soil organic C was modeled using the simple generalized model of Domke et al. [7]. 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.

2.6 Model Intercomparison

The Sortie-PPA and LANDIS-II model intercomparison for Harvard Forest (HF) EMS and Jones Ecological Research Center (JERC) RD flux towers was conducted using a collection of object-oriented functional programming scripts written in the R language for statistical computing [38]. The scripts were designed to simplify model configuration, parameterization, operation, calibration\validation, plotting, error calculation, and reproducibility of the presented results. 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 [22]. 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, RMSE follows the standard formulation, as shown in Equation 3.

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

Finally, the calculation of MAE is similarly unexceptional, per Equation 4.

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

While the Nash-Sutcliffe efficiency (NSE) is often found in a simulation model context, we selected the Bravais-Pearson interpretation of R^2 over NSE to simplify the presentation 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 [30]. 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, while 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., masking periodicity).

We compute R^2, RMSE, and MAE for the metrics described in Table 1 on page 9. 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 compare the models based on logistical criteria related to model 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 generalization
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

Both Sortie-PPA and LANDIS-II showed strong performance for the two model intercomparison sites, often achieving R^2 values approaching unity. Both models showed strong time-series correlations between predictions and observations across the range of metrics. On average, Sortie-PPA outperformed LANDIS-II across all sites and metrics tested (HF EMS $\overline{R^2} = 0.78, +0.07$, $\overline{RMSE} = 4.84, -1.53$; JERC RD $\overline{R^2} = 0.81, +0.02$, $\overline{RMSE} = 2.68, -0.19$. This result is based on calculating the 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

	Sortie-PPA			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, Sortie-PPA 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 flux tower and Jones Ecological Research Center RD flux tower.

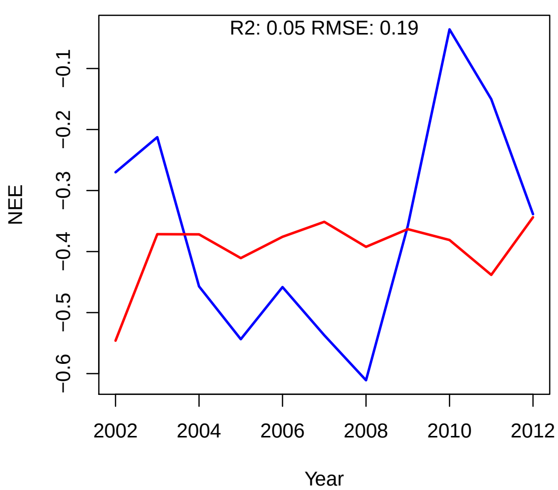
3.1 Harvard Forest EMS Tower

For the Harvard Forest EMS flux tower site, Sortie-PPA again showed higher R^2 values and lower RMSE and MAE values compared to LANDIS-II across the range of metrics tested. While Sortie-PPA 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 Sortie-PPA. Overall results for the Harvard Forest EMS flux tower site model intercomparison are shown in Table 3.

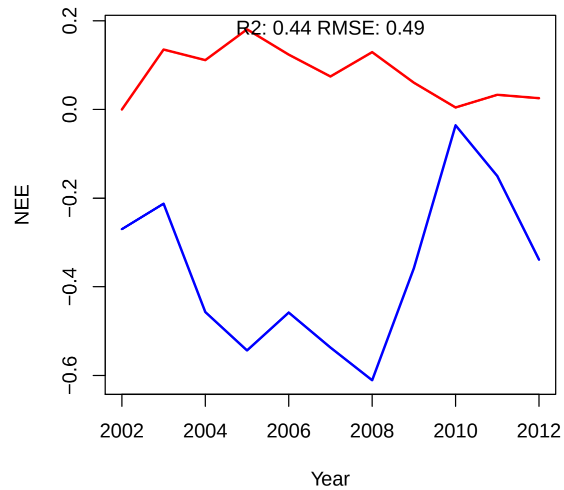
Table 3: Model fitness for Harvard Forest EMS tower

	Sortie-PPA			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}	...	0.58	0.58	...	1.07	1.07
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	0.78	4.84	4.67	0.71	6.37	6.29

