

Disturbance and Vegetation Dynamics in Earth System Models

Workshop Report



U.S. DEPARTMENT OF
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Disturbance and Vegetation Dynamics in Earth System Models Workshop

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By

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Cover Illustration

State Forest of Carite, Puerto Rico, in January 2018, four months after Hurricane Maria. The strong winds and heavy rain of Hurricane Maria resulted in canopy loss, tree mortality, and significant input of carbon and nutrients to the litter layer. Surviving trees began to grow and resprout within weeks to months after the hurricane. [Photo courtesy Kevin Krajick, Columbia University.]

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Executive Summary

This report summarizes discussion and outcomes from the March 2018 workshop, *Disturbance and Vegetation Dynamics in Earth System Models*, sponsored by the Office of Biological and Environmental Research (BER) within the U.S. Department of Energy Office of Science. The goals of this workshop, held in Gaithersburg, Maryland, were to (1) identify key uncertainties in current dynamic vegetation models limiting the ability to adequately represent vegetation in Earth System Models (ESMs) and (2) identify and prioritize research directions that can improve models, including forest structural change and feedbacks and responses to disturbance. Failure to capture disturbance dynamics and feedbacks limits the utility of ESMs for predictive understanding and application to societally important problems. This workshop considered (a) dynamic processes that significantly affect terrestrial ecosystems and the coupled Earth system and (b) the data constraints and modeling challenges important for future progress. There were three dominant workshop conclusions: vegetation changes, including disturbance-driven changes, are affecting climate and natural resources; these impacts are expected to increase in the future; and, yet, current models have insufficient data and process representations to adequately predict these changes.

Dynamic global vegetation models, developed to capture changes in the spatial distribution and local composition of plant functional types over time, have historically included some representation of the impacts of chronic and abrupt disturbances. However, these representations have been highly simplified in ways that cast doubt on model predictions. In particular, dynamic vegetation models do not yet accommodate all key processes that affect water, energy, and biogeochemical cycles at large scales or the risks to natural resources from environmental changes. A

variety of proposed new approaches may be able to better capture key vegetation response types, response times, and ecosystem vulnerabilities to extreme events.

Model projections of future ecosystem structure and function, including disturbance responses, commonly generate large predictive uncertainty, requiring use of diverse observational and experimental data in creative ways to understand and constrain this uncertainty. Workshop discussions focused on datasets, experimental capabilities, and modeling strategies to improve the data-model connections that lead to more reliable predictions. Participants identified a number of opportunities for new observations and experiments to inform predictions of disturbance and vegetation dynamics with large-scale vegetation models.

Key priority needs emerged from this workshop:

- **Synthesis efforts to exploit existing data and design new observations and experiments to inform future vegetation modeling efforts.** Scientific working groups targeting key areas of predictive uncertainty regarding vegetation dynamics and disturbances could enable this synthesis.
- **New empirical data that better quantify climate-disturbance-vegetation interactions to constrain vegetation model projections.** Experiments and monitoring designed expressly for this purpose are critical. Also needed is attention to the variables and spatiotemporal scales relevant for prediction, such as through integration of *in situ* observations and remote-sensing data.
- **New modeling approaches that adequately represent both process-based vegetation dynamics and disturbances.** Vegetation demographic models show promise but require further development and testing against observations and experiments across diverse ecosystem types.

1. Introduction

Anticipating the consequences of global change for terrestrial ecosystems is a goal of Earth system modeling. Variables driving ecosystem change include increasing atmospheric carbon dioxide (CO₂) and temperature, altered precipitation (IPCC 2013), and shifts in natural and anthropogenic disturbance regimes (Dale et al. 2001; Westerling et al. 2016; Raffa et al. 2008; Knutson et al. 2010). The frequency and intensity of fires, cyclonic storms, insect outbreaks, droughts, and floods are expected to increase in response to global change (Seidl et al. 2017). Vegetation dynamics, which dominate fluxes of carbon, water, and energy on land, are not only responding to global changes in temperature and precipitation directly, but also to the increasing frequency and intensity of large-scale disturbances. Ultimately, ecosystem responses to a changing atmosphere depend on interactions between vegetation and disturbance, each affecting the other. Earth System Models (ESMs) attempt to capture these changes and their influence on the larger Earth system (Bonan and Doney 2018). This report summarizes the state of scientific understanding and modeling approaches in these areas, highlighting research priorities identified at the March 2018 workshop, *Disturbance and Vegetation Dynamics in Earth System Models*. Held in Gaithersburg, Maryland, the workshop was sponsored by the Office of Biological and Environmental Research (BER) within the U.S. Department of Energy (DOE) Office of Science.

