Are more complex physiological models of forest ecosystems better choices for plot and regional predictions?

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ABSTRACT

Process-based forest ecosystem models vary from simple physiological, complex physiological, to hybrid empirical-physiological models. Previous studies indicate that complex models provide the best prediction at plot scale with a temporal extent of less than 10 years, however, it is largely untested as to whether complex models outperform the other two types of models at plot and regional scale in longer timeframe (i.e. decades). We compared model predictions of aboveground carbon by one representative model of each model type (PnET-II, ED2 and LINKAGES v2.2, respectively) with field data (19—77 years) at both scales in the Central Hardwood Forests of the United States. At plot scale, predictions by complex physiological model were the most concordant with field data, suggesting that physiological processes are more influential than forest composition and structure. Hybrid model provided the best predictions at regional scale, suggesting that forest composition and structure may be more influential than physiological processes.

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1. Introduction

Ecologists are increasingly interested in carbon dynamics at large temporal (e.g., decadal) and spatial (e.g., regional) scales (e.g., Thurner et al., 2014; Fang et al., 2014; Medvigy and Moorcroft, 2012). Forest ecosystem models are one of the primary tools used to predict future carbon dynamics of forest ecosystems (Rigo et al., 2013; Brown and Schroeder, 1999; Vanderwel et al., 2013; Malhi et al., 2006). Early forest ecosystem models are largely empirical-based while later models are increasingly process-based (Seidl et al., 2011; Bugmann, 2001). Based on complexity of physiological processes, most process-based forest ecosystem models can be classified into three types: simple physiological, complex physiological, and hybrid empirical-physiological.

Simple physiological models simulate carbon dynamics of forest ecosystems based on simple relationships between photosynthesis and environmental and biological variables (e.g., foliar nitrogen concentration). They operate at plot to watershed scales and usually use a monthly time step. Simple physiological models are applied to large areas (e.g., region) by dividing the area into raster cells, downscaling environmental variables to each raster cell, simulating carbon dynamics in each cell, and assembling the results for the region. This type of models is typically parameterized for forest ecosystem types (e.g., temperate deciduous forest), rather than individual species or plant functional type. Biomass is usually petitioned into different organs (e.g. root, stem and leaf) (Aber and Federer, 1992). Thus, simple physiological models do not simulate population-level processes such as competition and succession (e.g., Aber and Federer, 1992; Thornton et al., 2002). Furthermore, due to their coarse time steps, the coupling between atmospheric and physiological processes is relatively weak. However, this type of models is relatively easy to parameterize and requires the least computation power and time. PnET-II is an example of a simple physiological model and was originally designed to simulate forest ecosystem processes in a northern temperate forest (Aber and Federer, 1992).

Complex physiological models simulate carbon dynamics of forest ecosystems with close coupling between atmospheric conditions and physiological processes. They involve more variables than simple physiological models and use finer temporal scales (e.g., hourly) (e.g., Wang and Jarvis, 1990; Luo et al., 2001; Williams et al., 1996; Hanson et al., 2005). Similar to simple physiological models, complex physiological models simulate carbon dynamic with a grid cell system where environmental variables are

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downscaled to each cell and results from each cell can be assembled to represent a region. The models track plant functional types (e.g., early successional temperate deciduous tree) with forest structure information (e.g., tree density) (e.g., Grant, 2001; Moorcroft et al., 2001). Thus, complex physiological models can simulate simplified succession dynamics. Plant functional type-size cohorts are used to represent forest composition and structures. This type of model can typically simulate both C3 and C4 photosynthetic pathways. Complex physiological models are usually applied to broad regions with large grid cell sizes (e.g. 50 km), within which a small number of patches of land (typically <1 ha each) is simulated to represent the entire cell (Snell et al., 2014). They typically do not provide species-specific information, which may limit their value, especially when species-specific carbon dynamics are of interest. The Ecosystem Demography model version 2 (ED2) is a complex physiological model (Medvigy et al., 2009; Moorcroft et al., 2001).

Hybrid empirical-physiological models typically employ empirical age–size relationships to simulate aboveground woody biomass (AWB) dynamics for each individual plant instead of simulating carbon dynamics through physiological processes. Hybrid models may incorporate some mechanistic processes such as exchange of carbon with the atmosphere and soil (e.g., Friend et al., 1997, 1993; Seidl et al., 2005). Hybrid models typically operate at daily time steps and are designed to simulate plot scale (typically between 0.1 and 1 ha) carbon and soil nutrient dynamics. They track size and density by individual trees and mechanistically simulate succession and competition, and consequently the dynamics of forest composition and structure, which can be a strength for research on species-specific dynamics. The computation power and time needed by this type of model are between those of the simple and complex physiological models. LINKAGES v2.2 is a hybrid model that simulates dynamics of forest structure and composition at the spatial scale of a plot and temporal scale of decades (Wullschleger et al., 2003).

Comparing model predictions with field data can reveal levels of prediction uncertainty and identify strengths and weaknesses of different models (Reynolds et al., 2001; Xiong et al., 2014). Many comparisons between forest ecosystem model predictions and field data have been conducted to provide insight into the relationship between model prediction and model complexity (e.g., Hanson et al., 2004; Huber et al., 2012; Sterba and Monserud, 1997; Amthor et al., 2001; Bond-Lamberty et al., 2006; Wang et al., 2014). For example, Huber et al. (2012) compared predictions from three forest process-based models with different levels of complexity against a subset of National Forest Inventory data from Austria for 15 years and found that the more complex model provided better predictions of annual volume increments at a plot scale. Hanson et al. (2004) compared model predictions from 13 forest process-based models with field data for a temperate oak forest site and the complex physiological models using hourly time steps generated the best predictions of hourly, daily, and annual carbon and water budgets. These findings suggest that complex models may provide the best predictions at small temporal and spatial scales.

Complex physiological models require extensive climate data, detailed ecophysiological parameters, high computing power, and longer simulation time than the other two types of models (Huber et al., 2012). At regional scales, detailed, precise atmospheric and soil variables may not be available and effects of environmental heterogeneity are simplified through data imputation and aggregation (e.g., Falkowski et al., 2010; Cutler et al., 2007; Wilson et al., 2012; Liang et al., 2014). Modelers should weigh model performance against applicability (Buchman and Shifley, 1983; Huber et al., 2012); therefore, it is important to know whether complex physiological models are better than simpler models for predictions

at large temporal and spatial scales.

We compared predictions of forest carbon dynamics in terms of AWB by three forest process-based models with different complexity levels against decadal observations of field data at plot and regional scales under current climate. We chose one representative model from each of the three process-based models types: simple physiological model (PnET-II), complex physiological model (ED2), and hybrid empirical-physiological model (LINKAGES v2.2). In terms of physiological process, model complexity increases substantially from PnET-II to LINKAGES v2.2, and to ED2, however, in terms of forest composition and structure, model complexity increases from PnET-II to ED2, to LINKAGES v2.2 (Fig. 1). We hypothesized that at the plot scale, forest composition and structure may not be as influential as physiological processes on forest carbon dynamics because composition and structure are not likely to change significantly at small spatial scales. Therefore, complex or simple physiological models should perform adequately. We hypothesized that at the regional scale, forest composition and structure may be more influential than physiological processes and the hybrid empirical-physiological model should perform better than the physiological models. We applied each model to three forest sites in the Central Hardwood Region in the United States that have long-term, plot-scale observations: Sinkin Experimental Forest in Missouri (30 years of data), Vinton-Furnace Experimental Forest in Ohio (33 years of data), and Kaskaskia Experimental Forest in Illinois (77 years of data). We also carried out regional analysis of aggregated plots, based on the United States Forest Service Forest Inventory and Analysis (FIA) data, for each of the three ecological subsections that included one of the forest sites used for plot scale analysis: Current River Hills (21 years of data), Western Hocking Plateau (19 years of data), and Lesser Shawnee Hills (25 years of data). At this spatial scale, we tested whether simplified environmental heterogeneity could still lead to good match between mean model predictions and mean field data.

We addressed the following questions regarding prediction of forest AWB dynamics: 1) Can a complex process-based model outperform simple and hybrid empirical-physiological models in terms of mean and absolute bias at a decadal temporal scale and different spatial scales (plot and regional), given its detailed data requirements? 2) How do prediction biases change from plot to regional scales for the same model? Comparing the strength and weakness of these three types of models can help identify process-based model designs and formulations that are most suitable for specific types of applications at different spatial scales.

