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Publication Date

2017-09-18

DOI

10.1111/gcb.13910

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Article type : Research Review

Vegetation Demographics in Earth System Models: a review of progress and priorities.

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Running Title: Vegetation Demographics in Earth System Models

Keywords: Demographics, Earth System Model, Vegetation, DGVM, Ecosystem, Carbon Cycle

Abstract

Numerous current efforts seek to improve the representation of ecosystem ecology and vegetation demographic processes within Earth System Models (ESMs). These developments are widely viewed as an important step in developing greater realism in predictions of future ecosystem states and fluxes. Increased realism, however, leads to increased model complexity, with new features raising a suite of ecological questions that require empirical constraints. Here, we review the developments that permit the representation of plant demographics in ESMs, and identify issues raised by these developments that highlight important gaps in ecological understanding. These issues inevitably translate into uncertainty in model projections but also allow models to be applied to new processes and questions concerning the dynamics of real-world ecosystems. We argue that stronger and more

innovative connections to data, across the range of scales considered, are required to address these gaps in understanding. The development of first-generation land surface models as a unifying framework for ecophysiological understanding stimulated much research into plant physiological traits and gas exchange. Constraining predictions at ecologically relevant spatial and temporal scales will require a similar investment of effort and intensified inter-disciplinary communication.

Introduction

Ecological demographic processes govern terrestrial vegetation structure, and vegetation structure influences climatically important fluxes of carbon, energy, and water (Bonan, 2008). Better representation of vegetation demography in Earth System Models (ESMs) has repeatedly been identified as a critical step towards a more realistic representation of biologically mediated feedbacks in modeling future climates (Moorcroft *et al.,* 2001, 2006; Purves and Pacala 2008; Evans 2012; Thomas *et al.*, 2015). Model-data comparison is greatly assisted by increasingly realistic model abstraction methods. Similarly, a greater range of data can be used for parameterization and initialization, and in some cases, models improvements can be directly linked to better simulation of biodiversity (Levine et al. 2016). These improvements are traded off against increasing complexity and computation expense.

Dynamic global vegetation models (DGVMs) are the components of land surface models (LSMs) that try to predict the global distribution of vegetation types from physiological principles (Foley *et al*., 1996; Cao & Woodward, 1998; Sitch *et al.,* 2003; Woodward & Lomas, 2004). Traditionally, DGVMs represent plant communities using a single area-averaged representation of each plant functional type (PFT) for each climatic grid cell. This simplification and the resulting computational efficiency has allowed first generation DGVMs (hereafter g1DVMs) to be broadly adopted within ESMs (Cox, 2001; Bonan et al., 2003; Krinner *et al.,* 2005; Arora & Boer 2010).

This level of abstraction means, however, that g1DVMs do not capture many demographic processes considered important for the accurate prediction of ecosystem composition and function, including canopy gap formation, vertical light competition, competitive exclusion, and successional recovery from disturbance (Hurtt *et al.,* 1998; Moorcroft et al., 2001; Smith et al., 2001; Feeley *et al.,* 2007; Stark *et al.,* 2012).

In contrast, forest gap, (Bugmann *et al.*, 2001; Dietze & Latimer 2011) and 'individual based' models (IBMs) (Smith *et al*., 2001; Sato *et al*., 2007; Fyllas *et al*., 2014; Shuman *et al.,* 2014; Christoffersen *et al.,* 2016; Fischer *et al.,* 2016) represent vegetation at the level of individual plants. IBMs represent spatial variability in the light environment and thereby simulate competitive exclusion, succession, and coexistence of tree species (Pacala *et al.,* 1996; Smith et al. 2001). Simulation of individual trees in a spatially explicit, stochastic framework incurs a notable computational penalty, however. These challenges are typically addressed by limiting the spatial scope (Sakschewski *et al.,* 2015), temporal frequency, and/or reduced sampling of the potential ensemble of model outcomes (Sato *et al.,* 2007; Smith *et al.,* 2014).

As a compromise between the abstraction of g1DVMs and the computational expense of IBMs, many groups have developed 'cohort-based' models, whereby individual plants with similar properties (size, age, functional type) are grouped together (Hurtt *et al.,* 1998, Moorcroft *et al.,* 2001, Lischke *et al.,* 2006; Medvigy *et al*., 2009; Haverd et al. 2013; Scherstjanoi *et al.,* 2013; Smith *et al.,* 2014; Weng *et al.*, 2015). The cohort approach retains the dynamics of IBMs, with reduced computational cost, but removes stochastic processes that can enhance the representation of functional diversity (Fisher *et al.,* 2010).

Herein we refer to both individual and cohort-based models as ‘vegetation demographic models’ (VDMs). We define VDMs as a special class of DGVM, which include representation/tracking of multiple size-classes or individuals of the same PFT, which can encounter multiple light environments within a single climatic grid cell. We adopt this terminology since both individual and cohort models present similar opportunities and challenges as they are implemented within ESMs.

As in first-generation models the distributions of PFTs, and their associated traits, can be geographically and temporally 'filtered' in VDMs via the mechanisms of competition, differential recruitment and mortality. In VDMs, however, disturbance history and vertical light competition modulate interactions between plant traits and resource acquisition. Further, it is typical (but not universally the case) that *a priori* constraints on distribution (climate envelopes) are removed (Fisher *et al.,* 2015). Vegetation structure and distribution thus become entirely emergent model properties of ascribed plant functional traits and their interactions with abiotic environmental conditions. In addition, VDMs provide critical new opportunities for data-model integration owing to their higher fidelity representation of the structure of vegetation stands, as we will discuss in this review.

Several efforts to embed VDMs within ESMs are now coming to fruition, but understanding of their provenance, function and uncertainties remains specialized knowledge even within the land surface modeling community. In this review, we focus on those models currently resident in ESMs or regional atmospheric models. Many ‘offline’ VDMs exist, with novel and beneficial approaches (e.g. Scheiter *et al.,* 2012; Haverd et al. 2013; Pavlick *et al.,* 2013; Fyllas *et al.,* 2014; Scherstjanoi *et al.,* 2014; Sakschewski *et al.,* 2015). We focus on the particular challenges of large-scale implementations, coupled to atmospheric models, since this process imposes important boundary conditions on VDM functionality. For example, ESMs typically require land-atmosphere fluxes of carbon, water and energy at hourly or sub-hourly timescales, and these must be in exact balance to prevent erroneous model drift. Implementation must be global in principle, imposing computational restrictions, and many other processes (hydrology, snow, lakes, urban areas, biogeochemical cycles, land-use change) must be simulated consistently.

Underpinning the implementation of VDMs in LSMs are a set of processes whose representations require significant modification (compared to first-generation DGVMs) to provide the appropriate function in the context of multi-layer, multi-PFT ecosystems. These include the partitioning of light and other resources between individuals or cohorts, the representation of ecophysiological processes involved in carbon and nutrient uptake, allocation, mortality and recruitment within the newly resolved model dimensions, and the interpretations of land use, fire and other disturbances. These new model structures pose several research challenges and opportunities. In this review, which is the first to bring together expertise from such a diverse range of VDM groups, we:

i) summarize the state-of-the-art of VDM development,

ii) discuss model features specific to VDMs and alternative assumptions currently used,

iii) detail datasets available for validation and benchmarking, and

iv) outline future code development and data collection strategies needed to better constrain these new model elements.

We hope to both motivate research aimed at informing the representation of plant ecology in ESMs and highlight gaps in basic ecological theory that are now at the front line of simulating the biosphere's role in the climate system. We argue that it is too early to assert that any one methodology is the ideal representation of plant demographics to use within ESMs. Rather, until relevant data and knowledge gaps are filled through concerted empirical and model-based research, we expect that an ensemble of techniques will allow for more robust predictions of likely trajectories of vegetation structural changes, their impacts on biogeochemistry and climate feedbacks (Sanderson *et al.,* 2015; Koven *et al.,* 2015).

