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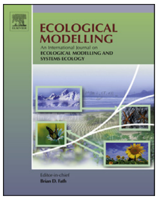

Toward more robust projections of forest landscape dynamics under novel environmental conditions: Embedding PnET within LANDIS-II

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ABSTRACT

Ecological models built on phenomenological relationships and behavior of the past may not be robust under novel conditions of the future because global changes are producing environmental conditions that forests have not experienced historically. We developed a new succession extension for the LANDIS-II forest landscape model, PnET-Succession, to simulate forest growth and succession using physiological first principles. PnET-Succession integrates the tree physiology model PnET-II with the existing LANDIS-II Biomass Succession extension. PnET-Succession simulates the competition of tree species cohorts for water and light as a function of photosynthetic processes driven by foliar nitrogen. Competition for water is simulated on each grid cell through a dynamic soil-water balance that receives precipitation and loses water through runoff, consumption in photosynthesis, and evapotranspiration. Competition for light is modeled by tracking solar radiation through canopy layers according to a standard Beer-Lambert formula. PnET-Succession requires average monthly photosynthetically active radiation, atmospheric CO_2 concentration, temperature and precipitation as inputs. The new extension also dynamically calculates species establishment probabilities in each time step as a function of water and radiation stress. We calibrated PnET-Succession to biomass and LAI measurements from the Duke Experimental Forest in North Carolina (USA) and tested the calibrated model against data from the Green Ridge State Forest in Maryland. The new extension shows considerable promise for studying forest response to climate change, including changes in carbon stocks.

1. Introduction

Forests around the world are being impacted by global shifts that affect forest growth and competition such as climate change (IPCC, 2007), variations in atmospheric composition (Pitelka et al., 1997; Thuiller et al., 2008) and introduced exotic pests (Aukema et al., 2010). Such alterations produce specific changes in landscape characteristics and dynamics at distinct spatial and temporal scales (Laughlin et al., 2004; He and Mladenoff, 1999). Many of these changes are unprecedented, and their effects and interactions with other ecological processes are uncertain. Models that use empirical relationships estimated under past conditions may not reliably predict future forest dynamics under a novel regime of fundamental ecosystem drivers (Gustafson, 2013; Williams and Jackson, 2007). In contrast, process-based models that use direct cause-and-effect relationships to link forest dynamics with fundamental drivers such as temperature, precipitation, and CO_2 concentrations can produce more robust predictions under novel conditions (Cuddington et al., 2013; Gustafson, 2013).

Forest landscape models simulate forest generative (establishment, development, aging) and degenerative (disturbance, senescence) processes over broad spatial and temporal scales (see reviews by Scheller and Mladenoff, 2007; He, 2008). By explicitly modeling spatial processes such as seed dispersal and disturbance spread while simultaneously modeling local competition among tree species, these models can account for ecosystem interactions in both time and space and across scales. Competition within these models is modeled in various ways. Many models have applied a phenomenological approach that probabilistically simulates the outcome of competition via a state transition matrix (Scheller and Mladenoff, 2007). By comparison, the LANDIS family of models simulate competition among tree species cohorts for growing space

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on a site (e.g., Scheller and Mladenoff, 2004) or stand thinning dynamics (Wang et al., 2013), resulting in nondeterministic successional pathways that are sensitive to tree species life history and their interactions with different disturbance types. While biotic processes of tree species cohort growth, competition, and death are explicitly modeled using the LANDIS framework, relationships with environmental drivers are generally indirect and crudely estimated.

Integration of tree physiology and competition amongst trees for the fundamental resources of water and light offers a comparatively advanced and robust approach that directly accounts for dynamic biophysical drivers of vegetation change. For example, TreeMig, uses a submodel that dynamically simulates competition for light only (Lischke et al., 2006; Thuiller et al., 2008). Another model, FireBGCv2, simulates competition for both light and water (Keane et al., 2011). FireBGCv2 uses a radiation balance and it is advanced in some of its hydrological calculations, for example by implementing an explicit catchment simulation. Although it simulates individual trees at its finest spatial scale, because it assumes a steady state relationship between individual tree C and stand C it does not implement a closed C balance to scale C up from the tree to the stand and landscape level. Instead, it implements empirical relationships for scaling (Keane et al., 2011).

In this paper, we describe a new extension (PnET-Succession) to the LANDIS-II forest landscape model (Scheller et al., 2007a) that simulates growth based on competition of species-age cohorts for both light and water. Although based on the Biomass Succession extension of Scheller and Mladenoff (2004), PnET-Succession replaces the cohort competition routines in Biomass Succession with a more detailed approach based on the PnET-II model of Aber et al. (1995). The purpose of the new approach is to link the succession process more directly to local competition for light and water, and to the fundamental drivers of climate and atmospheric chemistry, by incorporating the first principles of tree physiology and physical shading. We carefully balanced this implementation of fundamental drivers with the need to constrain complexity and the resulting model and parameter uncertainty (Cuddington et al., 2013; Keane et al., submitted for publication; Gustafson, 2013). The ultimate objective is to produce a more robust model for simulating landscape dynamics under multiple global changes.

2. Methods

2.1. Overview of model components

PnET-Succession integrates components of the spatially explicit forest biomass and demography Biomass Succession extension of LANDIS-II (Scheller and Mladenoff, 2004; Scheller, 2012) and the one-dimensional ecophysiology model PnET-II (Aber and Federer, 1992; Aber et al., 1995) into a single succession extension that dynamically simulates the most important ecophysiological processes that drive tree species responses to shading, climate and atmospheric chemistry. Instead of parameterizing Biomass Succession with outputs from a PnET-II simulation, as described by Scheller and Mladenoff (2004) and Xu et al. (2009) (c.f., Section 2.2.3), PnET-Succession includes PnET-II equations to simulate succession, growth, and senescence processes at a monthly time step. Local ecophysiological processes in PnET-Succession therefore respond dynamically to inputs and cohort composition changes that occur during a model run. This allows us to simulate above- and belowground biomass by species cohorts, and cumulative LAI, soil water and radiation at the site-level (Fig. 1).

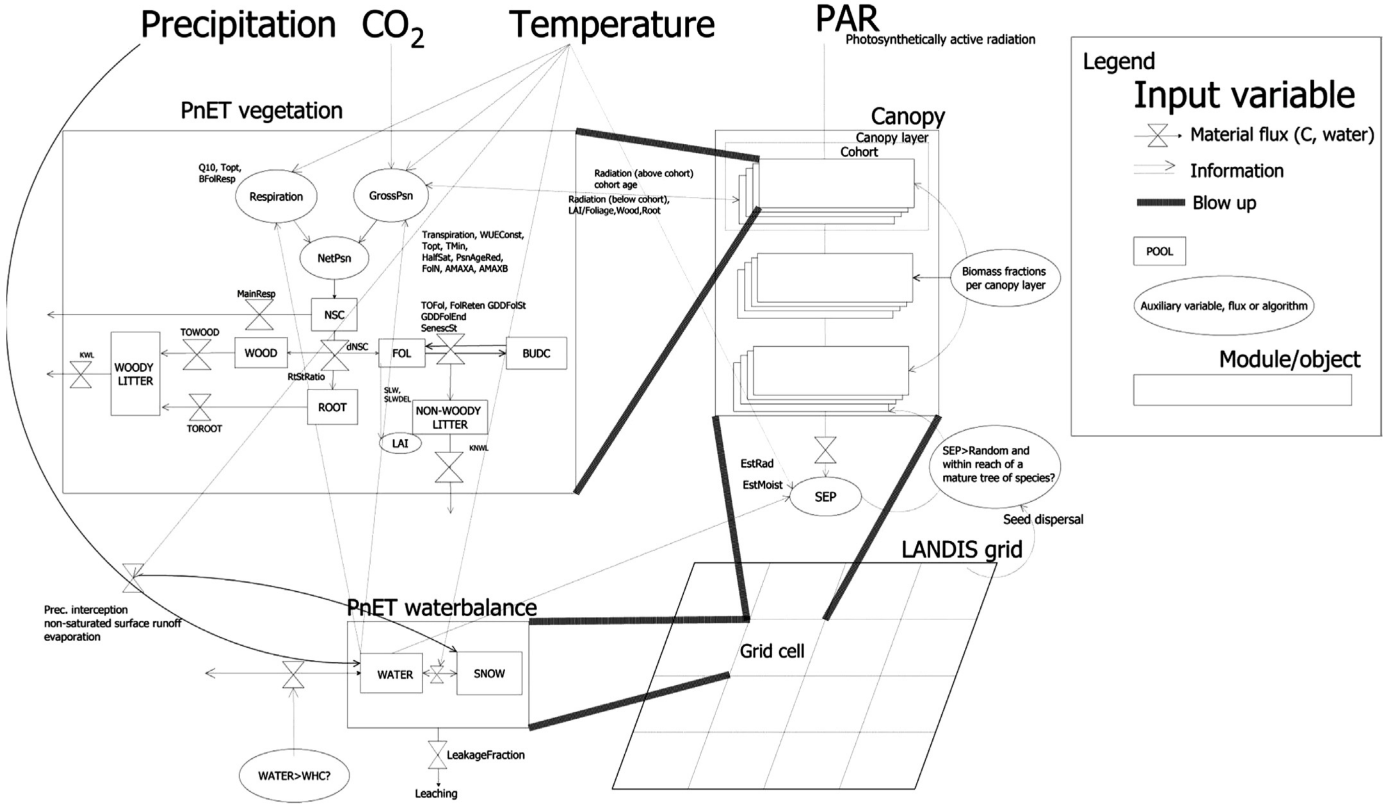

Fig. 1. Conceptual scheme of the PnET-Succession extension of LANDIS-II. Radiation and water stress are the two main feedbacks that determine photosynthesis. Species establishment probability (SEP) is determined by simulating the development of a new cohort with minimal biomass with radiation and moisture determined by the cohorts present on the site.