2. Methods

2.1. Description of models

2.1.1. Simple physiological model (PnET-II)

PnET-II (Aber et al., 1995) is a lumped-parameter model that simulates photosynthesis, evapotranspiration and net primary production of forest ecosystems and is an improved version of PnET (Aber and Federer, 1992). The design of PnET-II is based on two principles: (1) maximum potential net photosynthetic rate under light-saturated condition is a function of foliar nitrogen concentration, and (2) water use efficiency (mg C fixed per g H_2O transpired) is a function of vapor pressure deficit. Based on these two principles, a link between carbon dynamics and water transpiration has been established, and the computation load for water transpiration has been greatly reduced since it only depends on vapor pressure deficit. PnET-II estimates maximum potential net photosynthetic rate, which is under light saturation condition. And then, net photosynthetic rate is calculated, accounting for effects of light attenuation, temperature, water availability and vapor pressure
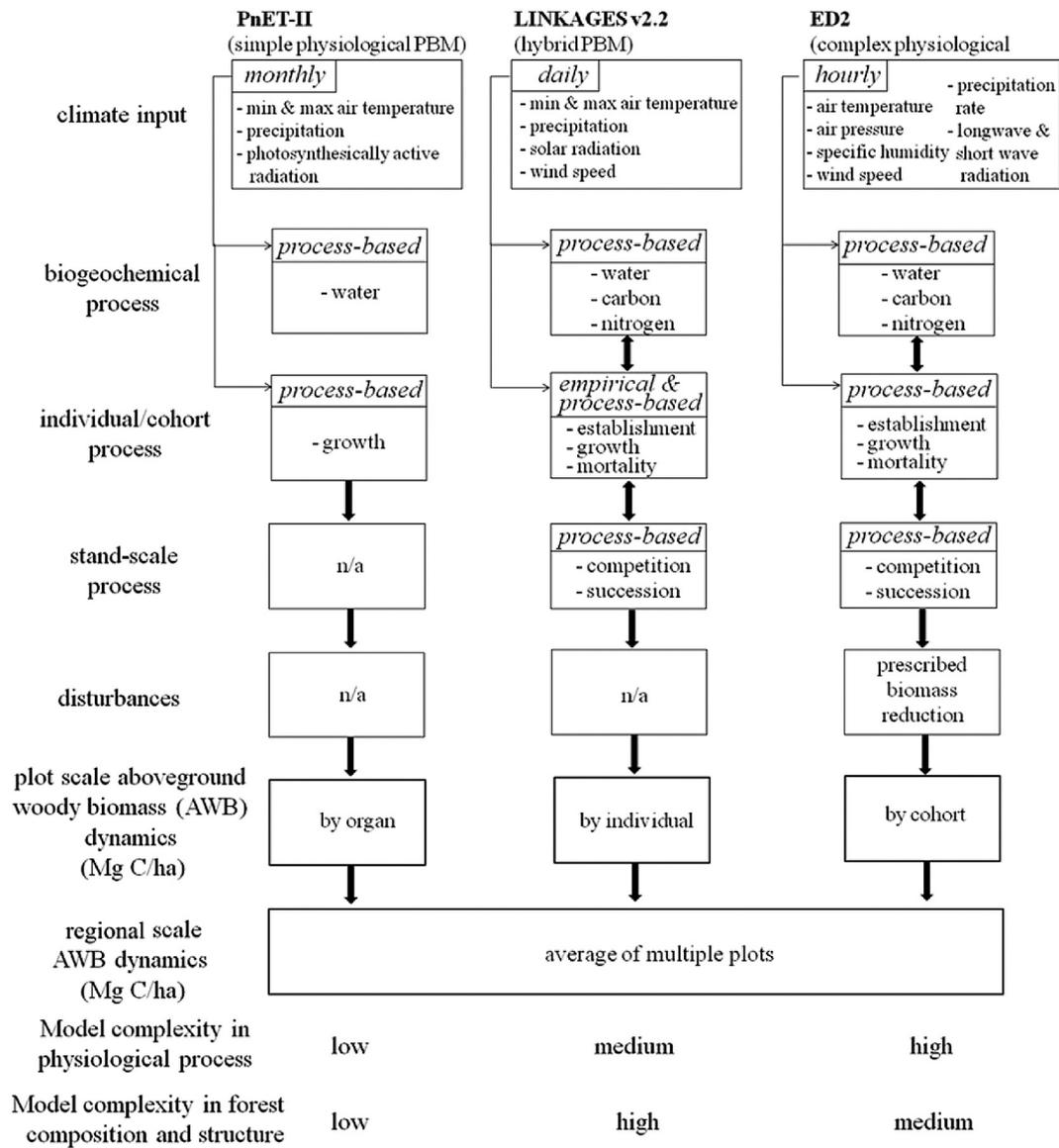
Fig. 1. Comparisons among three process-based models (PnET-II, LINKAGES v2.2, and ED2) in terms of climate inputs, biogeochemical, individual/cohort, stand-scale processes, disturbance, in what entity is aboveground woody biomass partitioned, and model complexities in physiological process and forest composition and structure. Items listed in the climate input and processes refer to those being incorporated and simulated in each model. For example, soil nitrogen is required in LINKAGES initiation and subsequently simulated and can ultimately affect the productivity.

deficit on photosynthesis, from the maximum potential net photosynthetic rate. The annual net primary productivity is summarized based on the net photosynthetic rate (Aber et al., 1995). Annual aboveground wood net primary productivity is allocated from the annual net primary productivity. The annual aboveground wood net primary productivity can be considered close to annual aboveground wood biomass increment (Zhao and Zhou, 2005; Whittaker et al., 1974). We add the annual aboveground wood net primary productivities to the initial aboveground wood biomass to obtain time series of biomass over the period of simulations. PnET-II operates on a monthly time-step. Input plot-level parameters include those regulating the physical and physiological processes such as light attenuation and photosynthesis, which could be obtained from field measurements or derived from literature. Water holding capacity is the only required soil parameter. Climate parameters include monthly minimum and maximum air temperature, total monthly precipitation and photosynthetically active radiation. PnET-II does not contain information pertaining to individual trees. We used the model to predict aboveground woody biomass in terms of carbon.

2.1.2. Complex physiological model (ED2)

ED2 predicts aboveground and belowground ecosystem structure, biomass, and the fluxes of water and carbon between the ecosystem and the atmosphere based on climate and soil properties (Medvigy et al., 2009). It incorporates phenomena operating at a wide range of temporal scales from fine scale plant physiological response to environmental factors (hourly), through changes in soil hydrology (weekly and seasonal), to long-term change in forest composition and belowground carbon storages (yearly to century) (Moorcroft et al., 2001). It subdivides the focal area into grid cells with side length typically varying from 10^{-1} km-10^2 km. Ecosystems are highly heterogeneous even at small scales, e.g., plot scale, however, environmental heterogeneity within each cell, especially when it is at relatively large scale, e.g., regional scale, are not represented by this model. ED2 employs a system of size- and age-

structured (SAS) partial differential equations to closely approximate the mean behavior of a corresponding individual-tree-based stochastic gap model to simulate biotic heterogeneity. This approach can be considered analogue to deriving the Navier—Stokes equations in statistical physics. Multiple simulation runs are commonly needed for stochastic gap models to provide ensemble averages of forest structure and composition, however, by using the SAS equations, ED2 can capture net effect of stochasticity at a much less computing cost (Moorcroft et al., 2001). ED2 does not represent individual plant species but simplifies the plant composition into several plant functional types. We used plant functional types early-, mid-, and late-successional temperate deciduous trees species, and southern pines species. Input parameters include elevation, slope, aspect, soil type, vegetation type, age since disturbance, and soil parameters such as soil carbon and nitrogen. Diameter at breast height (dbh), plant functional type, and stem density are also needed for vegetation conditions. Climate parameters include hourly air temperature, pressure, specific humidity, wind speed, precipitation rate, incoming longwave and shortwave radiations.

2.1.3. Hybrid empirical-physiological model (LINKAGES v2.2)

LINKAGES v2.2, is a hybrid empirical-physiological model that simulates the effects of climate change and inter- and intra-annual variation in climate on long-term forest dynamics and carbon—nitrogen cycles (Wullschleger et al., 2003). The hypothesis underlying LINKAGES v2.2 is that the interactions between demographic, microbial, climatic and geological dynamics may explain much of the observed variation in forest ecosystem structure, carbon and nitrogen storage and cycling. Climatic and geological dynamics, such as water availability, constrain plant demography, such as regeneration and mortality. Sequestration of atmospheric carbon by plants is partly limited by microbial production of ammonium; however, plants can also affect soil nitrogen availability by the amount and type of litter they return to the soil. Regeneration, growth and mortality of individual trees greater than 1.4 cm in dbh in a 1/12 ha plot are simulated at daily time steps. LINKAGES inputs, namely growing degree days, soil water availability, annual evapotranspiration, soil field moisture capacity, and wilting point, are calculated from daily temperature and precipitation. Decomposition of down wood and soil nitrogen availability are calculated from organic matter quantity and carbon chemistry, evapotranspiration, and degree of canopy closure. Tree reproduction is constrained by estimates of growing degree days, light levels, and water availability. Growing degree days and the availability of light, water, and soil nitrogen constrain tree growth and biomass accumulation. The estimated probability of tree mortality increases with age and slow growth rate (annual diameter increment less than 1 mm or less than 10% of the optimal diameter increment). LINKAGES contains stochastic processes in regeneration and age-dependent mortality. Seedling establishment is determined for each species based on light, growing degree days, soil moisture multipliers and a random number ranging from 0 to 1. Age-dependent mortality is stochastic so that about 1% individuals of a given species would survive up to maximum age. (Pastor and Post, 1985). Species-specific parameters derived from life history attributes (e.g. longevity, maximum height) of 72 species of upland tree species in the eastern United States are provided in the model documentation. Soil parameters include water holding capacity; wilting point; and average percentage of clay and sand. Climate parameters include daily maximum and minimal air temperatures, precipitation, solar radiation, and wind speed.

2.2. Study areas and sites

We chose three ecological subsections located in the Central Hardwood Region of the United States as regional scale areas for this study: Current River Hills, Lower Shawnee Hills, and Western Hocking Plateau, which are located in Missouri, Illinois and Ohio, respectively (Fig. 2). Ecological subsection is a unit in the United States National Hierarchical Framework of Ecological Units, which is delineated based on similar bedrock and soil formations, local climate, topographic relief, and vegetative conditions (McNab et al., 2007). We used FIA data to initiate simulations and to compare with model predictions at the regional level. The FIA program is a United States Department of Agriculture Forest Service program that conducts systematic inventories of forests across the country. These inventories make periodic repeated measurements of permanent sample plots with a sampling intensity of approximately one plot per 2430 ha (O'Connell et al., 2013). We chose one experimental forest site from each ecological subsection for our plot scale study: the Sinkin, Kaskaskia, and Vinton Furnace Experimental Forests (Fig. 2). These sites have some of the longest time series of forest inventory data in the eastern United States. Descriptions of ecological subsections and the experimental forest in each follow.
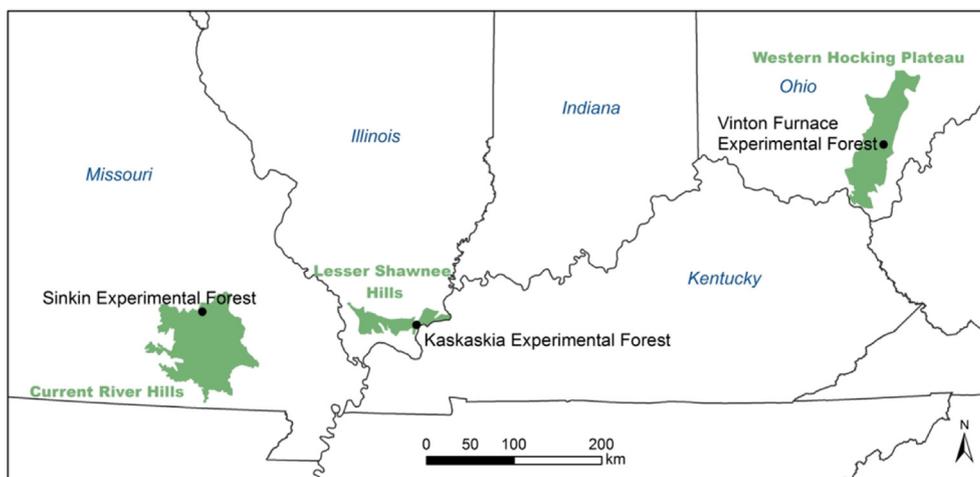
Fig. 2. Locations of experimental forests where study plots (black dots) were located and ecological subsections that represented regions (green polygons) used to evaluate model predictions of aboveground woody biomass dynamics at plot and regional scales in the Central Hardwood Region of the United States. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2.1. Current River Hills subsection – Sinkin Experimental Forest

The Current River Hills subsection is in the Ozark Highlands in southeast Missouri and is approximately 8.1×10^3 km^2 in area. This subsection is a mature dissected plateau with dolomite and sandstone bedrock, and soils primarily developed from cherty limestones (McNab et al., 2007). The average annual temperature is around 13 °C and average annual precipitation is 1100 mm. This area contains primarily mature upland oak, oak-hickory and oak-pine communities. The dominant species include white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lamb.), and scarlet oak (*Quercus coccinea* Muenchh.), bitternut hickory [*Carya cordiformis* (Wangenh.) K. Koch] and pignut hickory (*C. glabra* Miller) (Shifley and Brookshire 2000). Oaks and hickories dominated the Central Hardwood Forest landscape for the past 5000 years, and they are still keystone species. Fire has been an important disturbance in this region for hundreds of years (Nigh and Schroeder, 2002; Guyette et al., 2006). The past anthropogenic fire regimes have long-lasting influences on forest composition and structure, wildlife, calcium availability in soil, and aluminium concentrations in wood (Gueyette and Cutter, 1997). We used FIA data that was based on consistent protocols from 1989 to 2010, resulting in a 21-year data series.