Progress to date

In this section we detail the ongoing progress of implementing vegetation demographic models (VDMs) inside ESMs on a loose continuum from individual- to cohort-based approaches.

SEIB-DGVM

The SEIB-DGVM (Spatially-Explicit Individual-Based Dynamic Global Vegetation Model, http://seib-dgvm.com) is an IBM, representing variability of light in both the vertical and horizontal dimensions. Following initial implementation at a global scale (Sato *et al.*, 2007), SEIB-DGVM has been modified to represent plant population dynamics and biogeochemistry in south-east Asia (Sato 2009), Africa (Sato & Ise 2012), and Siberia (Sato *et al.*, 2010).

SEIB simulates a 30m x 30m patch of forest, where individual trees establish, compete, and die. Each tree is composed of a cylindrical crown and trunk, plus fine roots. Tree crowns are horizontally sliced into 10-cm deep 'disks,' for which photosynthesis is calculated separately with a daily physiological timestep. Leaf area is updated daily by turnover and growth. Crowns of different trees do not occupy the same physical space. To represent spatial plasticity, crowns are able to grow a given distance horizontally in response to light availability each year.

SEIB-DGVM is implemented within the MIROC-ESM (Watanabe *et al.,* 2011). In the ESM context, SEIB-DGVM is run once for each grid cell, representing one particular integration of the stochastic forest, to allow global applications.

LPJ-GUESS

The Lund-Potsdam-Jena General Ecosystem Simulator (Smith *et al.,* 2001, 2014) is also an IBM, but with multiple patches accounting for stochastic heterogeneity in composition and structure arising from succession following stand-destroying disturbance. Both 'individual' and more commonly used 'cohort' modes are implemented. In the cohort mode, tree or shrub individuals of the same age and PFT within patch are grouped together and simulated as an average individual, scaled to patch level via cohort density. Multiple PFTs may occur within a single patch, and compete for light, water and nitrogen. Photosynthesis, stomatal conductance, phenology, turnover and allocation follow LPJ-DGVM (Sitch *et al.,* 2003), with the addition (LPJ-GUESSv3.0 onward) of nitrogen cycling (Smith *et al*., 2014). The model includes the wildfire scheme of Thonicke *et al.,* (2001), and a new representation of fire dynamics is in development.

LPJ-GUESS is coupled to the RCA4 regional climate model (Wramneby *et al.,* 2010; Smith et al. 2011). It also accounts for land cover dynamics and carbon cycling within the EC-EARTH ESM (Hazeleger *et al.,* 2010; Weiss *et al.,* 2014). Daily meteorological fields are input to LPJ-GUESS and adjustments in leaf area index for separate `high' and `low' vegetation tiles, averaged across patches, are returned to the land surface physics scheme. Impacts on energy and water exchange with the atmosphere are manifested via albedo, evapotranspiration and surface roughness length. CO_2 is exchanged daily with the atmospheric transport model.

LM3-PPA

The Geophysical Fluid Dynamics Laboratory (GFDL) Land Model 3 with the Perfect Plasticity Approximation (LM3-PPA) is a cohort-based VDM (Weng *et al.,* 2015). The PPA assumes that tree crowns ‘perfectly’ fill canopy gaps through phototropism (plasticity) (Strigul *et al.,* 2008). Crowns thus self-organize into discrete canopy layers, within which all plants receive the same incoming radiation The LM3-PPA model extends earlier work on simpler tractable PPA models (Farrior *et al.,* 2013, 2016) to include prognostic energy, water and carbon cycling. The simpler PPA models allows ecosystem scale consequences of plant strategies to be rapidly predicted, allowing the properties of the complex model to be investigated in greater depth (Weng *et al.*, 2015).

LM3-PPA successfully captured observed successional dynamics of one site in Eastern US temperate forest (Weng *et al.*, 2015), and the changing relative abundances of deciduous and evergreen strategies over succession in three sites spanning temperate to boreal zones in North America (Weng *et al.*, 2016). Coupling to the GFDL ESM for site-level simulations has been completed, and global implementation is currently in progress.

Ecosystem Demography models

The Ecosystem Demography (ED) concept is also a cohort-based representation of vegetation dynamics (Hurtt *et al.*, 1998; Moorcroft *et al.*, 2001). In contrast to the LM3-PPA, ED discretizes the simulated landscape into spatially implicit ‘patches’ according to ‘age since last disturbance’, capturing the dynamic matrix of disturbance-recovery processes within a typical forest ecosystem in a deterministic manner (in contrast to LPJ-GUESS and SEIB). Within patches, individuals are grouped into cohorts by PFT and height class, and height-structured competition for light between cohorts drives successional dynamics. ED uses a patch fusion/fission scheme to track the landscape-scale age distribution resulting from disturbance. During fission, disturbance splits patch areas into undisturbed and disturbed fractions. During fusion, (to keep the number of patches from growing exponentially), patches that are similar in structure are merged. No sub-grid geographic information is retained. Similar fusion/fission routines exist for cohorts. At least three derivatives of the original ED concept have emerged since its inception, including:

ED

One implementation of the Ecosystem Demography concept (currently known solely as 'ED'), was developed from (Moorcroft *et al*., 2001) applied to the U.S by Hurtt *et al*., (2004) and Albani *et al*., (2006), and is now a global model (Fisk *et al.,* 2015). Advances in this version have focused on the inclusion of land-use as driver of demography (Hurtt *et al.,* 2006), transient effects of tropical cyclones (Fisk *et al.,* 2013), plant migration in response to climate change (Flanagan *et al.,* 2016), and detailed use of vegetation structure to initialize and test ecosystem dynamics (Hurtt *et al.,* 2004, Thomas *et al.,* 2008, Hurtt *et al.,* 2010, Fisk *et al.,* 2015, Hurtt *et al.,* 2016). This branch of ED has also been coupled to the RAMS mesoscale atmospheric model (Roy *et al.,* 2003) and the GCAM integrated Assessment Model (Fisk 2015) and also serves as base model of the NASA Carbon Monitoring System (Hurtt *et al.,* 2014), and the NASA-GEDI mission (Dubayah *et al.,* 2014).

ED2

The Ecosystem Demography Model v2 (ED2) (Medvigy *et al*., 2009, https://github.com/EDmodel/ED2) also uses the scaling concepts of Moorcroft *et al.,* (2001), with numerous subsequent developments. In ED2, grid cells are further disaggregated by similar edaphic conditions. Heterogeneity in light environment and canopy structure is integrated into the biophysical scheme, giving rise to differentiated horizontal and vertical micro-environments within grid-cells that vary in temperature, humidity, soil moisture and soil nutrient conditions. Recent developments include a plant hydrodynamic scheme, drought-deciduous phenology (Xu *et al.*, 2016), nitrogen fixers, boreal-specific PFTs, dynamic soil organic layers, and trait-based recruitment (Trugman *et al.*, 2016).

ED2 has been tested in boreal (Trugman *et al.*, 2016), temperate (Medvigy *et al.*, 2009, Medvigy and Moorcroft 2012, Medvigy *et al*., 2013, Antonarakis *et al.*, 2014), tropical (Kim *et al.*, 2012; Zhang *et al.*, 2015; Levine *et al*., 2016; Xu *et al*., 2016), tundra (Davidson *et al*., 2009), agricultural (Lokupitiya et al., 2016), and biofuel systems (LeBauer *et al.*, 2013). It has also been applied to ecosystems undergoing disturbance events such as fire, drought, elevated CO2, land-use change, and insect defoliation (Medvigy *et al.*, 2012, Zhang *et al.*, 2015, Miller *et al.*, 2016, Trugman *et al.*, 2016). ED2 is coupled to the Regional Atmospheric Modeling System (RAMS) (Knox *et al.*, 2015; Swann *et al.*, 2015).

