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A model comparison of fire return interval impacts on carbon and species dynamics in a southeastern U.S. pineland

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Abstract. Ecosystem process models can be used to predict forest response to disturbances at a range of scales. Selection of the spatial class of model should depend on the scale of the research or management question, and model type should depend on the ecosystem attributes of interest. In some cases, multiple classes of models could be used to address a single research question, with evaluations at each scale having potential benefits and drawbacks. This study examines two classes of models relative to how fire return intervals impact carbon and species dynamics in a southeastern U.S. pineland. A model that can be run as a global class model (ED) and a landscape class model (LANDIS-II) were parameterized with species inventory data from an experimental *Pinus Palustris* (longleaf pine) forest in southwest Georgia, and simulations were calibrated with literature values, then validated with eddy-covariance data from the study site. A variety of fire scenarios that included prescribed fire with a 2-yr return interval, fire exclusion, and three wildfire scenarios (20-, 50-, and 100-yr return intervals) were used for model runs. Results were compared and evaluated with regard to ecosystem carbon and species dynamics. Both models illustrated that prescribed fire provided the greatest carbon sequestration potential and most stable aboveground biomass through time when compared to the wildfire scenarios. The fire exclusion scenario for LANDIS-II was the only scenario where prescribed fire did not provide the greatest carbon sequestration potential. However, fire exclusion on the order of centuries was a condition of this outcome and the occurrence of such long fire-free periods is considered unrealistic in this fire-prone landscape. Differences between models were primarily the result of the underlying characteristics of each model class, namely the spatial resolution and number of species included. In the end, two vastly different scale models supported the conclusion that high frequency prescribed fire in southeastern U.S. pinelands stabilizes carbon and maintains species composition in an ecosystem that is a known ecological hotspot.

Key words: carbon sequestration; ecosystem demography; ecosystem modeling; fire emission; Ichauway; Jones Center; LANDIS-II; longleaf pine; prescribed fire; wildfire.

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Introduction

Ecosystem process models can be used to aid management decisions by predicting how various environmental changes may influence an ecosystems' composition, structure, and distribution. A wide range of models have been developed that balance the spatial and temporal scale of the model with the simulated complexity of biophysical and biogeochemical processes, such as forest succession, disturbance, competition, soil respiration, and nutrient dynamics (Turner et al. 2004, 2016, De Bruijn et al. 2014). The complexity at which these processes are represented within each model is a function of how realistic and necessary the processes are at various scales, which is also driven by computational demands. For instance, ecosystem process models parameterized at the stand, or gap level, emphasize biogeochemical and biophysical processes of individual trees or a small group of trees at fine spatial (meters) and temporal scales (~years). Forest landscape class models simulate spatially explicit processes, such as dispersal, nutrient cycling, and disturbance over larger areas (~1000 ha) and larger time steps (~centuries) (Lischke et al. 2006, Syphard et al. 2011, Xu et al. 2012, Jin et al. 2017, Wang et al. 2017), at the cost of some finer-scale attributes such as explicit tree location. Dynamic global vegetation models (DGVMs) operate globally with spatial resolutions on the order of degrees, with temporal resolutions similar to landscape models, and can often be coupled with global circulation models (GCMs) to simulate feedbacks to climate (Woodward et al. 1995, Cox 2001, Krinner et al. 2005, Sitch et al. 2008, Fisher et al. 2018). This class of model requires even more simplification of finer-scale attributes such as using plant functional types (PFTs) rather than individual tree species. Scaling strategies enable models built for a certain scale to function at other scales, but it is typical to trade complexity of the inherent simulated processes for increased spatial and temporal resolution (Sato et al. 2007, Sato and Ise 2012, Snell et al. 2014, Flanagan et al. 2019*b*).

Ecosystem process models are important to land managers because they provide predictions of how disturbances, particularly fire, alter ecosystem attributes (Hurtt et al. 2002, Lenihan et al. 2003, Beringer et al. 2007, Lawson et al. 2010, Scheiter et al. 2015, Littell et al. 2016). Fire is an ecosystem process that directly influences species composition, structure, and distribution in forests, and hence carbon sequestration potential, but response to fire and fire frequency is unique across ecosystems and their inherent attributes. For example, a slight increase in the frequency of repetitive fires might change the dominant species of an ecosystem but leave total biomass relatively stable (Kasischke et al. 2010). However, fire exclusion that decreases fire frequency can affect species composition, forest structure, and carbon balance in unique ways that have not been fully explored (Hurteau and Brooks 2011). A long interval between fires can alter the dominant species type and increase the quantity of available fuels such that future fires result in higher intensity and severity (Westerling and Bryant 2008). Following such a sequence, state shifts to different forest types, or even conversion from forests to grasslands, shrublands, or savannas can be common (Ryan and Frandsen 1991, Swezy and Agee 1991, Varner et al. 2007, 2009, O'Brien et al. 2010). Though these changes are not always permanent, they can alter species distribution and carbon sequestration potential for decades (Hurteau and North 2009). To mitigate some of these undesirable ecosystem changes, prescribed fires are used to manage vegetation composition and structure, reduce fuel loads, and maintain specific ecosystem types.

In the southeastern United States, pine forests have historically been maintained with frequent prescribed fire to promote the dominance of fire-adapted pine species, especially longleaf pine (*Pinus palustris*) in the Coastal Plain. This frequently burned ecosystem promotes high biological diversity (Dell et al. 2017) and reduces competition from broad-leaved tree species (Glitzenstein et al. 1995). The high fuel accumulation rate in this ecosystem makes it prone to high-intensity stand-replacing fires in as little as a decade if prescribed fire is withheld (Outcalt and Wade 2004). In as little as two decades, this ecosystem can transition to a hardwood dominated forest (Hartnett and Krofta 1989) that is still susceptible to a stand-replacing fire (Varner et al. 2005). Besides minimizing the potential of a stand-replacing fire, frequent fires provide other benefits, including maintaining quality trees for selective timber harvesting, conservation of rare species, and improving foraging habitat for game species such as white-tailed deer, wild turkey, and bobwhite quail (Kilburg et al. 2014, Cherry et al. 2017, Kamps et al. 2017, Stephens et al. 2019). However, if fire were to be completely excluded for many decades, a mature closed-canopy hardwood forest could potentially sequester more aboveground carbon than a pine forest but with a concomitant loss of biological diversity (Brown et al. 1997, Gonzalez-Benecke et al. 2015, Martin et al. 2015). Therefore, the trade-offs between carbon sequestration potential vs. other ecological benefits could be considered. Thus, the primary goal of this research was to understand these complex interactions between fire return interval, tree species composition, and carbon sequestration capacity by using ecosystem process models.