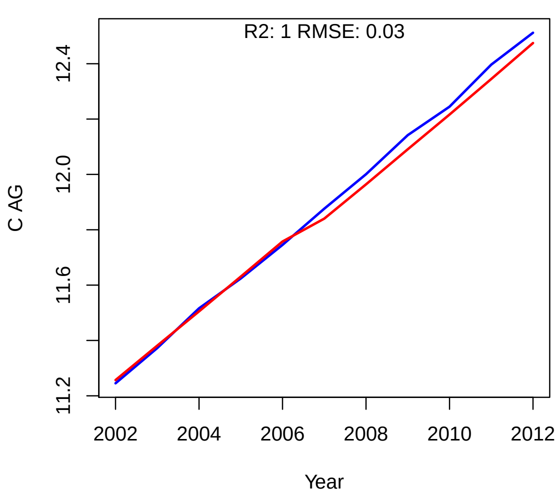
Analyzing figures for the Harvard Forest EMS flux tower site shows the temporal dynamics between observed and predicted values for both models. In Figure 5 below, we show the temporal differences in modeled NEE and aboveground C for the two models in comparison to observations for Harvard Forest EMS 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, Sortie-PPA outperformed LANDIS-II in aboveground C per both criteria. While LANDIS-II tended to underpredict aboveground metrics, Sortie-PPA tended to overpredict these metrics.



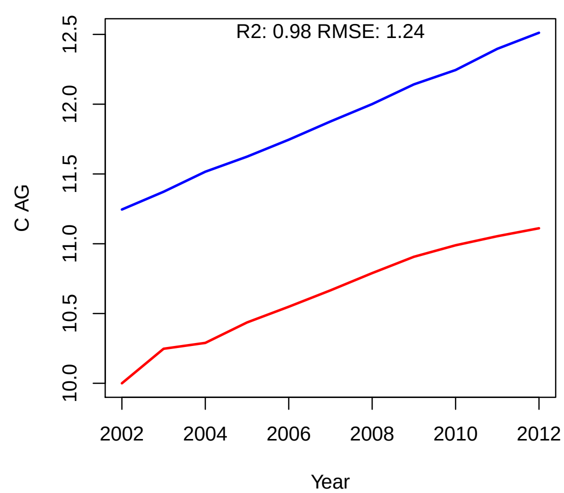
(a) Sortie-PPA NEE



(b) LANDIS-II NEE



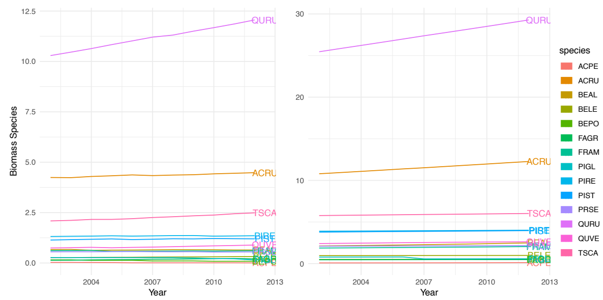
(c) Sortie-PPA C_{AG}



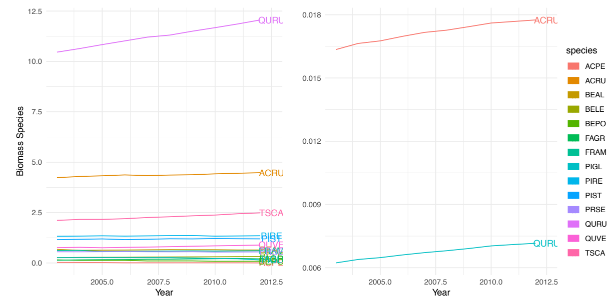
(d) LANDIS-II C_{AG}

Figure 5: Simulated and observed NEE and aboveground C
observations = blue, simulations = red

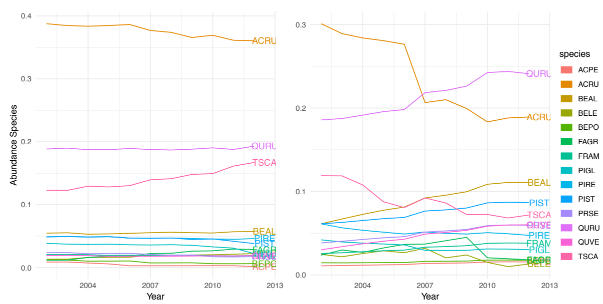
An analysis of simulated species biomass and abundance also shows greater fidelity of the Sortie-PPA model to data, as shown in Figure 6 below. As LANDIS-II does not contain data on individual trees, species relative abundance is calculated based on the number of cohorts of each species. The results for Sortie-PPA indicate the 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.