The Sinkin Experimental Forest is in southeastern Dent County, Missouri (37°29′N, 91°16′W). This site is dominated by black oak, scarlet oak, northern red oak (*Quercus rubra* L.), white oak, and post oak (*Quercus stellata* Wangenh.). Other species include hickories (*Carya spp.*), black gum (*Nyssa sylvatica* Marsh.), sassafras [*Sassafras albidum* (Nutt.) Nees], shortleaf pine (*Pinus echinata* Mill.), black cherry (*Prunus serotina* Ehrh.), maples (*Acer spp.*), flowering dogwood (*Cornus florida* L.), and black walnut (*Juglans nigra* L.). The understory is composed of hardwood tree species and shade-tolerant herbaceous plants (USDA, 2012). We used data from eleven 0.25 ha plots established in 1978 in undisturbed areas within the Sinkin Experimental Forest to monitor oak-hickory stand development. Trees with dbh greater than or equal to 1.5 cm were recorded in 1982, 1985, 1988, 1993, 1999, and 2008; resulting in a 30-year data series.

2.2.2. Lesser Shawnee Hills subsection – Kaskaskia Experimental Forest

The Lesser Shawnee Hills subsection is in the Interior Low Plateau-Shawnee Hills ecological section in southern Illinois and is approximately 2.0×10^3 km^2 in size. The landscape consists of sandstone bluffs, steep-sided ridges, and hills with broad valleys. Regional annual average temperature is 13 °C, mean annual precipitation is 1098 mm, and is distributed equally throughout the year. The average length of the growing season is 190 days. The soils are primarily Alford silt loam, Grantsburg silt loam, and Clarksville cherty silt loam. Oak-hickory forest is the primary vegetation type (McNab et al., 2007). Common species include northern red oak, black oak, white oak, chestnut oak (*Quercus prinus* L.) and sugar maple (*Acer saccharum* Marshall) (Van Kley and Parker, 1993). We used FIA data that was based on consistent protocols from 1985 to 2010, resulting in a 25-year data series.

The Kaskaskia Woods Natural Area is in the Kaskaskia Experimental Forest located in Hardin County in Southern Illinois (37°30′N, 88°30′W). The aspect of this site is generally northeast. The soils are well-drained silt loams and the productivity largely depends on soil moisture availability (Zaczek and Groninger, 2002). The site consists of mixed upland hardwoods with an overstory of yellow poplar (*Liriodendron tulipifera* L.), white oak, red oak, scarlet oak, pignut hickory, sugar maple, and slippery elm (*Ulmus rubra* Muhl.), and an understory of southern red oak (*Quercus falcata* Michx.), white ash (*Fraxinus americana* L.), mockernut hickory [*Carya tomentosa* (Lam.) Nutt.], red mulberry (*Morus rubra* L.), American elm (*U. americana* L.), flowering dogwood and sassafras (Adams et al., 2004). We used data from four 0.1 ha and two 0.2 ha permanent plots established in 1935 to monitor the growth of all-aged mixed-upland hardwoods in Kaskaskia Woods Natural Area. No major disturbances occurred in these plots after establishment and they were re-measured in 1940, 1958, 1962, 1963, 1973, 1978, 1983, 1992, 1997 and 2012; resulting in a 77-year data series.

2.2.3. Western Hocking Plateau subsection – Vinton Furnace Experimental Forest

The Western Hocking Plateau subsection is in the Southern Unglaciated Allegheny Plateau ecological section in southern Ohio, it is approximately 5.2×10^3 km^2 in size. This area is a mature dissected plateau with high hills, sharp ridges, and narrow valleys. Bedrock is mainly sandstone, siltstone, and shale with some limestone and coal. The climate is continental with a warm summer and cold winter. Precipitation in spring and summer is slightly higher than fall and winter, but water deficits are infrequent (McNab et al., 2007). Annual average temperature is 11 °C, and mean annual precipitation is 1000 mm in the form of mostly rain. The growing season includes 158 frost-free days (USDA, 2013). Oaks (*Quercus* spp.) dominate dry and dry-mesic ridge tops and slopes, while sugar maple and yellow poplar dominate mesic slopes and wet-mesic ravine bottoms (Hix, 1997). We used FIA data that was based on consistent protocols from 1991 to 2010, resulting in a 19-year data series.

The Vinton Furnace Experimental Forest is in Vinton County, Ohio (39°11′N, 82°22′W). This site was occupied by mixed oak forest that developed after clear-cutting over 100 years ago to produce charcoal for iron smelting. More recently the area was used for long-term prescribed fire and restoration studies (Dress and Boerner, 2003). The soils are unglaciated silt loam derived mostly from sandstones, siltstones, and shales. Common trees were chestnut oak on the ridges, scarlet oak and black oak growing downslope, white oak, red maple (*Acer rubrum* L.), and hickories on the midslope blending to yellow poplar in the mesic areas. Short-leaf pine was the major conifer species (USDA, 2013). We used data from two 0.2 ha plots and one 0.04 ha plot established in Study Area 25 in 1978. All three plots had not been harvested after the establishment. Tree species and dbh were periodically remeasured with the most recent measurement in 2011, resulting in a 33-year data series.

2.3. Tree species and allometric equations

All plots and regions are in the Central Hardwood Region, and despite the geographic span, they have similar tree species composition. We included tree species that comprised more than 90 percent of the total basal area for all sites and subsections. Overstory species were shortleaf pine, Virginia pine (*Pinus virginiana* Mill.), red maple, sugar maple, hickories, American beech (*Fagus grandifolia* Ehrh.), white ash, yellow poplar, black gum, American sycamore (*Platanus occidentalis* L.), white oak, scarlet oak, southern red oak, blackjack oak (*Quercus marilandica* Münchh.), chinkapin oak (*Quercus muehlenbergii* Engelm.), northern red oak, post oak, black oak, American basswood (*Tilia americana* L.), American elm, and slippery elm. As for understory species, flowering dogwood was included.

Since AWB is not directly measured in the field, we used allometric equations to estimate AWB based on dbh. We report AWB as mass of carbon and estimated it as half of the mass of woody structures (O'Connell et al., 2013). LINKAGES v2.2 uses the following allometric equation (adapted from Sollins et al., 1973) for all tree species:

$$AWB = 0.05965 \times dbh^{2.393} \tag{1}$$

where AWB is carbon in kilograms for the aboveground woody part of a living tree, dbh is diameter at breast height in centimeters. ED2, however, calculates AWB using different allometric equations for different plant functional types. We classified species into four plant functional types: southern pine (all pine species), early- (American sycamore), mid- (oaks, hickories, white ash, yellow poplar, black gum, American basswood and elms) and late-successional (maples, American beech and flowering dogwood) temperate deciduous trees. We calculated AWB using the following allometric equations (adapted from Moorcroft et al., 2001):for southern pines:

$$AWB = 0.0735 \times dbh^{2.238} \tag{2}$$

for early-successional temperate deciduous trees:

$$AWB = 0.01324 \times dbh^{2.95954} \tag{3}$$

for mid-successional temperate deciduous trees:

$$AWB = 0.08085 \times dbh^{2.4572} \tag{4}$$

for late-successional temperate deciduous trees:

$$AWB = 0.1175 \times dbh^{2.2518} \tag{5}$$

where AWB was reported as carbon in kilograms for aboveground structural woody part of a living tree and dbh was in centimeters. PnET-II does not have any built-in allometric equation so we used equations from both Sollins et al. (1973) and Moorcroft et al. (2001) to produce estimates comparable to LINKAGES v2.2 and ED2; we referred to these two approaches as PnET-II-S and PnET-II-M, respectively.

2.4. Model parameterization

The three models required different climate parameters at different time steps. We obtained site-specific climate data for ED2 (hourly time step) from the 4-times daily NCEP/NCAR reanalysis data set (Kalnay et al., 1996); parameters included hourly air temperature, air pressure, specific humidity, wind speed, precipitation rate, incoming longwave and shortwave radiations. We generated hourly data by linearly interpolating the original NCEP/NCAR 4-times daily data. Site specific climate data for LINKAGES v2.2 (daily time step) and PnET-II (monthly time step) were obtained from daily and monthly NCEP/NCAR reanalysis data set. Parameters for LINKAGES v2.2 included daily high and low air temperature, precipitation, solar radiation and wind speed. Parameters for PnET-II included monthly high and low air temperature, photosynthetically active radiation, and precipitation. Climate data for the centroid point of each ecological subsection was used as the area-specific climate data. The earliest year in NCEP/NCAR reanalysis data is 1948, and the earliest year in the field data of the Kaskaskia site is 1935, so we used climate data between 1948 and 1961for period between 1935 and 1948 where no data is available.

We used soil information from Web Soil Survey (Soil Survey Staff, 2013). We used water holding capacity for PnET-II; water holding capacity, wilting point, average percentage of clay, sand, and rock in the uppermost 1 m soil for LINKAGES v2.2; and soil textural classes and the depth of mineral soils for ED2. We used the NCEP/NCAR reanalysis data set to assign initial soil temperature (Medvigy et al., 2009). We used physiological parameters from Tjoelker et al. (2001), Reich et al. (1995), Scheller and Mladenoff

(2005), and Xu et al. (2009) for PnET-II and ED2. We accepted default values of parameters whenever site- or subsection-specific values were not available in the literature.