Most modeling studies select a single model to assess the impacts of management on future disturbance scenarios, but the inherent strengths and weaknesses of model selection on the consequences of altered fire frequencies have not been sufficiently evaluated (McGuire et al. 2012), particularly between classes of models. For the United States, numerous models exist that are not processed based on but operate at the landscape scale and can inform management decisions based on historical data. However, if a process-based landscape class model is needed but not readily available, often global class process models can be used for a preliminary evaluation at those sites (Silva et al. 2019). For this study, we explored how various fire return intervals impacted carbon and species dynamics in a southeastern U.S. pineland by using a previously parameterized landscape class process model [Landscape Disturbance and Succession II (LANDIS-II)] and a model that can function as a global class process model (Ecosystem Demography [ED]). Our central question was how well frequent prescribed fire stabilizes and maintains carbon and species dynamics in a southeastern U.S. pineland compared with wildfires. This work expands on our previous LANDIS-II research (Flanagan et al. 2019*a*) by utilizing the same fire scenarios from that study within the ED model. The five fire scenarios simulated were as follows: fire exclusion, a prescribed fire interval of 2 yr, and wildfire return intervals of 20, 50, and 100 yr. The new ED results were then used for an inter-model comparison that assessed the impact of each scenario on changes and differences in (1) total aboveground biomass (AGB), (2) net ecosystem carbon balance (NECB), and (3) species composition. Both models were also validated for net ecosystem exchange (NEE) of CO_2 with eddy-covariance (EC) site data. The similarities and differences for each model and pros and cons of using a given model class for this type of research question are discussed in detail.

Methods

Study area

For this study, we utilized the landscape of The Jones Center at Ichauway, located in southwestern Georgia, Unites States. It is a 115-km^2 (11,736 ha) research and conservation site in the Coastal Plan (31°13′N, 84°29′W; Fig. 1; Mitchell et al. 1999, Goebel et al. 2001). The climate is characterized as humid subtropical (Christensen 2013) with long, hot summers and short, cool winters that yield yearly temperatures ranging from 5 to 34°C and precipitation averaging 132 cm/yr, which is evenly distributed (Lynch et al. 1986, Palik et al. 1998). The karst landscape is weakly dissected by alluvial deposits with elevation ranges from 23 to 93 m above sea level (Holder and Schretter 1986). Soils are fine to moderately fine loamy or clay subsoils that range from poorly to excessively drained (Goebel et al. 2001).

For research purposes, The Jones Center is composed of several major ecological communities, with the most extensive (~6000 ha) being the longleaf pine ecosystem. This ecosystem is primarily second-growth forest and has had prescribed fire applied every two to four years for the last 80 yr. Thus, the overstory is dominated by 80- to 100-yr-old longleaf pines, with an understory of over 900 native plant species, including bunchgrasses, primarily wiregrass (*Aristida stricta*), many forb and grass species, and numerous hardwood species (Goebel et al. 2001). The hardwoods have generally remained small in stature because prescribed fire repeatedly top-kills aboveground plant parts, but some mature hardwoods are found in the overstory (Perkins and Conner 2004). For the landscape class model, we limited the study to 1267 ha within the longleaf ecosystem. This is because long-term modeling plots, which are needed to initialize the model, spanned the range of environmental conditions present in this ecosystem. For additional details of the study area, refer to Flanagan et al. (2019*a*).

Landscape disturbance and succession-II

Landscape disturbance and succession-II was chosen to represent the landscape class model and was parametrized with specific data from Fort Benning, GA (Martin et al. 2015, Swanteson-

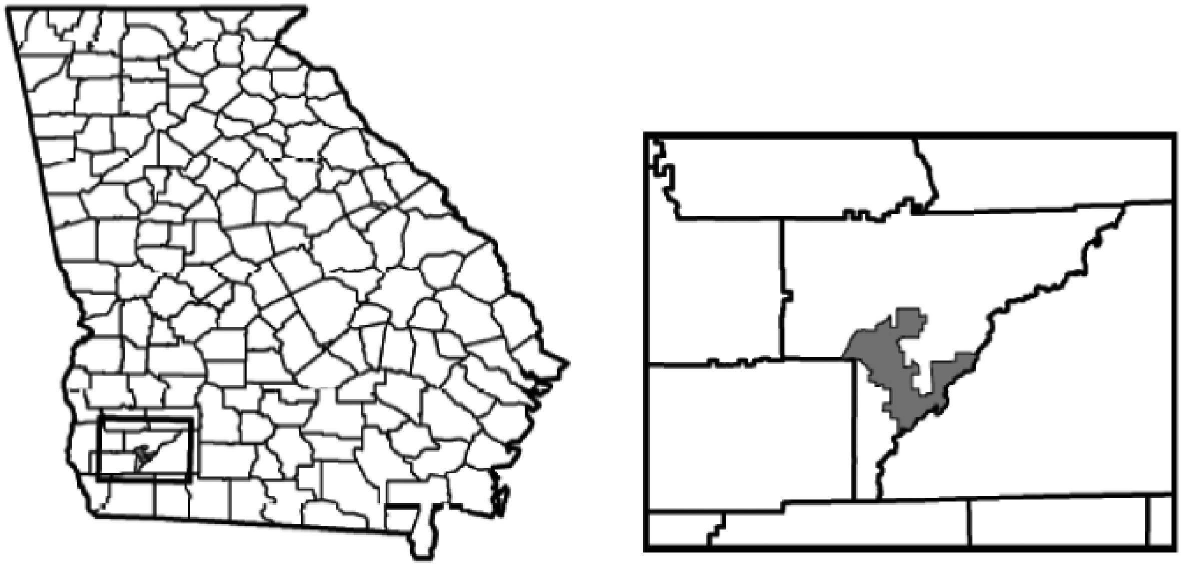

Fig. 1. Study site location illustrating a map of Georgia, USA (left), and its counties with the location of The Jones Center at Ichauway, Baker County, highlighted in gray and expanded on the right.