2.1.1. *LANDIS-II modeling platform*

LANDIS-II is a forest landscape modeling platform that consists of a core collection of libraries (Scheller and Domingo, 2006) and a collection of independent extensions that represent various ecological processes of interest (Scheller et al., 2007b). LANDIS-II simulates disturbances and forest succession in large landscapes (10^4–10^7 ha), with cell size typically ranging from 10 to 250 m. Individual cells are grouped into ecoregions with homogeneous climate and soil parameters. Consequently, disturbance regimes (e.g., fire, wind regime) are defined according to ecoregions, and the probability that tree species can successfully establish varies among ecoregions (Scheller and Mladenoff, 2004). To decrease model complexity and limit run-time and memory requirements, LANDIS-II tracks species-age cohorts rather than individual trees. User selected succession extensions simulate the processes of cohort establishment, growth, aging, and senescence. Depending on the succession extension, cohorts are represented by presence-absence or by a continuous measure of abundance (e.g., biomass) for each cohort. Cohort ages are binned into discrete classes that typically reflect the temporal integration unit (i.e., time step) used to model succession (Scheller and Mladenoff, 2004). Optional disturbance extensions simulate destructive ecological processes such as fire (Sturtevant et al., 2009), wind throw (Scheller et al., 2007b), timber harvests (Gustafson et al., 2000) and insect outbreaks (Foster, 2011; Foster et al., submitted for publication; Sturtevant et al., 2004). Extensions can each operate with a different time step determined by the user to best represent the process being simulated.

2.1.2. *LANDIS-II Biomass Succession*

The Biomass Succession extension of LANDIS-II uses aboveground biomass on grid cells as the ecosystem "currency," simulating the processes of tree species cohort establishment, cohort growth and competition for growing space, and cohort senescence and mortality (Scheller et al., 2007b). Biomass is allocated to just two aboveground pools: live and dead. Our modifications to Biomass Succession focus on the algorithms to simulate establishment, growth and senescence, so our description of the existing extension is limited to those processes. In Biomass Succession, a tree species cohort is considered to become established when seedlings emerge and survive one model time step. Establishment is determined stochastically based on a user-defined species establishment probability (SEP). Although SEP can be defined in Biomass Succession to vary at user-defined time steps (e.g., to reflect changing environmental conditions due to climate change or other perturbations), these changes do not reflect a response to dynamic site conditions. In addition, Biomass Succession assumes that shading is correlated with biomass on a cell, and establishment is further modified according to the shade tolerance of the tree species (Scheller and Mladenoff, 2004). Once established, tree species cohorts remain on a site until removed by disturbance, or until they reach a species-specific longevity.

Aboveground net primary productivity (ANPP) of a cohort depends on the maximum possible ANPP for the species in the ecoregion (ANPP_{max}) and on the ratio of current cohort biomass to the maximum biomass the site can support (B_{max}), which indicates how much "growing space" is available. Mortality-related losses in cell biomass are accounted prior to growth, so that ANPP may fill in space vacated by such losses. ANPP_{max} and B_{max} are external inputs to Biomass Succession and are typically estimated using finer-scale models such as PnET. Biomass Succession calculates initial biomass of cohorts (only species-age combinations are specified in initial conditions input file) by simulating a spin-up that covers a time span equal to the age of each cohort. Mortality depends both on biomass density (thinning) and on age (i.e., senescence). Mortality due to self-thinning is low when a cohort is young or small and accelerates with age. Biomass lost to senescence is transferred to the dead biomass pool that decays according to species and ecoregion-specific decay rates.

There are drawbacks to the use of B_{max} and ANPP_{max} that we addressed with PnET-Succession. The input parameter ANPP_{max} is based on the maximum observed or modeled ANPP for a monoculture of a species on a particular site. ANPP_{max} is sometimes derived from empirically observed growth rates in tree stands, i.e., 99th percentile of observed ANPP (Gustafson et al., 2010). However, it is unclear how tree growth might respond to novel future conditions (i.e., absence of typical competition, CO_2 enrichment, climate warming). Moreover, it is usually unclear what resource constraints and competition pressures may have been present when ANPP_{max} was observed. Alternatively, ANPP_{max} may be derived from other models (see Section 2.1.3), where ANPPmax is assumed to equal ANPP when canopy closure occurs. When ANPP_{max} is estimated using a model that includes some kind of resource constraint or competition (e.g., Xu et al., 2009), Biomass Succession essentially double-counts the effect of limiting factors when it also simulates competition for "growing space."

B_{max} represents a long-term steady state (i.e., in the absence of disturbance) of aboveground biomass that a site can support. Typically, B_{max} is derived from growth tables (Smith et al., 2006; Gustafson et al., 2013) or by assuming a rule of thumb such as $B_{\text{max}} = 30 \cdot \text{ANPP}_{\text{max}}$ (Scheller and Mladenoff, 2007) or other empirical relationship (e.g., Keeling and Phillips, 2007). Like tree growth, it is unclear how B_{max} might respond to novel future conditions.

2.1.3. *PnET-II*

The LANDIS-II input parameters, SEP and ANPP_{max} can be estimated using PnET-II in a loosely coupled meta-modeling approach (Fig. 2; Xu et al., 2009). PnET-II is a 1-dimensional "big leaf" ecophysiology model that couples carbon (C) and water balance to simulate species-age cohort biomass dynamics (Aber and Federer, 1992; Aber et al., 1995). C balance in PnET-II is driven by photosynthesis, which depends on radiation, soil moisture, leaf area index (LAI) and foliage N (optional). Multiplicative reduction factors are used to decrease the potential rate of photosynthesis according to

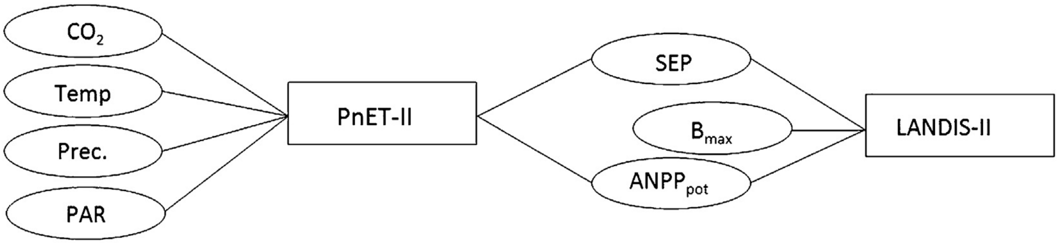

Fig. 2. Loosely coupled meta-modeling approach using PnET-II and LANDIS-II. The rectangles represent the models, and the ovals represent model input and output variables. ANPP: Aboveground Net Primary Production, SEP: Species Establishment Probability, B_{max}: Maximum biomass.
Adapted from Xu et al. (2009).

water stress, suboptimal radiation, vapor pressure deficit, and suboptimal temperature. Potential photosynthesis rates are based on laboratory data (Reich et al., 1990; Aber and Federer, 1992). Soil water is calculated in a "tipping bucket" (Jones and Kiniry, 1986) hydrology model that uses water inputs (precipitation) and losses (e.g., evaporation, surface runoff) to calculate the saturation of soil relative to WHC, which is used to calculate water stress to determine rate of photosynthesis and therefore transpiration. In PnET-II, atmospheric CO_2 affects the rate of photosynthesis by changing both the response to vapor pressure deficit and by increasing water use efficiency. PnET-II does not implement senescence. Driving variables in the PnET-II model are user-defined monthly average daily maximum temperature, monthly total precipitation and average atmospheric CO_2.

2.1.4. Traditional meta-modeling parameterization of Biomass Succession

The original PnET model (Aber and Federer, 1992) does not predict SEP and $ANPP_{max}$ directly. Because $ANPP_{max}$ is conceptually associated with the productivity of closed canopy forests prior to the onset of any age-related decline in productivity (Scheller and Mladenoff, 2004, p. 215), Xu et al. (2009) equated $ANPP_{max}$ to the ANPP predicted by PnET for a stand that has just achieved crown closure. Xu et al. (2009) further assumed that $B_{max} = 30.0 \cdot ANPP_{max}$ (Whittaker and Marks, 1975; Scheller and Mladenoff, 2007). While PnET-II does not model the process of establishment, Xu et al. (2009) used PnET-II to estimate SEP from the environmental adjusting factors (water, light) that affect photosynthesis, assuming that conditions that reduce photosynthesis will also reduce the probability of sapling establishment (Botkin et al., 1972; Pastor and Post, 1985).

The meta-modeling approach is flexible in that LANDIS-II Biomass Succession is not directly reliant on PnET-II if other methods are more desirable. For example, $ANPP_{max}$ can be derived from empirical calibration with growth volume tables or other tree growth data (e.g., Smith et al., 2006; Gustafson et al., 2013). A key strength of a coupled LANDIS-II PnET-II methodology is the ability to simulate long-term (i.e., century and longer) future forest conditions under dynamic and novel climatic and atmospheric conditions – something that neither model can achieve alone. The meta-modeling approach also introduces a number of conceptual inconsistencies for resulting simulations. For example, PnET is nonspatial and PnET inputs do not necessarily reflect the vegetation that LANDIS simulates in individual sites. PnET-II directly adjusts growth rates based on light transmission through LAI, whereas LANDIS-II only approximates this process via "available growing space" that is a function of actual biomass and B_{max}. However, Standing biomass and available light at the forest floor are not necessarily directly correlated (Vose et al., 1994). This has implications not only for growth reduction of established cohorts in the understory, but also for light conditions at the forest floor affecting SEP. Likewise, site water balance is dynamic within PnET-II due to interactions with supported leaf area, and such temporal variability in water balance may have implications for competitive interactions among tree species and cohorts (Valladares and Niinemets, 2008). Finally, a loose coupling of PnET-II misses the opportunity to better account for LAI and biomass of stem, root and foliage pools within LANDIS-II.

