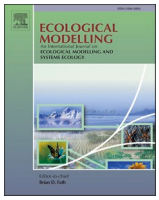
Ecological Modelling 490 (2024) 110657

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel



Overcoming conceptual hurdles to accurately represent trees as cohorts in forest landscape models

Eric J. Gustafson [a,*], Brian R. Sturtevant [a], Brian R. Miranda [a], Matthew J. Duveneck [b]

[a] Institute for Applied Ecosystem Studies, Northern Research Station, USDA Forest Service, 5985 Highway K, Rhinelander, WI 54501, USA
[b] Harvard Forest, Harvard University, Petersham, MA, USA

ARTICLE INFO

Keywords:
Forest landscape models
LANDIS-II
PnET-succession
Modeling cohorts
Gap dynamics
Light attenuation

ABSTRACT

Forecasting the response of vegetation to climate change and human actions at global to landscape scales often relies on system models. Many such models represent the composition and demography of vegetation using age class cohorts of species or vegetation types. Forest landscape models (FLM) simulate spatially explicit forest dynamics in response to disturbance and abiotic drivers and constraints at landscape spatial and temporal scales (10^5 – 10^8 ha, hundreds of years), and many represent trees as species-age cohorts on a grid of cells to make the model tractable at landscape scales. However, it has become evident that complications arise when calculating cell-level summaries involving multiple cohorts because one cannot assume that all cohorts simultaneously occupy the entire physical space of a cell. A fundamental assumption of a widely used FLM (LANDIS-II) is that cohorts are homogeneously distributed across the grid cells that they occupy. It is only implicitly assumed that the stems (trunks) and crowns (foliage) of the individual trees that make up the cohorts physically occupy some proportion of the cell's area with a non-clustered distribution, but the model does not track those proportions. In reality, when cohort biomass is reduced by disturbance or turnover (self-thinning), gaps are created that are at least temporarily unoccupied. In current versions of LANDIS-II, such gaps are ignored. We describe a new approach for cohort-based FLMs to estimate those proportions (including open space) and apply them to compute more realistic estimates of light attenuation and cell-level estimates of cohort and total cell biomass. This approach accounts for gap dynamics in a FLM where stems are not explicitly modeled, allowing cohorts to partially fill cells. These improvements allow more accurate simulation of forest "gap" dynamics in cohort-based landscape models to produce more accurate absolute biomass estimates at species, cell and landscape scales.

1. Introduction

Projecting the response of vegetation to climate change and human actions at global to landscape scales often relies on system models. Many such models represent the demography of vegetation using age class cohorts of species or vegetation types rather than individual stems (e.g., trees) as a foundational method for scaling detailed local dynamics to broad spatial and temporal scales. While the cohort construct is common, its implementation varies across models, and the specifics of how the cohort concept is integrated can have important consequences for long-term simulated dynamics (Fisher et al., 2017; Petter et al., 2020). At its core, cohort structure within a broad-scaled model represents a balance in the degree to which local heterogeneity is approximated. In this paper we focus specifically on the conceptual notion of representing vegetation as species-age cohorts in forest landscape models (FLM) with the aim of improving the realism of state variable projections.

1.1. Use of cohorts in ecological models

The use of cohorts to simplify the conception and simulation of complex ecological systems has been adopted in several broad classes of models, including forest landscape models (see below) and dynamic global vegetation models (DGVM) (Fisher et al., 2017)). The Lund-Potsdam-Jena General Ecosystem Simulator (LPJ-GUESS; Smith et al., 2001, 2014) is a DGVM that can optionally group together into cohorts the individual trees or shrubs of the same age and plant functional type (PFT) within a patch and simulate them as an average individual, using cohort stem density to scale them to the patch level. Multiple PFTs can occur within a patch and the competition for water, light and nitrogen is simulated. The Geophysical Fluid Dynamics

* Corresponding author.
E-mail address: Eric.Gustafson@usda.gov (E.J. Gustafson).

https://doi.org/10.1016/j.ecolmodel.2024.110657
Received 21 August 2023; Received in revised form 16 January 2024; Accepted 12 February 2024
Available online 21 February 2024

Laboratory (GFDL) Land Model 3 with Perfect Plasticity Approximation (LM3-PPA; Weng et al., 2015) is a cohort-based vegetation demographic model that assumes that tree crowns "perfectly" fill canopy gaps through phototropism (plasticity) (Strigul et al., 2008). Crowns self-organize into discrete canopy layers where all plants in the same layer are exposed to the same incoming radiation. The Ecosystem Demography (ED) concept is also a cohort-based representation of vegetation dynamics (Hurtt et al., 1998; Moorcroft et al., 2001). Individuals are grouped into cohorts by PFT and height class within patches, and successional dynamics are driven by height-structured competition for light among cohorts. CLM (ED) (Fisher et al., 2015) is a variant of the Community Land Model (CLM) (Lawrence et al., 2011; Oleson et al., 2013) that merges the ED and PPA concepts, allocating cohorts to canopy and understory layers, although a cohort may exist in multiple layers. Growth and competition are simulated via hydrology, canopy biophysics, photosynthesis, and respiration.

Models operating at a finer scale have adopted a diversity of approaches to simulating growth and competition of assemblages of plants. The "big-leaf" concept (e.g., PnET, Biome-BGC) scales leaf-level photosynthesis processes to an aggregate "canopy" representing all individuals of a species or assemblage of species (i.e., forest type) on a site by converting leaf-level instantaneous process rates to broader spatial and temporal scales (Hidy et al., 2016). Gap models (e.g., JABOWA, Botkin et al., 1972; Linkages, Post and Pastor 2013) and individual tree models (e.g., PICUS, Badeck et al., 2001; SORTIE, Pacala et al., 1993; iLand, Seidl et al., 2012; LAVESI, Kruse et al., 2018) simulate the growth, loss and establishment of individuals, but are therefore limited to relatively small land areas and/or time frames. Statistical growth and yield models (e.g., FVS, Crookston and Dixon 2005) project patterns of annual diameter increment and self-thinning using relationships based on destructive and non-destructive plot and stand-scale measurements and empirically derived growth rates.

Among ecological models, forest landscape models (FLMs) specifically simulate forest dynamics at landscape scale (10^5 – 10^8 ha) as cohorts (age classes) of species or PFTs respond successionally to disturbances. They have proved useful for generating insights into how disturbance regimes (including those directly and indirectly caused by human actions) interact with biotic and abiotic conditions to assess forest ecosystem change and resilience. Their strength is the ability to project the spatial and temporal pattern of forest state variables resulting from the successional response to spatially explicit simulation of disturbances and temporal changes in abiotic conditions (i.e., light, soil water and climate). Such models take a variety of modeling approaches, ranging from probabilistic state-and transition models (e.g. VDDT-TELSA, Beukema et al., 2003; RMLANDS, Cushman et al., 2011) to process-based simulation models (e.g., Fire-BGCv2, Keane et al., 2011; iLAND, Seidl et al., 2012; LANDIS-II, Scheller et al., 2007) that use a mixture of phenomenological and mechanistic approaches to mimic the many processes that drive forest ecological dynamics (Gustafson 2013).

FLMs described generally by Shifley et al., 2017) and Petter et al., 2020) typically represent landscapes as either polygons or grid-cells, tracking composition by species or PFT and age over time scales of decades to centuries. TreeMig (Lischke et al., 2006) models tree range shifts over millennial time scales and it tracks forest composition by species-height classes. Similar to DGVMs, some FLMs track the aggregate state variables of species-age cohorts rather than individual stems to more efficiently scale the dynamics of gap models to landscapes (Roberts 1996; Mladenoff 2004). A common assumption of this approach is that cohorts represent individual trees of the same species and age that are homogeneously distributed across a grid-cell (Mladenoff et al., 1993; Scheller and Mladenoff, 2004). However, it is easy to think of individual trees when mentally visualizing cohorts, so it is important to keep in mind that when death or disturbance impacts individual trees, the effect on the cohort to which they belong may be a minor change in its mean attributes.