Franz et al. 2018), and literature values (Botkin et al. 1972, Pastor and Post 1986, Burns and Honkala 1990, Sutherland et al. 2000, Bachelet et al. 2001, Wimberly 2004, Hendricks et al. 2006, Scheller et al. 2011*a*, *b*, Samuelson et al. 2014). Validation was done by comparing outputs with eddy-covariance data (see Methods: Validation with Eddy-covariance data). In this section, we provide brief details on LANDIS-II parameterization for this study. For a more detailed description of parameterization and calibration of all the components used for LANDIS-II, see Flanagan et al. (2019*a*). All parameters and output processing scripts can be found in the LANDIS-II GitHub repository, https://github.com/ LANDIS-II-Foundation, under Project-JonesEcological ResearchCenter-2019.

At its core, LANDIS-II is used to study forest dynamics at landscape scales over long time periods through the integration of ecosystem processes and disturbances. In a gridded landscape, where the user determines the grid spatial scale, each cell simulates how cohorts of a species at a given age progress through time. This is governed by growth rates, competition, reproductive ability, and response to disturbance events. Such events can include, but are not limited to, insects, wildfire, prescribed fire, wind, harvesting, fuel treatments, and climate change, and can be species-specific (Scheller et al. 2007). Of the numerous extensions available beyond the core package of LANDIS-II, the Net Ecosystem Carbon and Nitrogen (NECN) Succession (v4.2; Scheller et al. 2011*b*) and Biomass Harvest (v3.1.6; Gustafson et al. 2000) extensions were used. The NECN extension is derived from the CENTURY model (Parton et al. 1987, 1988) and tracks above- and belowground carbon and nitrogen through time as determined by a species age, growth rate, ability to compete for resources (water, nitrogen, light), and responses to various disturbances. The Biomass Harvest extension was chosen to simulate fire scenarios to make these disturbance events deterministic and comparable between prescribed fire and wildfire scenarios (Flanagan et al. 2019*a*).

Initial vegetation communities were represented as a species distribution map with inherent age classes. The initial communities were determined by long-term monitoring (LTM) plots provided by The Jones Center. Twelve species were used for the initial vegetation communities. LANDIS-II defines each species by individual characteristics and a plant functional type (PFT), which were conifer and hardwood. The conifer PFT included longleaf pine, slash pine (*P. elliotti*), and pond cypress (*Taxodium ascendens*). The hardwood PFT had eight oaks, live (*Quercus virginiana*), southern red (*Q. falcata*), laurel (*Q. hemisphaerica*), blue jack (*Q. incana*), turkey (*Q. laevis*), sand post (*Q. margaretta*), water (*Q. nigra*), post (*Q. stellate*), and also swamp tupelo (*Nysa biflora*).

Ecosystem demography

The ED model was selected as the global class model as it had already been parameterized for the area with a similar harvest function (Flanagan et al. 2016, 2019*b*, Silva et al. 2019). The ED model (Hurtt et al. 1998, Moorcroft et al. 2001) now has numerous variations that have been published (Hurtt et al. 2002, 2010, Medvigy et al. 2010, Dietze et al. 2011, Medvigy and Moorcroft 2012, Flanagan et al. 2016, 2019*b*). The version chosen here follows the adjustments made by Hurtt et al. (2002) for North American tree species, with the modifications made by Flanagan et al. (2016, 2019*b*). Previous research successfully implemented this version in North America (Hurtt et al. 2004, 2016, Fisk et al. 2013, Flanagan et al. 2016, 2019*b*, Dolan et al. 2017) and had a harvest function similar to that of LANDIS-II added for charcoal extraction studies in Mozambique (Silva et al. 2019). A version running the same core code but with downscaled inputs is currently being used in NASA's Carbon Monitoring System (CMS) (Hurtt et al. 2019) and the NASA Global Dynamics Investigation (GEDI) mission (Dubayah et al. 2020).

Ecosystem demography is a mechanistic model that approximates the first moment of the spatial stochastic ("gap") ecosystem model. The approximation relates size, age, and structure in a pseudo-spatial framework to minimize computational time when compared to spatially explicit simulations. PFTs are grouped into classes dependent on physiognomy, leaf form, photosynthetic pathway, and other characteristics, and compete for water, nutrients, and light governed by submodels of growth, soil water availability, phenology, disturbance, and biogeochemistry. The two PFTs used for this region were cold deciduous and pine. This version runs at a half-degree resolution, so due to the size of the region, only a single grid cell was simulated. ED typically starts a simulation from bare ground, meaning it does not start with an initial community distribution as LANDIS-II does, but can be restarted with the species distribution it generated. Therefore, as the current vegetation distribution would not exist without the continuous presence of fire, the mortality factor for the deciduous species was increased in a spin-up run so that the percentage of pine vs. deciduous species on the landscape were similar to the percentage of conifer vs. hardwood species in LANDIS-II. This increased mortality factor was not used for the actual scenarios.