CLM(ED)

CLM(ED) (Fisher *et al.*, 2015) is a variant of the Community Land Model (CLM) (Lawrence *et al.*, 2011; Oleson *et al.*, 2013), integrating the ED concept within the architecture of the Community Earth System Model (Hurrell *et al.*, 2013). CLM(ED) includes a merging of the ED and PPA concepts, allocating cohorts to canopy and understorey layers. It deviates from the standard PPA as it does not allocate canopy levels according to a definitive height threshold (z*, Purves *et al.*, 2008; Strigul *et al.*, 2008) and instead splits growing cohorts between canopy layers - the fraction of each cohort remaining in the canopy a continuous function of height (in principle increasing the probability of coexistence, Fisher *et al.*, 2010).

Canopy biophysics, hydrology, photosynthesis, and respiration all follow CLM4.5 (Oleson *et al.*, 2013) subject to disaggregation into cohort-level fluxes. CLM(ED) includes new representations of phenology and carbon storage and a modified SPITFIRE fire model (Thonicke et el. 2010). CLM(ED) was applied regionally, focusing on the sensitivity of biome boundaries to plant trait representation (Fisher *et al.*, 2015) and will be re-named FATES (Functionally Assembled Terrestrial Ecosystem Simulated) in future references.

Approaches to model structure and process representation

Historically, demographic models (typically IBMs) have been distinct from models with detailed plant physiological representation. In the VDMs discussed here, however, demographics (recruitment, growth, mortality) arise primarily as functions of physiological functions and so the two are intimately linked. Thus, design decisions in physiological algorithms have potentially critical impacts on the emergent population dynamics. In this section, we discuss the process modifications that are required when moving from a g1DVM model to a size-structured VDM. These include higher-order representation of competition for light, water and nutrients, demographic processes (recruitment, mortality) and disturbance (fire, land use). Our intention is to 1) illustrate the logic behind the inclusion of new model features, 2) highlight process uncertainties that remain or emerge (by way of motivating new research themes), and 3) provide context for the following discussion of model evaluation data.

Competition for light

Land surface models calculate radiation partitioning and the within-canopy radiation regime using radiative transfer models (RTM). RTMs simulate the reflectance, interception, absorption, and transmission (into the ground) of shortwave radiation (0.3 to 2.5 microns) through a canopy comprised of scattering elements (leaves, wood, soil and snow). Incoming radiation is typically partitioned into direct and diffuse streams. Interception of direct radiation by scattering elements results in reflected and transmitted fluxes of diffuse radiation. Upwards-reflected diffuse radiation affects leaves higher in the canopy, preventing a simple solution to the partitioning of energy. To resolve this, iterative methods calculate upwards and downwards diffuse fluxes until a solution is reached (Goudriaan, 1977; Norman, 1979). Other approaches use the ‘two-stream approximation’ (Dickinson, 1983; Sellers, 1985), a system of two coupled ordinary differential equations which can be analytically solved (Liou 2002) assuming a continuum with homogenous reflectance and transmission characteristics. The two-stream approximation is used for a single canopy divided into sun/shade fractions in CLM4.5 (Bonan *et al.*, 2011) and as a set of canopy layers each with its own 2-stream solution for JULES (Mercado *et al.,* 2007), ORCHIDEE-CAN (Naudts *et al.*, 2015), ED2 (Medgivy *et al*., 2009) and CLM(SPA) (Bonan *et al.,* 2014).

In VDMs, the RTM is necessarily more complex than standard LSMs because of the need to have more than one PFT within a given vertical structure canopy, invalidating the homogeneity assumptions of the two-stream model. VDMs must further determine 1) how to partition leaves and stems of cohorts/individuals into discrete scattering elements within which there can be an assumption of homogeneity and 2) how to arrange these scattering elements relative to each other, to discern the influence of plant height on radiation interception. The details of how these issues are resolved control the nature of the feedback between plant size and light acquisition, and thus are a pivotal component of any trait-filtering architecture (Fisher *et al.*, 2010; Scheiter *et al.*, 2012).

Solving these problems efficiently is a significant component of the implementation of VDMs in ESMs. Here, we summarize the status of the existing schemes, their advantage and disadvantages, and suggest ways in which these might be developed further. Alternative schemes are represented in Fig. 1.

Individual-based approach: SEIB

In SEIB-DGVM, each individual crown has an x-y location in space, and shading of trees by their neighbors is explicitly simulated. Direct and diffuse photosynthetically active radiation (PAR) are estimated for each crown disk. For diffuse PAR, all disks at the same height receive the same radiation, attenuated by the leaf area index (LAI) above each disk using Beer's law (Goudriaan *et al.*, 1977). For direct light, a 'virtual cylinder' is calculated for each canopy disc. The cylinder extends South, at 0.86 x the midday solar angle (Sato et al. 2007), and available PAR is attenuated (also using Beer's law) by the leaves located within the cylinder. The grass layer is horizontally divided into 1x1 m cells, each of which receives PAR attenuated by the LAI above. Some simplifications are employed to efficiently simulate individual trees (daily timestep, static solar angle, few or no replicates). In contrast, cohort models (below) have a lower computational footprint, but must designate rules by which light is distributed to cohorts of differing height in the absence of direct spatial competition.

Infinitely thin flat crowns: ED, ED2

Perhaps the most straightforward method for representing how cohort leaves are aligned with respect to incoming light is the 'flat-top crown' idea; wherein the total leaf area of each cohort is conceptually distributed evenly across the entire canopy area of a patch (one infinitely thin layer). The cohort-layers are stacked vertically and the two-stream model is used to determine radiation absorbed by each layer at its midpoint. Each cohort thus is shaded by all taller cohorts.

The flat-top method is relatively straightforward to implement, but suffers from the biologically unrealistic outcome that marginally taller cohorts outcompete their neighbors in terms of light availability. This can lead to systematic growth biases (compared to observations) where the tallest trees grow too fast and next-tallest trees more slowly, making coexistence of multiple PFTs more difficult to achieve (Fisher *et al.*, 2010). Further, there is no representation of the effects of space on canopy structure (Farrior *et al.*, 2016). In ED2, these negative effects have been partially mitigated by (1) the consideration of cohort crown area, which allows partial, rather than complete, shading among cohorts and, (2) a cohort splitting algorithm that prevents a single cohort from accumulating a leaf area index above a predetermined maximum LAI threshold.

Vertically overlapping crowns: LPJ-GUESS

LPJ-GUESS adopts an approach similar to ED2 but with three-dimensional crowns evenly distributed across the area (c. 0.1 ha) of each stochastic patch, and uniformly distributed in the vertical dimension from ground level up to the current maximum height of each individual or cohort. A multi-layer Beer’s law integration partitions incoming PAR among cohorts by relating light absorptance of each layer to that layer’s leaf area using a single fixed extinction coefficient (Smith *et al.*, 2001). A herbaceous layer captures PAR not absorbed by the canopy.

Perfect Plasticity Approximation: LM3-PPA

The PPA assumes that trees can forage for light in a ‘perfectly plastic’ manner horizontally within a patch. Starting with the tallest tree, the crown area of each successively shorter tree is assigned to the canopy layer until the cumulative canopy crown area equals or exceeds the patch ground area. Once the 'canopy' is filled with tree crowns, the next shorter trees inhabit the first understory layer and are shaded by the trees in the canopy. If the first understory layer is also full, then a additional understory layers are created. All crowns in the same layer receive the same incoming radiation streams, and penetration of light through each crown is determined using Beer's law (Weng *et al.*, 2015). The radiation streams penetrating the crowns of a layer are averaged before passing to the next lower layer. Light reflected by the soil can be absorbed by the leaves above. Physiologically-based PPA models Dybzinski et al. 2011, Farrior et al. 2015, Weng et al. 2015] include a gap fraction parameter (η), whereby only $1-\eta$ of each layer can be filled. This allows more light to reach the understory, and thus more realistic understory behavior, but does not fundamentally change the PPA algorithm.

Discretized PPA: CLM(ED)

The CLM(ED) follows a similar logic to the PPA, and resolves radiation streams between canopy layers, and also discretizes direct and diffuse fluxes into 'leaf layers' within cohorts. To reduce computational intensity, cohorts are merged together for flux calculations, such that all leaves of each PFT are represented by a three-dimensional matrix of PFT, canopy layer, and leaf layer. An iterative, layered solution, following Norman (1979), calculates equilibrium upwards and downwards radiation fluxes.