The term *vegetation dynamics* is used here to include plant demographic processes of growth, mortality, and reproduction, as well as the interactions among plants that share common resources (e.g., light, water, and soil nutrients; see Fig. 1, p. 3). It also includes seed production and dispersal, which govern vegetation migration when climate and environment change. Within the broader field of ecology, these processes are referred to as *population and community dynamics*. To predictively scale such dynamics across diverse ecosystems and the globe, vegetation dynamics research requires

study of functional traits that influence plant resource acquisition and use, demographic rates, and response to disturbances. Vegetation dynamics processes determine the structure and functional composition of ecosystems, influencing exchanges of energy, water, and carbon between the atmosphere and land surface. Contemporary changes in demographic rates are attributed to changes in climate, atmospheric chemistry, and management, as well as to changes in landscape disturbances.

Physical and biological disturbances can accelerate, slow, or dramatically alter the character of vegetation dynamics. *Disturbance* processes range from individual tree falls to landscape-altering fires, insect outbreaks, and hurricanes. Landscape-scale disturbances were the focus of the workshop. The *disturbance regime* (i.e., spatial and temporal characteristics such as frequency, severity, and size of disturbances) depends on interactions between the physical environment and vegetation, and it shapes the composition and structure of vegetation. The effects of disturbance are not uniform across the landscape and increase landscape heterogeneity, for example, with varied burn severity following fire or with hurricane effects ranging from defoliation to complete blowdown of all canopy trees. Regional-scale models attempt to capture the emergent properties of processes operating at fine scales, without necessarily tracking each event or accounting for the important spatial variability that, in turn, influences vegetation dynamics and ecosystem processes.

Disturbance and vegetation responses to climate and environmental changes are interdependent. For example, higher temperatures that exacerbate water stress or drought can leave trees more vulnerable to bark beetle attack. Similarly, fire behavior can be influenced strongly by the sizes and density of trees in a forest, which are influenced by climatic, land-management, and disturbance histories. Challenges for observation and prediction include the complexity of interacting variables that can contribute to highly nonlinear responses, such as abrupt plant community changes