Model properties

Each model had slightly different climate and soil properties. LANDIS-II used 16 yr of climate data (2000–2016) from the Georgia Automated Environmental Monitoring Network (GAEMN 2015). ED used 21 yr of data (1989–2010) from the Multi-Scale Synthesis and Terrestrial Model Intercomparison Project (MsTMIP) conducted by the North American Carbon Program (NACP) (Huntzinger et al. 2013, Wei et al. 2014). This is a combination of the National Centers for Environmental Prediction (NCEP) and Climate Research Unit (CRU) climatologies at global half-degree resolution. Both models used soil data from the National Resources Conservation Service Soil Survey Geographic Database (NRCS SSURGO). The differences in model parameters and other general information are shown in Table 1. As LANDIS-II is a landscape class model, the climate and soil attributes were used to create nine different ecoregions across the 1267-ha area at a 1-ha resolution. ED being used as a global class model had only one climate and soil combination that ran for its half-degree resolution.

Fire scenarios

Five fire scenarios with fire return intervals informed by literature and empirical data were run for both models. They were as follows: a frequent prescribed fire regime (2-yr return interval), fire exclusion, and three infrequent wildfire scenarios (20-, 50-, and 100-yr return intervals). When a fire (prescribed or wildfire) occurred, it was applied to the entire domain. ED required this with its resolution, and although LANDIS-II was parameterized to allow for different areas to burn at different time intervals, previous research showed no impact on the general trend of results (Flanagan et al. 2019*a*) and this approach facilitated a consistent comparison between the models. The prescribed fire and fire

Table 1. Model parameters and general information.

Model	LANDIS-II	ED
Resolution	1 ha, for 1267 total sites	Half degree (~60 km by 60 km), for one total site
Timescale (300 yr of simulations)	Monthly predictions outputted yearly	Monthly predictions outputted yearly
Species	12 species of age-cohorts	Two plant functional types (PFTs)
Climate inputs	Minimum temperature, maximum temperature, total precipitation	Temperature, precipitation, specific humidity or dewpoint, photosynthetically active radiation (PAR)
Soil inputs	Depth, drainage, field capacity, wilting point, percent sand, percent clay	Depth, conductivity, degree of saturation, maximum moisture content, texture
Ecoregions (soil and climate combinations)	Nine combinations	One combination
Simulation type	Stochastic	Deterministic
Growth	Age- and species-based	Age and PFT- and height-based

exclusion scenarios served as controls where maximum AGB was compared to literature values. For fire exclusion, each model ran from initial conditions with no additional disturbance and a transition from a pine to a hardwood forest with a maximum AGB of ~250 Mg/ha, similar to Brown et al. (1997), was observed. Prescribed fire was applied every 2 yr as it is the mean return interval at The Jones Center. This scenario removed a species-dependent percentage of vegetation from each model such that when the ecosystem was stable, the total AGB was similar to Gonzalez-Benecke et al. (2015) for an unthinned longleaf pine stand and the percentage of longleaf to hardwoods on the landscape was similar to Loudermilk et al. (2011). When the slightly longer return intervals used by Gonzales-Benecke and Loudermilk (3-yr and 2.85-yr return intervals, respectively) are accounted for, our final prescribed fire AGB results of ~195 Mg/ha vs. ~230 Mg/ha and percent hardwoods that occupied 5% of the landscape vs. 8% were reasonable based on known trends.

For the wildfire scenarios, Outcalt and Wade (2004) found that in the absence of fire, some longleaf ecosystems experienced stand-replacing fires in as little as a decade due to rapid fuel accumulation. Varner et al. (2007) also found 91% overstory mortality for a site that had not experienced fire for 45 yr. Therefore, a conservative lower bound of 20 yr for a stand-replacing wildfire was chosen, with 50- and 100-yr return intervals used to represent other forest successional stages, as well as a wide range of carbon sequestration and emissions possible within each model. For further consistency between models, we used each model's harvest functions to simulate a deterministic fire regime. This surrogate approach eliminated inconsistencies of stochastic fire events that confound model comparisons and simulated survival of the youngest cohorts (ages 1–3) without the need to reseed or resprout the domain after a wildfire. All other age classes were removed as a single event during a simulation. With this approach, the soil carbon pools were also appropriately adjusted after fire events to match literature values. For the prescribed fire scenario, values for consumption rates in a longleaf ecosystem of 30% of woody AGB and 77% of leaf litter were used (Ottmar et al. 2016). For the wildfire scenarios, 81% and 100% of the respective pools were adjusted (Regelbrugge and Smith 1994). All simulations were run for 300 yr. Each fire scenario was run once for ED because it is strictly deterministic. For LANDIS-II, our methodology created an environment where deterministic fire events dominated the inherent stochastic physiological processes. Therefore, each LANDIS-II fire scenario was run for five simulations. We compared each model's outputs of AGB, NEE, NECB, and species dynamics. For more details on model parameterization, scenario development, and validation, see Flanagan et al. (2019*a*).

Validation with eddy-covariance data

Model validation involved comparison to eddy-covariance (EC) data taken from The Jones Center (Starr et al. 2015, 2016). Three flux tower sites, which experienced biannual burning (every odd year) from January 2009 to December 2013 (Whelan et al. 2013), were compared to each model's outputs. As LANDIS-II requires the user to input climate data, climate from these explicit times was used for a truly independent validation. As ED's climate is precomputed, no changes were made and the representative year was used. Each model's predicted NEE, where negative values represented sequestration, was compared with the EC data.

Results

Eddy covariance

The average net ecosystem exchange (NEE) over this five-year period was -0.73 Mg C$\cdot$m$^{-2}\cdot$yr^{-1} for the EC data, -0.94 Mg C$\cdot$m$^{-2}\cdot$yr^{-1} for LANDIS-II, and -0.40 Mg C$\cdot$m$^{-2}\cdot$yr^{-1} for ED (Fig. 2).