Modifying extreme assumptions

The existing methodologies for the division of solar radiation in cohort models represent two extreme assumptions at either end of a continuum. The flat-top assumption implies that small differences in relative height lead to large changes in light availability (within a patch), whereas the PPA assumption means that differences in height, however extreme, only affect light availability at the boundaries between canopy layers (canopy vs. understory). In reality, canopy trees all receive equivalent light from above, but the amount of lateral light they receive depends on their height relative to their neighbors. An ideal framework might include the capacity of the PPA to represent the impact of space on competition for overhead light, while adding change in lateral light availability with height among canopy trees. A spatially-implicit scheme that could capture both of these features would enhance the ability of VDMs to capture size-related variation in light availability, and thus presumably size-related variation in growth and survival.

Water acquisition and its influence on plant physiology

In comparison with competition for light, competition for water is less well-understood, and model representations remain poorly developed, especially in terms of how water is distributed among competing plants, as well as in how water acquisition affects plant processes.

Representing competition for water

Shared vs. partitioned water resources:

Models use contrasting assumptions of how water resources are divided horizontally within a grid-cell. Some VDMs represent a single ‘pool’ of water from which all plants draw equally (CLM(ED), LM3-PPA, SEIB-DGVM, Fig. 2, panel b). Other models (ED2, LPJ-GUESS) divide water resources by patch (Fig. 2, panel a). Real ecosystems are unlikely to conform to either of these simplifications. In reality, whether water resources are shared across patches depends on the relative characteristic length scales of disturbance and of horizontal water redistribution (Jupp & Twiss, 2006). Where canopy gaps and thus patches are small, we might expect that water would be effectively shared between patches of different ages; in contrast, where disturbance events are larger-scale (blow-downs, fires) and patches accordingly larger, we might expect little or no such water sharing. No VDMs track length scales or arrangement of disturbance events by default, nor do they represent inter-patch water fluxes The impact of this type of effect can be important for the surface energy balance (Shrestha et al., 2016).

Spatial aggregation of water resources:

A rich literature exists on the spatial partitioning of water resources in semi-arid regions (Rodriguez-Iturbe *et al.,* 1999; Van Wijk & Rodriguez-Iturbe 2002; Meron *et al.,* 2004; d'Odorico *et al.,* 2007; Scanlon *et al.,* 2007; Gilad *et al.,* 2007; Borgogno *et al.,* 2009; Meron 2011), the focus of which is the tendency for soil moisture states to shift away from the mean due to vegetation-mediated positive feedback mechanisms (Fig 2. Panel c), including root foraging for water, and impacts of vegetation on infiltration and recruitment (Shachak *et al.,* 2008, Ivanov *et al*., 2010). These mechanisms allow patchy vegetation to persist where the spatial mean moisture state might prevent viable vegetation growth. LSMs typically assume spatial homogeneity of moisture, leading in principle to underestimations of vegetation survival.

Size symmetry of water competition:

The degree to which competition for belowground resources is asymmetric with regard to plant size is unclear. VDMs typically allow partitioning of water between plants of differing root depth (Ivanov *et al*., 2012) but within a given soil volume assume perfectly symmetric competition. Schwinning and Weiner (1998) argued that, where a large plant is in competition with a small plant, the fraction of the small plant's root zone affected by the resulting resource depletion is larger than the affected fraction of the root system of the large plant, (Fig 2. Panels d and e) suggesting the likelihood of size asymmetry, but the degree to which this is a dominant phenomenon remains unclear (DeMalach *et al.*, 2016; Schenk, 2006).

Impacts of water on plant physiology

LSMs have used simplistic representations of the responses of plants to acquired soil moisture since their inception (McDowell *et al.*, 2013). Recently, plant hydraulics theory (Sperry *et al.*, 1998), offline models (Williams *et al.*, 2001; Bohrer *et al.*, 2005; Hickler *et al.*, 2006; Janott *et al.*, 2011; McDowell *et al.*, 2013; Gentine *et al.*, 2015) and datasets (Choat *et al.*, 2012; Maréchaux *et al.*, 2016; Christoffersen *et al.*, 2016) have improved substantially, giving rise to the potential for inclusion of 'hydrodynamics' (prognosis of moisture states and fluxes within plants) in LSMs. These methods have shown promise for improving simulations of carbon, water, and energy fluxes, particularly during dry conditions (Williams *et al.*, 2001; Fisher *et al*., 2006, 2007; Bonan *et al.*, 2014; Christoffersen *et al.*, 2016). Prediction of internal plant moisture status might also allow more realistic representation of drought deciduousness (Xu *et al.*, 2016), sink limitations on growth (Fatichi *et al.*, 2014), and stress-induced tree mortality (Anderegg et al. 2012)

Considerable effort is currently being expended on the implementation of such hydrodynamic schemes within VDMs (Xu *et al.*, 2016; Christoffersen *et al.*, 2016). Key challenges include 1) parameterization of hydraulic trait trade-offs and coordination across functional types and tissues, 2) understanding the impact of segmentation of the hydraulic continuum, 3) representing characteristic timescales of xylem embolism refilling (Mackay *et al.*, 2015), 4) linking stomatal responses to plant hydraulic states/fluxes (Bonan *et al.*, 2014; Sperry & Love

2015; Sperry *et al.,* 2016; Christoffersen *et al.,* 2016), 5) integrating plant hydraulic status with existing growth and allocation schemes and demography, and 6) integration with appropriate benchmarking data.

Below-ground competition for nutrients:

Nutrient cycling (nitrogen, rarely phosphorus) is now represented in several LSMs (Wang *et al.,* 2010; Zaehle *et al.,* 2010; Smith et al. 2014) yet uncertainties remain concerning the appropriate representation of many processes (Zaehle & Dalmonech 2011; Xu *et al.,* 2012; Brzostek *et al.,* 2014; Zaehle *et al.,* 2014). VDMs inherit these uncertainties, and are subject to further structural degrees of freedom, derived from size/age structured representations of nutrient supply and demand. In principle, similar concerns of tiling impacts, aggregation, and asymmetric competition apply to nutrient as well as water uptake. One difference is that nutrients tend to be more abundant near the ground surface than at depth, thus may allow for more size-symmetric competition than for water. An advantage of VDMs is that they might better resolve some features of nutrient cycling that are difficult to include in typical LSMs, such as explicit representation of the successional status of nitrogen-fixing versus non-fixing plants, and release of nutrient competition following disturbance. Of the models described here, ED2, LPJ-GUESS, and LM3-PPA have nutrient cycling schemes (Trugman *et al.,* 2016; Smith et al. 2014; Weng et al. 2016)

Vegetation Demographics: recruitment & mortality

g1DVMs typically include representations of plant demography (recruitment, mortality) (Sitch *et al.,* 2003; Melton and Arora 2016). Where, in g1DVMs, mortality and recruitment rates only impact mean vegetation biomass and PFT distributions, in size-structured VDMs, these processes also impact emergent forest structure and PFT composition, which in turn affect light competition and feed back on PFT filtering. There is thus a strong imperative to constrain demographic processes in VDMs.

Mortality

Tree mortality is represented in g1DVMs as either a constant (in basic models) or as a function of various 'proxies' - carbon balance, hydraulic stress, growth efficiency, plant traits, size, or age (McDowell *et al.*, 2011, 2013). Persistent uncertainty about the major drivers of plant death means that a consensus on model structure is not yet justified. Some models now account for several additional sources of mortality, including biotic damage (Hicke *et al.,* 2012, Dietze and Matthes 2015; Jönsson et al. 2012), atmospheric pollutants (Dietze and Moorcroft 2011), wind damage (Lagergren et al. 2012) and herbivory (Pachzelt et al. 2015) but relative importance of these various processes remains unclear. Representations of height structures and hydrodynamics in VDMs should improve the fidelity of mortality proxy prediction, given that mortality can be strongly related to tree size (Muller-Landau *et al.,* 2006; Lines *et al.*, 2010; Bennet *et al.*, 2015).