LANDIS-II is an open-source forest landscape modeling platform (Scheller et al., 2007) where specific extensions (modules) are plugged in to simulate specific ecological processes as needed for the research question being addressed. PnET-Succession is a succession extension (i.e., simulates growth and competition) developed by our research group (de Bruijn et al. 2014), built by embedding the algorithms of the PnET-II ecophysiology model (Aber et al., 1995) into the Biomass Succession extension (Scheller and Mladenoff, 2004) of LANDIS-II. A major difference between PnET-Succession and most other biomass-based succession extensions in LANDIS-II is the explicit modeling of leaf area index (LAI), canopy layering, and light attenuation through each canopy layer, more analogous to the design of some DGVMs described above. Specifically, one to several vertical canopy layers are allowed by the user and cohorts are dynamically assigned to a layer based on their relative biomass (i.e., larger cohorts are above smaller cohorts). However, these canopy dynamics and consequent growth patterns add complexity that is currently ignored within other succession extensions of LANDIS-II. While other cohort-based FLM platforms also include explicit canopy layering (e.g., TreeMig, Lischke et al., 2006; LandClim, Schumacher et al., 2004), methods diverge widely with respect to how vertical and horizontal heterogeneity in the canopy are addressed. The objective of this paper is to describe these complexities and outline our solution within PnET-Succession. Our goal is to catalyze even deeper thinking about ways to estimate state variables more accurately within cohort-based simulation models that explicitly model canopy dynamics.

1.2. Cell-level heterogeneity in a cohort model

While the cohort concept is widely recognized as a simplifying scaling methodology, it nonetheless enables a degree of heterogeneity to be simulated at the scale of a cell, the width of which can be flexible within LANDIS-II and is typically set between 10 m and 250 m. In the case of a tree species-age cohort FLM such as LANDIS, the cohort concept allows both compositional heterogeneity and age heterogeneity, with the latter often serving as a surrogate for size or structure. Such heterogeneity enables nondeterministic successional dynamics to emerge from competitive interactions among tree species cohorts subjected to different stressors and disturbance agents at local and landscape scales (Mladenoff, 2004). For example, the presence of tree species cohorts affects shade conditions at the ground level, serving as a filter on the establishment of new tree species age cohorts based on life history traits (i.e., shade tolerance).

For most biomass-based LANDIS-II succession extensions, tree species cohorts compete for generic "growing space" – representing the combination of limited resources of water, light and (optionally) nutrients using the assumption that cohorts with more biomass have a competitive advantage. Canopy dynamics are therefore only implicitly modeled. By contrast, PnET-Succession scales leaf-level processes of photosynthesis, respiration, and transpiration to the grid cell by integrating light extinction and water consumption in stacked canopy layers and computing a dynamic soil water balance, based on the physiological first principles of the PnET-II forest ecophysiology model (Aber et al., 1995). At the center of the design of PnET-II and PnET-Succession is the simulation of cohort photosynthesis within stacked sublayers of foliage that are processed from top to bottom so that both light and water are consumed (by attenuation and transpiration) within each sublayer. PnET-Succession additionally organizes cohorts into major canopy layers (where the canopies of the cohorts within a layer are approximately the same height) that are also processed from highest to lowest and attenuate light according to the attenuation by the cohorts within each canopy layer. This conceptual design is meant to mimic the vertical stratification of multi-cohort canopies found in natural forests and the vertical arrangement of foliage within individual tree canopies. The design of PnET-Succession is analogous to that of ecophysiologically-based DGVMs that explicitly model vertical heterogeneity at the cell-level. However, this requires explicit definition of rules for canopy layering and light extinction. The added complexity of

vertical heterogeneity as described previously by Lischke et al. (1998) underscores the question of whether horizontal spatial heterogeneity should also be considered. Cell-level spatial heterogeneity is a factor that has been addressed in the context of DGVMs – in part because their spatial resolution is typically quite coarse (e.g., half-degree of latitude/longitude, McCabe and Dietz, 2019).

Modeling horizontal heterogeneity must account for the observation that trees (particularly large trees) generally exhibit "crown shyness" (Hajek et al., 2015) such that individual tree crowns in the same canopy layer have very little horizontal overlap, so vertical light extinction through the crown of a tree primarily occurs through leaves of a single species. LANDIS generally simulates cell-level dynamics as a function of intermixed pools of biomass, or in the case of PnET-Succession, intermixed pools of biomass and vertically stratified but spatially intermixed pools of LAI. However, we must understand that the LANDIS assumption that cohorts are homogeneously distributed across a cell means that the spatial distribution of stems of a cohort is not clustered or anisotropic but is instead even or random. It clearly should not imply that each cohort occupies 100% of the cubic space on and above the cell because occupancy of the same physical space by two physical entities (e.g., trees) is impossible. Homogeneous distribution further implies that the stems (trunks) and crowns (foliage) of the individuals of each cohort physically occupies some proportion of the cell's area with a non-clustered distribution, but LANDIS never specifies those proportions.

When cohort biomass is reduced by disturbance there is an implied opening of space (gaps) that are at least temporarily unoccupied, and these may vary by canopy layer. A new approach is needed that makes assumptions to estimate those proportions (including the open space) and apply them to compute realistic estimates of light attenuation and transpiration, and cell-level estimates of cohort and total cell biomass. In this paper we describe a new approach to account for spatial heterogeneity in a forest landscape model in which stems or stem density are not explicitly modeled.

2. Conceptual models

Here we describe in detail two conceptual models for representing trees as cohorts in FLMs, specifically by comparing the methods used in prior and current versions of the PnET-Succession extension of LANDIS-II.

2.1. Stacked canopy method (version 4.x)

2.1.1. Canopy dynamics

In PnET-Succession, the foliage of multiple cohorts on a cell is represented as multiple major canopy layers that are stacked vertically and higher layers (greater biomass) shade lower layers. Within a major canopy layer the foliage of each cohort is further subdivided into vertically stratified sublayers, each of which attenuates light as it passes through the foliage in the sublayer. The original PnET-Succession foliage algorithm (de Bruijn et al., 2014) assumed that all cohorts within a major canopy layer had completely interleaved foliage (i.e., every cubic centimeter of a canopy layer had equal amounts of foliage of each cohort in the layer), and that light attenuation was the sum of attenuation by all cohorts in the layer. Furthermore, the canopy of a single cohort could span multiple major canopy layers. Although allowing multiple cohorts to each occupy an entire canopy layer seems to honor the fundamental LANDIS assumption that cohort occupancy of cells is homogeneous, allowing foliage to mix between layers is computationally complicated. It also ignores the reality that "crown-shyness" is observed in natural forests (Hajek et al., 2015). Summing attenuation through all sublayers of all cohorts within a canopy layer assumes that the sublayers of all cohorts are stacked and results in greater light attenuation (less light) than expected (from empirical observations) at the bottom layers of the simulated canopy.

Beginning with PnET-Succession v3.0, a simplification was made to assign all the foliage of an individual cohort to a single canopy layer (rather than sharing across layers). The number of these major canopy layers depends on the number and relative sizes of the cohorts. The height of a cohort is not modeled or tracked in PnET-Succession, so the height of a cohort's canopy layer relative to that of other cohorts is approximated by its relative size, using woody biomass as a surrogate for height. Cohorts of similar size (biomass) are grouped into the same canopy layer (i.e., assuming similar stature). A cohort may grow rapidly enough to leave its current layer and move up into the layer above (overtopping). In this way, canopy layering is dynamic and self-organizing. Because the height of individual stems (in nature) is usually not reduced by the loss of other individuals or branches, the cohort's lifetime maximum biomass is used to determine its canopy position to prevent cohorts from being demoted to a lower canopy layer when they lose biomass (e.g., disturbance or senescence). The attenuation of light is computed sequentially by cohort, which conceptually assumes that all cohorts fully occupy the area of the cell and are cumulatively stacked within their canopy layer. The order of processing cohorts is randomized at each timestep to prevent bias in access to light and water. A problematic consequence of this computational method is that each cohort is a *de facto* functional canopy layer, and light attenuation becomes severe on sites with many cohorts.

2.1.2. Scaling biomass estimates from the cohort to the cell

Because this method assumes that all cohorts simultaneously occupy 100 % of the cell area (a physical impossibility), cell-level biomass is estimated as the sum of the biomass density (gDW/m^2) values of the cohort of all cohorts on the cell. This sometimes produces values considerably higher than empirical measures of total tree biomass, and such discrepancies prompted us to develop an alternative method.