Aboveground biomass

Both models predicted maximum AGB of ~250 Mg/ha after ~100 yr in the fire exclusion scenario and remained relatively stable for the duration of that simulation (Fig. 3). Also, both models predicted maximum AGB of ~195 Mg/ha in the prescribed fire scenario with a decrease in AGB toward the end of the scenario. As this is a second-growth forest of relatively the same age dominated by one species, either longleaf pine or the pine PFT for LANDIS-II and ED, respectively, age-related mortality was responsible for this trend. When the scenarios were extended past this time frame, total AGB rebounded from this age-related perturbation and returned to the established maximum AGB due to recruitment of new individuals into the stand. The wildfire scenarios showed that LANDIS-II's representation of multiple similar species on the landscape (the eight oak species) quickly achieved maximum predicted total biomass and was made for a smoother curve. In LANDIS-II, this was ~80 yr after a fire event, while ED was still not at maximum predicted AGB when fire was excluded 100 yr after a fire event.

Net ecosystem carbon balance

Net ecosystem productivity (NEP), which does not account for biomass removed by fire, also showed the impact of ED not reaching maximum

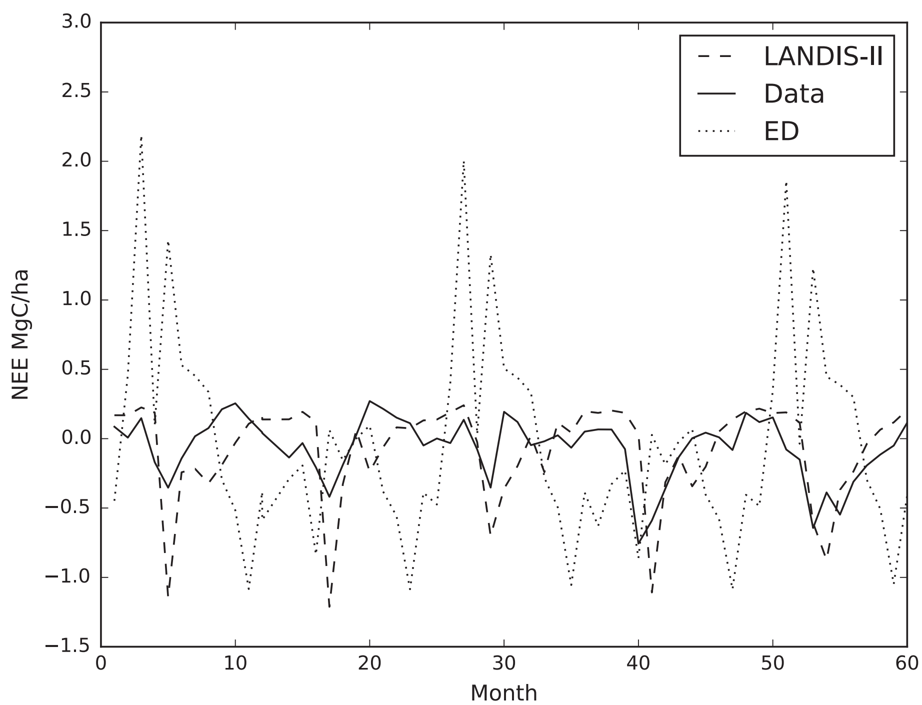

Fig. 2. Monthly predicted net ecosystem exchange (NEE) of the models and the eddy-covariance (EC) data. Negative values represent sequestration, and positive values represent emission.

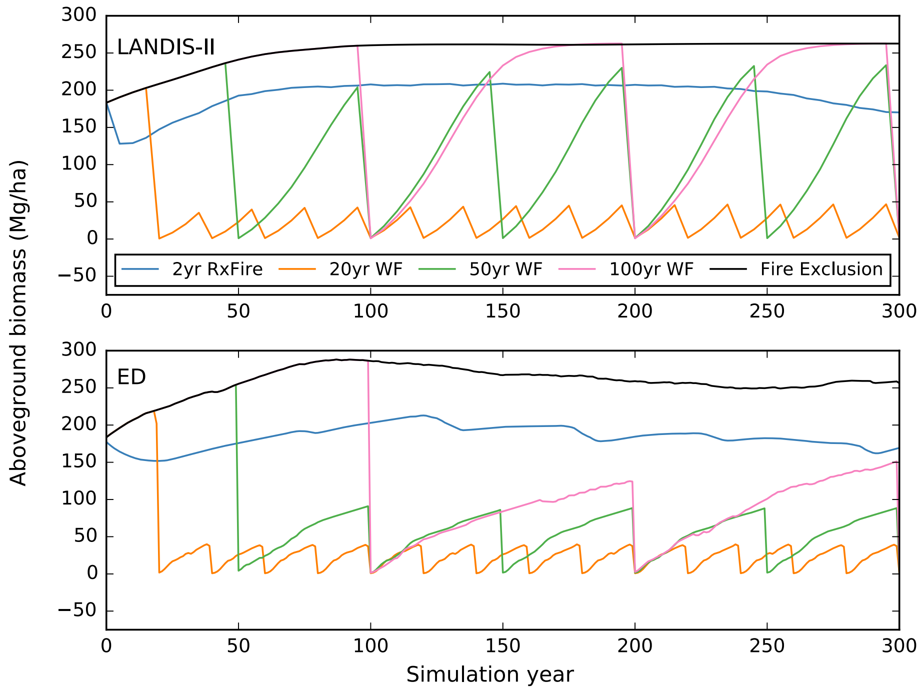

Fig. 3. Yearly model predicted aboveground biomass (AGB) for all scenarios.

biomass. Both models predicted emissions after a fire event (negative values) and then sequestration (positive values) a few years later (Fig. 4). However, as LANDIS-II had reached maximum potential AGB by the end of the 100-yr wildfire return scenario, and reached near-maximum values (~80–90% of maximum) in the 50-yr wildfire scenario (Fig. 3), predicted NEP was zero or near zero (Fig. 4) for these scenarios. As ED did not reach maximum potential AGB in any of the wildfire scenarios (Fig. 3), it continued to predict positive NEP until the next fire event (Fig. 4). To calculate NECB, NEP was combined with the loss of biomass from fire. This was tracked through time cumulatively, with ED predicting slight net carbon gains (sequestration) for all scenarios, whereas LANDIS-II predicted slight net losses of C (emissions) (Fig. 5). ED predicted prescribed fire to have the greatest carbon sequestration potential, while LANDIS-II predicted it second to the fire exclusion scenario.