The likelihood of increased climate-stress related mortality (Anderegg *et al.,* 2013) has motivated numerous experimental and observational studies in recent years (McDowell *et al.,* 2008, 2011, 2013, 2015; Zeppel *et al.,* 2011; Xu *et al.,* 2013; Anderegg *et al.,* 2012, 2015). One goal of this effort is to empirically relate hypothesized physiological proxies to rates of tree death at relevant scales.

At the scale of individual plants, mortality is a discrete process, occurring after some threshold of physiological stress is reached. If a model, however, predicted that all members of a given cohort died on the day that their average stress exceeded some threshold, that cohort would be extinguished across the whole landscape. Given ESM gridcells are often very large (>100km resolution) this outcome would be ecologically unrealistic because of heterogeneity within the real population represented by that cohort. Cohort-based models therefore require empirical linkages between physiological proxies of death and mortality rates at the scale of model predictions. On a stand scale, the population represented by a cohort is heterogeneous due to variations in resource availability, genotype diversity, herbivory and disease. Across a landscape, the population represented by a cohort might also encounter heterogeneity in soil texture, topography, aspect, microclimate etc. Therefore we expect a looser connection between average physiological stress and landscape-scale mortality rates as the scale of prediction increases. In principle, the slope of the relationship between average physiological stress and landscape-scale mortality requires scale-dependent calibration (Fig. 3).

Recruitment

There is some evidence that establishment rates may be considerably more sensitive to environmental filters than selection of adult plants, thus, compositional shifts are as likely to be driven by changes in recruitment as by adult growth and mortality (Ibanez *et al.,* 2008, 2009). All demographic models represent plant recruitment processes (seed production, dispersal & germination), albeit simplistically. The rate of seed production is typically highly idealized; in ED-type models, it is a fixed fraction of net primary productivity (NPP) for plants that are in positive carbon balance (Moorcroft *et al.,* 2001). Most VDMs do not consider dispersal among grid cells, given the complexities of this process (Sato and Ise 2012; Nabel *et al.,* 2015). To simulate germination, VDMs typically impose a minimum size threshold below which physiological processes and demography are not resolved and the emergence of new recruits is thus a phenomenological formulation (Farrior *et al*., 2013), modulated in some VDMs by climate envelopes (LPJ-GUESS, SEIB-DGVM), empirical proxies (forest-floor potential NPP, Smith et al. 2001) or plant traits and environmental conditions (Trugman *et al.* 2016).

Disturbance Regimes: Fire & land use

Fire

Most ESMs contain representations of the impacts of fire, in g1DVMs, however, the impact of fire-induced tree mortality is simply to reduce the overall number density (individuals/m^2) in the next timestep (Hantsen *et al.,* 2016). VDMs' tracking of size and age structure provides three opportunities to improve representation of fire-vegetation interactions. First, age-since-disturbance structured models can natively represent disturbance-recovery mosaics that arise as a result of frequent fire regimes and fire-vegetation feedback processes (wind speed, flammability, recruitment) within those regimes. Second, vertical canopy structure can capture size-structured mortality resulting from fire events and thus represent the dynamics of the 'fire-trap' in savanna-type ecosystems (Hoffmann & Solbrig, 2003; Hoffmann *et al.* 2012).

Land Use

Capturing the impact of human land-use and land-cover change on the carbon cycle, hydrology and other biogeophysical systems is a key application of ESMs (Pongratz *et al*., 2009; Shevliakova *et al*., 2009; Jones *et al*., 2011; de Noblet-Ducoudré *et al*., 2012; Brovkin *et al*., 2013). For the CMIP inter-comparison process, a single consolidated set of land-use transitions are specified (with carbon estimates from the 'ED' model as described above, Hurtt *et al.,* 2011), providing a matrix of transitions between land use classes (e.g. primary forest, secondary forest, pasture, cropland) through time (Lawrence *et al.*, 2016). In traditional LSMs, land-use transitions must be translated into annual land-cover maps that specify the fraction of the land surface occupied by each PFT (Lawrence *et al*., 2012). A principal advantage of VDMs is that these land-use transitions can be directly implemented without the need for translation into PFT fractions, since they can explicitly simulate ecosystem disturbance and recovery (Shevliakova *et al*., 2009).

Representing human managed systems such as croplands, pasturelands, and plantation forests also requires the specification of transitions and management practices (e.g. harvest, grazing) (Shevliakova *et al.*, 2009, Lindeskog *et al.*, 2013). Implementing standardized representations of these processes directly will emerge as a challenge as VDMs become more common elements of ESM structure. A further advantage of VDMs relates to the impacts of shifting cultivation. The impact of gross land use transitions has been estimated to generate emissions that are 15-40% higher than the net transitions alone (Hansis *et al*., 2015; Stocker *et al*., 2014; Wilkenskjeld *et al.*, 2014). This effect can be captured using age-since-disturbance mosaic approaches but is not directly possible with traditional LSMs.

Benchmarking VDMs

On the need for VDM specific benchmarking data

Benchmarking and validation activities for LSMs have become increasingly numerous and sophisticated in recent years. These include comparisons against global or regional gridded data products (Luo *et al.*, 2012), comparisons of relationships between two or more properties (emergent constraints), comparisons against intensively measured individual sites (including flux towers) (Schwalm *et al.*, 2010) and against manipulation experiments (de Kauwe *et al.*, 2013; Zaehle *et al.*, 2014). The International Land Model Benchmarking Project (www.iLAMB.org) maintains a set of standard benchmarking products used for this purpose. Expanding this set of standardized data products to match the scope of VDMs will be a critical challenge in years to come (Hoffman et al., 2017). In this section, we describe potential metrics for benchmarking the novel aspects of VDMs described above. For some components, benchmarking datasets are already available, but for many they are scarce. We hope to illustrate potential platforms for future model-data integration made possible by the additional realism of VDM components.

Further to this, numerous model inter-comparison projects in recent years have attempted to compare the outputs of large and complex Earth Systems Model components (including LSMs) against various types of benchmarking data. Vegetation demographics, in particular, are the emergent properties of a very large array of other simulated processes in VDMs, and so it is not clear that a straight inter-comparison between the featured approaches would generate a clear comparison of how different methods for abstracting ecosystems into models compare. Given the lack of consensus on the parametric and structural approaches employed in the physiological and biophysical algorithms of all said models, it is notoriously difficult to assign differences in model performance to individual attributes, such as their demographic representation (c.f. Zaehle et al. 2014). This difficulty provides a motivation for assessing the skill of individual component parts (e.g. radiation transfer schemes, hydrodynamic representations, allocation, mortality, and recruitment models,). Illustrating that VDMs have these components in common might provide a framework for future more refined inter-comparison studies.

Validation of radiation transfer and canopy organization

Radiation transfer models have two main components: The first is the underlying scheme;

how radiation interacts with the scattering elements, reflectance and transmittance properties, and the treatment of diffuse radiation. Validating these representations is arguably an existing field of research, particularly in the realm of assessing canopy structure from remote sensing data (Smolander & Sternberg 2005; Widlowski *et al.*, 2009, 2015).

The second feature of VDM RTMs are the assumptions controlling the arrangement of scattering elements with respect to each other. e.g. Is a discrete-layered PPA-like structure a good approximation of a forest canopy? How much do adjacent crowns affect each other's light interception? These questions might be addressed using detailed 3D observations on the arrangement of leaves and crowns in space, via high-density airborne or ground-based LiDAR (Stark *et al.*, 2012; 2015, Detto *et al.*, 2015), and then applying more complex 3D radiative transfer models (Morton *et al.*, 2015) to assess how alternate VDM RTM structures perform. These exercises should be prioritized, since the impact of size on resource acquisition is such a fundamentally important process in determining ecological demographics.