2.2. Proportional cohort occupancy method (version 5.x)

Revised methods using Proportional Cohort Occupancy (PCO) instead of stacking to model canopy dynamics (light attenuation, canopy "gaps") and to compute cell-level cohort biomass (accounting for fraction of cell occupied) have been implemented beginning with PnET-Succession v.5.0 (www.landis-ii.org/extensions/PnET-Succession). Where attributes of multiple cohorts were formerly summed to compute cell light attenuation and cell-level biomass density, proportionally weighted averages are now used as described here.

2.2.1. Canopy dynamics

In light of the empirical evidence for "canopy shyness" (Hajek et al., 2015), we have found it useful to conceive of the canopy of each cohort on a cell as a cube (i.e., all the individual crowns of a cohort are collected into a single conceptual cube) and that a major canopy layer is made up of all the side-by-side cubes of similar-sized cohorts and suspended above the cell, with the relative horizontal dimension of each cube being proportional to cohort occupancy within the cell (Fig. 1). The proportional size (PCanArea) of a cohort's cube is computed as current leaf area index (LAI) of the cohort relative to its maximum potential LAI (MaxLAI), which is either provided as specific species parameter or estimated from other species parameters (Gustafson et al., 2023). Within each cohort cube, the foliage of the cohort is allocated to a fixed number (user-defined, typically 5) of vertically stratified sub-canopy layers, and light attenuates as it passes through each cohort sublayer according to its LAI and light extinction coefficient (Monteith, 1975). Photosynthesis computations (including consumption of both light and water) are executed for each cube independently within a major canopy layer, and within a cube each cohort canopy sublayer is processed sequentially from top to bottom. The light exiting from the bottom of a major canopy layer is the weighted average of the light exiting from the bottom of each canopy cube (mimicking the diffuse nature of light passing through a heterogeneous canopy layer), and all cohorts in the next lower major

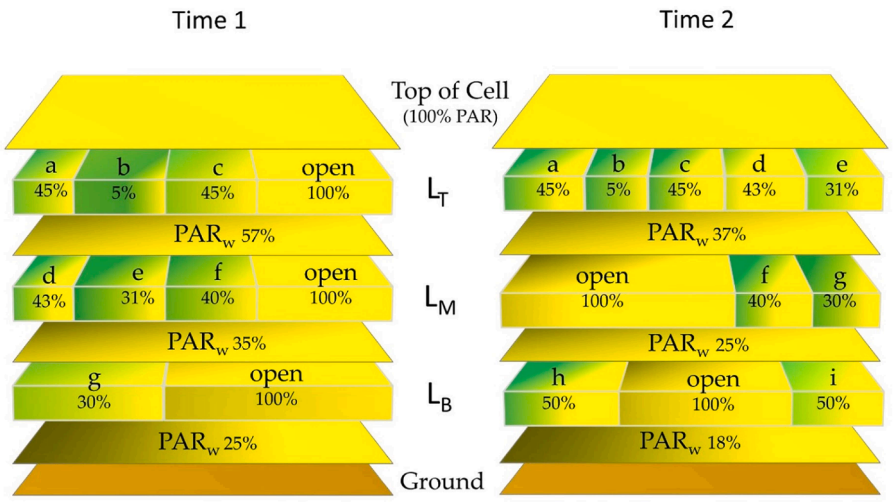


Fig. 1. Conceptual diagram of light dynamics in a single grid cell for cohort canopies using the PCO method. Time 1 illustrates several cohorts (green/yellow cubes) within three separate canopy layers (L_T, L_M, L_B) for top, middle, and bottom, respectively. The gradient of green/yellow and percentage listed represents how much light (yellow) is able to pass through each cohort's cube. For example, 'a' might represent a 90-year-old white pine cohort in the top layer with 45 % light passing through and 'g' a 5-year-old red oak cohort in the bottom layer with 30% of light passing through. Light attenuates through the canopy, thus cohorts at the top receive more light than those lower. Light attenuation is determined by the LAI and extinction coefficient of the species' foliage. A weighted average of PAR (PAR_w) is the light available to all cohorts in the next lower canopy layer (or ground for regeneration). Sublayers within each major canopy layer are not shown but described in the text. Time 2 shows the same cell after many years of growth and establishment. Each cohort occupies an area of the cell proportional to cohort size (biomass). The maximum cube area for each layer is equal to the sum of the species maximum LAI. Thus, at any given time, layers may be "full" (e.g., L_T of time 2), or may include open space (e.g., L_T of time 1) (For interpretation of the references to color in this figure, the reader is referred to the web version of this article).

canopy layer receive the same intensity of light from above.

The calculation of PCanArea (proportional size) of cohort (i) assumes that its canopy cube would completely fill the area of a cell (proportion = 1) when its cohort reaches its maximum LAI. Evidence from FACE experiments suggests that Maximum LAI may be relatively stable even under novel conditions (e.g., elevated CO_2) (Norby et al., 2003). Maximum LAI also defines when the foliage reaches its maximum density (depth) within the canopy cube.

$$PCanArea_i = LAI_i / MaxLAI_i$$

The horizontal proportion of a major canopy layer on a cell that is occupied by all of its cohort canopy cubes ($PCanArea_{Layer}$) is the sum of the proportions of the cohort canopy areas in the layer.

$$PCanArea_{Layer} = \sum_{i}^{n} PCanArea_i$$

A major canopy layer is considered filled (the cubes have expanded horizontally to eliminate all gaps (i.e., when the sum of cohort proportions ≥1). This represents canopy closure within a layer. With the assumption of non-overlapping cohort canopies within a layer (Hajek et al., 2015), the sum of the proportional canopy areas is subsequently constrained to not exceed 1. If $PCanArea_{Layer}$ is greater than 1, then $PCanArea_i$ for each cohort is proportionally rescaled ($PCanAreaAdj_i$) to make $PCanArea_{Layer}$ equal 1, mimicking stem exclusion mortality when a new competitor is introduced to the layer.

$$PCanAreaAdj_i = PCanArea_i / PCanArea_{Layer}$$

We note that the application of a strict limitation of $PCanArea_{Layer}$ <= 1can cause undesirable artifacts associated with abrupt transfers of cohort foliage between adjacent layers when cohorts have different growth characteristics. An optional generic parameter (CanopySumScale) can be used to scale the rate at which the constraint that cumulative canopy proportions cannot exceed 1 is applied, allowing a cohort entering a layer from below to more gradually fit into its new canopy layer. When CanopySumScale = 1 the constraint is abruptly applied (i.e., $PCanArea_{Layer}$ is never allowed to exceed 1), and behaves as described above. When CanopySumScale <1, the constraint is gradually applied at a rate proportional to CanopySumScale, and when CanopySumScale =0, there is no constraint on the value of $PCanArea_{Layer}$. (i.e., $PCanArea_{Layer}$ may exceed 1). Thus, CanopySumScale scales the relative rate at which excess canopy proportion is removed while adjusting to the space available to each cohort now sharing a layer. The canopy proportion for each cohort is calculated once each simulation year, so CanopySumScale conceptually represents the annual rate of stem exclusion mortality caused by the introduction of a new competitor cohort.

$$PCanAreaAdj_i = \left(\frac{PCanArea_i}{PCanArea_{Layer}} - PCanArea_i \right) * CanopySumScale + PCanArea_i$$

A cohort proportion that is constrained in this way is treated as a permanent cap (MaxCanopyProp) on how much horizontal 'space' the cohort can occupy within a layer. This assumption is based on the premise that once canopy closure has been reached, a cohort has limited ability to expand its canopy horizontally by branch growth and conceptually cannot add new stems. This simplification of canopy structure is similar in kind to the "perfect plasticity approximation" applied to the canopy structure within certain cohort-based dynamic global vegetation models (e.g., Weng et al., 2015, Fisher et al., 2017). If a cohort dies or is partially disturbed, the horizontal dimensions of its "cube" are removed or reduced, respectively, creating "open space" that may be filled by other cohorts growing in size (upward from a lower canopy layer) (see below).