Species distribution

In the prescribed fire scenario, both models predicted a stand dominated by longleaf pine (Fig. 6 Rx). In the fire exclusion scenario, both models predicted a transition to a hardwood-dominated forest (Fig. 6 Exclusion) with a higher maximum total AGB than the prescribed fire scenario. The 20-yr wildfire scenarios showed similar results for both models as well. The major differences were between the 50- and 100-yr wildfire scenarios as LANDIS-II reached maximum potential biomass quicker than ED.

Discussion

In this model comparison, two classes of models, a landscape scale and DGVM, predicted that prescribed fire benefits long-term carbon sequestration and stable AGB in a southeastern U.S. pineland (Figs. 3, 5). Given the large discrepancies between resolution, independent core model development, inherent processes, and species dynamics, the model outputs were remarkably similar, particularly when fires occurred either very frequently or were excluded for the entire time frame (Fig. 6: Rx, 20 yr, Exclusion). This convergence in model outputs gives confidence in the generality of this conclusion. Model similarities were also supported by their validation against an independent data set of NEE (Fig. 2).

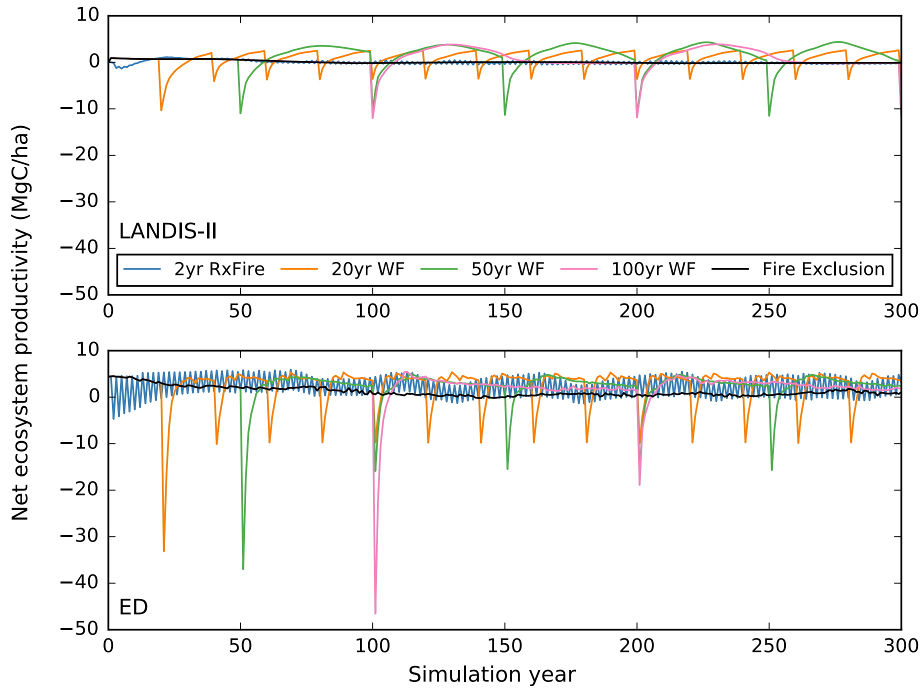

Fig. 4. Yearly model predicted net ecosystem productivity (NEP) for all scenarios. Negative values represent emission, and positive values represent sequestration.

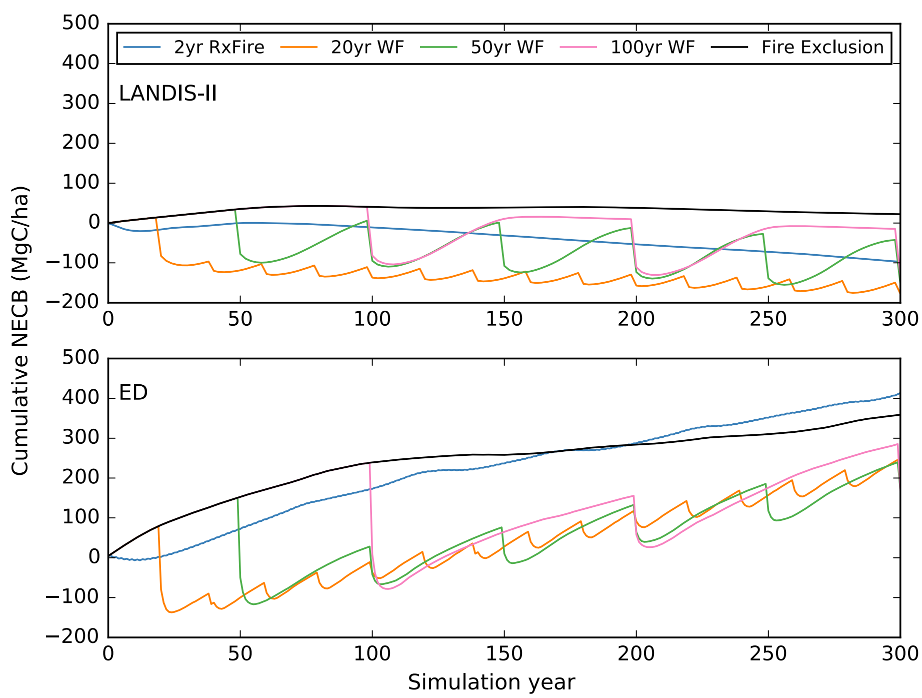

Fig. 5. Cumulative predicted net ecosystem carbon balance (NECB) for all scenarios. Negative values represent emission, and positive values represent sequestration.