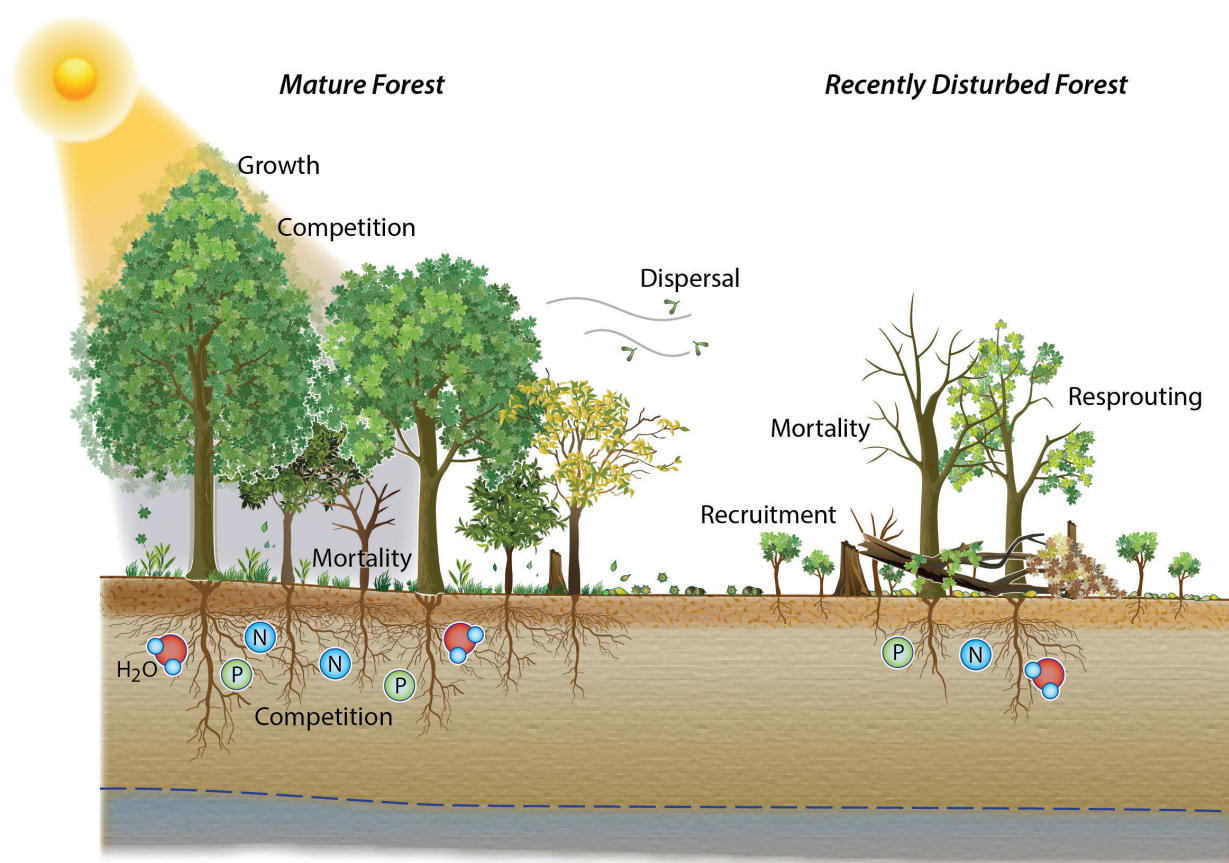


Fig. 1. Vegetation Dynamics Affecting Structural Properties and Biogeochemical Functioning of Ecosystems. These dynamic processes include plant growth, mortality and recruitment, seed dispersal, and competition among individuals and species for light, water, and soil nutrients such as nitrogen and phosphorus. Physical and biotic disturbances alter vegetation structure and trajectories of vegetation dynamics, as can chronic environmental changes. [Figure courtesy Lawrence Berkeley National Laboratory.]

and hysteresis, where transitions from one vegetation type to another may be hard to reverse. There also can be significant time lags between disturbance events and vegetation mortality or between ecosystem disruption and vegetation recovery.

This report focuses on critical elements of vegetation dynamics and their response to chronic and abrupt

environmental changes, including altered disturbance regimes; examines how vegetation dynamics and disturbance are and, in the future, could be represented in ESMs; and summarizes the empirical research available and needed to support predictive modeling under continued global change.

2. Why Incorporate Explicit Vegetation Dynamics and Disturbance in Models to Anticipate Ecosystem Change?

Large uncertainties in prediction of climate and biosphere change are due, in part, to uncertainties in projected changes in vegetation dynamics and disturbance (Friend et al. 2014). The link between these two uncertainties results from the fact that demographic processes such as tree growth and mortality and the severity and frequency of disturbances alter biogeochemical cycles on landscapes. Further, vegetation structure and large-scale disturbances can affect the surface albedo and fluxes of energy and water, from ecosystems to the atmosphere (Jackson et al. 2008; O'Halloran et al. 2012; Lu and Kueppers 2012; Rogers et al. 2013).

Vegetation dynamics occur in the absence of perturbations, but the individual processes (e.g., mortality, recruitment, and competition) can be increased, arrested, or set onto novel trajectories because of chronic perturbation (e.g., rising CO₂ or temperature) or abrupt disturbances (e.g., wildfire or insect outbreaks). For example, the mortality rate of undisturbed old-growth forests has more than doubled in the last four decades across much of the Americas, potentially due to chronic environmental changes (McDowell et al. 2018). This doubling of mortality will halve terrestrial carbon storage within 50 years if increases in growth and recruitment do not offset the mortality loss. Less is known about changes in regeneration dynamics over time, but recent tree recruitment is occurring in only a subset of the full geographic range of some North American tree species (e.g., Zhu et al. 2012; Dobrowski et al. 2015), with unknown consequences for ecosystem carbon balance and disturbance regimes. Accurately capturing the response of vegetation dynamics to chronic environmental changes is essential to the accurate prediction of future climate forcing associated with vegetation, a challenge some models have begun to address.