2.5. Design of simulation experiments

2.5.1. Plot scale experiments

We simulated AWB for plots at Sinkin Experimental Forest, Kaskaskia Experimental Forest, and Vinton Furnace Experimental Forest sites for periods corresponding to the data collection at each site (1978–2008, 1935–2011, 1978–2011, respectively). We initiated LINKAGES v2.2 and ED2 simulations with dbh records from each site for the first year of the simulation period. Since PnET-II does not use dbh data, we derived initial biomass from dbh using each set of allometric equations used in LINKAGES v2.2 and ED2, and then added net primary productivity predicted by PnET-II to obtain biomass. All plots at each Experimental Forest site were collectively simulated and the field data estimates were derived by averaging all plots. The raw simulation output from PnET-II was wood annual net primary production; we calculated AWB as the sum of wood annual net primary production. The simulation outputs from LINAKGES v2.2 and ED2 were AWB. Since LINKAGES v2.2 is a stochastic model, the average of 200 simulations was used as the simulation result for each site. ED2 runs on a grid cell system, and the cell length was set to 10^{-1} km. None of the three sites experienced major natural and anthropogenic disturbances during the period in which the field data were recorded, so we did not include disturbance in the plot scale simulations.

2.5.2. Regional scale experiments

We conducted simulations for three subsections over different time periods: 1989–2010 for the Current River Hills, 1985–2010 for the Lower Shawnee Hills, and 1991–2010 for the Western Hocking Plateau. The start years of simulation periods corresponded to the year consistent FIA protocols began in each area and we used FIA plots from the first year to initiate the simulations. We combined FIA plots from 1999 to 2001 and 2009–2011 to compare to model predictions for 2000 and 2010, respectively. We divided each ecological subsection into smaller subunits for our simulations to represent environmental and vegetation heterogeneities. For LINKAGES v2.2, we divided subsections into six land types: southwest slope, northeast slope, ridge, upland drainage, bottomland, and gentle slope. We divided subsections into $0.33° \times 0.33°$ grid cells for ED2. PnET-II simulations followed the spatial configurations used for LINKAGES v2.2 and ED2. We assumed that within each land type or grid cell abiotic conditions were homogeneous and could be represented by the mean condition. We used more than 1800 FIA plots across all land types and grid cells for simulation initiation and comparisons with model predictions of LINKAGES v2.2 and ED2. At each time point (namely initialization, 2000, and 2010), on average, each land type and each $0.33° \times 0.33°$ grid cell contained 33 and 32 FIA plots, respectively. Nearly 70% of the forest stands in the study areas were between 50 and 80 years old (USDA Forest Service, 2014), thus variations in aboveground woody biomass were relatively small among plots in a subunit. Average standard deviations of aboveground woody biomass for each land type and each $0.33° \times 0.33°$ grid cell were 5.9 and 7.2 Mg C/ha, respectively. Given the relatively small standard deviations, it would be reasonable to use average conditions of aggregated FIA plots to represent the vegetation conditions within each subunit. Although aggregation of FIA plots eliminated spatial variations in aboveground woody biomass within each subunit, since this study focused on the density of aboveground woody biomass, lack of spatial variations was not given concerns. Spatial variations in abiotic conditions, however, were represented by different land

types and grid cells over the study areas.

2.6. Data analyses

We plotted model predictions and field data together to visually examine model performance at the plot and regional scales. Visual examination is an intuitive and, in most cases, effective way to evaluate model performances (Bennett et al., 2013). However, visual examination alone may not be able to differentiate performance of multiple models, especially when differences between model predictions and field data are small and subtle; therefore we also quantitatively compared model predictions to field data.

At the plot scale, we used linear mixed model for repeated measurements to examine the slope and intercept of the regression between year and biomass. And the temporal effect was set to be random. We also tested the hypothesis that there was no significant difference between model predictions and field data ($P < 0.05$) with a Wilcoxon paired-sample signed-rank test, which tests if the ranked absolute differences between pairs of model predictions and field data are centered on 0. We calculated bias as the mean of residuals (Equation (6)); positive and negative values indicate over- and under-prediction, respectively. Positive and negative residuals can cancel each other out and result in a zero bias so we also calculated root mean square error (RMSE; Equation (7)). Residuals were squared and became positive when calculating RMSE so larger

residuals contributed more, which could be more relevant to model users (Bennett et al., 2013). We averaged the field data and model predictions for plots within each of the three sites by year. Bias, percent bias, and RMSE for all models were calculated using average field data and corresponding average model predictions at given years. Bias and RMSE were calculated from the following equations (Bennett et al., 2013):

$$\text{bias} = \frac{\sum_{i=1}^{n}(\hat{x}_i - x_i)}{n} \tag{6}$$

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}(\hat{x}_i - x_i)^2}{n}} \tag{7}$$

where $\hat{x}_i$ is the model prediction, x_i is the field data, n is the number of time points.

At the regional scale, bias, percentage bias, and RMSE were calculated for each model by comparing average model predictions for all subunits within each of the three subsections to corresponding FIA data for year 2000 and 2010. We calculated ratio of model predictions to field data in gross productivity and mortality of four models (except mortality in PnET-II as it does not simulate mortality) at plot and regional scales. A ratio equal to one means perfect match, ratios smaller than one and larger than one suggest
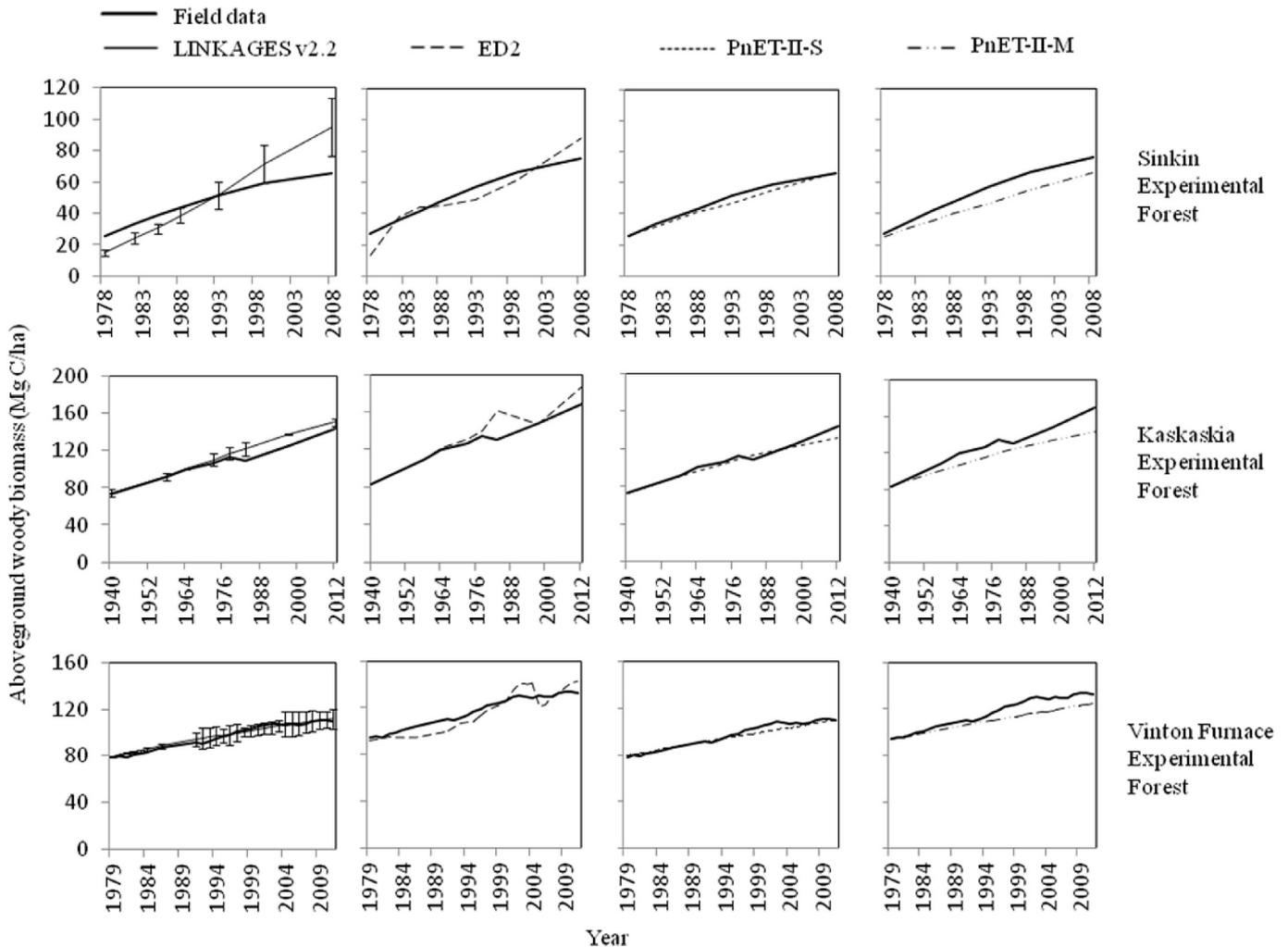

Fig. 3. Model predictions of AWB compared with the field data for each study plot in the Central Hardwood Region of the United States. LINKAGES v2.2 is the only stochastic model, error bars represent standard error of 200 repetitions.

Table 1
Repeated linear mixed regression statistics relating model predictions of aboveground woody biomass over time to field data at three sites in the Central Hardwood Region of the United States. All slopes were significantly different than 0 ($P < 0.001$). Bias, percent bias, and root mean square error (RMSE) of each model are based on comparison of model predictions to field data over the whole period of simulation.

Site	Allometric equation	Field data and model	Slope	Intercept	Bias (mg C/ha)	Bias (%)	RMSE (mg C/ha)
Sinkin Experimental Forest $n = 7$	Sollins	Field data	1.35	−2643.8	–	–	–
		LINKAGES	2.71	−5351.2	1.16	−5.35	13.5
		PnET	1.36	−2660.1	−2.20	−4.87	2.83
	Moorcroft	Field data	1.65	−3230.2	–	–	–
		ED	2.11	−4154.4	−1.87	−7.30	8.10
		PnET	1.36	−2664.3	−7.52	−14.3	8.23
Kaskaskia Experimental Forest $n = 8$	Sollins	Field data	0.93	−1730.3	–	–	–
		LINKAGES	1.09	−2034.2	5.30	4.54	7.10
		PnET	0.82	−1515.1	−2.50	−1.98	4.92
	Moorcroft	Field data	1.11	−2071.6	–	–	–
		ED	1.35	−2534.5	7.30	5.20	12.8
		PnET	0.82	−1504.0	−11.4	−8.18	13.5
Vinton Furnace Experimental Forest $n = 28$	Sollins	Field data	1.10	−2104.8	–	–	–
		LINKAGES	1.01	−1929.6	0.70	0.91	2.08
		PnET	0.94	−1789.5	−1.90	−1.71	3.11
	Moorcroft	Field data	1.35	−2584.6	–	–	–
		ED	1.69	−3251.9	−1.30	−1.43	6.62
		PnET	0.94	−1774.4	−6.90	−5.50	8.34

under- and over-prediction.