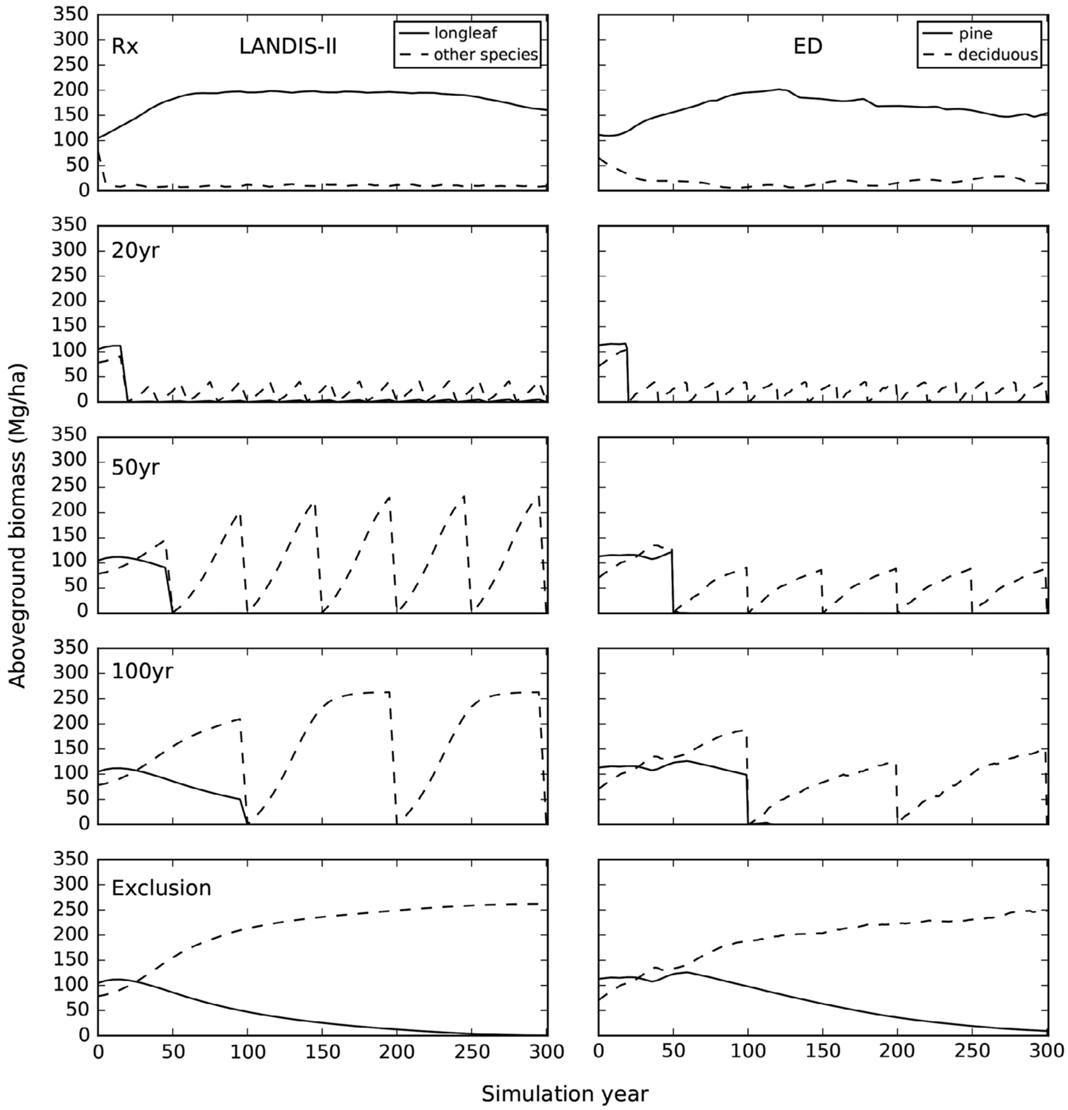

Fig. 6. Yearly model predicted aboveground biomass (AGB) for longleaf vs. other species (LANDIS-II) and pine vs. deciduous (ED).

Our results were focused on yearly predictions, which were similar, but were the product of monthly temporal patterns that showed more variation. The average NEE over this five-year period was -0.73 Mg C·ha^{-1}·yr^{-1} for the EC data, -0.94 Mg C·ha^{-1}·yr^{-1} for LANDIS-II, and -0.40 Mg C·ha^{-1}·yr^{-1} for ED. This illustrated a ~±0.3 Mg C^{-1}·ha^{-1}·yr^{-1} difference in mean NEE between models and data, which is quite small, especially given the flux tower data were not used to calibrate either model. The LANDIS-II predictions tracked particularly well as the scenarios were run with explicit climate data related to the time period of the EC data. ED's predictions were reasonable particularly in light of the precomputed climate input data used. At a yearly time step, this study showed that either model can be reliably used to predict the effects of changes in fire frequency on landscape carbon flux within this ecosystem type.

The two models were similar with respect to AGB, NEP, and species distribution results for prescribed fire, fire exclusion, and the 20-yr wildfire return (Figs. 3, 4, 6). Differences occurred in the predictions for the 50- and 100-yr wildfire scenarios because of the underlying species dynamics (Fig. 6). Both models showed the dominance of hardwoods in the absence of fire, but the underlying species dynamics impacted the time to reach maximum potential AGB. In these scenarios, where LANDIS-II had eight similar species (the oak species) growing on the landscape vs. one (cold deciduous PFT) for ED, LANDIS-II was able to reach maximum potential AGB at ~80 yr while ED did not reach maximum AGB until beyond the 100-yr scenario. Even though in ED the deciduous PFT had less competition for resources, growth was still limited by the number of new individuals the PFT could produce in a year. With only one dominant PFT per scenario, and one soil and climate type for the entire domain, ED's response to disturbance events was not as smooth (Figs. 3, 6) as LANDIS-II's response, where the multiple oak species compensated for a specific species change in growth. Ultimately, the inherent discrepancies between models were only notable when the heterogeneity (or lack thereof) was simulated for sufficient time (here, >20 yr) to reveal their respective differences in growth responses after a disturbance. Here, at short fire return intervals, the growth potential of multiple species is not different enough between models to manifest notable discrepancies, and at extremely long intervals or no disturbance at all, the ABG pattern predictions converged.