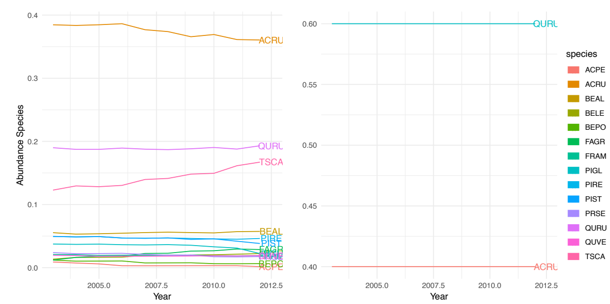
(a) Sortie-PPA B_{Sp}



(b) LANDIS-II B_{Sp}



(c) Sortie-PPA n_{Sp}



(d) LANDIS-II n_{Sp}

Figure 6: HF EMS: Simulated and observed species biomass and abundance left = observations, right = predictions

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, Sortie-PPA 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 Sortie-PPA demonstrated higher correlations and lower errors for most metrics tested, LANDIS-II outperformed Sortie-PPA in a few cases. This includes lower error magnitude for NEE, aboveground N, belowground biomass (dry weight), SOC, and SON. However, Sortie-PPA showed correlations equal or higher for all metrics, with lower errors for all other metrics. Overall results for the JERC RD flux tower site model intercomparison are shown below in Table 4.

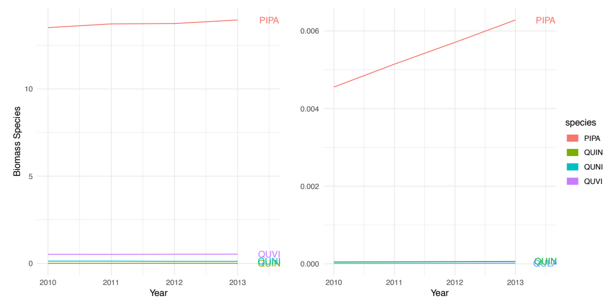
Table 4: Model fitness for Jones Ecological Research Center RD tower

	Sortie-PPA			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}	...	0.62	0.62	...	2.50	2.50
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	0.81	2.68	2.47	0.79	2.87	2.63

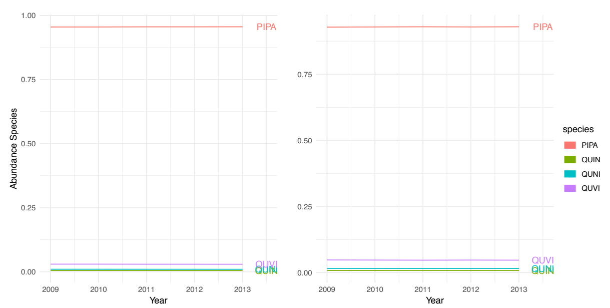
While both models shower higher performance for the JERC RD site, an analysis of simulated species biomass and abundance again indicates greater fidelity of the Sortie-PPA model to data, as shown in Figure 7. While LANDIS-II overpredicts the rate of longleaf pine growth, Sortie-PPA almost perfectly matches observed species abundance and biomass trajectories for all of the species. While the correlations are high, Sortie-PPA overpredicts the biomass magnitude.

Our results for the Harvard Forest EMS tower and Jones Ecological Research Center RD tower model intercomparison exercise clearly indicate strong performance by both models for the two sites. The results for JERC RD tower are particularly close between the two models. However, Sortie-PPA demonstrated better fidelity to observational data across a range of metrics on average. Next, we assess results related to the logistics of model deployment.