3. Results

3.1. Plot scale comparisons

Visual examination showed that the estimates of AWB from field data and model predictions increased over time at all sites, and all models seemed to be able to capture the observed trend in AWB (Fig. 3). The AWB predictions by ED2 were not significantly different from the field data at all sites; PnET-II-M and PnET-II-S were significantly different at all sites and one site, respectively; and LINAKGES v2.2 was significantly different at one site (Table 2). Thus, based on the Wilcoxon paired-sample signed-rank test, ED2 provided the best AWB predictions among the three models. LINKAGES v2.2 and ED2 tended to overpredict biomass, and PnET-II tended to underpredict (Fig. 4). In terms of absolute value, no single model had the smallest bias at all three sites. LINKAGES v2.2 had the smallest bias of 1.16 and 0.70 Mg C/ha, at Sinkin and Vinton Furnace Experimental Forest sites, respectively. PnET-II-M had the largest bias at all sites. No single model had the smallest percent bias at all three sites; however, PnET-II-M had the largest percent bias at all sites. No model constantly had the smallest or largest RMSE at all three sites (Table 1). When averaged across all three sites, ED2 and PnET-II-M had the smallest and largest biases and percent biases, respectively. PnET-II-S and PnET-II-M had the smallest and largest RMSE, respectively (Fig. 4). Ratios of model predictions to field data in gross productivity were larger than one in LINKAGES v2.2 and ED2, and were smaller than one in PnET-II. And ratios of model predictions to field data in gross mortality were both smaller than one in LINKAGES v2.2 and ED2 (Fig. 5).

3.2. Regional scale comparisons

The field data and model predictions all indicated increase in AWB in all subsections at the regional scale (Fig. 6). We compared model predictions to field data averaged across the three regions for both 2000 and 2010. LINKAGES v2.2 yielded the smallest bias (1.25 Mg C/ha), percent bias (2.94%), and RMSE (4.09 Mg C/ha). PnET-II-M had the largest bias (−6.45 Mg C/ha). PnET-II-S had the largest percent bias (11.9%) and RMSE (9.66 Mg C/ha). The bias (−3.71 Mg C/ha), percent bias (−7.32%) and RMSE (5.51 Mg C/ha) of ED2 were between those of LINKAGES v2.2 and PnET-II (Fig. 4). Biases were larger at the regional scale for ED2 and PnET-II-S than those at the plot scale; percent biases were larger at the regional scale for all models; RMSE were smaller at the regional scale for all models except PnET-II-S (Fig. 4). Ratios of model predictions to field data in gross productivity were larger than one in LINKAGES v2.2, ED2 and PnET-II-S; and was smaller than one in PnET-II-M. Ratio of model predictions to field data in gross mortality was smaller than one in LINKAGES v2.2, and was larger than one in ED2 (Fig. 5).

4. Discussion

Comparing predictions by models with different designs is challenging because target simulation entities can be different among models. Wood annual net primary production, structural wood, and woody aboveground biomass were the simulation entities for the simple physiological model, complex physiological model, and hybrid model, respectively, used in our study. In addition, forest composition and structure were represented at different levels of complexity among the three models. The simple physiological model did not represent forest composition and structures;

Table 2
P-values from Wilcoxon rank sum test for the comparison between the field data and model predictions at the plot scale for three sites. Field data measured in 1978, 1982, 1985, 1988, 1993, 1999, and 2008 were used for comparison at Sinkin Experimental Forest site. Field data measured in 1940, 1958, 1963, 1973, 1983, 1992, 1997 and 2012 were used for comparison at Kaskaskia Experimental Forest site. Field data measured in 1979–1984, 1986, 1991–2011 were used for comparison at Vinton Furnace Experimental Forest site.
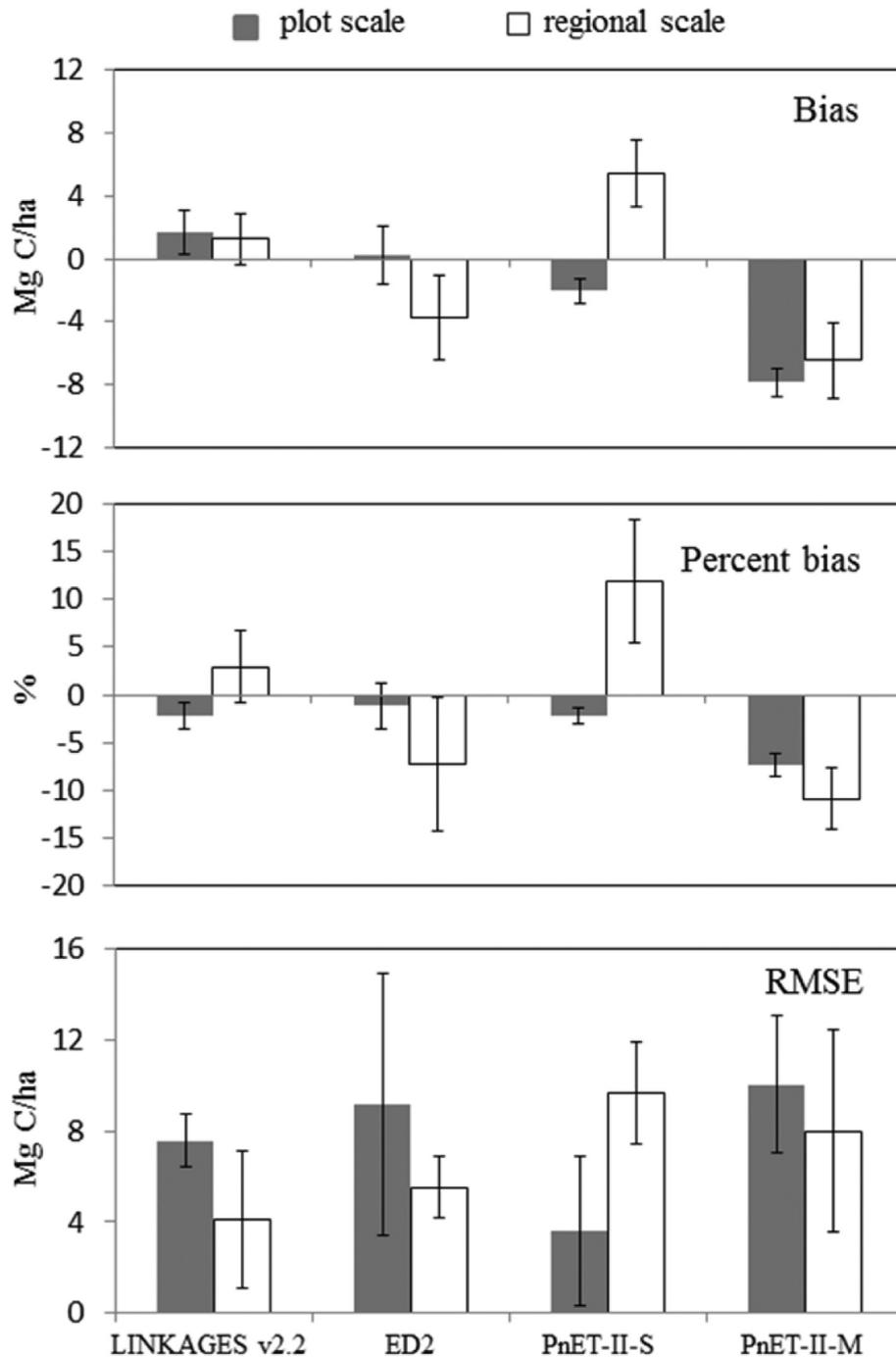
Allometric equation	Model	Site		
		Sinkin experimental forest $n = 7$	Kaskaskia experimental forest $n = 8$	Vinton Furnace experimental forest $n = 28$
Sollins	LINKAGES v2.2	0.9391	0.0239	0.2692
	PnET-II	0.0632	0.1002	0.0001
Moorcroft	ED2	0.5781	0.1016	0.2614
	PnET-II	0.0174	0.0197	<0.0001

Fig. 4. Comparisons of bias, percent bias, and root mean square error (RMSE) of LINKAGES, ED2, PnET-II-S, and PnET-II-M between plot and regional scales in the Central Hardwood Region of the United States. Error bars represent standard error.

the complex physiological model simulated cohorts for each plant functional type; and the hybrid model simulated individuals for each species. We used a framework that converted different simulation results to AWB as a common "currency" and compared predictions of AWB for all three models against field data at both plot and regional scales.

4.1. Plot scale comparisons

PnET-II, the simple physiological model, under predicted the AWB with both sets of allometric equations. Hanson et al. (2004)