Validation of plant water use

Establishing credible boundary conditions (soil moisture, meteorology, vegetation structure) and appropriate validation data (sap flow, leaf water potential, gas exchange) is a challenging prerequisite for testing alternative hypotheses about the physics and physiology governing plant water utilization. The number of locations for which this validation is possible is small but growing. Such intensive ecosystem physiology observations have proven extremely valuable, however, illustrated by their repeated use in model validation exercises (Williams *et al.*, 2001; Fisher *et al.*, 2007; Zeppel *et al.*, 2008; Plaut *et al.*, 2012; Poyatos *et al.*, 2013; Joetzer *et al.*, 2014; Matheny *et al.*, 2016). Since plant water status is fundamentally linked to both height, (on account of gravitational effects) and canopy position (in relation to differing evaporation rates) vertically-resolved models are critical to allowing direct model-data comparison exercises. Christofferson et al., for example, Christofferson et al. (2016) illustrate the importance of canopy position in correctly simulating daytime leaf water potential at the Caxiuana throughfall exclusion experiment in Amazonia, thus, g1DVMs with aggregated plant water status might be difficult to compare directly with plant hydraulics observations.

New datasets documenting stem water storage (Matheny *et al.*, 2015, Carrasco *et al.*, 2015), remotely sensed plant water status (Konings & Gentine, 2016) and solar induced florescence (Guanter *et al.*, 2016), also have the potential to provide additional metrics for evaluation of hydrodynamic model predictions.

Validation of canopy structure

Tests against plot-scale size structure data:

The canopy structure (tree size frequency per plant type) predicted by a VDM can be validated using ecological census data from permanent sample plots. Predicted canopy structure is a high-level emergent property, however, and is influenced by radiation transfer, photosynthesis, respiration, allocation, and demographics (recruitment and mortality). Thus where discrepancies arise, it is difficult to diagnose the model specific errors that led to the poor predictive power.

Using the PPA, Farrior *et al.*, (2016) circumvent this problem by collapsing the details of growth and demographic rates at a given location into constant rate parameters, which vary only with canopy status and PFT. This approach successfully captures the size distribution of a tropical rainforest, in particular, the observed shift in structure between understory trees (which approximate a power-law distribution) and canopy trees (which do not). This result highlights 1) the need to account for asymmetric availability of light across size classes (in contrast to West *et al.*, 1999; Enquist *et al.*, 2009), 2) that simulation of small-scale disturbances is critical in the tropics, necessitating a model inclusive of gap formation and 3), that representation of the plant canopy as distinct strata (canopy and one or more understory layers) is a useful simplification.

Tests against remote sensing of canopy structure:

Existing Earth Observation products can detect phenological signals (Hansen *et al.,* 2002) and vegetation stature (Lefsky *et al.,* 2005; Simard *et al.,* 2012). This allows a remote detection of `traditional' PFTs (defined by phenology and growth habit). As such, DVMs have historically been tested against these vegetation classification maps (Sitch *et al.,* 2003; Bonan *et al.,* 2003; Arora & Boer 2006; Fisher *et al.,* 2015). Emerging data products that observe high spectral resolution (i.e. "hyperspectral") data streams can be used to discern the properties of plant surfaces, which themselves can be linked to leaf or canopy traits (Asner *et al.,* 2012; Singh *et al.,* 2015; Shiklomanov *et al.*, 2016). In principle, VDMs specified using PFTs that align with traits that can be detected using hyperspectral sensing (e.g. leaf nutrient and photosynthetic properties, moisture/temperature features, leaf thickness & venation) could be validated using these types of observation (Antonarakis *et al.,* 2014; Asner *et al.*, 2016; Serbin *et al.*, 2015). Use of LIDAR to detect individual tree height and crown diameter (Hurtt *et al.,* 2004, 2010, 2016; Thomas *et al.,* 2006; Barbier *et al.,* 2010; Garrity *et al.,* 2012; Jucker *et al.,* 2016) can be used to constrain model vegetation structure predictions.

Validation of demographic rates (recruitment, growth, mortality).

Tests against plot-scale demographic data:

Recruitment, growth and mortality rates can be estimated from repeated censuses at permanent sample plots (Lewis *et al.*, 2004; Philips *et al.*, 2010). The direct use of plot data is hindered by the need to drive models with local climate data, however, and as such is typically limited to more intensively observed field sites (Powell *et al.* 2013). Emergent relationships, such as the change in mortality with environmental gradients (Philips *et al.*, 2010) other ecosystem properties such as NPP (Delbart et al. 2010) and regional extrapolation of mortality rates (Lines *et al.*, 2010; Johnson *et al.*, 2016) should also prove useful as benchmarks that a model might be expected to capture.

Tests against remotely sensed demographic data:

Recent developments in remote sensing-based disturbance detection, including a high-resolution (30 m x 30 m) global disturbance database (Hansen *et al.*, 2013), provide opportunities to evaluate large tree mortality events at global scales. At smaller scales, (Garrity *et al.*, 2013) illustrate the potential for detection of tree mortality using 1m resolution QuickBird imagery. Hyperspectral and airborne LIDAR techniques will likely improve our ability to remotely detect tree mortality rates (Eitel *et al.*, 2016). Remaining limitations of these approaches include the fact that they primarily detect mortality of canopy trees (McDowell et al., 2015), and that issues related to return frequency, cloud cover, sensor lifetime impact the ability to detect the exact timing of mortality events, impeding attribution of their drivers.

Broader issues concerning the inclusion of Vegetation Demographics in ESMs

Plant trait information

The use of plant trait data for parameterization of LSMs in general (Reich 2014; Reich *et al.*, 2014; Verheijen *et al.*, 2015) and VDMs in particular has been covered extensively elsewhere

(Scheiter *et al.,* 2012; Pavlick *et al.,* 2013; Fyllas *et al.,* 2014; Fisher *et al.,* 2015; Sakschewski *et al.,* 2015; Pappas *et al.,* 2015). VDMs are primarily designed as 'trait filtering' models, in that they predict the differential demographic performance (in terms of growth mortality and recruitment) from plant traits and environmental conditions, and thus in turn predict/filter the distribution of those traits across the landscape. The success of trait filtering approaches is linked to the fidelity with which trait trade-off surfaces are prescribed to the model (Scheiter *et al.,* 2012). Designing balanced trade-offs is a particular concern with this approach. Specifically, allowing traits to vary such that one particular PFT gains a large growth advantage -without sufficient attendant cost- will result in the runaway dominance of that PFT, particularly given positive feedbacks between growth, resource acquisition, and reproductive success (Pacala and Tilman 1994; Fisher *et al.,* 2010, 2015; Bohn *et al.,* 2011). Deriving balanced trade-off surfaces from plant trait datasets is also problematic if environmental variation affects plant trait expression. For example, Reich *et al.,* (2014) find that leaf lifespan of needleleaf trees varies with temperature, breaking the more typical global correlation with leaf mass per unit area. Thus, geographical datasets can conflate the causes of trait variability, as can impacts of shade on trait plasticity (Keenan & Niinemets 2016). We strongly advocate for detailed analyses of emerging trait databases to provide relevant trait relationships for VDM simulations (e.g. Christofferson et al., 2016).

Improving Informatics

Working with VDMs presents notable challenges in informatics and statistics due to their complexity, input requirements and output dimensionality. Recently, model informatics systems have emerged to meet these challenges, including the Predictive Ecosystem Analyzer (PEcAn) (Dietze et al., 2013, 2014; LeBauer et al., 2013). The primary goals of PEcAn are to reduce redundancy and improve reliability in the workflows associated with running, parameterizing, validating, calibrating and reporting ecosystem models. PEcAn consists of a suite of open-source workflow and statistical tools (https://github.com/PecanProject/pecan) and a web interface, (pecanproject.org). Tools include sensitivity analysis and variance decomposition, model-data assimilation, Bayesian calibration, as well as generation of common meteorological drivers, validation data streams, benchmarking, and visualizations. These common protocols allow analyses to be replicated across models, making inter-model comparison easier. Further, PEcAn employs a database to track workflows across researchers and institutions, allowing robust provenance tracking. PEcAn currently supports ten different ecosystem models, including most of the models discussed in this paper (ED2, CLM(ED), LM3-PPA, LPJ-GUESS). PEcAn is an open community project, and is extensible for novel analyses and modules.