Profound shifts in disturbance regimes are already under way in response to environmental changes, further highlighting the need to improve prediction of diverse disturbance types and vegetation responses. For example, the intensity of storms that affect U.S. coastlines and territories is increasing (Emmanuel 2017), and ocean warming has been intensifying hurricanes in the North Atlantic (Knutson et al. 2010). Further, many regions have seen prolonged fire seasons and increased size of individual fires (Westerling 2016; Littell et al. 2009). Changing fire regimes engage the feedbacks between vegetation fuels and microclimate that determine reburn severity (Coppoletta et al. 2016; Harvey et al. 2016a). Finally, insect outbreaks intensify tree stress, due in part to changing climates (Seidl et al. 2017; Hicke et al. 2016; Foster 2017). Warming accelerates insect development, while extreme drought and heat waves can weaken trees, increasing the frequency and intensity of insect outbreaks (Bentz et al. 2010; Cudmore et al. 2010; Hicke et al. 2013; Raffa et al. 2008). This emerging understanding of shifting disturbance regimes is not yet reflected in ESMs.

Changes in disturbance regimes and disturbance-vegetation interactions affect many ecosystem and Earth system processes. For example, hurricane and wind storm debris can dramatically impact short-term carbon fluxes to the soil and atmosphere (see Fig. 2, p. 5; Chambers et al. 2007; Lindroth et al. 2009; Zeng et al. 2009; Chen et al. 2015), and high wind, which is the dominant mode of tree mortality in forests from Europe to the Amazon (Seidl et al. 2014; Boose et al. 1994; Chambers et al. 2013; Nelson et al. 1994), affects ecosystem structure and productivity (Negrón-Juárez et al. 2015, 2018; Xi 2015; Foster et al. 1998). Changes in fire regimes have regionally specific effects. For example, with increasing fire activity plus aridity, boreal forests are likely to shift



Fig. 2. State Forest of Carite, Puerto Rico, in January 2018, Four Months after Hurricane Maria. The strong winds and heavy rain of Hurricane Maria resulted in canopy loss, tree mortality, and significant input of carbon and nutrients to the litter layer. Surviving trees began to grow and resprout within weeks to months after the hurricane. [Photo courtesy Kevin Krajick, Columbia University.]

to a higher occurrence of deciduous canopies (Johnstone et al. 2010a, 2010b), altering water and carbon cycles and albedo. Spatially extensive, insect-induced tree mortality can change surface-water, energy, and carbon budgets (Edburg et al. 2012; Dymond et al. 2010). While a full accounting requires consideration of post-disturbance regrowth, outbreaks of mountain

pine beetle in British Columbia yielded greenhouse gas emissions comparable to ~5 years of emissions from Canada's transportation sector (Kurz et al. 2008) and may have led to an initial summer warming of ~1°C through effects on albedo and evapotranspiration (Maness et al. 2013). Land management can further alter climate-disturbance-vegetation interactions through effects on soils and altered vegetation structure and composition (Berner et al. 2017; Clark et al. 2016; Vanderwel and Purves 2014; D'Amato et al. 2018). Inadequate representation of these ecosystem- and climate-altering disturbance-vegetation interactions contributes to significant uncertainty and bias in Earth system projections.

Affecting the trajectory of ecosystems following disturbance are disturbance severity and size and regeneration strategies, including seedbanks and resprouting, which differ among species and vary with regional and local climate (Turner et al. 1998; Ruehr et al. 2014; Harvey et al. 2016b; Alexander et al. 2012). For example, after a stand-replacing disturbance, seedlings dependent on near-surface moisture (Irvine et al. 2002; Ruehr et al. 2014) are vulnerable to heating and leaf damage (Comita et al. 2009). Necromass and understory light and temperature often increase after disturbance, sometimes inducing short-term carbon and nutrient losses (McDowell and Liptzin 2014; Shiels and González 2014; Silver et al. 2014; Waide et al. 1998; Erickson and Ayala 2004; Law et al. 2001). Changes in soil biogeochemistry following disturbance can last from days to decades (McLauchlan et al. 2014; Trahan et al. 2015). At the same time, depending on the severity and extent of the disturbance, growth and net ecosystem productivity may actually be enhanced by increased resource availability after disturbance (Curtis and Gough 2018). Complex and fine-scale controls on post-disturbance recovery, which are challenging to model, are critical needs for capturing the emergent character of ecosystem development and spatial heterogeneity.