found that 8-year mean annual net primary production predicted by PnET-II for 1993–2000 was 29.4% lower than biometric estimates for plots in an upland, oak-dominated forest in eastern Tennessee, United States. The underestimated annual net primary production could be explained, at least partly, by an underestimated annual leaf growth simulated by PnET-II. The predicted leaf growth was only about half the observed value. We calculated the ratio of model predictions to field data in terms of gross productivity; they were 0.977 and 0.923 for PnET-II-S and PnET-II-M, respectively (Fig. 5). PnET-II was the only model in this study that did not include mortality and succession, which suggests biases
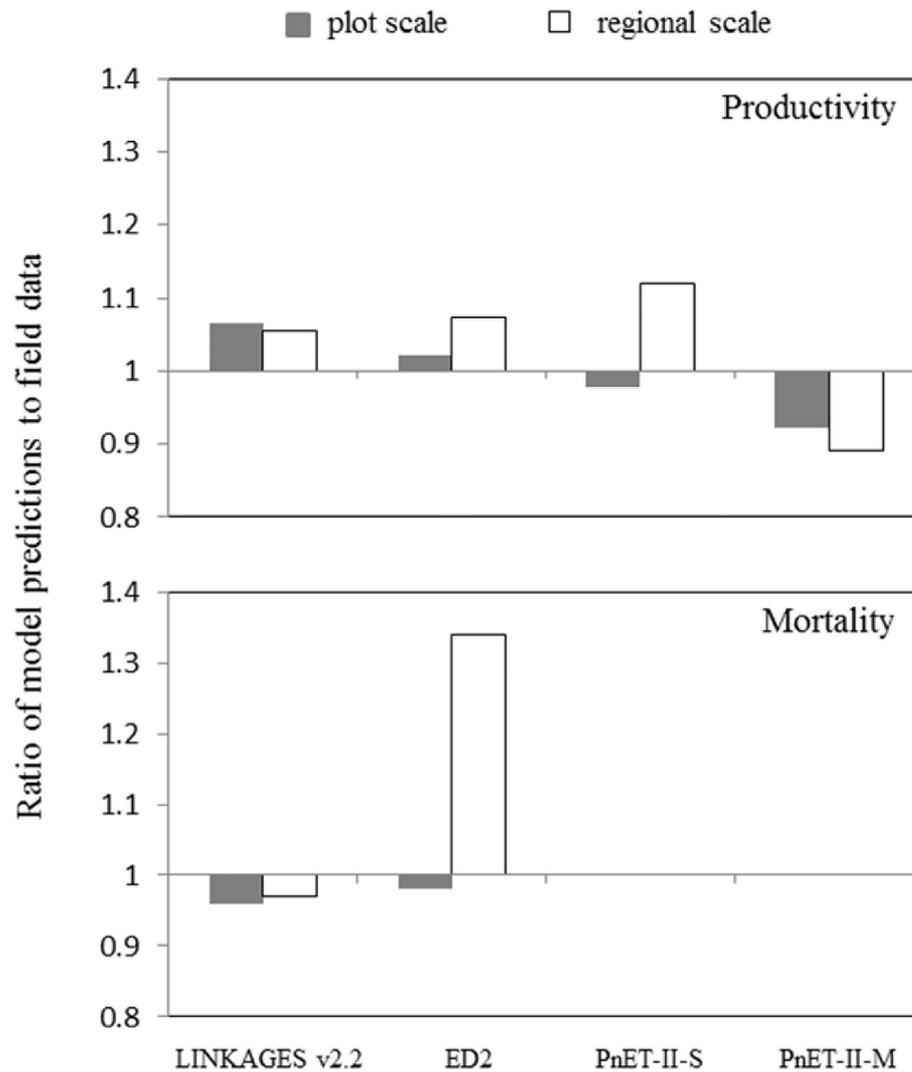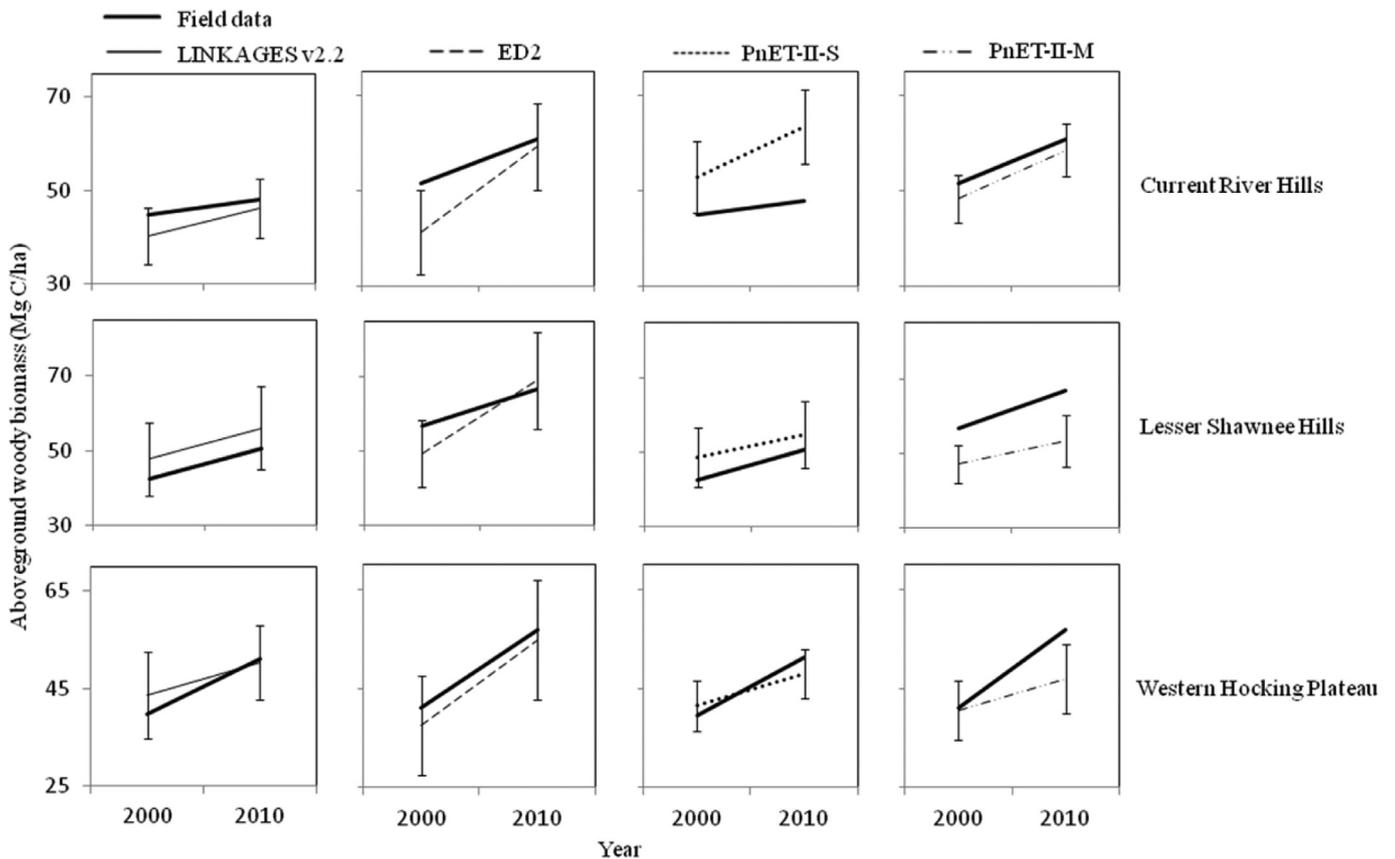
Fig. 5. Comparisons of ratio of model predictions to field data in gross productivity and mortality of LINKAGES, ED2, PnET-II-S, and PnET-II-M at plot and regional scales in the Central Hardwood Region of the United States.

were due to insufficient productivity rather than mortality or successional change. Succession results in changes in species composition and affects the long-term trend in biomass (Peet, 1981).

LINKAGES v2.2, the hybrid empirical-physiological model, showed a positive bias that was smaller than that of PnET-II and larger than that of ED2 in absolute values. LINKAGES v2.2 had a larger ratio of model predictions to field data in productivity (1.065) than PnET-II and ED2. And the ratio in mortality (0.96) was smaller than that of ED2 (0.98) (Fig. 5). Taken together, they explained a positive bias in LINKAGES v2.2 and why it was larger than that of ED2.

ED2, the complex physiological model, provided the best predictions of AWB at plot scales based on bias, percent bias, and the Wilcoxon paired-sample signed-rank test. Ratios of model predictions to field data in both productivity and mortality were 1.022 and 0.98, respectively (Fig. 5). The complex physiological model may have been more accurate because it operated at an hourly time step, and simulated fine-scale physiological processes in response to fast-changing environmental drivers (e.g., shortwave radiation). Simulations of fine-scale processes could better take environmental changes into account and are critical to simulate the effects of environmental changes on forest dynamics (Baldocchi and

Wilson, 2001; Huber et al., 2012). The complex physiological model may have had better performance at the plot scale because it simulates more complex physiological processes that are more closely linked with environmental drivers; however, forest composition and structure are not as well represented as in the hybrid model. If carbon dynamics are analyzed from a productivity and mortality perspective, the complex physiological model had a ratio of model predictions to field data closest to 1 in both productivity and mortality (Fig. 5). This seems to support our hypothesis that at the plot scale, forest composition and structure may not be as influential as physiological processes on forest carbon dynamics. However, ED2 did not have the smallest root mean square error (RMSE), rather it had the second largest one (9.18 Mg C/ha) (Fig. 4). Large RMSE and small bias suggest noticeable fluctuations of model predictions around the field data (Fig. 3). We suggest that this is partly because ED2 only modeled four plant functional types while LINKAGES v2.2 modeled 22 species; if mortality occurred in a few cohorts in ED2 it would likely cause greater biomass decreases than LINKAGES v2.2. Nevertheless, at the plot scale, such simplification in forest composition representation did not seem to affect the fact that ED2 had the best prediction in terms of bias, percent bias, and the Wilcoxon paired-sample

Fig. 6. Model predictions of aboveground woody biomass compared with the field data for each region in the Central Hardwood Region of the United States. Error bars represent standard deviations.

signed-rank test.

4.2. Regional scale comparisons

The percent bias of all models was larger at the regional scale than the plot scale. Abiotic environmental heterogeneity at the regional scale could be one of the factors contributing to the larger percent bias at the regional scale. Even though we used ecological subsections as our regional scale study areas—areas where the vegetation and environmental factors are considered relatively homogenous (McNab et al., 2007), the environmental heterogeneity within each subsection would still be higher than that at each plot-scale site. Small-scale abiotic environmental variations, such as difference in water availability at different slope positions of the same soil type, have been ignored in this regional scale study, and summarized environmental factors were used to represent the average physical situations across the entire subsection.

The simple physiological model, PnET-II, also performed the worst at the regional scale. The hybrid model, LINKAGES v2.2, performed better than the complex physiological model at the regional scale based on bias, percent bias, and RMSE and its error bars overlapped with the field data. The ratio of model predictions to field data for LINKAGES v2.2 was closer to 1 for productivity (1.054) and mortality (0.97) than was ED2 (1.074, 1.34; respectively) (Fig. 5). Overestimation of mortality by ED2 likely caused negative bias and percent bias in AWB and was due to over-prediction of the decline in the early successional plant functional type. Successional changes simulated by LINKAGES were more realistic. We believe these results support our hypothesis that forest composition may be more influential than physiological processes on biomass

dynamics at the regional scale.

While LINKAGES v2.2 had the best overall performance at the regional scale, ED2 also had a reasonable match with the field data; all but one of its error bars overlapped with the field data (Fig. 6). Because detailed environmental variables required by ED had to be aggregated or summarized at the regional scale, environmental heterogeneity was reduced, which may have limited the potential value of its complexity. Biomass accumulation simulated by the hybrid model is based on empirical growth curves derived from life history attributes of specific tree species. Abiotic environmental variables (growing degree days, soil moisture and nitrogen availability) are simplified to a scale from zero (no growth) to one (optimal conditions) in the simulation (Pastor and Post, 1985; Wullschleger et al., 2003). This type of model is less sensitive to abiotic environmental variables than the complex physiological model (Kramer et al., 1996). Thus, aggregation of environmental variables may have lesser effects on hybrid model than on complex physiological model, which may partly explain why the hybrid model performed better than the complex physiological model at the regional scale.

Predictions based on empirical relationships like those in the hybrid model may not hold true under changing environments in the future, since those relationships were established based on observations in the past (Gustafson, 2013; Cuddington et al., 2013). However, predictions based on empirical life history attributes might retain validity in the future due to niche conservatism (Crisp et al., 2009; Wiens et al., 2010). For example, the tolerance range of growing degree days of a given plant species may remain largely constant despite climate change.