2.2. New PnET-Succession extension

2.2.1. Advantage of PnET-Succession

There are advantages to the direct coupling of Biomass Succession and PnET-II (*PnET-Succession*) compared to the loose coupling approach:

1. PnET-Succession replaces the input parameters $ANPP_{max}$ and B_{max} of Biomass Succession dynamic calculations of growth and senescence that depend on site-level conditions and the effect of competing vegetation on soil and light availability. Consequently, establishment and growth are emergent properties of the model and are explicitly linked to changing fundamental drivers such as climate and CO_2 concentrations.
2. Dynamic calculations of foliage and LAI allow cohorts to die prior to senescence when respiration exceeds productivity, typically due to shading, water competition, drought, diseases or pests. This allows more realistic simulation of cohort death in the course of stand development (i.e., mortality is highest in the younger cohorts), and a more realistic accounting of biomass accumulation. An added benefit of implementing cohort deaths is that run times are reduced because the number of cohorts to be simulated is reduced.
3. PnET-Succession allows a more explicit simulation of species' survival strategies, by implementing a dynamic competition for light and water in a spatially specific water and radiation balance that is driven by incoming radiation and precipitation on the one hand, and light interception and transpiration on the other. For example, one can parameterize species or species-group combinations of respiration losses and water use efficiency to implement competitive advantages or disadvantages for particular species on sites with sub-optimal water and/or light.

2.2.2. Model structure

We will limit our discussion of the new succession extension to descriptions of its fundamental principles. A more formal documentation (equations and parameter values) is supplied in Appendix A. PnET-Succession replaces the simple growth and competition algorithms from Biomass Succession with the photosynthesis and respiration equations from PnET-II to simulate growth of specific cohort biomass components (root, foliage, wood, Non-Structural Carbon (NSC)) as a competition for light and water. These equations are embedded at the tree cohort level to calculate growth as a function of light availability and extinction through a stratified multi-species canopy, competition for soil water, and responses to climatic and atmospheric conditions (Fig. 1).

While PnET-II simulates growth for a "lumped forest" (Aber and Federer, 1992), the PnET-Succession model must explicitly simulate multiple cohorts that coexist on a single site, where each cohort is represented by a single PnET simulation. To reduce run times, several simplifications of PnET-II were made for PnET-Succession, primarily by broadening the scale of integration operations. For example, the time step in PnET-Succession is one month, whereas PnET-II completes soil water calculations daily. Additionally, PnET-Succession integrates photosynthesis calculations over 5 vertically stratified sub-canopy layers within a cohort canopy layer, with each sub-layer representing 20% of the total cohort LAI, where PnET-II uses 50 layers. Simulation results obtained with 50 foliage layers were compared with results obtained with 5 layers to ensure that these simplifications were reasonable.

Additionally, some parameters and algorithms were simplified. The hydrology calculations in the PnET-II model contain separate loss fractions of precipitation for evaporation (PrecIntFrac) that is subtracted from incoming precipitation and for crack flow or runoff (FastFlowFrac), which is subtracted from the sum of incoming precipitation and melting water. PnET-Succession combines these two losses into the PrecLossFrac parameter. PnET-Succession uses a somewhat different allocation of carbohydrate resources. PnET-II calculates a pool called PlantC, but its biological interpretation is not clear (Aber and Federer, 1992). In PnET-Succession, we use a 'nonstructural carbon' pool (NSC, Appendix A.1 Eqs. (14)–(17)) that has the advantage of representing a measurable property of plant tissue (i.e. the total starch, sucrose, glucose, fructose and other carbohydrates, Hoch et al., 2003). Changes we made to the implementation of NSC aim to improve simulations of extreme drought stress, an anticipated future use of the PnET-Succession model. Additionally, the implementation of water stress in the PnET-II model is through a coefficient (f_{water}) that is defined as transpiration (T) over a potential transpiration (PT) defined by potential rates of photosynthesis. PnET-Succession defines T as the minimum of water uptake capacity and a water demand that depends on photosynthesis. Because PT is only known at the end of a time step, however, f_{water} would down-scale photosynthesis only at the next time step, which would lead to delays in the seasonality of modeled soil water. Moreover, our experience with PnET-II is that of the two parameters involved in water uptake (i.e., WUEconst and f in Aber and Federer, 1992), simulation output was sensitive only to WUEconst (i.e., a reference water use efficiency), while simulation results changed with f only when f was unreasonably low. In PnET-Succession, f_{water} is therefore implemented according to an exponential stress curve which can be used in the time step for which it is calculated because it does not depend on potential photosynthesis (Appendix A.1, Eq. (5)).

Using PnET-II within LANDIS required us to prioritize the access of individual cohorts to water and radiation. In forests, individual trees have access to light depending primarily on height and proximity to other trees. Analogous to Biomass Succession, PnET-Succession assumes that LAI and biomass are spatially homogeneous at the site (i.e., cell) scale. PnET-Succession uses cohort biomass as a surrogate for canopy layers, where it assigns cohorts with larger biomass to upper canopy layers (Fig. 1-canopy). Canopy layers can be added as a site ages, and cohorts are assigned to canopy layers such that the largest (by biomass) cohort is assigned to the top layer, and successively smaller cohorts are assigned to layers according to user-specified proportions of biomass. For example, the user can specify that 100% of the cohorts are assigned to the lowest layer while the maximum cohort age <20 years, and 10% of the cohorts are assigned to the upper layer, 30% to the middle layer and 60% to the lowest layer after that. There is no limit to the number of canopy layers or age categories that can be specified. The absorption of light by canopy layers is computed using the Beer-Lambert formula as in PnET-II (Aber and Federer, 1992). All species age cohorts within a canopy layer have equal access to light.

Net photosynthetic production (Appendix A.2) is allocated to NSC. NSC is then allocated to wood, root and foliage biomass. Allocation to foliage increases with the net photosynthesis of the lower foliage layers. Allocation to the stem (wood) is not straightforward because wood allocation in a forest may be increased by height competition, which is not explicitly simulated by PnET-Succession. Because PnET-II does not simulate fine root specifically and because LANDIS simulates species-age cohorts rather than individual trees, we ignored changes to root:shoot ratios that are caused by competition (Dybzinski et al., 2011) and instead chose the simplifying assumption that root to shoot biomass ratio is a prescribed constant that is maintained by allocating C to conserve the root to stem ratio.

Unlike PnET-II, PnET-Succession must account for changes in tree physiology with age, and how trees die of old age. PnET-Succession does not account for specific age-related tree senescence factors, such as decreased efficiency of plant-internal transport processes (Drake et al., 2011; Gower et al., 1996). Instead, senescence is implemented as a reduction of gross photosynthesis with age. A user-defined reduction factor determines the shape of the growth reduction curve, which reaches zero at the longevity defined for the species. A cohort dies when NSC becomes <1% of the total of the other biomass pools, which typically occurs prior to the prescribed longevity age, but never exceeding it.

New species cohorts establish on a grid cell if the following conditions are met: (1) propagules exist on the cell, which is simulated with a dispersal kernel and (2) SEP > random variate [0,1], where SEP is the probability of establishment for the species on the site. SEP depends on the climate at the time of establishment, and is therefore calculated at each time step using empirical relationships that predict how suboptimal soil moisture, temperature and light availability affect SEP for each species (Fig. 1).

PnET-Succession requires an initial vegetation map as input that specifies species and age combinations on each site. It uses monthly climate data (maximum average monthly temperature, monthly total precipitation and monthly average atmospheric CO_2) as driving variables. Additionally, PnET-Succession uses species-specific parameters from both the original PnET-II model and the Biomass Succession extension. Similarly, PnET-II hydrological parameters that are used to calculate runoff and interception are associated with ecoregions in PnET-Succession. Like Biomass Succession, PnET-Succession uses a spin-up simulation to derive species cohort initial biomass.

2.3. *Site-level calibration of PnET-Succession*

PnET-Succession inherits a few non-measureable parameters from PnET-II, and therefore must be calibrated. We calibrated the extension using empirical data from two experiments at the Duke Experimental Forest (North Carolina: hereafter Duke EF) (Hui and Luo, 2004; Drake et al., 2011). Diameter at breast height (dbh), LAI, wood and root biomass were measured in 12 sites of differing ages in a forest dominated by loblolly pine (*Pinus taeda* L.) and various oak species (*Quercus* spp.) in 2008 (Drake et al., 2011). C increments in wood and coarse roots were calculated by applying species specific allometric regressions to annual dbh measurements of individual trees (Drake et al., 2011). The relative contribution of pines and hardwoods to total LAI was estimated from litter collections and local measurements of specific leaf area after correcting for petiole mass. Pine LAI was estimated as the difference between summer maximum ecosystem LAI (optical method) and hardwood LAI (litterfall method). Hui and Luo (2004) measured soil water in three additional sites with 14 year-old loblolly pine. The sites were established under very similar conditions in terms of land use history, initial stocking densities, management history and soil types. Soils are heavily weathered, clay-rich Alfisol soils of the Helena series with relatively low nitrogen and phosphorus availability. The main distinguishing feature between the sites was the age of the trees, with pines varying from 14 to 115 years old, and oaks from 1 to 102 years. We downloaded historic temperature and precipitation data from NOAA National Climatic Data Center (http://www.ncdc.noaa.gov/) for the weather station nearest to the Duke EF. Global values of historic CO_2 concentrations were obtained from IPCC (2007).

We used biomass measurements made by Drake et al. (2011) from the 12 sites with mixed oak/pine vegetation as a chronosequence showing the temporal dynamics of aging and succession from a pine to an oak dominated forest; this was done by applying PnET-Succession to represent a homogeneous site using a one-pixel map. Simulated biomass values that were calculated during the spin-up period were compared with measured biomass. We used an iterative parameter-generation minimum squares method to calibrate. We selected parameters that were calibrated according to their definition (i.e., non-measureable 'tuning parameters') or their (high) uncertainty (Appendix A.5). We evaluated model performance criteria (RMSE, average modeled and measured values, optical plotting) for each individual measurement type (LAI, Wood, Root, soil water). Additionally, we compared LAI simulated using 5 within-canopy integration steps, with LAI simulated using 50 canopy integration steps, to test if accurate results can be obtained with 5 just layers (see Section 2.2.2).