For the purpose of computing cohort-level growth, light travels downward through the sublayers of each cube independent of other cubes in the layer and each cohort consumes light according to the LAI and extinction coefficient of the cohort's foliage as it progresses through its individual sublayers. Light exiting the bottom of a major canopy layer is therefore estimated as the weighted average of the light attenuation through each cohort (as a function of the light extinction coefficient (k) and LAI_i), taking into account any open space, and this light is available to all cohorts in the canopy layer just below it (Fig. 1).

$$Transmissivity_i = e^{-k*LAI_i}$$

$$Transmissivity_{Layer} = \sum_{i=1}^{n} PCanAreaAdj_i \times Transmissivity_i$$

However, when CanopySumScale < 1, a canopy layer with multiple cohorts can temporarily exceed a total canopy proportion of 1. In this case, the simple proportionally weighted average of light attenuation is not a good representation of the light reaching the layer below because the weights do not sum to 1. When the sum of $PCanAreaAdj_i$ >1, there is no empty space in the layer, and the total light attenuation through the layer is calculated as a power function:

$$Transmissivity_{Layer} = \prod_{i=1}^{n} Transmissivity_i^{PCanAreaAdj_i}$$

Layer-level LAI (LAI_{Layer}) is calculated as the proportional sum of the LAI of the cohorts within the layer, where "open" PCanArea has an LAI value of zero.

$$LAI_{Layer} = \sum_{i=1}^{n} PCanAreaAdj_i \times LAI_i$$

LAI for the cell (LAI_{Cell}) is calculated as the sum of the layer LAIs.

$$LAI_{Cell} = \sum LAI_{Layer}$$

where light reaching the ground surface is a function of light attenuation through LAI_{Cell}.

2.2.2. Scaling biomass calculations from the cohort to the cell

The conceptualization of tree species cohort canopies acting as non-overlapping cubes within a layer also means that the woody biomass (stems) supporting those cubes is restricted to a subset of the area within the cell. PnET-Succession (v.5.x) therefore computes biomass in units that represent a biomass density (gDW/m^2) proportional to their cohort space (cube). Prior versions of PnET-Succession assumed that all cohorts equally (and simultaneously) occupy the entire space of the cell, so our new PCO method is a significant change that requires a shift in the underlying logic governing biomass-size assumptions. In general, cell-level estimates of all cohort attributes are computed according to the proportion of the cell area that the cohort occupies, and that proportion is estimated by PCanArea (or PCanAreaAdj). Thus, a cohort biomass density estimate represents the cohort's density wherever it (i.e., individual trees) is found on the cell and the cell-level biomass density estimate represents the cohort's average density across the entire cell area (i.e., including both where its individuals ARE found and where they are NOT found on the cell).

This distinction between cohort biomass density vs. cell-level biomass density is necessary to appropriately estimate cell-level biomass density as it would be empirically estimated in the field. If cohort biomass density was not rescaled within the layer, then cell-level biomass density could be overestimated by not recognizing that cohorts are competing for horizontal growing space when sharing a layer. Thus, given the assumption that cohorts within a layer do not physically share horizontal space (canopy shyness), a weighted average of the cohorts on the cell – including empty space – is the best way to represent an attribute at the cell level, and canopy proportion (PCanArea) is used as the weighting factor. Cell-level biomass density ($Biomass_{Cell}$) is computed by:

$$Biomass_{Cell} = \sum Biomass_i \times PCanAreaAdj_i$$

where $Biomass_i$ is cohort (i)'s cohort-level biomass density.

This method of scaling cohort-level densities to the cell scale applies to all values that are densities (unit of mass / unit of area), including all forms of biomass, non-structural carbon (reserves), LAI, photosynthetic output, respiration and senescence. Attributes that have only cell-level values or are not cohort-specific (e.g., leaf litter, coarse woody debris) are weighted by PCanArea at the time the cohort contributions to the cell are added (e.g., senescence). Scaling using PCanArea is applied only when reporting cell-level attributes to which cohort-level values are contributing. These cell-level averages (weighted by canopy proportions) are directly comparable to most empirical estimates of cohort attributes (Reese et al., review, 2024). When other LANDIS-II extensions require site-level attributes for a cell (e.g., fire or harvesting extensions), the cell-level values are provided.

Some examples will help illustrate the logic and consequence of the PCO approach. Consider a cell that carries 10,000 g/m^2 of cohort biomass density in one cohort, and 3000 g/m^2 of cohort biomass density in another cohort (see example A in Table 1). If cohorts are assigned to different layers when the biomass of one is less than half of the other's, then these two cohorts would be assigned to separate canopy layers; an upper layer with 10,000 g/m^2 cohort biomass density and a lower layer with 3000 g/m^2 cohort biomass density. In this example, the upper layer is fully occupied, but the lower layer is only 67 % occupied because its LAI is less than its maximum LAI, meaning that 33 % of the cell area is 'open' in this lower layer. The cell-level biomass density is the sum of the proportion-weighted cohort biomass density of the two layers: 12,000 g/m^2 biomass (i.e., 10,000 + (3000 * 0.67)). Compare that situation with one having two cohorts with 10,000 g/m^2 cohort biomass density, and a third with 3000 g/m^2 cohort biomass density (Example B in Table 1). The layering algorithm will place the two cohorts with 10,000 g/m^2 cohort biomass density into the upper canopy layer, and the cohort with 3000 g/m^2 cohort biomass density into a lower layer. In this example, the two larger cohorts each have a canopy cube area equal to half the area of the cell. Their cohort biomass density of 10,000 g/m^2 exists on the portion of the cell occupied by their foliage, but since their canopies each occupy only half of the cell, the biomass density of each individual cohort when scaled to the entire cell area is $10{,}000 \times 0.5 = 5000$ g/m^2. But the weighted average for the entire layer (i.e., over the entire area of the cell) is the sum of their cell-level biomass density, or 10,000 g/m^2. In the lower layer there is just one cohort with a cohort biomass density (3000 g/m^2), but because it occupies just 67% of the cell, its cell-level biomass density is 2000 g/m^2, and because it is the only cohort in the layer, the cell-level layer biomass density is also 2000 g/m^2. The total cell-level biomass density is equal to the sum of the biomass densities of both layers (i.e., 12,000 g/m^2). Example B clearly illustrates how not accounting for cohort occupancy produces an overestimation of cell-level biomass (summing cohort-level biomass would give 23,000 g/m^2, i.e., the sum of the second column).

In examples A and B (Table 1), at least one canopy layer is fully occupied (i.e., canopy closure has been reached and there is no open space within that layer). Example C (Table 1) shows the computations when there is open space (sum of PCanAreaAdj(i) in layer <1.0) in both layers due to mortality (Cohort 2) or small size (Cohort 3). Note that Cohort 1 has its PCanAreaAdj capped at 0.5 because that was its value when it reached its MaxLAI (Example B). Example D shows Cohort 3 gaining size (and height) and consuming open space created by the reduction (disturbance) of Cohort 2 in the upper layer. This example used CanopySumScale=1.0 (see above) and illustrates the ephemeral discontinuity in cell total biomass density caused by the transition of a cohort to a different canopy layer. Collectively, these examples illustrate how the PCO method produces more accurate estimates of individual (and total) cohort biomass densities at the cell-level.

3. Case study examples

To further illustrate the effect of these changes to the algorithms for simulating the attenuation and competition for light in tree canopies in PnET-Succession, we compared the behavior through time of selected state variables of multiple cohorts on a single grid-cell between the prior method (stacked cohort foliage) and the new (PCO) method. PnET-Succession (v5.1) contains an option to select the cohort processing algorithm to be applied and it can report some state variables at both

Table 1
Illustrative examples of how cell-level biomass scaling and canopy layering are computed. Cell Biomass Density is the cell-level biomass density of a cohort within a canopy layer and the Layer Biomass Density is sum of the cell-level biomass densities within the layer.