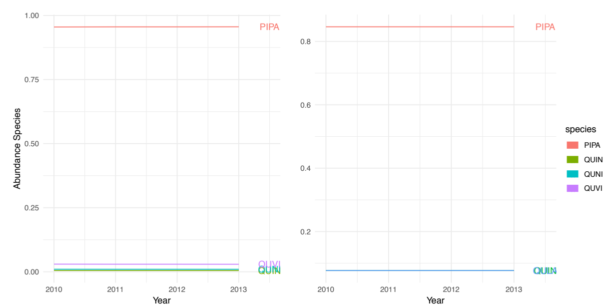
(a) Sortie-PPA B_{Sp}



(b) LANDIS-II B_{Sp}



(c) Sortie-PPA n_{Sp}



(d) LANDIS-II n_{Sp}

Figure 7: JERC RD: Simulated and observed species biomass and abundance left = observations, right = predictions

3.3 Model Usability, Performance, and Transferability

While the two models share a similar purpose and basis in forest dynamics and biogeochemistry modeling, they differ in notable practical and conceptual terms. The command-line version of the Sortie-PPA model used in this work, version 5.0, consists of approximately 500 lines of R code and is thus readily deployable across platforms, including cloud providers. Meanwhile, the LANDIS-II model core and Net Ecosystem Carbon and Nitrogen (NECN) succession extension are an estimated 2,000 and half a million lines of code, respectively. While this version of Sortie-PPA 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 [34], similar to the MC1 model [2]. This carries important implications for model parameterization needs. While Sortie-PPA relies on information on 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

First, we begin with an assessment of model usability.

1. Ease of installation
   While LANDIS-II requires the installation of one or more Windows executable files, depending on the options desired, Sortie-PPA 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 Sortie-PPA requires an order of magnitude fewer parameters. While some of these parameters can be difficult to locate in the literature, they may often be generalized at the genus level.

3. Ease of program operation
   Both models are run from the command line and are thus equally easy to operate. However, Sortie-PPA uses comma-separated-value (CSV) files for input tables, which are easier to work with than tables nested in raw text files. This additionally allows for simplification in designing model application programming interfaces (APIs), or model wrappers, a layer of abstraction above the models.

4. Ease of parsing outputs
   All Sortie-PPA outputs are provided in CSV files in a single folder while LANDIS-II generates outputs in multiple formats and in multiple folders. While the Sortie-PPA format is simpler and easier to parse, the image output formats used by LANDIS-II carry benefits in spatial applications.

3.3.2 Model Performance

Next, we assess model performance. 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 results sections. As shown in Table 5 below, Sortie-PPA was approximately 300% faster in our timing tests. This was somewhat surprising given that Sortie-PPA model individual trees in an interpreted language while LANDIS-II is written in a compiled language. The difference in speed is likely attributable to the simplicity of the Sortie-PPA model.

Table 5: Simulation timing results

Site	Model	Duration (years)	Elapsed (sec)
HF EMS	Sortie-PPA	11	8.51
HF EMS	LANDIS-II	11	30.08
JERC RD	Sortie-PPA	5	2.25
JERC RD	LANDIS-II	5	8.02

3.3.3 Model Transferability

Here, we discuss model transferability. In this section, we assess how easy or difficult it is to apply the models to new locations or to transfer the models to another computer system. Both are important for the logistics of model deployment.

1. Model generalization
   Both models appear to generalize effectively to different forested regions of the world. 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 Sortie-PPA, it may often be possible to rely on published parameters. Meanwhile, the growth, mortality, and fecundity parameters used by Sortie-PPA are easy to calculate with common field data.

3. Size of the program
   Sortie-PPA 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 be on the way with Microsoft .NET Core, LANDIS-II is written in C# and is thus Windows-based. Sortie-PPA is written in R and thus has full cross-platform support.

5. Ease of training new users
   While both models have a learning curve, the practical simplicity of Sortie-PPA makes it easy to train new users. While LANDIS-II contains more features, these come at the cost of training new users.

4 Conclusion

In conclusion, both Sortie-PPA and LANDIS-II effectively captured dynamics that were 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" that drive interannual and decadal variation in NEE [50]. While Sortie-PPA indicated stronger performance across the range of metrics tested, including the logistics of model deployment, LANDIS-II also performed well across these metrics. Further studies are needed to compare more aspects of the two models in a structured manner. We hope that this study serves as the basis for future forest ecosystem model intercomparisons in the North American continent, similar in spirit to the former TDE Ecosystem Model Intercomparison project [13]. Similarly, the aims of this work are 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 this regard, there are beneficial aspects to both modeling approaches and the trade-offs presented largely depend on the desired application.

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Appendix A

Supplementary Materials

All model parameters files and R scripts used in this model intercomparison exercise are available at our project GitHub repository.