As ecosystems adjust to changing environmental conditions, thresholds in ecosystem structure or functioning may be crossed that are difficult to reverse.

Some disturbance drivers, such as temperature, are undergoing chronic increases and could yield state changes in ecosystems (e.g., from forest to shrublands to grasslands; McDowell et al. 2017). The likelihood of exceeding thresholds for state changes increases following disturbances such as fires, insect outbreaks, and windstorms. Threshold exceedance often involves interactions, such as between weather and fuels in the

case of fire. Whereas the high fuel moisture content typical of many forest stands reduces burn risk, once forests are transformed to grasslands, the ensuing increase in fire frequency can resist reforestation. Once a threshold has been exceeded, resulting changes can alter the ecosystem's capacity to recover (Raffa et al. 2008; Johnstone et al. 2016).

3. Current Modeling Approaches

Because vegetation dynamics and disturbance can influence ecosystem function and climate at regional scales, and over days to decades, ESMs increasingly seek to capture the key features of these interactions to improve predictions of biosphere change. Nevertheless, many of the important disturbance types and ecosystem responses are not yet included even in the most advanced vegetation models. Workshop discussions considered the current state of the vegetation models embedded within ESMs as a basis for moving forward. This section summarizes the main points of these discussions, beginning with several general concepts.

3.1 Concepts

Current vegetation models include both **deterministic** and **probabilistic** approaches, and the methods for quantifying uncertainty are unique to each approach. In deterministic models, uncertainty estimates are generated from ensembles of runs, each with different (stochastic) model inputs, or prediction summaries of multiple models. Fully probabilistic model predictions rely on probability distributions for all model inputs. **Generative models** are probabilistic models that predict the data used to fit the model and may be invertible in multiple ways, that is, to predict the response data (i.e., forward simulation), to estimate parameters (i.e., model fitting), and to predict the input data (i.e., inverse prediction) (Clark et al. 2013, 2017). **Ecosystem models**, as well as fully integrated ESMs, are traditionally deterministic models, while **ecological models** of vegetation dynamics and disturbance often have stochastic elements.

Workshop discussions revisited the long-standing challenge of **scaling** information (data and models) and theory to translate responses at the leaf and organism scale to the biome scale (Ehleringer and Field 1993). “Bottom-up models” propagate physiology and individual behavior at scales ranging from minutes up to landscapes and decades. “Top-down models” take

an aggregate view, exploiting evidence to make predictions at the scale of interest. Both methods have limitations. The error in predictions from bottom-up models expands with space and time, as when canopy-level processes are parameterized with leaf-level responses (Jarvis 1993) or when population-level models are parameterized from individual responses (Clark et al. 2011; Ghosh et al. 2015). However, there rarely are adequate data to fully constrain top-down models of ecosystem properties of interest. Extrapolating beyond the conditions and observations used to build either type of model results in unknown error. Efforts to combine bottom-up and top-down approaches can offer unique advantages in understanding and prediction (Jarvis 1993; Norman 1993). These diverse approaches also can lend complementary insights and inform ESM representations of vegetation dynamics and disturbance (Seidl et al. 2011).

3.2 Vegetation Modeling Approaches for Earth System Models

Discussions at the meeting considered both bottom-up representation of vegetation processes and top-down controls provided by remote-sensing products and distributed ground-based observations, but these deliberations produced only limited examples of predictive checks. Bottom-up modeling approaches include **individual-based models** (IBMs; e.g., the process-based forest-disturbance-landscape model iLand, Seidl et al. 2012) and cohort-based forest landscape models (e.g., LANDIS-II, Mladenoff 2004), with environmental constraints defined at the level of individual trees or cohorts. IBMs induce heterogeneity in plant growth and predict a distribution of individual responses to environmental variation such as disturbance (e.g., ZELIG-TROP, Holm et al. 2014, or SORTIE, Uriarte et al. 2009); early generations of these models emphasized typical canopy gap-sized patches (Shuman et al. 2014, 2015). Population, community, and ecosystem dynamics are predicted

from the responses of many individual plants to environmental conditions, which in turn are affected by neighboring plants and canopy properties (Larocque et al. 2016). Continental-scale simulations are feasible (Shugart et al. 2015; Shuman et al. 2017) but computationally impractical, and these models typically do not simulate physical feedbacks and processes (e.g., soil hydrology and land-atmosphere interactions) that would connect with an ESM (but see Sato and Ise 2012). The need for large ensembles with stochastic parameters may make coupling stochastic IBMs to ESMs too computationally costly, at least in the near term. IBMs also fail to incorporate key physiological processes and parameters.