Summary

We describe the major modifications to traditional dynamic vegetation models that are necessary to allow structured representation of ecological demographic processes inside the architecture of Earth System Models. These developments open a number of avenues for better data-model integration, and highlight gaps in ecological observation and understanding that we hope could be a major focus of future scientific endeavor.

Priority areas for VDM development include

1. Partitioning of solar radiation between competing plant canopies, and the physics of shading within and between individuals and cohorts.
2. Representation of plant hydrodynamics in models, and improving parameterizations and linkages to observations.
3. Distribution of below-ground resources (nutrients and water) between size classes, PFTs,

and patches.

4. Representation of demographic processes (mortality and recruitment), scaling of reductionist physiological models of plant mortality across heterogeneous landscapes, calibration using emerging remote sensing products, and trait impacts on recruitment rates.

5. Better representation of land use processes and fire disturbance. For fire, this includes size-structured impacts of burning, as well as recovery and fire-vegetation feedback processes. For land use change, challenges include mapping transitions into clear impacts on ecosystem structure and management and global parameterization of heterogenous anthropogenic impacts.

These foci integrate many potential avenues for novel model-data-fusion effort that are made plausible via the implementation of demographic models. We advocate for more intensive and innovative usage of ecological data streams in model validation and argue that the many different avenues for development of VDMs will benefit from coordinated approaches to these topics. The development of common, widely-available intensive (plot-scale) and distributed (network and remote-sensing scale) testbeds, accessible via commonly-used online tools (e.g. iLAMB, PEcAn) will provide the greatest chance of constraining future trajectories of the land biosphere in ESMs

Acknowledgements

The outline for this manuscript was identified during a workshop focused on VDM implementation in ESMs held at the National Center for Atmospheric Research in January 2016. NCAR is sponsored by the National Science Foundation. CDK, BC, RK, JH, TP, JS, CX & SPS were supported by the Next-Generation Ecosystem Experiments (NGEE Tropics) project that is supported by the Office of Biological and Environmental Research in the Department of Energy, Office of Science. TV and SPS were supported by NASA Terrestrial Ecology grant NNX14AH65G and through the United States Department of Energy contract No. DE-SC0012704 to Brookhaven National Laboratory. ATT was partially supported by a National Science Foundation Graduate scholarship. BS acknowledges support from the Strategic Research Fellowship Area MERGE. ML was funded by FAPESP (grant 2015/07227-6)" AMM was supported by U.S. National Science Foundation Hydrological Science grant 1521238. GH acknowledges the support of NASA. JL and TZ were funded by USDA agreements 11-JV-112423-059 and 16-JV-11242306-050. DM acknowledges support from the US Department of Energy, Office of Science, Office of Biological and Environmental Research, Terrestrial Ecosystem Science (TES) Program under award number DE-SC0014363.

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Tables

Table 1: Table of attributes of vegetation demographics models discussed in this paper.

Model acronym	Name	Vegetation Representation	Coupled to ESM?	Stochastic?	Canopy Structure	Disturbance history patches?
SEIB	Spatially-Explicit Individual-Based model	Individual	MIROC-ESM	Yes	Individuals	No
LPJ-GUESS	Lund Potsdam Jena General Ecosystem Simulator	Individual or Cohort	EC-Earth, RCA-GUESS	Yes (optional for some processes)	Flat-top	Yes
LM3-PPA	Perfect Plasticity Approximation	Cohort	GFDL-ESM	No	PPA	No
ED	Ecosystem Demography Model	Cohort	RAMS	No	Flat-top	Yes
ED2	Ecosystem Demography model v2	Cohort	RAMS	No	Flat-top	Yes
CLM(ED)	Community Land Model with Ecosystem Demography	Cohort	CESM	No	PPA	Yes

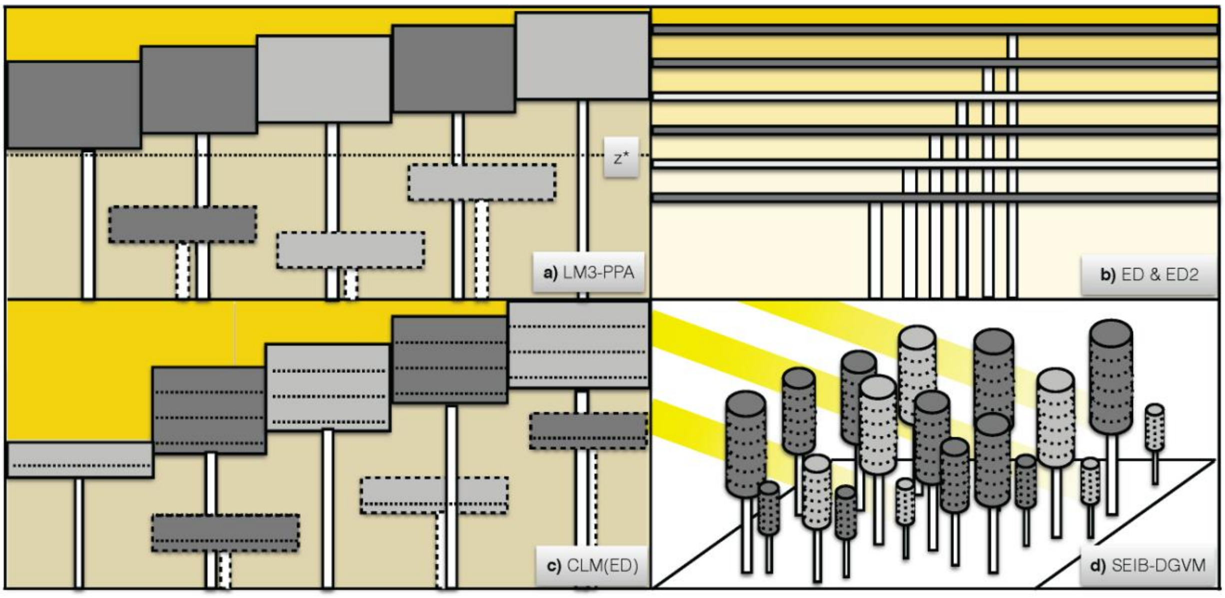
Figure Captions

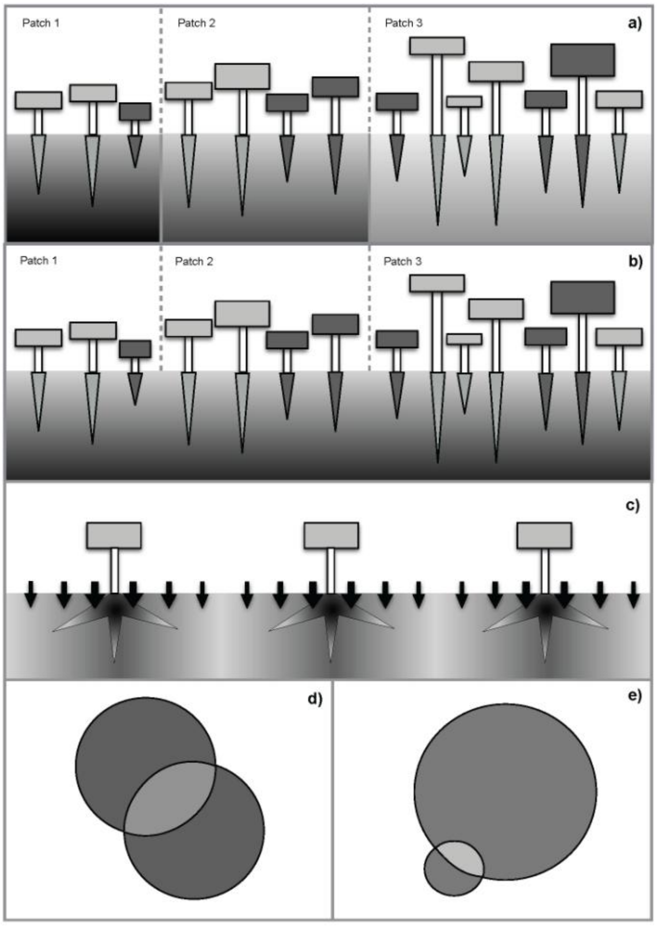
Figure 1: Organization of canopy schemes in four vegetation demographic models. Shades of yellow represent incident light levels, while shades of grey indicate alternative plant functional types (PFTs). Boxes represent cohorts as represented by ED & ED2, LM3-PPA and CLM(ED). Dotted cohort boundaries denote cohorts that belong to the understory, all of which receive identical light levels, in the PPA schemes of the LM3-PPA and CLM(ED) models. Note that in the LM3-PPA there can be more than one understory layer, but in CLM(ED) there cannot. In the cohort-based schemes, horizontal positioning is for illustrative purposes only and not represented by the model, which is one-dimensional. Dotted lines in the CLM(ED) figure illustrate within-canopy leaf levels resolved by the radiation transfer scheme. In the LM3-PPA, ‘z*’ indicates the cohort height above which canopy/understory status is defined. In the CLM(ED), there is no ‘z*’ threshold, and larger cohorts in the