2.4. Prediction of landscape-level aboveground biomass and LAI

Parameter values optimized during the calibration procedure were used to evaluate model performance in a simulation of forest dynamics at Green Ridge State Forest (GRSF) in Maryland. GRSF was selected because input maps and parameters were available from prior studies (Sturtevant and Seagle, 2004; Townsend et al., 2003, 2004; Foster, 2012). Model results obtained with PnET-Succession were compared with equivalent results obtained using the Biomass Succession model coupled with PnET-II. The predicted distribution in biomass of both models was compared with the distribution of biomass measured in GRSF in CFI data. Additionally, LAI predicted by PnET-Succession was compared to LAI measurements by Sturtevant and Seagle (2004). GRSF is located in the central Appalachian highlands in the Ridge and Valley physiographic region of the eastern United States, just east of the Allegheny Plateau, in the state of Maryland. The area receives 1000 mm of precipitation annually, distributed evenly throughout the year. Annual temperatures range from −5 to 28 °C with an average of 10.6 °C. Most soils at GRSF are derived from shale or sandstone and are relatively shallow to bedrock and well drained. Elevation ranges from approximately 200 to 600 m (Foster, 2011). The historic vegetation in GRSF was an oak-chestnut forest type, but logging, extensive burning, and exotic pests such as the chestnut blight have replaced most of the original forest (Sturtevant and Seagle, 2004). Disturbances have been less frequent since ∼1950 and most of GRSF is now covered with secondary forests dominated by several species of oak (white oak: *Quercus alba* L., scarlet oak: *Q. coccinea* Muenchh., northern red oak: *Q. rubra* L., chestnut oak: *Q. prinus* L.) that attain dominance according to moisture gradients that are defined by topography. Virginia pine (*Pinus virginiana* Mill.), white pine (*P. strobus* L.) and hemlock (*Tsuga canadensis* L.) grow on moister, north facing slopes. GRSF management by the State of Maryland aims to continue an oak/pine forest type (Foster, 2011).

2.4.1. Simulation of GRSF

Maps of current vegetation, management areas and ecoregions were derived from baseline simulations by Foster (2011). A forest community type map was developed from hyperspectral AVIRIS imagery, maps of harvest polygons dating from 1969 to 2000, and continuous forest inventory (CFI) data from a network of 436 plots sampled by the MD DNR in 1999 and 2000 (Maryland Department of Natural Resources (MD DNR); Townsend et al., 2003; Foster, 2011). Ecoregions were derived from the Soil Survey Geographic Database (SSURGO) based on seven soil variables: field capacity (water, 1/3 bar), wilting point (water, 15 bar), available water capacity, silt, sand, and clay content (%), and soil pH, each averaged up to a soil depth of 40 cm. The climate was identical for each ecoregion except the parameter for fraction of precipitation loss that was varied according to aspect and elevation. Planned harvest regimes were included as baseline disturbances. Harvesting prescriptions were derived from the latest management map for GRSF, in which 57% of approximately 19,100 ha had been designated for timber management (MD DNR January 2011). Prescriptions ranged from salvage cuts of senescing pine and black locust to white pine release and pre-commercial thinning of mixed oaks. We parameterized the model to harvest 1% of the managed area annually on average, in accordance with a 100-year rotation. We assumed a continuation of the climate from 1980–2000 to the next two centuries, where climate was generated using randomly drawn years from 1980 to 2000.

2.4.2. Criteria to compare PnET-Succession with Biomass Succession

1. To evaluate predictive performance, biomass from the PnET-Succession spin-up was compared with observed biomass in GRSF as reported in CFI. Additional, simulated Leaf Area Index was compared with values reported by Sturtevant and Seagle (2004). The comparison of LAI with values reported by Sturtevant and Seagle (2004) is only a rough indication of model performance, because Sturtevant and Seagle (2004) selected mature forested stands (i.e., they do not represent the full range of stands simulated within PnET-Succession). However, no other LAI measurements are available. Model performance was compared to the equivalent results from the Biomass Succession model. Both models predict aboveground biomass, but only PnET-Succession predicts LAI (Foster, 2011; Sturtevant and Seagle, 2004). The criterion for good model performance is that the model spin-up creates a distribution of biomass and/or LAI that is within the uncertainty limits (>95% overlap) of the measurements.
2. Because PnET-Succession does not use a parameter $B_{\max}$ that caps potential biomass stocks, it is important to show that biomass remains within biologically reasonable limits. We compared PnET-Succession biomass predictions with predictions of the Biomass Succession module during a 200-year simulation. The criterion for good model performance is that PnET-Succession predicts biomass dynamics that we considered biologically plausible. Additionally, we compared the proportional abundance of aboveground biomass among three classes of tree species: oak, pines and other species.
3. Unlike Biomass Succession, PnET-Succession links cohort establishment directly to site soil water and radiation conditions. To evaluate how well the model captures these interactions, we compared spatial patterns of establishment for sugar maple and scarlet oak, two species with different ecological niches. The criterion for model performance is that ecological relationships (LAI, soil water) agree with theoretical and observed trends found in the literature, and that predicted establishment patterns concur with ecological knowledge of the species in terms of drought resistance and shade tolerance.

3. Results

3.1. Calibration of the PnET-Succession extension with Duke EF data

Modeled projections of wood and root biomass, and available soil water showed excellent agreement with empirical data from Duke EF (Table 1 and Fig. 3). In the Duke EF, simulated LAI of loblolly pines was highest at about 30 years of age, after which it reached a lower, stable level from 50 to 120 years of age. LAI of oak spp. reached a stable level by about 30 years of age. PnET-Succession modeled this pattern well (Fig. 3 and Table 1). Reducing the number of canopy integration steps from 50 to 5 had very little influence on model behavior (Fig. 3: striped versus solid lines see Section 2.2.2).

3.2. Landscape analysis comparison based on GRSF data with PnET-Succession and Biomass Succession

3.2.1. Comparison of biomass and LAI

PnET-Succession described initial aboveground biomass (AGB) at GRSF stands with accuracy similar to the Biomass Succession model (Fig. 4A,C and Table 2). Both Biomass Succession and PnET-Succession predicted AGB well within the uncertainty ranges that were associated with CFI measurements (Table 2). The largest modeled AGB values for a cell by PnET-Succession (∼500 Mg DW ha^{-1}) and Biomass Succession model

Table 1
Comparison of PnET-Succession predictions with measurements taken at the Duke EF. Values are mean and standard deviation. The simulation model was run once on each of the 12 Duke EF sites.

Parameter	Species	*N*	Modeled	Measured	RMSE	R^2
LAI (m^2)	*Pinus taeda* L.	19	2.8 ± 0.1	2.7 ± 0.2	0.5	0.70
	Quercus spp.	9	1.3 ± 0.1	1.7 ± 0.3	0.7	0.41
Wood ($kg\,m^{-2}$)	*Pinus taeda* L.	9	11.8 ± 0.4	7.7 ± 1.0	5.0	0.22
	Quercus spp.	9	2.1 ± 0.4	2.8 ± 0.4	0.8	0.76
Root ($kg\,m^{-2}$)	*Pinus taeda* L.	9	4.1 ± 0.1	3.8 ± 0.4	0.9	0.23
	Quercus spp.	9	0.8 ± 0.1	1.2 ± 0.2	0.5	0.87
Soil water	N/A	24	324 ± 14	342 ± 12	32	0.81

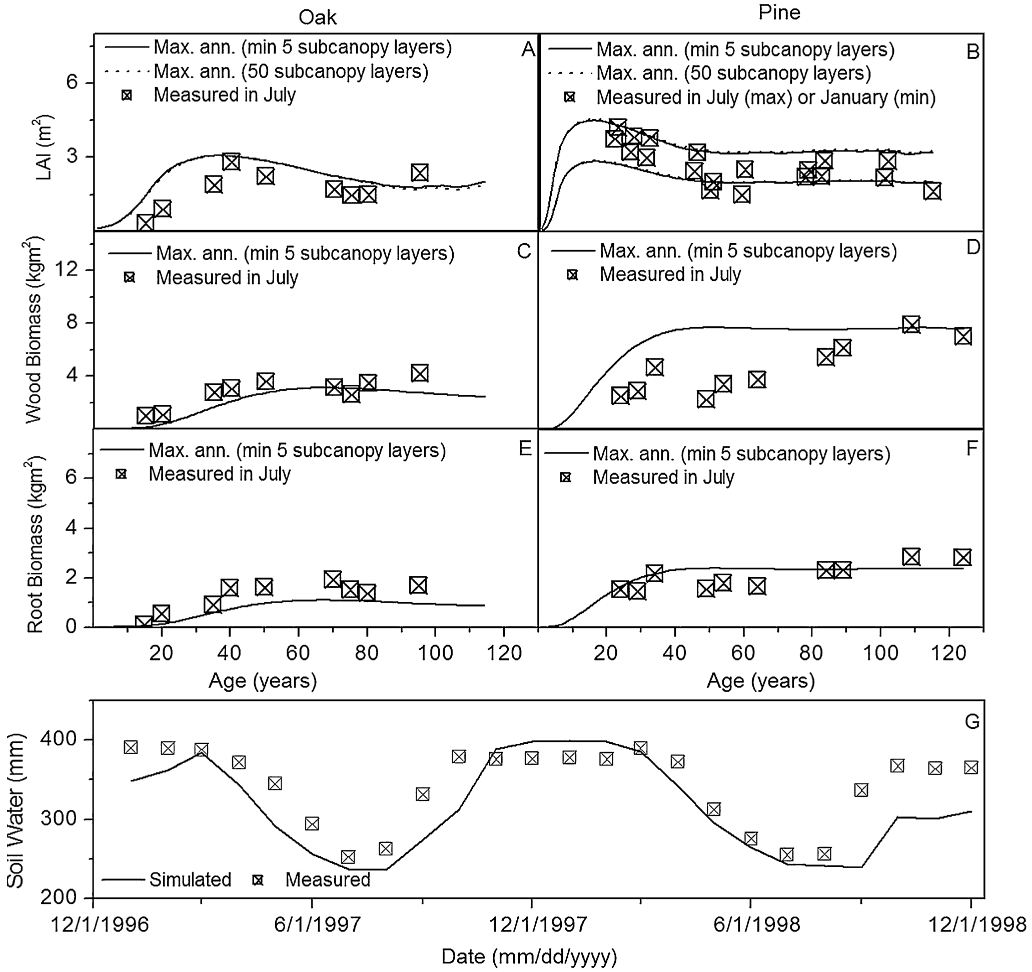

Fig. 3. Calibration results for PnET-Succession derived from the data from Duke EF. Simulated annual biomass of loblolly pine (*P. taeda* L.) in A, C, E and oak spp. B, D, F cohorts of different ages compared with observed biomass at 12 sites in Duke EF (Drake et al., 2011). The dotted lines in A and B are simulated minimum and maximum LAI in simulations performed with 50 within-canopy layers, where the default solid lines are LAI integrated in 5 steps. The second solid line in B is winter LAI for the (coniferous) *P. taeda*; winter LAI for oak spp = 0.0. G: simulated soil moisture for a site with 9-year old oaks and 14-year old loblolly pine compared with soil moisture observed by Hui and Luo (2004).