Dynamic global vegetation models (DGVMs), which represent vegetation dynamics, disturbance, and land use within ESMs, predict the global distribution of vegetation types based on physiological relationships (Sitch et al. 2003; Woodward and Lomas 2004). Early DGVMs (Cox 2001; Bonan et al. 2003; Krinner et al. 2005; Arora and Boer 2006) recognized that shifts in biome boundaries (e.g., from tundra to forest) affect the biophysical exchange of energy, carbon, and water with the atmosphere. “Bioclimate envelopes” were estimated from current biome distributions and used to predict future vegetation distributions, ignoring individual plants and cohorts. DGVMs are increasingly used within ESMs to examine variability in the contemporary carbon cycle (Ahlström et al. 2015; Le Quéré et al. 2018). However, the sensitivity of vegetation to climate, and vice versa, presents challenges (Chapin et al. 2005; Sitch et al. 2008). In particular, a lack of functional diversity and the structure that results from demography within biomes leads to errors in DGVM sensitivity to climate and disturbance (Cox et al. 2000; Powell et al. 2013). Because vegetation changes can affect climate regionally (Snyder et al. 2004; Swann et al. 2018), effective global simulation of future transient vegetation within ESMs remains an important challenge.

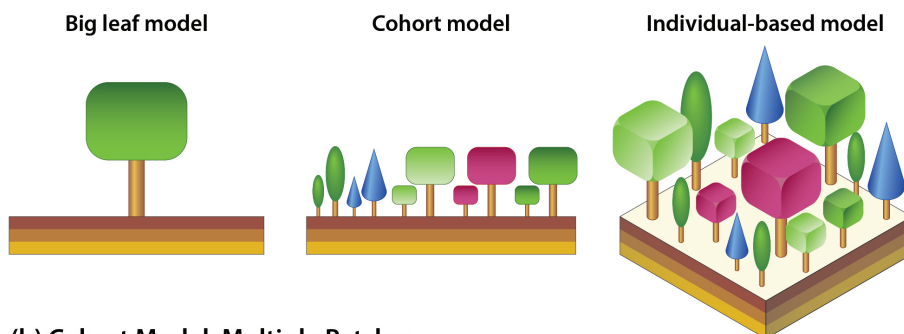
Vegetation demographic models (VDMs) offer an approach to vegetation dynamics and disturbance different from early DGVMs (Fisher et al. 2018) by

explicitly accounting for plant demography and often representing a greater diversity of plant sizes and plant functional types (PFTs; Hurtt et al. 1998; Moorcroft et al. 2001; Smith et al. 2001). VDMs explicitly simulate disturbance and recovery, and they may include spatially resolved fire-vegetation interactions and the physiological drivers of plant mortality such as hydraulic failure and carbon starvation. The larger number of represented processes connects these models to a richer set of observations for parameterization and testing, which can generate ecological insight as well as identify needs for further model development (e.g., McDowell et al. 2013; Powell et al. 2013). A number of recent VDMs simplify vegetation dynamics as representative cohorts (i.e., size classes), thus allowing different scales for plant growth, mortality, reproduction and recruitment, and competition without representing individual trees (Medvigy et al. 2009; Fisher et al. 2018). **Cohort-based approaches** predict a common growth or mortality rate for all trees in the same size class and canopy position and, therefore, are intermediate between “big-leaf” and individual-based models (see Fig. 3, p. 9). As a forest patch develops, differences among cohorts and functional types in their light and water limitations result in unequal resource capture. Allocation of carbon to growth of above- and belowground tissues and to reproduction and storage are generally assigned as fixed fractions of an idealized allometry.