Example A	Cohort Biomass Density (g/m2)	Layer	LAI	MaxLAI	Adjusted PCanArea	Cell Biomass Density (g/m2)	Layer Biomass Density (g/m2)
Cohort 1	10,000.00	Upper	3.50	3.50	1.00	10,000.00	10,000.00
Cohort 2	3000.00	Lower	2.00	3.00	0.67	2000.00	2000.00
		Cell Total Biomass Density (g/m2):				12,000,00	12,000.00
Two similar cohorts sharing the top layer							
Example B	Cohort Biomass Density (g/m2)	Layer	LAI	MaxLAI	Adjusted PCanArea	Cell Biomass Density (g/m2)	Layer Biomass Density (g/m2)
Cohort 1	10,000.00	Upper	3.50	3.50	0.50	5000.00	–
Cohort 2	10,000.00	Upper	3.50	3. 50	0.50	5000,00	10,000,00
Cohort 3	3000.00	Lower	2.00	3.00	0.67	2000,00	2000,00
		Cell Total Biomass Density (g/m2):				12,000,000	12,000.00
Removal of Cohort 2							
Example C	Cohort Biomass Density (g/m2)	Layer	LAI	MaxLAI	Adjusted PCanArea	Cell Biomass Density (g/m2)	Layer Biomass Density (g/m2)
Cohort 1	10,000.00	Upper	3.50	3.50	0.50	5000.00	–
Cohort 2	0.00	Upper	0.00	3. 50	0.00	0.00	5000.00
Cohort 3	3000.00	Lower	2.00	3.00	0.67	2000.00	2000.00
		Cell Total Biomass Density (g/m2):				7000.00	7000.00
Reduction of Cohort 2; Cohort 3 has grown into gap in top layer; Adjusted PCanAreascaled to sum to 1.							
Example D	Cohort Biomass Density (g/m2)	Layer	LAI	MaxLAI	Adjusted PCanArea	Cell Biomass Density (g/m2)	Layer Biomass Density (g/m2)
Cohort 1	10,000.00	Upper	3.50	3.50	0.28	2837.84	–
Cohort 2	3000.00	Upper	1.50	3.50	0.24	729.73	–
Cohort 3	5000.00	Upper	2.50	3.00	0.47	2364.86	5932.43
		Cell Total Biomass Density (g/m2) :				5932.43	5932.43

cohort-level and site-level. We calibrated species parameters of selected species independently under each option, matching simulated single-species growth to the same growth curve targets (e.g., as in Gustafson et al., 2020). When calibrating the different algorithms, a few parameters must have slightly different settings to successfully hit the same target. Thus, because each option was calibrated to produce the same species-specific growth behavior and the same model version was used, any variation in state variables can be attributed to the differences in the cohort processing algorithms. The cases described here established different assemblages of cohorts on the single cell (representing a northern Wisconsin forested site having a silt-loam soil and historical climate) and simulated them through time. We set the model to prevent the random establishment of new cohorts to keep the cases simple, recognizing that the establishment of new cohorts would allow cohorts to grow into any open space from below, which would be more realistic.

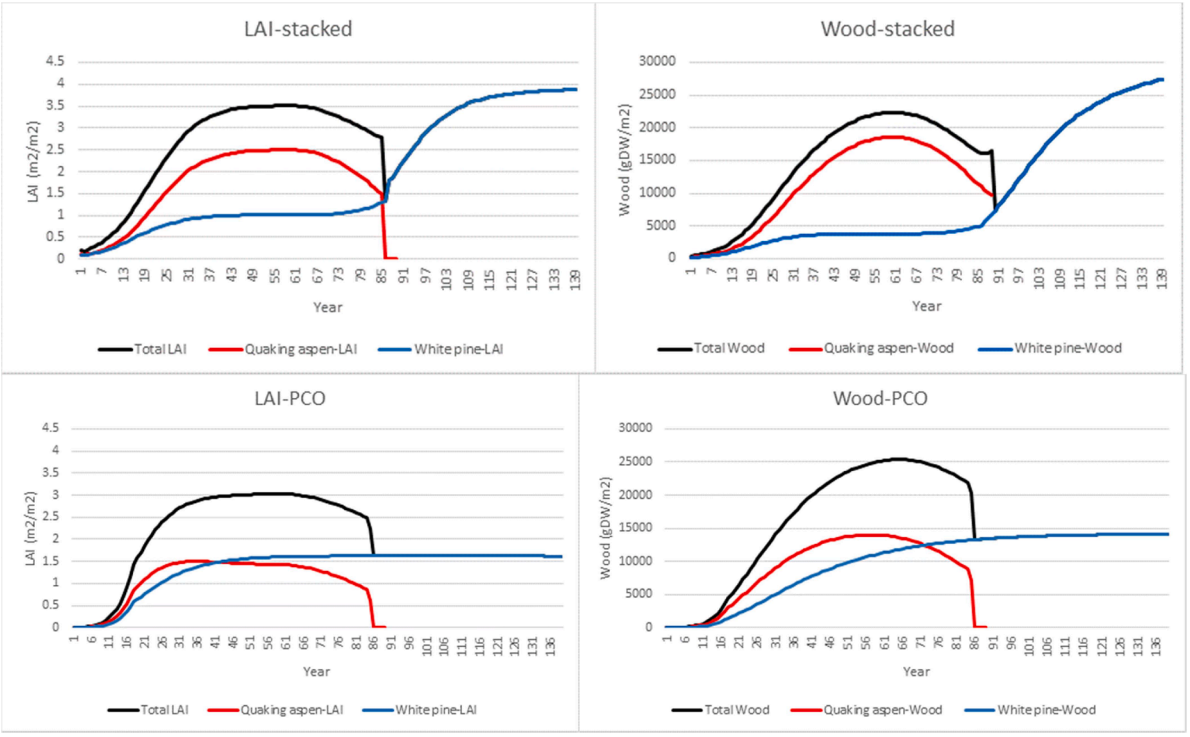


Fig. 2. Comparison of site-level leaf area index (LAI) and living above-ground woody biomass of two cohorts (quaking aspen and white pine) simulated using stacked or PCO processing algorithms. Note that white pine LAI equals total LAI after aspen dies.

3.1. Case 1

When a cohort of the very shade-intolerant quaking aspen (*Populus tremuloides*) was established with a cohort of the intermediate shade-tolerant white pine (*Pinus strobus*) under the stacked algorithm (Fig. 2), white pine was suppressed (in a lower major canopy layer) until the aspen senesced (shorter longevity). This happened because the stacked version assumes that the other cohort is completely filling the layer above, reducing the light available for the white pine. In the PCO version, the white pine is sharing the top layer with the aspen and thus has more access to light. Under the PCO algorithm, the two species coexisted in the same canopy layer, with aspen growing somewhat faster until it began senescing. When aspen died from senescence, white pine was constrained from expanding laterally into the open space because that would imply adding stems, which is not possible for a mature cohort.

3.2. Case 2

We also simulated cohorts of five species having increasing shade-tolerance (quaking aspen, black cherry (*Prunus serotina)*, red oak (*Quercus rubra*), red maple (*Acer rubrum*) and sugar maple (A. *saccharum*)), with the first two species (most shade-intolerant) being established 20 years prior to the most shade-tolerant species (sugar maple) and the second two 10 years prior to sugar maple (Fig. 3). With the stacked algorithm, the most shade-intolerant species quickly overtopped (and suppressed) the others until they senesced, at which time the next most shade-intolerant species overtopped the remaining cohorts until eventually only the most shade-tolerant species remained (Fig. 3). With the PCO algorithm, species with similar shade-tolerance tended to share a canopy layer, and when the overtopping species senesced, the release of sub-dominant cohorts was limited because PCO assumes that established cohorts cannot add new stems to fill newly opened space (Fig. 3). It is important to note that red oak and sugar maple coexisted in the same canopy layer with another cohort for some time and thus were constrained in their growth when they were released. Note also that maple has a long senescence in which LAI declines; in a landscape simulation, newly established cohorts would take advantage of this decline, using the associated increase in light availability to grow into the opening space. When upper canopy cohorts are removed by disturbance, the brief coexistence of cohorts trending in opposite directions would not occur and the release of lower-canopy cohorts would not be constrained.

A comparison of cohort- and site-level estimates of cohort attributes through time shows that failing to account for fractional occupancy of cohorts on a cell and canopy layer gaps (i.e., summing cohort-level estimates) can produce elevated estimates, many of which are clearly unreasonably high (Fig. 4).