Table 2
Comparison of PnET-Succession predictions with empirical measures on the GRSF by Sturtevant and Seagle (2004) for LAI and continuous forest inventory (CFI) for biomass. Values are mean and standard deviation.

	PnET-Succession	Biomass succession	Measured
Aboveground biomass ($Mg\,DW\,ha^{-1}$)	140 ± 7	145 ± 46	143 ± 61[a]
LAI (m^2)	3.4 ± 0.7		2.2 ± 1.0[b]

[a] Derived from continuous forest inventory data.

[b] Sites were selected to represent a suite of topographic moisture conditions, excluding floodplains and riparian zones. Additionally, all sites were chosen to represent mature forest (age >80 years) that were primarily deciduous and located a minimum of 100 m from any forest opening >30 m in width (Sturtevant and Seagle, 2004).

(~400 $Mg\,DW\,ha^{-1}$) exceeded the largest measured biomass values (~300 $Mg\,DW\,ha^{-1}$). Mean modeled LAI was 50% greater than the mean LAI in the observed data, but because the uncertainty in LAI measurements is very large, it fell within the 95% confidence interval of measured LAI (Fig. 4B,D and Table 2).

Simulated average AGB (with PnET-Succession) increased from 148 $Mg\,ha^{-1}$ in 2000 to 189 $Mg\,ha^{-1}$ in 2040 (Fig. 5A). After 2040, biomass declined to 151 $Mg\,ha^{-1}$ in 2200. This is very similar with the predictions of the Biomass Succession model, in which biomass increased from 142 $Mg\,ha^{-1}$ in 2000 to a maximum of 202 $Mg\,ha^{-1}$ in 2064, declining to 157 $Mg\,ha^{-1}$ by 2200 (Fig. 5B). Both models show a biomass optimum around simulation year 2050. However, the increase and decline in biomass is more pronounced in Biomass Succession. Oak biomass remains nearly constant in the

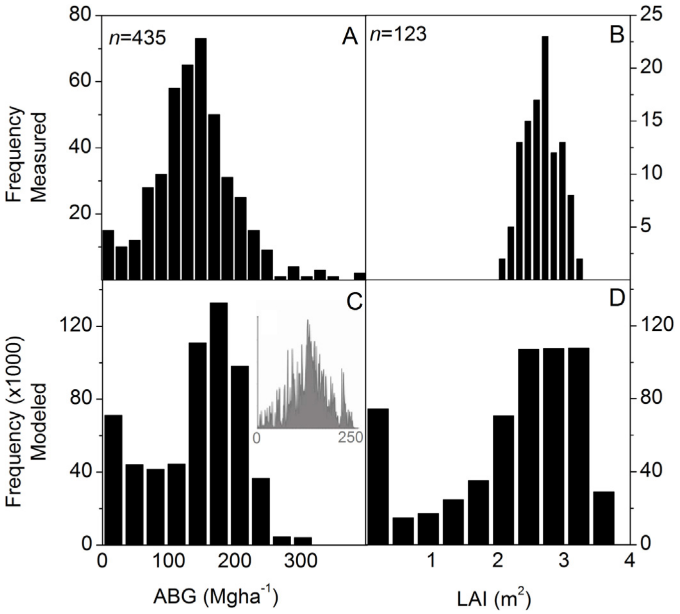

Fig. 4. (A) Measured aboveground biomass (AGB) in 2001 based on CFI data. (B) Measured LAI in 2001 according to Sturtevant and Seagle (2004). (C) AGB simulated with PnET-Succession in 2001 (inlay: simulated AGB with Biomass-Succession) and (D) LAI modeled with the PnET-Succession module.

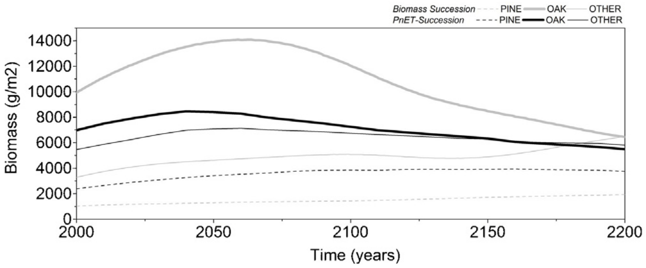

Fig. 5. Total aboveground biomass (ABG) predictions for 200 years in Green Ridge State Forest (GRSF).

PnET-Succession model, whereas it is greater according to Biomass Succession. PnET-Succession simulates a reduction of pine biomass in later years while pine biomass increases under Biomass Succession. Finally, PnET-Succession simulates a slight decrease of non-oak or pine species whereas Biomass Succession simulates a considerable increase in non-oak or pine species in particular after 2150.

3.2.2. *Species establishment dynamics, water and radiation*

Simulated LAI tends to be strongly and positively correlated with simulated soil moisture when LAI exceeds approximately 0.5 m^2 (Fig. 6). Since below-canopy radiation is negatively correlated with LAI, scarlet oak (a drought tolerant but shade intolerant species) has high establishment on low LAI/low soil water sites typical of dry ridge tops, while sugar maple (a shade tolerant but drought intolerant species) has high establishment on wet sites where LAI is typically high (Fig. 7B). An exception to the negative correlation between LAI and soil moisture occurs in sites that were recently disturbed (i.e., where LAI is less than 0.5 m^2; Fig. 6). This exception occurs because stand-replacing disturbance removes leaf cover that temporarily interrupts transpiration. Consequently, establishment probabilities in disturbed sites are high for both shade tolerant/drought intolerant and for shade intolerant/drought tolerant trees (Fig. 7C–F).

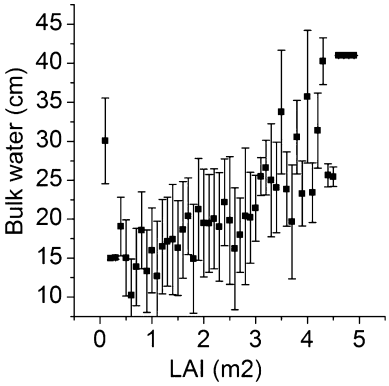

Fig. 6. Relationship between modeled LAI and modeled soil water on individual sites in Green Ridge State Forest (GRSF) at time 0.

4. Discussion and conclusion

4.1. *Insights and improvements*

Development in FLMs is shifting toward additional site-level complexity to allow interactions among endogenous and exogenous drivers affecting spatiotemporal change in tree species composition and structure over large land areas. For example, the LANDIS-II Century Succession embeds a simplified version of the Century model (Parton et al., 1994) as a soil chemistry submodel to simulate long-term soil carbon and nitrogen dynamics (Scheller et al., 2011). As these extensions operate within a common modeling platform (LANDIS-II), there is potential for subsequent integration of above and below-ground processes. LANDIS PRO is another version of LANDIS that explicitly simulates stem density based on stand development theory (Oliver, 1981) within a separate modeling platform (LANDIS PRO, Wang et al., 2014). Relative to LANDIS PRO, PnET-Succession trades stand structural detail for deep integration of physiological first principles. TreeMig uses a site-level tree population model and detailed seed-dispersal kernels embedded within an FLM environment to capture relevant stand dynamics and responses to environmental drivers, but has limited integration of ecophysiology and does not include competition for soil water (Lischke et al., 2006). FireBGC2 is a hybrid of a gap model, biogeochemical model, and an FLM (Keane et al., 2011). It addresses similar questions as PnET-Succession, but uses greater model complexity. Biomass Succession, designed a decade ago, was a simple yet elegant method to add more realistic stand dynamics, competitive effects, carbon dynamics and allow partial disturbances within an FLM framework originally designed to simulate only the presence or absence of tree species cohorts (Scheller and Mladenoff, 2004). The direct coupling of PnET-II to LANDIS-II succession is a natural evolution of the model consistent with the original design, allowing deeper integration of shading and soil water balance relationships with endogenous (vegetation) and exogenous (atmosphere, climate, disturbance) drivers. This deeper integration provides multiple advantages.