Although the general ranking order by scenario of NECB was similar between models, there were also some distinct differences. For all scenarios (Fig. 5), ED predicted slight net carbon sequestration, while LANDIS-II predicted slight net carbon emissions; except for the fire exclusion scenario, ED predicted maximum carbon sequestration potential with prescribed fire, while LANDIS-II predicted maximum sequestration potential to occur under the fire exclusion scenario; that is, no fire on the order of centuries. Although the latter prediction is probably correct from a theoretical standpoint, we note that total absence of fire is unrealistic given the fire-prone nature of the forest type and landscape in question (Mitchell et al. 2014, Krofcheck et al. 2017). The LANDIS-II prescribed fire scenario represented the second best opportunity to *minimize* carbon emissions. While the slopes of the two model predictions of NECB were opposite, the yearly difference between the models NECB was only ~1 $Mg \cdot ha^{-1} \cdot yr^{-1}$—a very minor difference in magnitude. These values, but not the slope or the ranking order of the simulations, are influenced by the amount of AGB converted to detrital carbon following fire. With the inherent differences in these models, the relative similarity of their outputs vis-à-vis frequent prescribed fire provides strong evidence of the carbon sequestration benefits provided by prescribed fire in the southeastern United States.

Model uncertainties and sensitivities are critical considerations when using or comparing model performance. In this study, there was limited sensitivity to fire behavior within the models because the harvest functions were used as a proxy for fire to standardize fire frequencies and effects within each model and improve comparisons. As such, though each model was previously parameterized and validated for the region, underlying sensitivities in the species dynamics of each model were the main source of sensitivity to the results as previously reported. As for uncertainties, ED is deterministic and therefore has no uncertainties in predicted results. LANDIS-II has stochastic physiological processes, but the fire events dominate these processes in driving long-term ecosystem dynamics to the extent that the range of values is not visible on the figures.

Future work could improve predictions of NECB with the inclusion of new submodels that represent the current research progress in quantifying recalcitrant forms of carbon, and black carbon (char and soot) in particular (DeLuca and Aplet 2008). These long-term carbon stores that are produced in every fire event are relatively poorly quantified in the models in terms of production rates, especially for small particulates, but these almost certainly could contribute to the carbon sequestration potential in these fire-prone systems. While some studies have incorporated black carbon production in landscape modeling studies (Marconi et al. 2017), this is not incorporated as a matter of course and needs more robust assessment due to the long-lasting nature of these particulates (Samuelson et al. 2017). Furthermore, a comparison of these two models with finer-scale gap-level models could provide for more detailed information on nutrient dynamics at the tree level (Lavoie et al. 2010) in response to regular low-intensity surface fires (Wright et al. 2013). Predictions related to climate change and other disturbances (pests, disease, windstorms) could be incorporated to examine their impact and variability on carbon balance response. Climate change is particularly important because species and species interactions may respond in unique ways to increased temperature and more variable rainfall, particularly in this region (Mitchell et al. 2014). These scenarios present many avenues for future research on the complex relationships between longleaf pine, hardwoods, and fire frequency.

Model decision support

When choosing a model, there is a trade-off between input requirements and time needed for model parameterization and the effect on desired model realism. ED has high transportability because many inputs are precomputed but with limited modifiability and lack of species-level resolution. LANDIS-II is highly tunable and can model individual species responses but requires a longer parameterization (at least 9 months). With this detail, however, it provides greater flexibility in "scenario" testing (climate change, fire, insects outbreaks, harvesting, etc.) than ED. When users are uncertain about data requirements or availability, one approach is to begin with an already-constructed DGVM, such as ED, and examine the initial outputs. If the results recommend a more in-depth analysis, time investment would increase to build the more complex landscape class model. Ultimately, these decisions should be based on the objectives for model application—for example, what research or management question is being addressed, or how the model output will be applied.

Finally, it is important to note that the domain sizes of ecosystem process models, and particularly ED and LANDIS-II, are gradually moving in convergent directions. ED was recently downscaled for a 90-m resolution study of three northeastern states (Hurtt et al. 2019) and is in the works for the contiguous United States at a yet-to-be-determined resolution (coarser than 90 m but finer than half degree) as it is being used in the NASA CMS and GEDI missions. LANDIS-II is being parameterized for the southern Appalachians (3.5 M ha) at 4-ha resolution and is in the process of being parameterized for the entire USDA Forest Service area of the Southern Research Station (all 13 southern states) at a yet-to-be-determined coarser resolution. Once these projects are complete, the transportability factor for both models should be improved for this region.

Conclusions

This model comparison study provided projections of ecosystem carbon dynamics and species composition for a southeastern U.S. pineland under various fire return intervals from two classes of ecosystem process models. Both models support the application of frequent low-intensity prescribed fires in southeastern pinelands as a means to provide the most stable aboveground biomass and species distributions. Prescribed fire provides the greatest carbon sequestration benefits, while preventing potential stand-replacing wildfires in this fire-prone ecosystem, while maintaining a global hotspot of biodiversity.

This study also illustrated that two very different scales of models could be useful for estimating changes in C and AGB in response to various scenarios of wildland fire and resulting fire effects. The similarities between models were remarkable at high fire frequencies, yet the discrepancies found at the intermediate fire frequencies emphasized model differences and potential unknowns on growth patterns during long periods without fire. Assessing the appropriate choice of model for management application will depend on the research or management objectives and the time, resources, and skill available to parameterize each model. In this ecosystem, coarser-scale questions related to general patterns of landscape C sequestration could benefit from using ED, while LANDIS-II would provide similar information but with more inputs and time needed for parameterization. If finer-scale questions are desired, related to individual species response to competition and explicit disturbances (climate change, fire, insects, disease, land use, harvesting) and their interactions, then LANDIS-II is more appropriate. The convergence of model results in this study does provide confidence in the predicted outcomes and suggests each works well for assessing fire management decision space for frequently burned ecosystems.

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Data Availability

Data are available from Zenodo: http://doi.org/10.5281/zenodo.5649270