4. Discussion

The scaling of cell- or individual-level plant processes to site or landscape scales in simulation models has always been a challenge. For example, FireBGCv2 (Keane et al., 2011) is a FLM that implements a gap model (FireSUM, Keane et al., 1990) to simulate individual trees and gap dynamics on a single site and imputes the results to all the landscape grid cells having similar conditions. Simulating individual trees avoids many of the assumptions that our approach is required to use, but when conditions on individual sites diverge significantly through time because of disturbances, the individual tree approach may become untenable. iLAND (Seidl et al., 2012) is one of several FLMs that upscales an individual tree model to landscape scale using a hierarchical multi-scale method where dynamics emerging from lower hierarchical levels feed into processes at higher levels, and feedbacks from higher hierarchical levels apply constraints on processes at lower levels. The methods used in these two models can account for compositional, age, vertical, and horizontal heterogeneity at the grid-cell level. Despite reliable advances in computing performance spanning decades (Schaller, 1997), such detailed scaling of individual trees to landscapes still limits the spatial extent to which such methods may be realistically applied (Sturtevant

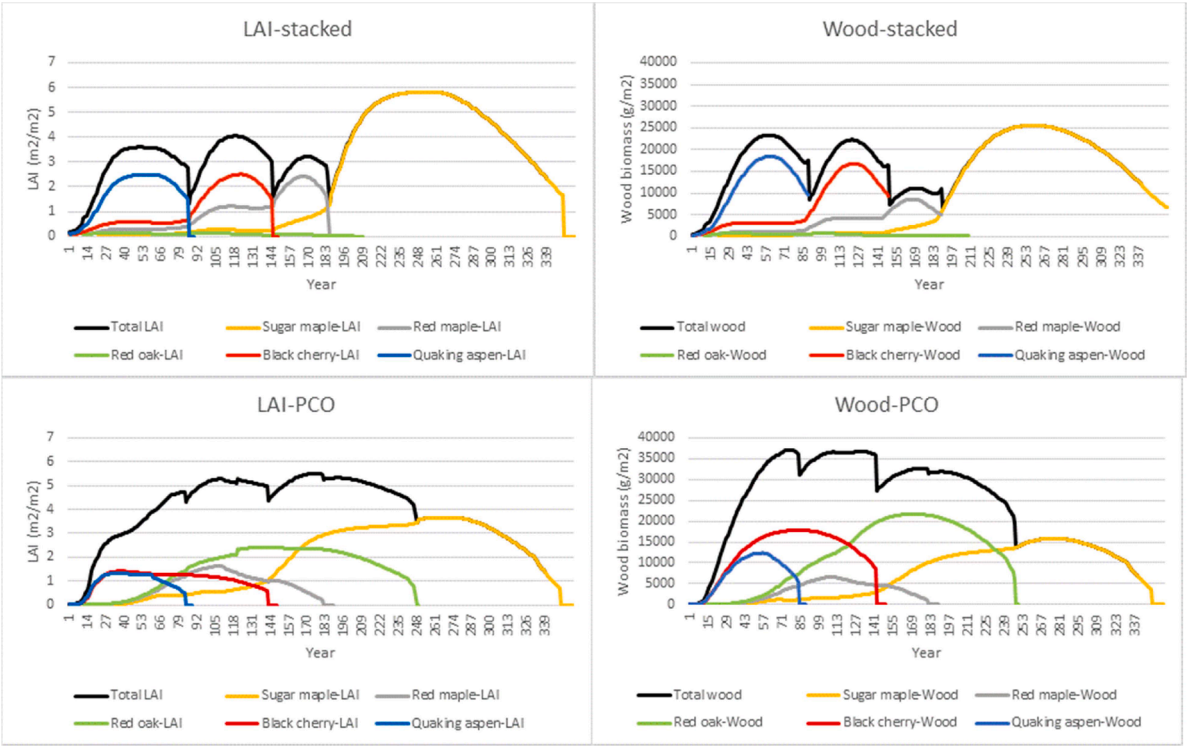


Fig. 3. Comparison of site-level leaf area index (LAI) and living above-ground woody biomass of five cohorts (Case 2) simulated using stacked or PCO processing algorithms.

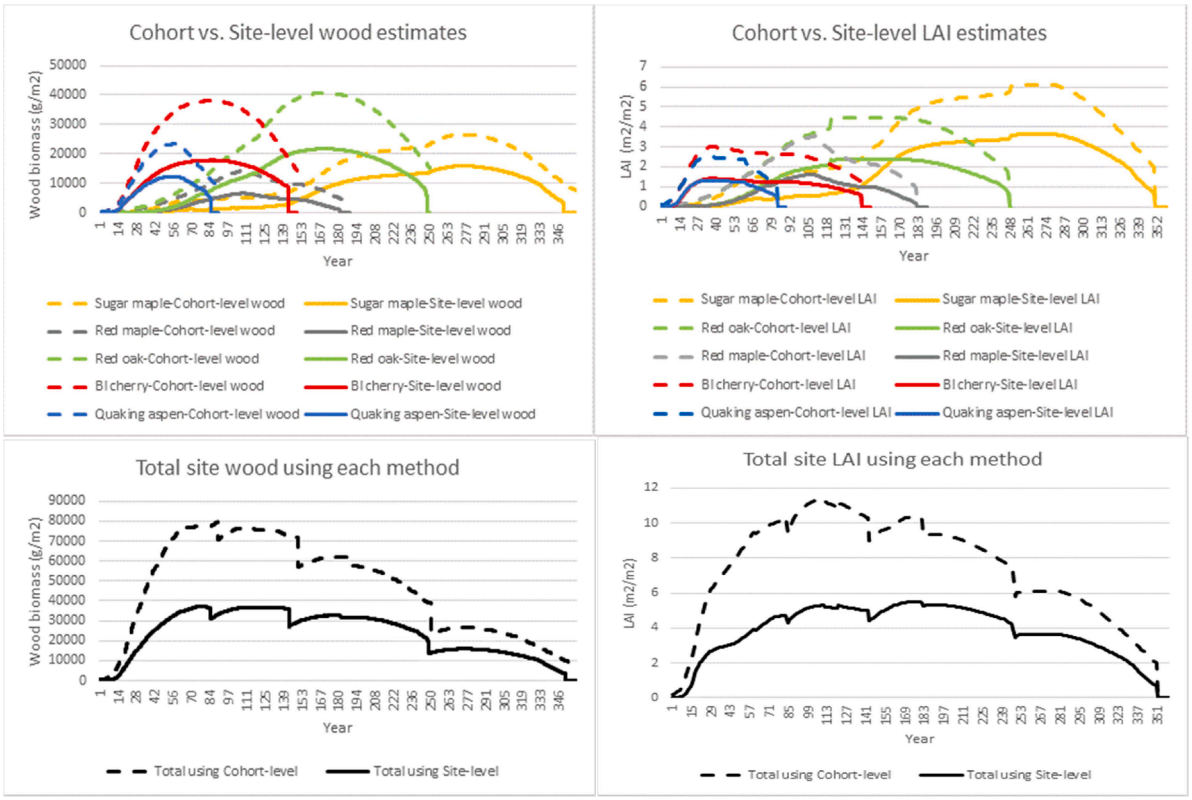


Fig. 4. Comparison of cohort-level vs. site-level cohort attributes through time on a cell with five cohorts (Case 2). Cohort-level estimates represent values on the proportion of the cell where the cohort is found, and site-level estimates reflect the average of the entire cell (i.e., where the cohort is found and where it is not found).

and Fortin, 2021). By contrast, TreeMig (Lischke et al., 2006) models horizontal and vertical heterogeneity via height classes of tree species distributed spatially to Poisson distributions at the cell level but do so via comparatively coarse-resolution cells (typically 1 × 1 km resolution).

Every FLM adopts simplifying assumptions, conceptual frameworks and algorithmic solutions to strike a balance among geographic (i.e., ecosystem) portability, computational intensity, capacity to simulate large extents and/or fine resolution, and robustness to novel conditions. The tree species cohort design of the LANDIS family of models enables efficient scaling of nondeterministic successional pathways to broad landscapes and regions (Mladenoff et al., 2004). Most biomass-based succession extensions within LANDIS-II focus on compositional and age heterogeneity, with other dimensions of heterogeneity modeled implicitly rather than explicitly. However, there are compelling reasons to more explicitly model canopy dynamics in a way more consistent with contemporary cohort based DGVMs. For example, competition for light contributes substantively to size-growth asymmetry in species-diverse forests (Purves and Pacala, 2008; Dye et al., 2019). However, overly simplistic assumptions regarding canopy stratification, such as each cohort occupies distinct vertical space (i.e., “cohort stacking”) tend to amplify small advantages with long-term consequences for species dominance and coexistence (Fig. 2, Fig. 3; Fisher et al., 2010). Similar simplifying assumptions have been applied in other cohort-based FLMs that include canopy layering (e.g., Schumacher et al., 2004).

In this paper we offer a methodology by which cell-level vertical and spatial heterogeneity are integrated within a cohort-based FLM. Representing vegetation demography with species-age cohorts is a common approach with specific challenges that are not always fully appreciated. Here we have highlighted one of those challenges and proposed a solution that produces more realistic dynamics for light attenuation through tree canopies and improved estimates of vegetation biomass (size) at cell and landscape scales.