PnET-Succession dynamically links growth and establishment to temperature, radiation balance and water availability, and forces species cohorts to compete for light and water. The model can therefore better evaluate how changes in climate, management or natural-disturbances play out in a larger landscape, based on the sensitivity of tree species to light and water availability, reflecting adaptive strategies and ecological niches. As an example, tolerance to shade and drought impose conflicting demands on photosynthetic mechanisms; thereby favoring certain species and balances between groups (i.e., conifer or hardwood) at the site scale associated with these life history traits, depending on actual

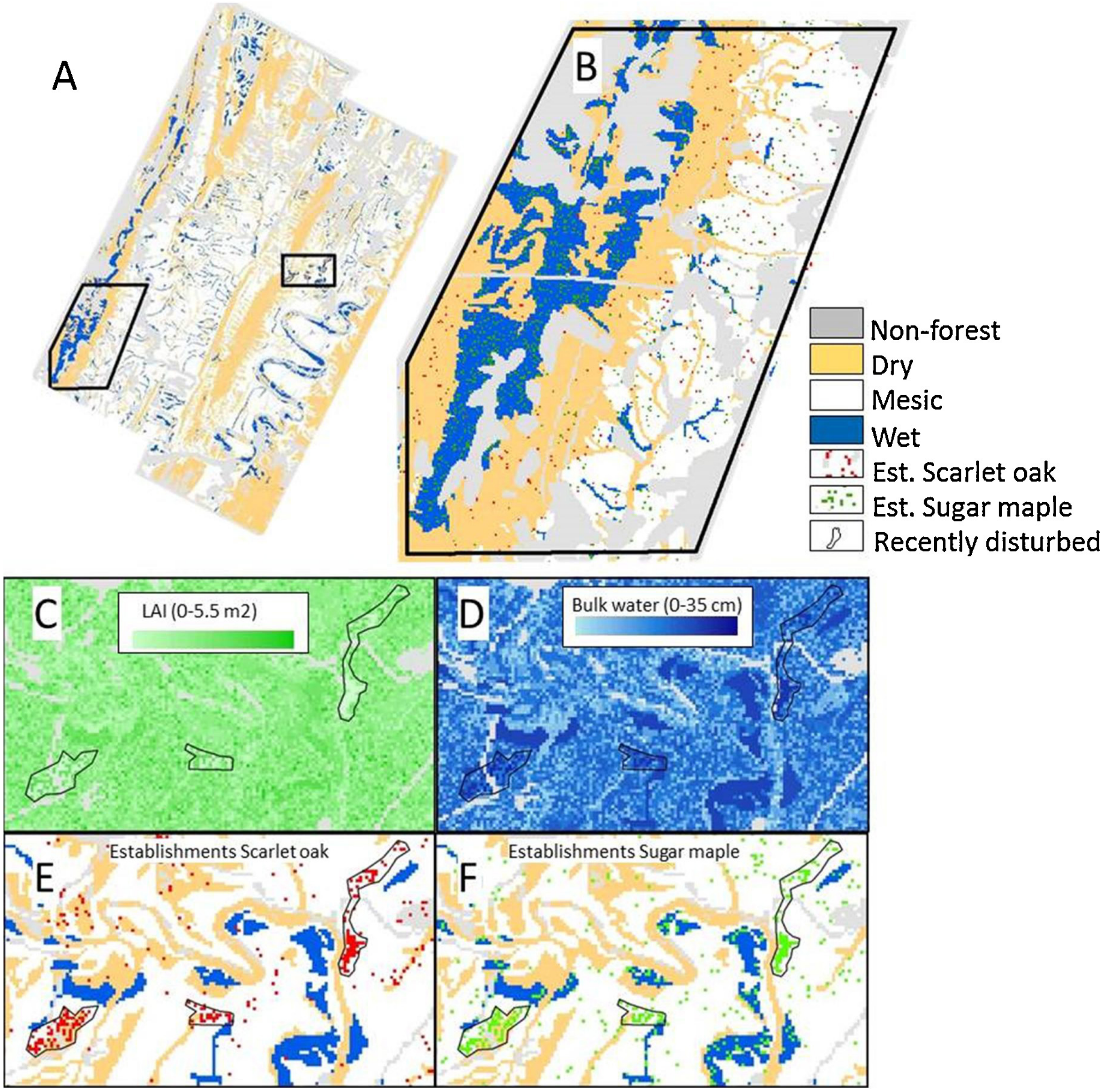

Fig. 7. Establishment probability in Green Ridge State Forest (GRSF) from 2000 to 2010 as a function of Leaf Area Index and soil water. (A) Overview of the map of GRSF, with two selections that are presented in B–F. Ecoregions are pooled in dry, mesic and wet. (B) Detail of establishment of a drought-tolerant scarlet oak, and a drought-intolerant sugar maple in a region that contains both dry, mesic and wet ecoregions. (C) Leaf area index in a section where several small harvests occurred. (D) Bulk soil water in a section where several small harvests occurred. (E) Detail of establishments of scarlet oak. (F) Detail of establishments of sugar maple.

light and water regimes (Allen, 1991; Valladares and Niinemets, 2008). Within undisturbed forests, equilibrium is generally reached between LAI and soil moisture, where LAI increases with increasing water availability (Asner et al., 2003; Sturtevant and Seagle, 2004). These responses of growth and establishment will lead to a configuration of tree species that generally responds to soil hydrology via LAI (i.e., scarlet oak establishes and competes best on exposed ridges and slopes, sugar maple on mesic sites). When disturbances disrupt the normal balance between LAI and soil water (Latif and Blackburn, 2008; Gray et al., 2002), SEP responds accordingly within the model, as illustrated by the distribution of establishment by drought sensitive and shade tolerant sugar maple versus the distribution of drought tolerant scarlet oak in response to the combination of environmental gradients and harvesting in the GRSF (Fig. 7). Hence, disturbance creates light and water availability resources that can have important consequences for the spread of either desirable (e.g., reintroduced) or undesirable (e.g., invasive) tree species (Greene et al., 1999). We expect forest vegetation and establishment within the ridge and valley physiographic province to be particularly sensitive to soil water balance as it falls within the rain shadow created by the Appalachian Plateau (Brown and Brown, 1984). The interaction between soil moisture balance, disturbance, and tree species migration has yet to be examined in the context of climate change.

The new extension allows more realistic simulation of stand dynamics by directly simulating the light regime via LAI. Because shade is now decoupled from biomass, stand development is less deterministic, providing a process by which cohorts can die from competitive effects. In PnET-Biosucession, the death of cohorts is simulated when cohorts that are unable to meet respiration demand (i.e., when simulated Non-Structural Carbon <1.0) are removed. Within the GRSF simulations, both PnET-Succession and Biomass Succession projected an initial increase in aboveground live biomass, followed by a decline to a lower quasi-equilibrium. This general pattern is consistent with a maturing, primarily even-aged oak-dominated forest after transitioning from the stand dynamics stage of stem exclusion (Morrissey et al., 2008) toward an uneven-aged forest structure associated with understory re-initiation (Oliver and Larson, 1996). However, we attribute the more pronounced increase and decline indicated by Biomass Succession to excessive establishment and persistence of understory cohorts that stagnated without a method for competitive exclusion of cohorts (Fig. 5). Although not directly demonstrated here, the explicit simulation of LAI and shade provides more realistic growth responses to shade, including species-specific growth responses to shading effects, and appropriate responses to partial disturbances such as defoliation that directly reduces LAI or thinning treatments that reduce biomass but largely maintain LAI.

Direct linkage between vegetation dynamics (i.e., establishment, growth, competition) and environmental drivers via ecophysiology is a robust method to project future forest conditions under changing climate and atmospheric conditions. Phenomenological models that rely heavily on empirically derived relationships as surrogates for mechanisms force their users to define how those relationships will be altered under novel future conditions. Because those conditions do not currently exist for the study of how systems will respond to them, users are required to extrapolate beyond the domain of data or make assumptions. Another difficulty is accounting for interactions among model components that are each simulating a process under novel conditions. When there are explicit links between fundamental drivers and processes simulated using first principles, the projected dynamics of the system as a function of novel variations in the fundamental drivers is expected to be more robust than under a phenomenological approach (Gustafson, 2013).

4.2. Model evaluation

Calibrated parameters based on the data from Duke EF were successfully applied to predict vegetation dynamics at GRSF. It is instructive to compare our parameter values (Appendix A.5) with those published in PnET literature. PnET literature reports different combinations of N response parameters AmaxA and AmaxB (Aber and Federer, 1992; Aber et al., 1995; Ollinger et al., 1995). We preferred AmaxA and AmaxB estimates from Reich et al. (1990) because they were species-specific. Reich et al. (1990) supply combinations of AmaxA, AmaxB for *Acer rubrum*, *Prunus serotina* and *Quercus ellipsoidalis*. Because additional reported values are unavailable, AmaxA, AmaxB for *Acer rubrum* were applied to *Acer* spp., and *Quercus ellipsoidalis* was applied to *Quercus* spp. Other species were parameterized with combinations that are traditionally used in other PnET literature, i.e., AmaxA, AmaxB = 5, 21.5 for broadleaved tree species, and AmaxA, AmaxB = −46, 71.9 for conifers (Appendix A.5).

4.3. Assumptions and caveats

We discuss here the most important assumptions upon which our extension was built.

1. We assumed that cohort age is a surrogate for canopy height when calculating light extinction through the canopy. We also assumed that all species in an age cohort had equal access to the light available to that cohort. PnET-Succession cannot predict when trees will lose access to light because they are lagging behind same-aged trees of another species, thereby facing a progressively increasing loss of access to resources. In particular, this may have implications when simulating slow growing (shade tolerant) trees alongside fast growing pioneer tree species (Messier et al., 1999). As a result, slower growing species in the model may experience better competitive success in gaps than would be expected from empirical observation. We are currently working on methods to address this issue. For example, the criterion for canopy layer groupings, currently age, could shift to biomass, or alternatively, we could try to explicitly model tree height and use it as a criterion for the canopy grouping in the future.
2. PnET-Succession does not implement a dynamic, temperature dependent evaporation from the surface, but rather treats evaporation as a constant of precipitation. This is related to its inheritance from the PnET model that does not simulate evaporation, because it is not intended to simulate water dynamics of non-vegetated surfaces. However, in a spatial model that implements disturbances, differences between evaporation from bare soil and transpiration from a vegetation surface are more important, and ignoring evaporation may lead to overestimated water availability within canopy openings.
3. PnET-Succession also assumes that excessive water (i.e., when soil water exceeds the soils' water holding capacity) is removed from the surface. PnET-Succession can therefore not be used to simulate forest dynamics within wetland, nor can it address species interactions related to subsurface adaptations (e.g., taproot vs. shallow root systems). It also does not implement water table depth by which species with deep taproots might have more access to water in a drought than those with more shallow root systems.
4. PnET- Biosuccession does not simulate nutrient dynamics. Besides water and light, competition for N and P in particular can be important determinants of the outcome of competition between trees. A weakness of PnET-II, and therefore of PnET-Succession, is that it assumes a constant concentration of nitrogen in foliage, which is regarded as a species-specific trait. In reality, nitrogen concentrations in foliage fluctuate according to environmental conditions, particularly according to the availability of N in the soil (Springer et al., 2005) and canopy position. Nitrogen availability varies through time due to accumulation of organic material and some species can fix atmospheric N. There are other versions of PnET that include nutrient dynamics (PnET-BGS, PnET-CN, Driscoll et al., 2001; Aber et al., 1996), but we chose not to include these processes at this time to minimize model complexity and parameter uncertainty.
5. PnET uses many relationships that are based on controlled-environment studies. However, many of the combinations of conditions found in the field have not been explicitly studied under controlled conditions. We resolved this by calibrating the model with measurements from the Duke forest, but nevertheless, the heterogeneity and complexity of forested landscapes introduces uncertainty that is difficult to model.
6. Three physiologically active biomass pools (root, wood and foliage) improves upon most comparable forest dynamics simulation models, but remains a simplification with potential consequences to the accuracy of the model calculations. In particular, turnover rates of branches and of roots vary substantially. For example, it is known that there is a great physiological difference between fine roots and coarse roots. Fine roots, have turnover rates in a similar order of magnitude as foliage, while coarse roots may not die naturally except due to severe disturbances or tree death (Norby and Jackson, 2000). Similarly, the turnover rate of aboveground woody biomass is in reality the sum of turnover of branches because senescence of boles is normally equivalent to the death of the tree, whereas the pool of aboveground woody biomass represents the sum of branches and boles. We therefore justify the use of a single turnover rate for the pool of aboveground biomass by the lack of appropriate data for characterizing finer resolution in biomass pools.