understory may in principle be taller than the shorter cohorts in the canopy layer (reflecting imperfect competition processes, per Fisher *et al*., 2010). Note that for ED-derived models (ED, ED2, CLM(ED)), cohort organization is illustrated only for a single patch, though each model represents a multitude of patches having different ages since disturbance within a single site.

Figure 2: Illustration of unresolved belowground resource partitioning issues in vegetation demographic models. Panels a) and b) show two alternative depictions of resource partitioning in an age-since-disturbance resolving (ED-type) model. In a) resources (water/nutrients) are resolved for each age-since-disturbance patch, meaning that different extraction levels can affect resource availability over the successional gradient, a situation made more likely by large spatial-scale disturbances. In b) all patches share a common pool, a situation more relevant to smaller (individual) scale disturbances. Panel c) illustrates two mechanisms of water resource concentration in a semi-arid system, including greater infiltration rates near vegetation (differentially sized vertical arrows) and spatially extensive root systems that move water to the site of individual plants. Both allow greater local water availability than is possible using the grid cell mean soil moisture value. Panels d) and e) illustrate a mechanism for size asymmetric in resource competition. In d) two similar-sized root zones intersect, depleting the resource where they overlap. Since they are the same size, neither has an advantage. In e) the smaller root system has most of its resource uptake soil volume depleted, whereas the larger root system is only mildly affected by the overlap, thus the larger root system gains an asymmetric advantage analogous to that of large trees in the forest canopy competing for light.

Figure 3: Scale-dependence in extrapolating cohort-level mortality proxies to landscape-scale predictions of mortality. Panel a) illustrates a plausible multi-annual trajectory for mortality proxies throughout a chronic drought (solid line) and a hypothetical threshold whereby decline in this proxy is predictive of death (dashed line). Panel b) illustrates potential evolution of between mortality proxies and numbers of individuals through time (left to right). Long dashes represent a threshold-based mortality algorithm, whereby all individuals in a given cohort die in the same timestep. Short dashes illustrate a scaling from individual to landscape where there is a low level of heterogeneity across individuals, and the dotted line illustrates a condition with higher heterogeneity. In this case, parts of the grid cell (or genetic population) experience mortality at much lower degrees of average stress, and others are resilient under a given set of climatic drivers. As local mortality rates (gap scale) vary in comparison to landscape scale (entire forest), the slope of these lines requires calibration to a specific spatial scale.


z*
a) LM3-PPA
b) ED & ED2
c) CLM(ED)
d) SEIB-DGVM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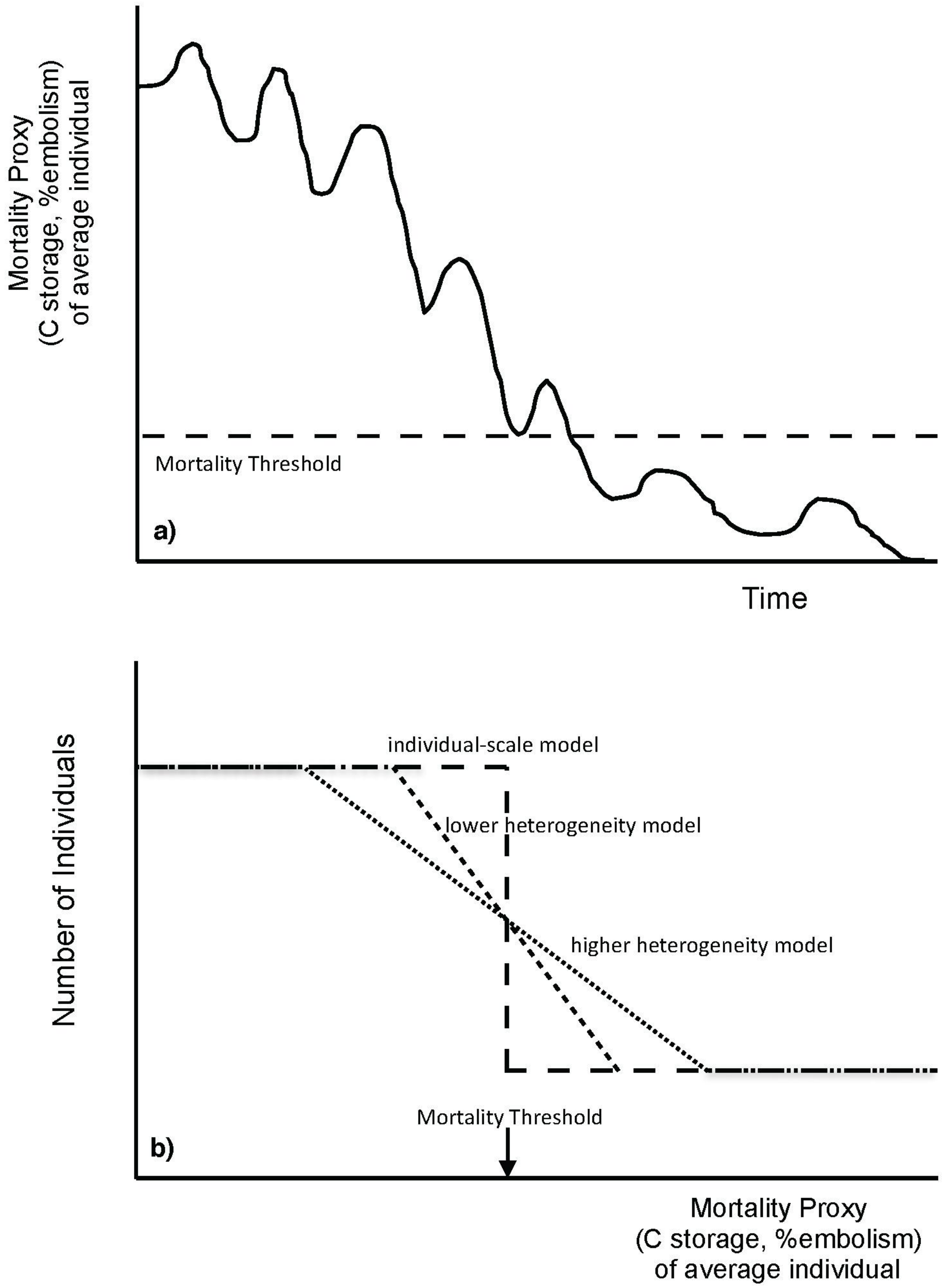
Mortality Proxy
(C storage, %embolism)
of average individual
Mortality Threshold
a)
Time
individual-scale model
lower heterogeneity model
higher heterogeneity model
Number of Individuals
Mortality Threshold
b)
Mortality Proxy
(C storage, %embolism)
of average individual