Our PCO approach to processing cohorts offers several advantages. Our approach allows emergent canopy dynamics consistent with the formation of distinct canopy layers as well as co-occupancy of those layers in species-rich systems (Oliver and Larson, 1996), and natural gaps in the canopy that become increasingly important as forest stands age and mature (West et al., 2009). The approach enables more explicit competition for growing space in vertical and horizontal dimensions, recognizing that cohort biomass density is not uniformly distributed across cells in these dimensions. In our experience, we have found that accounting for cell-level heterogeneity better constrains cell-level biomass accumulation as an emergent property of tree species age cohort competition, without the need to cap biomass using some theoretical maximum value that may not reflect varying site, compositional, climatic, and atmospheric conditions. We have demonstrated here that failing to account for proportion of the cell occupied by a given tree species age cohort when aggregating attributes such as biomass or LAI to the cell-level can overestimate such attributes (Fig. 3). Our approach further improves the comparability of model outputs with empirical data that typically use units of biomass (or wood volume) per large unit of area (acre or hectare). Model users often calibrate the parameters controlling growth by comparing simulated growth with empirical measures of growth from sources typically representing simple conditions (i.e., even-aged, monocultures, etc.; Reese et al., prep).

Some model behavior illustrated in this paper suggests that our new method can be further improved. The PCO approach sometimes generates discontinuities (through simulated time) in cell-level estimates of biomass pools when cohorts are lost or change canopy layers (e.g., LAI, Fig. 3). We applied a phenomenological solution (i.e., CanopySumScale parameter) that softens this transition by allowing summed canopy proportions in a layer to temporarily exceed 1, but that solution might be improved via closer connections to ecological processes such as self-

thinning of stands. Likewise, the rule that a cohort cannot expand its proportion of the canopy area once crown closure occurs is likely too rigid. While it is true that a cohort cannot expand its coverage via addition of new stems, the silvicultural practice of thinning is premised on the ability of existing trees to expand branches and leaf area into new space in response to partial disturbances (Oliver and Larson, 1996). Some artifacts in cohort dynamics may therefore be expected because of the canopy occupancy rules, particularly with respect to partial disturbances affecting filled canopy layers. For example, a disturbance that partially reduces the canopy proportion of one species cohort in a filled canopy layer would have the ability to refill its vacated space, but a species coexisting in that same layer unaffected by the disturbance would be constrained to remain within its existing canopy proportion. Individual tree-based approaches are more naturally suited to handle such dynamics – nonetheless partial disturbance effects and ecosystem responses remains an important frontier in cohort-based forest modeling (e.g., Kautz et al., 2018). Future improvements to our PCO method will target the rules underlying space allocation within canopy layers to address the above realities.

Another way to achieve results similar to our PCO method might be to simply reduce the cell size. The PCO method is necessary when many cohorts coexist within a layer on a cell. But, as cell size approaches the diameter of a single tree canopy, fewer cohorts would compete within each layer. The PCO approach allows larger cell sizes, which in turn makes it feasible to simulate increasingly large landscapes. Additional study is needed to determine the optimal combination of approaches for both simulation speed and accuracy of computation of cell-level state variables.

5. Conclusion

FLMs are increasingly being used as a research tool to understand how various global changes can be expected to alter forest ecosystem goods and services and as a decision-support tool to evaluate the long-term consequences of alternative forest management strategies and climate futures. Refinements of their algorithms improve their utility for these purposes. The improvements described in this paper allow more accurate simulation of forest "gap" dynamics in models that represent vegetation demography using cohorts, to produce more accurate absolute biomass estimates at cell, species and landscape scales. This is particularly important for studies that assess carbon stocks under alternative climates and/or forest management strategies.

CRediT authorship contribution statement

Eric J. Gustafson: Conceptualization, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Brian R. Sturtevant:** Conceptualization, Methodology, Validation, Writing – original draft. **Brian R. Miranda:** Conceptualization, Methodology, Software, Validation, Visualization, Writing – review & editing. **Matthew J. Duveneck:** Conceptualization, Methodology, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgments

We thank our colleagues who meet regularly to discuss the cross-fertilization of PnET and LANDIS-II, especially Zaixing Zhou, Scott Ollinger, Andy Ouimette, Jane Foster, Danelle Laflower, and Dustin Bronson. Such discussions expand our thinking and reveal model logic that can be improved. Funding for the development and application of PnET-Succession has been provided over a period of many years by the Northern Research Station of the USDA Forest Service, the USDA Agriculture and Food Research Initiative, the Eastern Region of the USDA Forest Service, and the Great Lakes Restoration Initiative (GLRI, Focus Area 5; Project Template #936: Planning Informed by Alternative Future Watershed Ecosystem Services). We also thank three anonymous reviewers for helpful critical reviews that resulted in an improved manuscript.

References

Aber, J.D., Ollinger, S.V., Federer, C.A., et al., 1995. Predicting the effects of climate change on water yield and forest production in the northeastern United States. Clim. Res. 5, 207–222.

Badeck, F.W., Lischke, H., Bugmann, H., Hickler, T., Hönninger, K., Lasch, P., Lexer, M. J., Mouillot, F., Schaber, J., Smith, B., 2001. Tree species composition in European PrisMatsumatotine forests: comparison of stand data to model predictions. Clim. Change 51, 307–347.

Beukema, S.J., Kurz, W.A., Klenner, W., Merzenich, J., Arbaugh, M., Arthaud, G.J., Barrett, T.M., 2003. Applying TELSA to assess alternative management scenarios. In: Systems Analysis in Forest Resources. Managing Forest Ecosystems, 7. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-0307-9_16.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. J. Ecol. 60, 849–872.

Crookston, N.L., Dixon, G.E., 2005. The forest vegetation simulator: a review of its structure, content, and applications. Comput. Electron. Agric. 49, 60–80.

Cushman, S.A., Wasserman, T.N., McGarigal, K., 2011. Modeling landscape fire and wildlife habitat. In: McKenzie, D., Miller, C., Falk, D. (Eds.), The Landscape Ecology of Fire. Ecological Studies (Analysis and Synthesis). Springer, Dordrecht, pp. 223–245. https://doi.org/10.1007/978-94-007-0301-8_9.

de Bruijn, A., Gustafson, E.J., Sturtevant, B.R., Foster, J.R., Miranda, B.R., Lichti, N.I., Jacobs, D.F., 2014. Toward more robust projections of forest landscape dynamics under novel environmental conditions: embedding PnET within LANDIS-II. Ecol. Modell. 287, 44–57.

Dye, A., Ross Alexander, M., Bishop, D., Druckenbrod, D., Pederson, N., Hessl, A., 2019. Size–growth asymmetry is not consistently related to productivity across an eastern US temperate forest network. Oecologia 189, 515–528.

Fisher, R., McDowell, N., Purves, D., Moorcroft, P., Sitch, S., Cox, P., Huntingford, C., Meir, P., Ian Woodward, F., 2010. Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations. New Phytol. 187, 666–681.

Fisher, R.A., Muszala, S., Verteinstein, M., Lawrence, P., Xu, C., McDowell, N.G., Lawrence, D., 2015. Taking off the training wheels: the properties of a dynamic vegetation model without climate envelopes. Geosci. Model. Dev. 8, 3293–3357.

Fisher, R.A., Koven, C.D., Anderegg, W.R.L., et al., 2017. Vegetation demographics in Earth System Models: a review of progress and priorities. Glob. Change Biol. 24, 35–54. https://doi.org/10.1111/gcb.13910.

Gustafson, E.J., 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, 1429–1437.

Gustafson, E.J., Kern, C.C., Miranda, B.R., Sturtevant, B.R., Bronson, D.R., Kabrick, J.M., 2020. Climate adaptive silviculture: how much will it take to produce resilient forest landscapes? For. Ecol. Manage. 470-471, 118208 https://doi.org/10.1016/j.foreco.2020.118208.

Gustafson, EJ., BR. Sturtevant, BR. Miranda. 2023. PnET-Succession v 5.1: comprehensive description of an ecophysiological succession extension within the LANDIS-II forest landscape model. Published on the Internet by the LANDIS-II Foundation. URL.