4.4. Potential applications

PnET-Succession provides a new and more robust model to study how forest ecosystems will respond to disturbances. Because our new extension features a more mechanistic approach to model growth and competition as a function of fundamental drivers that are rapidly changing (e.g., climate, CO_2 and ozone concentrations), projections of future forest dynamics should be more robust to these novel environmental conditions (Gustafson, 2013). For example, it is difficult to parameterize Biomass Succession to simulate the interaction of increased CO_2 concentrations and drought because there are not a lot of empirical data from such conditions to parameterize the model. However, because PnET-Succession has independent mechanistic functions relating CO_2 concentration and water stress to photosynthesis (growth), the model is able to simulate their interaction as an emergent property.

Tree species composition can have important consequences for carbon sequestration. For example, widespread conversion of oak-dominated forests in the eastern USA to species with faster decay rates (e.g., red maple) (Abrams, 1998; Fei et al., 2011) may have consequences for carbon storage potential of those forests. Further, different genera and species of trees have individualistic responses to novel changes in climate and disturbances, especially invasive insects and disease (Moser et al., 2009). Hence projecting future competitive interactions among species subject to novel changes becomes critical for projecting future carbon storage potential. As a case in point, PnET-Succession can simulate how the migration of tree species depends on interactions of regional climatic circumstances and local disturbances. This is important, for example in studies of invasive (exotic) tree species, but also in studying how a desired tree species (for example, blight-resistant chestnut) could potentially reestablish within a landscape that is affected by disturbances that are natural (e.g., windthrow), semi-natural (invasive species) or anthropogenic (harvests).

A major issue for simulating competition amongst tree species is that previous spatial models, such as Biomass Succession, would not specifically deal with how disturbances actually attack the trees, i.e., what biomass components are attacked by a particular disturbance. For example, it can be expected that foliage-eating insects have a very different effect on trees than, for example, the chestnut blight, which causes girdling stem cankers. Tolerance to the loss of tree components that are typically very dynamic, such as foliage or fine roots may be very different as compared to the loss of bark or stem wood. By implementing biomass in terms of the three components (root, stem, foliage) we expect to be better able to simulate changes in forest growth caused by specific disturbances.

Acknowledgements

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Appendix A. Documentation of PnET-Succession

Each LANDIS tree cohort requires an instance of a PnET-II simulation. A PnET-simulation in LANDIS consists of a photosynthesis part and an allocation part.

A.1. Photosynthesis

Radiation decreases through a canopy layer according to a Lambert-Beer relationship ($\mathrm{PAR}_i = \mathrm{PAR}_0 \cdot e^{(-k\cdot \mathrm{LAI})}$; where LAI represents leaf area index). Photosynthesis is calculated for each canopy layer i according to a linear relationship between foliar nitrogen concentration and assimilation rates under optimal growth conditions to estimate the potential rate of net photosynthesis ($\mathrm{NetPsn_{pot}}$):

$$\mathrm{NetPsn_{pot}} = \mathrm{AmaxA} + \mathrm{AmaxB} \cdot N_{\mathrm{fol}}(\mathrm{nmol/g/s}) \tag{1}$$

where N_{fol} is the nitrogen concentration in foliage biomass, AmaxA and AmaxB are the intercept and slope of the response. Net photosynthesis increases linearly with higher concentrations of atmospheric CO_2 in PnET-II. Parameters for this relationship were derived from leaf-based laboratory research. $\mathrm{NetPsn_{pot}}$ is used to derive potential gross photosynthesis ($\mathrm{GrossPsn_{pot}}$) and potential respiration ($\mathrm{Resp_{pot}}$) from a standard rate of respiration BaseFolResp:

$$\mathrm{GrossPsn_{pot}} = (1 + \mathrm{BaseFolResp}) \cdot \mathrm{NetPsn_{pot}}(\mathrm{gC/g\ foliage}) \tag{2}$$

$$\mathrm{Resp_{pot}} = \mathrm{BaseFolResp} \cdot \mathrm{NetPsn_{pot}}\,(\mathrm{gCO_2/gFol}) \tag{3}$$

Multiplicative reduction factors f_{water}, f_{RAD}, f_{VPD} and $f_{T,P}$, f_{age} reduce GrossPsn for water stress, suboptimal radiation, vapor pressure deficit, temperature and age:

$$\mathrm{GrossPsn} = f_{\mathrm{water}} \cdot f_{\mathrm{RAD}} \cdot f_{\mathrm{VPD}} \cdot f_{T,P} \cdot f_{\mathrm{age}} \cdot \mathrm{GrossPsn_{pot}}\,(\mathrm{gCO_2/gFol}) \tag{4}$$

where f_{water} is a reduction factor calculated according to:

$$f_{\mathrm{water}} = \left(\frac{\mathrm{water} - \mathrm{PWP}}{\mathrm{WHC} - \mathrm{PWP}}\right)^{\mathrm{GrMstSens}} (-) \tag{5}$$

Eq. (5) implies that GrossPsn is reduced more when water content < water holding capacity (WHC) and when GrMstSens or permanent wilting point is large.

Transpiration (T) is the minimum is calculated from $\mathrm{GrossPsn}_i$ and water use efficiency (WUE)

$$T = \frac{\mathrm{GrossPsn} \cdot M_{\mathrm{CO_2}}/M_{\mathrm{C}}}{\mathrm{WUE}} (\mathrm{mm}) \tag{6}$$

where $M_{\mathrm{CO_2}} = 44$ and $M_{\mathrm{C}} = 12$ are the molar weights of CO_2 and carbon. WUE is calculated from a reference WUE ($\mathrm{WUE_{const}}$) which increases with supra-optimal CO_2 concentrations

$$\mathrm{WUE} = d_{\mathrm{gs}} \cdot \mathrm{WUE_{const}}/\mathrm{VPD}\,(\mathrm{g/mm}) \tag{7}$$

where d_{gs} is a correction factor (>1) that depends on atmospheric CO_2 (not shown here, see Aber and Federer, 1992 for more details). Atmospheric CO_2 is a PnET-II driver input parameter that is supplied in monthly values.

Soil water (w_s) is calculated in a bulk-hydrology model that updates soil water and snow depending on precipitation, air temperature and consumption by the tree cohorts. A fraction of PrecLossFrac is subtracted from precipitation to account for interception, crack flow and runoff. f_{VPD} is a correction parameter that reduces potential gross photosynthesis with high vapor pressure deficit

$$f_{\mathrm{vpd}} = \mathrm{DVPD1} \cdot \mathrm{VPD}^{\mathrm{DVPD2}}(-) \tag{8}$$

Vapor pressure deficit (VPD) is calculated from the temperature fluctuations during the day (not shown). Photosynthesis rate reduction due to suboptimal temperature ($f_{T,P}$) is calculated according to:

$$f_{T,P} = \frac{(\mathrm{Psn}T_{\mathrm{max}} - T_{\mathrm{day}}) \cdot (T_{\mathrm{day}} - \mathrm{Psn}T_{\mathrm{min}})}{((\mathrm{Psn}T_{\mathrm{max}} - \mathrm{Psn}T_{\mathrm{min}})/2)^2}(-) \tag{9}$$

where daytime temperature (T_{day} in °C) is derived from minimum daily temperature ($T_{\min}$ in °C) and maximum daily temperature ($T_{\max}$ in °C) that are model inputs, supplied in monthly averages

$$f_{\text{age}} = 1 - (\text{Age}/\text{longevity})^{\text{PsnAgeRed}}(-) \tag{10}$$

where Age is the age of a tree cohort, PsnAgeRed is a tuning parameter of photosynthesis reduction as a function of age. Shade is expressed as a reduction factor ($f_{\text{rad},i}$), which is a fraction of maximum photosynthetic activity that can be obtained with incoming photosynthetically active radiation (PAR) that depends on a species-specific half saturation intensity of radiation for photosynthesis (HalfSat)

$$f_{\text{rad},i} = 1 - e^{-\text{PAR}_i \frac{\log(2)}{\text{halfSat}}} \tag{11}$$

Actual respiration (Resp) is estimated from Resp_{pot} taking into account day length (L_{day} in seconds) and night length (L_{night} in seconds) in the given latitude and day of the year and a temperature response factor

$$\begin{aligned}\text{Resp} = -\text{Resp}_{\text{po}} \cdot t^{\text{dWater}}(L_{\text{day}} \cdot Q_{10}^{(T_{\text{day}}-T_{\text{opt}})/10} \\ + L_{\text{night}} \cdot Q_{10}^{(T_{\text{night}}-T_{\text{opt}})/10)}(\text{gC/month})\end{aligned} \tag{12}$$

where Q_{10} represents the multiplication fraction of respiration activity, with a 10 °C increase in ambient temperature. Actual net rate of photosynthesis ($\text{NetPsn}_{\text{act}}$) is calculated as the sum of GrossPsn and Resp

$$\text{NetPsn}_{\text{act}} = \sum_{i=0}^{\text{IMAX}} \text{GrossPsn} + \text{Resp}(\text{g cm}^{-2}) \tag{13}$$