None of the models we examined simulate forest landscape

processes, which are spatially continuous and temporally dynamic processes (e.g., fire disturbance). Forest landscape processes are likely to have greater contribution to forest ecosystem responses than climate variables alone (Gustafson et al., 2010; Kurz et al., 2008; Girardin and Mudelsee, 2008; Li et al., 2013). Therefore, greater bias could occur if forest landscape processes are not included in the prediction of forest ecosystem dynamics (Reynolds et al., 2001). One reason PnET-II, ED2, and LINKAGES v2.2 performed reasonably well in our study is likely that there were no major disturbances in our study areas and sites in the study period.

Superiority of complex physiological model at the plot scale was achieved at the price of more detailed input data, longer time of simulation, and more simplified representation of forest composition. While the hybrid model was the best model at the regional scale, it cannot provide carbon dynamics at a fine temporal scale

characteristics, to help select the best model for their application in forest biomass and carbon modeling.

Acknowledgments

Appendix 1. List of parameters used for PnET-II and ED2.

Model	Parameter name	Definition (unit)	Value
PnET-II	BaseLeafRespFrac	Respiration as a fraction of maximum photosynthesis	0.1
	NetPsnMaxA	Intercept of relationship between foliar N and net maximum photosynthetic rate	−16
	NetPsnMaxB	Slope (μmoles CO_2 m^{-2} sec^{-1})	71.9
	PsnTMax	Maximum temperature for photosynthesis (°C)	40
	PsnTOpt	Optimum temperature for photosynthesis (°C)	20
	PsnTMin	Minimum temperature for photosynthesis (°C)	0
	HalfSat	Half saturation light level (J m^{-2} sec^{-1})	200
	WUEConst	Constant in equation for water use efficiency as a function of vapor pressure deficit	10.9
	FastFlowFrac	Fraction of water inputs lost directly to drainage	0.1
	f	Soil water release parameter	0.04
	CFracLeaf	Carbon as fraction of foliage mass	0.45
	CFracWood	Carbon as fraction of wood mass	0.5
	CFracRoot	Carbon as fraction of fine root mass	0.45
	RootAllocA	Intercept of relation between foliar and root allocation	130
	RootAllocB	Slope	1.92
	LeafGRespFrac	Foliar growth respiration, fraction of allocation	0.25
	WoodGRespFrac	Wood growth respiration, fraction of allocation	0.25
	WoodMRespFrac	Wood maintenance resp., fraction of allocation	0.35
	RootGRespFrac	Fine root growth respiration, fraction of allocation	0.25
	RootMRespFrac	Fine root maintenance resp., fraction of allocation	0.5
ED2	MPHOTO_TEC3	Stomatal slope for conifers and temperate C3 plants	7.2
	BPHOTO_BLC3	Cuticular conductance for broadleaf C3 plants (μmoles m^{-2} leaf sec^{-1})	10,000
	BPHOTO_NLC3	Cuticular conductance for needleaf C3 plants (μmoles m^{-2} leaf sec^{-1})	1000
	KW_TREE	Water conductance for tree (m^2 year^{-1} kg^{-1}C in root)	600
	GAMMA_C3	Dark respiration factor for C3 plants	0.035
	DO_TREE	Transpiration control in gsw (DO) for all trees	0.016
	ALPHA_C3	Quantum yield of all C3 plants.	0.08
	RRFFACT	Factor multiplying the root respiration factor	1
	LWIDTH_BLTREE	Leaf width for broadleaf trees (m)	0.1
	LWIDTH_NLTREE	Leaf width for conifer trees (m)	0.05
	Q10_C3	Q10 factor for C3 plants	2.4
	GAMM	Gamma coefficient for momentum	13
	GAMH	Gamma coefficient for heat	13
	TPRANDTL	Turbulent Prandtl number	0.74
	RIBMAX	Maximum bulk Richardson number	0.5
	LEAF_MAXWHC	Maximum water that can be intercepted by leaves (kg m^{-2} leaf)	0.11
	UBMIN	Minimum wind speed at the top of the canopy air space (m sec^{-1})	0.65
	UGBMIN	Minimum wind speed at the leaf level (m sec^{-1})	0.25
	USTMIN	Minimum friction velocity (m sec^{-1})	0.05

(e.g., daily carbon sequestration) like the complex physiological model can. The simple physiological model provided the worst prediction. Although we primarily focused on density of aboveground woody biomass, other traits associated with forest ecosystems (e.g., forest composition, basal area) are often of interest in ecosystem and landscape modeling. Data preparation and simulation time are also often, if not always, of concern. We suggest modelers can use the comparisons in model performance from our study, along with evaluating tradeoffs in other model

References

Aber, J.D., Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. Oecologia 92 (4), 463–474.

Aber, J.D., Ollinger, S.V., Federer, C.A., Reich, P.B., Goulden, M.L., Kicklighter, D.W., Melillo, J.M., Lathrop, R.G.J., 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. Clim. Reserch 5, 207–222.

Adams, M.B., Loughry, L., Plaugher, L., comps, 2004. Experimental Forests and Ranges of the USDA Forest Service. Gen. Tech. Rep. NE-321. Newtown Square, PA, U.S. Department of Agriculture. Forest Service, Northeastern Research

Station, 178.

Amthor, J.S., Chen, J.M., Clein, J.S., Frolking, S.E., Goulden, M.L., Grant, R.F., Kimball, J.S., King, A.W., McGuire, A.D., Nikolov, N.T., Potter, C.S., Wang, S., Wofsy, S.C., 2001. Boreal forest CO_2 exchange and evapotranspiration predicted by nine ecosystem process models: intermodel comparisons and relationships to field measurements. J. Geophys. Res. Atmos. 106 (D24), 33623—33648.

Baldocchi, D.D., Wilson, K.B., 2001. Modeling CO_2 and water vapor exchange of a temperate broadleaved forest across hourly to decadal time scales. Ecol. Model. 142 (1—2), 155—184.

Bennett, N.D., Croke, B.F.W., Guariso, G., Guillaume, J.H.A., Hamilton, S.H., Jakeman, A.J., Marsili-Libelli, S., Newham, L.T.H., Norton, J.P., Perrin, C., Pierce, S.A., Robson, B., Seppelt, R., Voinov, A.A., Fath, B.D., Andreassian, V., 2013. Characterising performance of environmental models. Environ. Model. Softw. 40 (0), 1—20.

Bond-Lamberty, B., Gower, S.T., Goulden, M.L., McMillan, A., 2006. Simulation of boreal black spruce chronosequences: comparison to field measurements and model evaluation. J. Geophys. Res. Biogeosciences 111 (G2). G02014.

Brown, S.L., Schroeder, P.E., 1999. Spatial patterns of aboveground production and mortality of woody biomass for eastern U.S. forests. Ecol. Appl. 9 (3), 968—980.

Buchman, R.G., Shifley, S.R., 1983. Guide to evaluating forest growth projection systems. J. For. 81 (4), 232—234, 254.

Bugmann, H., 2001. A review of forest gap models. Clim. Change 51, 259—305.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P., 2009. Phylogenetic biome conservatism on a global scale. Nature 458 (7239), 754—756.

Cuddington, K., Fortin, M.J., Gerber, L.R., Hastings, A., Liebhold, A., O'Connor, M., Ray, C., 2013. Process-based models are required to manage ecological systems in a changing world. Ecosphere 4 (2). Article 20.

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A., Hess, K.T., Gibson, J., Lawler, J.J., 2007. Random forests for classification in ecology. Ecology 88 (11), 2783—2792.

Dress, W.J., Boerner, R.E.J., 2003. Temporal and spatial patterns in root nitrogen concentration and root decomposition in relation to prescribed fire. Am. Midl. Nat. 149 (2), 245—257.

Falkowski, M.J., Hudak, A.T., Crookston, N.L., Gessler, P.E., Uebler, E.H., Smith, A.M.S., 2010. Landscape-scale parameterization of a tree-level forest growth model: a k-nearest neighbor imputation approach incorporating LiDAR data. Can. J. For. Res. 40 (2), 184—199.

Fang, J., Guo, Z., Hu, H., Kato, T., Muraoka, H., Son, Y., 2014. Forest biomass carbon sinks in east Asia, with special reference to the relative contributions of forest expansion and forest growth. Glob. Change Biol. 20 (6), 2019—2030.

Friend, A.D., Schugart, H.H., Running, S.W., 1993. A physiology-based gap model of forest dynamics. Ecology 74 (3), 792—797.

Friend, A.D., Stevens, A.K., Knox, R.G., Cannell, M.G.R., 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (hybrid v3.0). Ecol. Model. 95 (2—3), 249—287.

Girardin, M.P., Mudelsee, M., 2008. Past and future changes in Canadian boreal wildfire activity. Ecol. Appl. 18 (2), 391—406.

Grant, R.F., 2001. A review of the Canadian ecosystem model ecosys. In: Shaffer, M. (Ed.), Modeling Carbon and Nitorgen Dynamics for Soil Management. CRC Press, Boca Raton, Florida, USA, pp. 173—264.

Gueyette, R.P., Cutter, B.E., 1997. Fire history, population, and calcium cycling in the current river watershed. In: Pallardy, et al. (Eds.), Proceedings of the 11th Central Hardwood Forest Conference. Gen.Tech. Rep. NC-188. U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, MN, pp. 355—373.

Gustafson, E., 2013. When relationships estimated in the past cannot be used to predict the future: using mechanistic models to predict landscape ecological dynamics in a changing world. Landsc. Ecol. 28 (8), 1429—1437.

Gustafson, E.J., Shvidenko, A.Z., Sturtevant, B.R., Scheller, R.M., 2010. Predicting global change effects on forest biomass and composition in south-central Siberia. Ecol. Appl. 20 (3), 700—715.

Guyette, R.P., Stambaugh, M.C., Muzika, R.M., Dey, D.C., 2006. Fire scars reveal variability and dynamics of eastern fire regimes. In: Fire in Eastern Oak Forests: Delivering Science to Land Managers, Proceedings of a Conference. U.S. Department of Agriculture, Forest Service, Northern Research Station, Columbus, OH, p. 304.

Hanson, P.J., Amthor, J.S., Wullschleger, S.D., Wilson, K.B., Grant, R.F., Hartley, A., Hui, D., Hunt, J.E.R., Johnson, D.W., Kimball, J.S., King, A.W., Luo, Y., McNulty, S.G., Sun, G., Thornton, P.E., Wang, S., Williams, M., Baldocchi, D.D., Cushman, R.M., 2004. Oak forest carbon and water simulations: model intercomparisons and evaluations against independent data. Ecol. Monogr. 74 (3), 443—489.

Hanson, P.J., Wullschleger, S.D., Norby, R.J., Tschaplinski, T.J., Gunderson, C.A., 2005. Importance of changing CO_2, temperature, precipitation, and ozone on carbon and water cycles of an upland-oak forest: incorporating experimental results into model simulations. Glob. Change Biol. 11 (9), 1402—1423.