Hajek, P., Seidel, D., Leuschner, C., 2015. Mechanical abrasion, and not competition for light, is the dominant canopy interaction in a temperate mixed forest. For. Ecol. Manage. 348, 108–116. https://doi.org/10.1016/j.foreco.2015.03.019.

Hidy, D., Barcza, Z., Marjanović, H., Ostrogović Sever, M.Z., Dobor, L., Gelybó, G., Fodor, N., Pintér, K., Churkina, G., Running, S., Thornton, P., Bellocchi, G., Haszpra, L., Horváth, F., Suyker, A., Nagy, Z., 2016. Terrestrial ecosystem process model biome-BGCMuSo v4.0: summary of improvements and new modeling possibilities. Geosci. Model. Dev. 9, 4405–4437. https://doi.org/10.5194/gmd-9-4405-2016.

Hurtt, G.C., Moorcroft, P.R., Pacala, S.W., Levin, S.A., 1998. Terrestrial models and global change: challenges for the future. Glob. Chang. Biol. 4, 581–590.

Kautz, M., Anthoni, P., Meddens, A.J., Pugh, T.A., Arneth, A., 2018. Simulating the recent impacts of multiple biotic disturbances on forest carbon cycling across the United States. Glob. Chang. Biol. 24, 2079–2092.

Keane, R.E.; Loehman, R.A.; Holsinger, LM. 2011. The FireBGCv2 landscape fire and succession model: a research simulation platform for exploring fire and vegetation

dynamics. Gen. Tech. Rep. RMRS-GTR-255. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 137 p.
Keane, R.E., Arno, S.F., Brown, J.K., 1990. Simulating cumulative fire effects in ponderosa pine/douglas-fir forests. Ecology 71, 189–203. https://doi.org/10.2307/1940259.
Kruse, S., Gerdes, A., Kath, N.J., Herzschuh, U., 2018. Implementing spatially explicit wind-driven seed and pollen dispersal in the individual-based larch simulation model: LAVESI-WIND 1.0. Geosci. Model Dev. 11, 4451–4467.
Lawrence, D.M., Oleson, K.W., Flanner, M.G., Thornton, P.E., Swenson, S.C., Lawrence, P.J., Bonan, G.B., 2011. Parameterization improvements and functional and structural advances in version 4 of the Community Land Model. J. Adv. Model. Earth. Syst. 3 (1), M03001.
Lischke, H., Löffler, T.J., Fischlin, A., 1998. Aggregation of individual trees and patches in forest succession models - capturing variability with height structured random dispersions. Theor. Popul. Biol. 54 (3), 213–226. https://doi.org/10.1006/tpbi.1998.1378.
Lischke, H., Zimmermann, N.E., Löffler, T.J., Bolliger, J., Rickebusch, S., 2006. TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. Ecol. Modell. 199, 409–420. https://doi.org/10.1016/j.ecolmodel.2005.11.046.
McCabe, T.D., Dietze, M.C., 2019. Scaling contagious disturbance: a spatially-implicit dynamic model. Front. Ecol. Evol. 7 https://doi.org/10.3389/fevo.2019.00064.
Mladenoff, et al., 1993. LANDIS: a spatial model of forest landscape disturbance, succession, and management. In: Proceedings of the 2nd International Conference on Integrating Modeling and GIS. NCGIA. Breckenridge, CO.
Mladenoff, D.J., 2004. LANDIS and forest landscape models. Ecol. Modell. 180 (1), 7–19.
Moorcroft, P.R., Hurtt, G.C., Pacala, S.W., 2001. A method for scaling vegetation dynamics: the ecosystem demography model (ED). Ecol. Monogr. 71, 557–586.
Monteith, J.L., 1975. Principles of Environmental Physic. Edward Arnold, London.
Norby, R.J., Sholtis, J.D., Gunderson, C.A., Jawdy, S.S., 2003. Leaf dynamics of a deciduous forest canopy: no response to elevated CO2. Oecologia 136, 574–584.
Oleson, K., Lawrence, D., Bonan, G., Drewniak, E., Huang, M., Koven, C., Yang, Z. 2013. Technical description of version 4.5 of the Community Land Model (CLM), NCAR Technical Note NCAR/TN- 503+STR, 420 pp. 10.5065/d6rr1w7m.
Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics, Update Edition. John Wiley and Sons, Inc, New York, p. 520. p.
Pacala, S.W., Canham, C.D., Silander Jr., J.A., 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. Can. J. For. Res. 23, 1980–1988. https://doi.org/10.1139/x93-249.
Petter, G., Mairota, P., Albrich, K., Bebi, P., Brůna, J., Bugmann, H., Haffenden, A., Scheller, R.M., Schmatz, D.R., Seidl, R., Speich, M., Vacchiano, G., Lischke, H., 2020. How robust are future projections of forest landscape dynamics? Insights from a systematic comparison of four forest landscape models. Environ. Model. Softw. 134, 104844.
Post, W.M., Pastor, J., 2013. LINKAGES: An Individual-Based Forest Ecosystem Biogeochemistry Model. ORNL DAAC, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ORNLDAAC/1166.
Purves, D., Pacala, S., 2008. Predictive models of forest dynamics. Science (1979) 320 (5882), 1452–1453.
Reese, G.C., C.C. Dymond, K.M. Quigley, M.J. D., M.S. Lucash, E.J. Gustafson, R.M. Scheller, M.B. Russell, B.R. Miranda, B.R. Sturtevant.2024 In review. Applying growth and yield data and models to the calibration of forest landscape models. Can. J. For. Res.
Reese, G.C., Gustafson, E.J., Vogeler, J.C., Miranda, B.R., Quigley, K.M., Suvada, J., Sturtevant, B.R., 2024b. Evaluation of biomass, composition, and hydrologic dynamics of a forest landscape model using historical datasets. J. TBD.
Roberts, D.W., 1996. Landscape vegetation modelling with vital attributes and fuzzy systems theory. Ecol. Modell. 90, 175–184.
Schaller, R.R., 1997. Moore's law: past, present and future. IEEe Spectr. 34 (6), 52–59. https://doi.org/10.1109/6.591665.
Scheller, R.M., Mladenoff, D.J., 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. Ecol. Modell. 180, 211–229.
Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible temporal and spatial resolution. Ecol. Modell. 201, 409–419. https://doi.org/10.1016/j.ecolmodel.2006.10.009.
Schumacher, S., Bugmann, H., Mladenoff, D.J., 2004. Improving the formulation of tree growth and succession in a spatially explicit landscape model. Ecol. Modell. 180 (1), 175–194.
Seidl, R., Rammer, W., Scheller, R.M., Spies, T.A, 2012. An individual-based process model to simulate landscape-scale forest ecosystem dynamics. Ecol. Modell. 231, 87–100. https://doi.org/10.1016/j.ecolmodel.2012.02.015.
Shifley, S.R., He, H.S., Lischke, H., Wang, W., Jin, W., Gustafson, E.J., Thompson, J.R., Thompson, F.R., Dijak, W.D., Yang, J., 2017. The past and future of modeling forest dynamics: from growth and yield curves to forest landscape models. Landsc. Ecol. 32, 1307–1325. https://doi.org/10.1007/s10980-017-0540-9.
Smith, B., Prentice, I.C., Sykes, M.T., 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Glob. Ecol. Biogeogr. 10, 621–637.
Smith, B., Warlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., Zaehle, S., 2014. Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. Biogeosciences. 11, 2027–2054.
Strigul, N., Pristinski, D., Purves, D., Dushoff, J., Pacala, S., 2008. Scaling from trees to forests: tractable macroscopic equations for forest dynamics. Ecol. Monogr. 78, 523–545.
Sturtevant, B.R., Fortin, M.J., 2021. Understanding and modeling forest disturbance interactions at the landscape level. Front. Ecol. Evol. 9 https://doi.org/10.3389/fevo.2021.653647.
Weng, E.S., Malyshev, S., Lichstein, J.W., Farrior, C.E., Dybzinski, R., Zhang, T., Pacala, S.W., 2015. Scaling from individual trees to forests in an Earth system modeling framework using a mathematically tractable model of height-structured competition. Biogeosciences 12, 2655–2694.
West, G.B., Enquist, B.J., Brown, J.H., 2009. A general quantitative theory of forest structure and dynamics. In: Proceedings of the National Academy of Sciences, 106, pp. 7040–7045.