A.2. Allocation and senescence

$\text{NetPsn}_{\text{act}}$ can be allocated directly to foliage, or be added to non-structural carbon (NSC) from where it can be transported to root or stem biomass (Fig. 2). Eq. (11) ensures that $\text{NetPsn}_{\text{act}}$ decreases with each foliage layer due to a lower light level. The ratio of productive foliage layers (i.e., ProductiveCanopyFraction = the count of i in which $\text{NetPsn}_{\text{act}} > 0/\text{IMAX}$) is used to allocate photosynthates to foliage assuming that the plant decreases allocation to foliage when extra foliage does not result in higher photosynthesis. $\text{NetPsn}_{\text{act}}$ is initially allocated to NSC. A constant fraction of NSC is released per time step:

$$\delta\text{NSC}/\delta t = \text{DNSC} \cdot \text{NSC}(\text{g cm}^{-2}\,\text{month}^{-1}) \tag{14}$$

can be allocated to the production of foliage, root and stem biomass according to:

$$\delta\text{Fol}/\delta t = \text{PCF} \cdot \delta\text{NSC}/\delta t\,(\text{gDW m}^{-2}) \tag{15}$$

where $\delta\text{Fol}/\delta t$ is foliage growth, DNSC is a tuning parameter and $\%C$ is the fraction of C in biomass. Allocation to wood and root biomass follows from released NSC and a species sp ecific root to stem ratio (RootStemRatio) according to:

$$\delta\text{Wood}/\delta t = (1 - \text{PCF}) \cdot \delta\text{NSC}/\delta t\,(\text{gDW m}^{-2}) \tag{16}$$

when Root/Wood > RootStemRatio, or alternatively

$$\delta\text{Root}/\delta t = (1 - \text{PCF}) \cdot \delta\text{NSC}/\delta t\,(\text{gDW m}^{-2}) \tag{17}$$

Constant fractions are subtracted from Root and Wood to represent turnover. Foliage loss is seasonal only.

A.3. Seasonality

All the trees lose foliage at a species-specific user-specified Julian day, the difference between deciduous and coniferous trees is simply expressed in a fraction of foliage lost <1 for conifers. A fraction FolReten·Fol is retracted back to NSC, while the remaining foliage (1-FolReten)·Fol is lost to the litter pool. Foliage allocation in the spring is triggered by a species-specific minimum cumulative temperature (GDD in °C).

A. Species-specific parameters.

Description	AmaxA[a]	AmaxB[a]	FolNCon[a,b]	Longevity[c] (yr)
	N-response parameter	N-response parameter	Foliage N (%)	
acerrubr	6[e]	34[e]	2.39	300
acersacc	6[e]	34[e]	2.39	300
caryglab	−11[f]	53.6[f]	2.55	300
fraxamer	5[g]	21.5[g]	2.3	300
juglnigr	5[g]	21.5[g]	2.4	154
lirituli	5[g]	21.5[g]	4.12	250
magnacum	5[g]	21.5[g]	2.4	250
nysssylv	5[g]	21.5[g]	2.6	250
pinuechi	−46[h]	71.9[h]	2.4	200
pinupung	−46[h]	71.9[h]	2.4	300
pinurigi	−46[h]	71.9[h]	2.4	675
pinustro	−46[h]	71.9[h]	2.6	450
pinuvirg	−46[h]	71.9[h]	1.1	200
prunsero	16[g]	41.3[g]	3.7	250
quercus spp	−11[h]	53.6[h]	2.49	600
queralba	−11[h]	53.6[h]	2.49	200
quercocc	−11[h]	53.6[h]	2.09	400
querprin	−11[h]	53.6[h]	2.72	400
querrubr	−11[h]	53.6[h]	2.3	225
quervelu	−11[h]	53.6[h]	2.54	100
robipseu	5[g]	21.5[g]	2.4	500
sassalbi	5[g]	21.5[g]	2.4	140
tiliamer	5[g]	21.5[g]	3.92	800
tsugcana	5[g]	21.5[g]	2.4	300
ulmuamer	5[g]	21.5[g]	2.4	350

[a] Measured or prescribed with fixed values (i.e., either 'expert judgment' or values frequently used in various published PnET-II applications).

[b] Sturtevant and Seagle (2004).

[c] http://bigtree.cnre.vt.edu/TreeAge.htm, with adjustments according to forest inventory ages, i.e. if reported initial ages of cohorts exceed longevity, PnET-Succession will not be able to simulate them. In these cases we assumed higher longevity.

A.4. Establishment probability (P_{est})

Establishment of a cohort species depends on the temperature and GDD requirements that effect mature trees of the same species. $P_{\text{est}} = 0.0$ when temperature and cumulative temperature are not sufficiently high for mature trees of a species to be physiologically active. Alternatively, P_{est} depends on ambient temperature, soil moisture and subcanopy radiation according to:

$$P_{\text{est}} = f_{T,P} \cdot f_{\text{moist}} \cdot \text{frad}(-) \tag{18}$$

where $f_{T,P}$ is equal to the growth reduction factor for photosynthesis (Eq. (10)), f_{moist} depends on soil moisture according to

$$f_{\text{moisture}} = (\text{water}/\text{WHC})^{\text{EstMoist}}(-) \tag{19}$$

where ρ_m is a tuning parameter and WHC is water holding capacity (cm).

A.5. Parameterization

B. Category specific parameters.

	Const[a]	Dec.[b]	Conf[c]	DT[d]	ST[e]	Description
FolTurnover[f]	–	1	0.33	–	–	Foliage turnover (yr^{-1})
FolReten[f]	0.3	–	–	–	–	Foliage C retention (g/g)
RootTurnover[g]	0.01[h]	–	–	–	–	Root turnover (yr^{-1})
WoodTurnover[g]	0.01[i]	–	–	–	–	Wood turnover (yr^{-1})
BaseFolRespFrac[f]	0.1[j]	–	–	–	–	Base foliage respiration fraction (–)
GrowthMoistureSensitivity[g]	–	–	–	5[k]	6[k]	Tuning parameter on water stress (–)
RespQ10[f]	2[j]	–	–	–	–	Respiration Q10 (10 °C^{-1})
SLWmax[f]	–	100[j]	170[j]	–	–	Maximum specific leaf weight (g m^{-2})
SLWDel[f]	0.2[j]	–	–	–	–	Reduction of SLW with canopy depth (–)
k[f]	–	0.58[j]	0.5[j]	–	–	Light extinction coefficient (–)
DVPD1[f]	1[j]	–	–	–	–	Tuning parameter on photosynthesis sensitivity to VPD (–)
DVPD2[f]	–	2[j]	2[j]	–	–	Tuning parameter on photosynthesis sensitivity to VPD (–)
InitialFol[f]	10[l]	–	–	–	–	Initial foliage biomass (g m^{-2})
GDDFolStart[f]	300[j]	–	–	–	–	Growing Degree Days at which tree becomes physiologically active (°C)
SenescStart[f]	260[j]	–	–	–	–	Julian day where tree becomes inactive
AmaxFrac[f]	–	1[j]	0.75[j]	–	–	Tuning factor on photosynthesis
PsnTMin[f]	5[j]	–	–	–	–	Minimum temperature for photosynthesis (°C)
PsnTOpt[f]	24[j]	–	–	–	–	Optimum temperature for photosynthesis (°C)
WUEConst	–	–	–	10.9[f]	5.64[m]	Constant in water use efficiency calculation (g/mm)
DRESP[g]		–	–	0.001[k]	0.0001[k]	Respiration rate of biomass tissue (yr^{-1})
DNSC[g]	0.97[l]	–	–	–	–	Release rate of Non Structural Carbon (yr^{-1})
RootStemRatio[g]	–	0.2[n]	0.25[n]	–	–	Root to stem biomass ratio (–)
WiltingPoint[f]	–	–	–	0.1[o]	0.2[o]	Permanent Wilting Point (–)
HalfSat[f]	–	–	–	350[j]	150[j]	Half-light saturation (W m^{-2})
PsnAgeRed[o]		MAXINT[p]	1.5[p]	–	–	Age determined decline in phostynthesis
EstRadSensitivity[g]	–	–	–	30[k]	3[k]	Tuning parameter on species establishment sensitivity to shade (–)
EstMoistureSensitivity[g]	–	–	–	3[k]	10[k]	Tuning parameter on species establishment sensitivity to drought (–)

[a] Constant parameters: applied to all tree species.

[b] Deciduous: parameters applied to all deciduous trees.

[c] Coniferous: parameters applied to all conifers.

[d] Drought tolerant: parameters applied to drought tolerant tree species.

[e] Shade tolerant: parameters applied to shade tolerant tree species.

[f] Measured or prescribed with fixed values (i.e., either 'expert judgement' or values frequently used in various published PnET-II applications).

[g] Calibrated parameter values.

[h] Allowable range was 0–0.2, based on expert judgment. Field measurements of root turnover are not directly applicable because PnET-II does not model fine and coarse root separately and the ratio of fine and coarse roots changes considerably.

[i] Allowable range was 0–0.01, based on expert judgment.

[j] Aber and Federer (1992) and other published PnET-II applications.

[k] No allowable range was prescribed (i.e., unmeasurable parameter).

[l] Prescribed small value, the model is not sensitive to this parameter except when unreasonable high values are used (i.e., >1000 g).

[m] Allowable ranges were a prescribed range of 1.8–21 gCO$_2$/mm, based on a diversity of tree species and ecoregions (Webb et al., 1978; Lindroth and Ciencials, 1996; Benzarti, 1999).

[n] Allowable range was 0–1.0 (assuming that stem biomass is always larger than root biomass).

[o] Expert judgment.

[p] Drake et al. (2011) found no reduction in photosynthetis rates in aging hardwoods, and a small effect in aging conifers.

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