Hix, D.M., 1997. Forest ecosystems of the Marietta Unit, Wayne National Forest, southeastern Ohio: multifactor classification and analysis. Can. J. For. Res. 27 (7), 11—17.

Huber, M.O., Eastaugh, C.S., Gschwantner, T., Hasenauer, H., Kindermann, G., Ledermann, T., Lexer, M.J., Rammer, W., Schörghuber, S., Sterba, H., 2012. Comparing simulations of three conceptually different forest models with National forest inventory data. Environ. Model. Softw. 40, 88—97.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Leetmaa, A., Reynolds, R., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J.,

Jenne, R., Joseph, D., 1996. The NCEP/NCAR 40-year reanalysis project. Bull. Am. Meteorol. Soc. 77 (3), 437—471.

Kramer, K., Friend, A., Leinonen, I., 1996. Modelling comparison to evaluate the importance of phenology and spring frost damage for the effects of climate change on growth of mixed temperate-zone deciduous forests. Clim. Res. 7 (1), 31—41.

Kurz, W.A., Stinson, G., Rampley, G., 2008. Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances? Philos. Trans. R. Soc. Lond B Biol. Sci. 363 (1501), 2261—2269.

Li, X., He, H.S., Wu, Z., Liang, Y., Schneiderman, J.E., 2013. Comparing effects of climate warming, fire, and timber harvesting on a boreal forest landscape in northeastern China. PLoS One 8 (4), e59747.

Liang, Y., He, H.S., Wu, Z., Yang, J., 2014. Effects of environmental heterogeneity on predictions of tree species' abundance in response to climate warming. Environ. Model. Softw. 59, 222—231.

Luo, Y., Medlyn, B., Hui, D., Ellsworth, D., Reynolds, J., Katul, G., 2001. Gross primary productivity in duke forest: modeling synthesis of CO_2 experiment and eddy—flux data. Ecol. Appl. 11 (1), 239—252.

Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Quesada, C.A., SalomÃO, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., MartÍNez, R.V., Vinceti, B., 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. Glob. Chang. Biol. 12 (7), 1107—1138.

McNab, W.H., Cleland, D.T., Freeouf, J.A., Keys Jr., J.E., Nowacki, G.J., Carpenter, C.A., 2007. Description of ecological subregions: sections of the conterminous United States [CD-ROM]. In: Gen. Tech. Report WO-76B. U.S. Department of Agriculture, Forest Service, Washington, DC, p. 80.

Medvigy, D., Moorcroft, P.R., 2012. Predicting ecosystem dynamics at regional scales: an evaluation of a terrestrial biosphere model for the forests of north-eastern North America. Philosophical Trans. R. Soc. B Biol. Sci. 367.

Medvigy, D., Wofsy, S.C., Munger, J.W., Hollinger, D.Y., Moorcroft, P.R., 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: ecosystem demography model version 2. J. Geophys. Res. 114 (G1). G01002.

Moorcroft, P.R., Hurtt, G.C., Pacala, S.W., 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). Ecol. Monogr. 71 (4), 557—585.

Nigh, T.A., Schroeder, W.A., 2002. Atlas of Missouri Ecoregions. Missouri Department of Conservation, Jefferson City, MO, 212pp.

O'Connell, B.M., LaPoint, E.B., Turner, J.A., Ridley, T., Boyer, D., Wilson, A.M., Waddell, K.L., Pugh, S.A., Conkling, B.L., 2013. The Forest Inventory and Analysis Database: Database Description and Users Manual Version 5.1.6 for Phase 2. USDA Forest Service.

Pastor, J., Post, W.M., 1985. Development of a linked forest productivity-soil process model. In: ORNL/TM-9519. Oak Ridge National Laboratory, Oak Ridge, TN.

Peet, R., 1981. Changes in biomass and production during secondary forest succession. In: West, D., Shugart, H., Botkin, D. (Eds.), Forest Succession. Springer, New York, pp. 324—338.

Reich, P.B., Walters, M.B., Kloeppel, B.D., Ellsworth, D.S., 1995. Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. Oecologia 104 (1), 24—30.

Reynolds, J., Bugmann, H., Pitelka, L., 2001. How much physiology is needed in forest gap models for simulating long-term vegetation response to global change? Challenges, limitations, and potentials. Clim. Chang. 51 (3—4), 541—557.

Rigo, D., Barredo, J., Busetto, L., Caudullo, G., San-Miguel-Ayanz, J., 2013. Continental-scale living forest biomass and carbon stock: a robust fuzzy ensemble of IPCC tier 1 maps for Europe. In: Hřebíček, J., Schimak, G., Kubásek, M., Rizzoli, A. (Eds.), Environmental Software Systems. Fostering Information Sharing. Springer, Berlin Heidelberg, pp. 271—284.

Scheller, R.M., Mladenoff, D.J., 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. Glob. Chang. Biol. 11 (2), 307—321.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganičová, K., Netherer, S., Arpaci, A., Bontemps, J.-D., Bugmann, H., González-Olabarria, J.R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.-J., Mohren, F., 2011. Modelling natural disturbances in forest ecosystems: a review. Ecol. Model. 222 (4), 903—924.

Seidl, R., Lexer, M.J., Jäger, D., Hönninger, K., 2005. Evaluating the accuracy and generality of a hybrid patch model. Tree Physiol. 25 (7), 939—951.

Shifley, S.R., Brookshire, B.L.E., 2000. Missouri ozark forest ecosystem project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. In: General Technical Report NC-208, p. 314. St. Paul, MN.

Snell, R.S., Huth, A., Nabel, J.E.M.S., Bocedi, G., Travis, J.M.J., Gravel, D., Bugmann, H., Gutiérrez, A.G., Hickler, T., Higgins, S.I., Reineking, B., Scherstjanoi, M., Zurbriggen, N., Lischke, H., 2014. Using dynamic vegetation models to simulate plant range shifts. Ecography 37 (12), 1184—1197.

Soil Survey Staff. Web Soil Survey. Natural Resources Conservation Service, United States Department of Agriculture 2013 cited July 3, 2012. Available from http://websoilsurvey.nrcs.usda.gov/.

Sollins, P., Reichle, D.E., Olson, J.S., 1973. Organic Matter Budget and Model for a Southern Appalachian Liriodendron Forest.

Sterba, H., Monserud, R.A., 1997. Applicability of the forest stand growth simulator prognaus for the Austrian part of the Bohemian Massif. Ecol. Model. 98 (1), 23–34.

Thornton, P.E., Law, B.E., Gholz, H.L., Clark, K.L., Falge, E., Ellsworth, D.S., Goldstein, A.H., Monson, R.K., Hollinger, D., Falk, M., Chen, J., Sparks, J.P., 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. Agric. For. Meteorol. 113 (1–4), 185–222.

Thurner, M., Beer, C., Santoro, M., Carvalhais, N., Wutzler, T., Schepaschenko, D., Shvidenko, A., Kompter, E., Ahrens, B., Levick, S.R., Schmullius, C., 2014. Carbon stock and density of northern boreal and temperate forests. Glob. Ecol. Bio-geogr. 23 (3), 297–310.

Tjoelker, M.G., Oleksyn, J., Reich, P.B., 2001. Modelling respiration of vegetation: evidence for a general temperature-dependent Q10. Glob. Chang. Biol. 7 (2), 223–230.

USDA, 2012. Sinkin Experimental Forest. USDA Forest Service-Northern Research Station cited January 24, 2013. Available from: http://nrs.fs.fed.us/ef/locations/mo/sinkin/.

USDA, 2013. Vinton Furnace State Experimental Forest. cited 2014. Available from: http://www.nrs.fs.fed.us/ef/locations/oh/vinton-furnace/.

USDA Forest Service, 2014. FIA Datamart. Available at: http://www.fia.fs.fed.us/tools-data/default.asp (accesed 13.09.14.).

Van Kley, J.E., Parker, G.R., 1993. An ecological classification system for the central hardwoods region: the Hoosier National forest. In: Gillespie, A.R.P., George, R., Pope, Phillip E., Rink, George (Eds.), Proceedings of the 9th Central Hardwood Forest Conference. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, MN, pp. 308–326.

Vanderwel, M.C., Coomes, D.A., Purves, D.W., 2013. Quantifying variation in forest disturbance, and its effects on aboveground biomass dynamics, across the eastern United States. Glob. Chang. Biol. 19 (5), 1504–1517.

Wang, W.J., He, H.S., Spetich, M.A., Shifley, S.R., Thompson Iii, F.R., Dijak, W.D., Wang, Q., 2014. A framework for evaluating forest landscape model predictions using empirical data and knowledge. Environ. Model. Softw. 62 (0), 230–239.

Wang, Y.P., Jarvis, P.G., 1990. Description and validation of an array model — MAESTRO. Agric. For. Meteorology 51 (3–4), 257–280.

Whittaker, R.H., Bormann, F.H., Likens, G.E., Siccama, T.G., 1974. The Hubbard Brook ecosystem study: forest biomass and production. Ecol. Monogr. 44 (2), 233–254.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Jonathan Davies, T., Grytnes, J.-A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecol. Lett. 13 (10), 1310–1324.

Williams, M., Rastetter, E.B., Fernandes, D.N., Goulden, M.L., Wofsy, S.C., Shaver, G.R., Melillo, J.M., Munger, J.W., Fan, S.M., Nadelhoffer, K.J., 1996. Modelling the soil-plant-atmosphere continuum in a Quercus–Acer stand at Harvard Forest: the regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties. Plant Cell Environ. 19 (8), 911–927.

Wilson, B.T., Lister, A.J., Riemann, R.I., 2012. A nearest-neighbor imputation approach to mapping tree species over large areas using forest inventory plots and moderate resolution raster data. For. Ecol. Manag. 271 (0), 182–198.

Wullschleger, S., Gunderson, C., Tharp, M.L., West, D., Post, W., 2003. Simulated patterns of forest succession and productivity as a consequence of altered precipitation. In: Hanson, P., Wullschleger, S. (Eds.), North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes. Springer, New York, pp. 433–446.

Xiong, X., Grunwald, S., Myers, D.B., Kim, J., Harris, W.G., Comerford, N.B., 2014. Holistic environmental soil-landscape modeling of soil organic carbon. Environ. Model. Softw. 57, 202–215.

Xu, C., Gertner, G.Z., Scheller, R.M., 2009. Uncertainties in the response of a forest landscape to global climatic change. Glob. Chang. Biol. 15 (1), 116–131.

Zaczek, J., Groninger, J., 2002. Stand dynamics in an old-growth hardwood forest in southern Illinois, USA. Nat. Area J. 22 (3), 211–219.

Zhao, M., Zhou, G.-S., 2005. Estimation of biomass and net primary productivity of major planted forests in China based on forest inventory data. For. Ecol. Manag. 207 (3), 295–313.