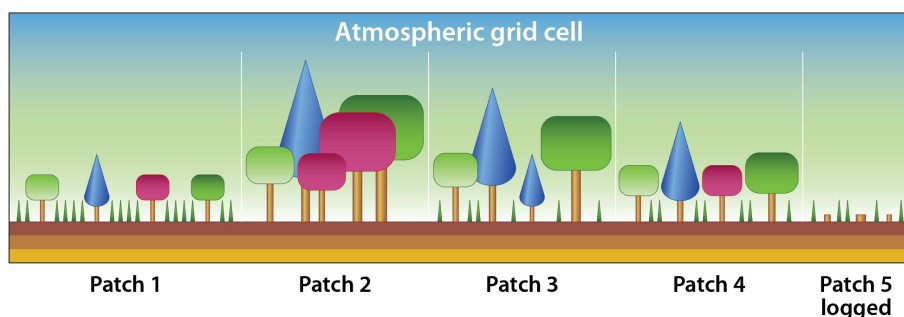
Examples of VDMs operating within ESMs at a global scale include the following (for more details, see Fisher et al. 2018):

- SEIB-DGVM, embedded within the JAMSTEC ESM (Japan), is a spatially explicit IBM that simulates an ecosystem with stochastic demography, replicated within each grid cell to generate an ensemble prediction of vegetation states and fluxes (Sato et al. 2007). Long time steps (i.e., daily) for physiological processes, limited replication, and small patch sizes reduce the computational burden necessary for application in a global or ESM context.

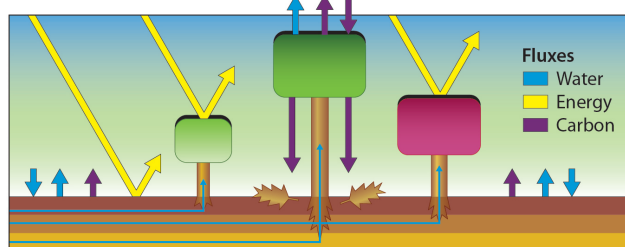
(a) Model Types



(b) Cohort Model: Multiple Patches



(c) Cohort Model: Fluxes



(d) Cohort Model: Time Since Disturbance

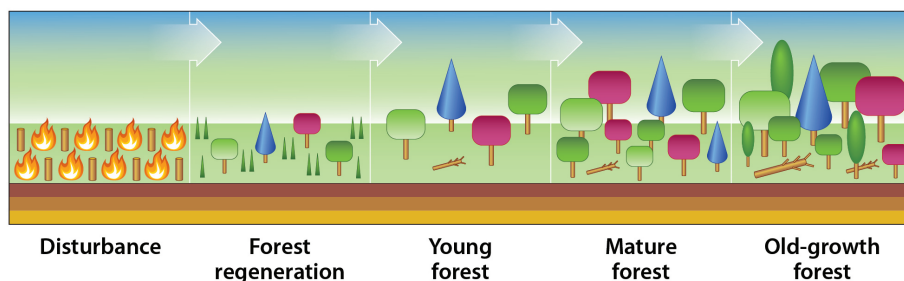


Fig. 3. Vegetation Model That Tracks Cohorts on Patches Through Time and Calculates Ecosystem Fluxes and Vegetation Dynamics. (a) Cohort-based models are an intermediate solution between unstructured, “big-leaf” models and stochastic individual-based models (IBMs). (b) Each land-atmospheric grid cell of a cohort model is divided into multiple patches with different forest stand structures. (c) Fluxes of water, energy, and carbon are calculated for each cohort and patch and aggregated to the grid cell. (d) Vegetation dynamics of recruitment, growth, and mortality transform individual patches through time, for example, regenerating a forest following disturbance by fire. [Additional information: Medvigy et al. 2009 and Bartels et al. 2016.]

- LPJ-GUESS, embedded within the EC-EARTH ESM (pan-European), represents cohorts of plants and passes information on canopy structure (i.e., tree and nontree) to its host land model. This model separately calculates surface exchange of carbon, water, energy, and momentum (Weiss et al. 2014). LPJ-GUESS uses the concept of replicate patches to capture variation in disturbance history.
- LM3-PPA, embedded within the GFDL ESM (United States), is being expanded to allow global simulations (Weng et al. 2015). The LM3-PPA model assumes that plants are organized into discrete canopy layers and that each layer experiences the same light conditions.
- FATES, based on the Ecosystem Demography (ED) concept (Moorcroft et al. 2001; Fisher et al. 2015), uses cohorts to approximate size- and age-structured vegetation through succession and across landscapes. FATES is an independent component within the land model coupled to the U.S. Energy Exascale Earth System model (E3SM) and Community Earth System Model (CESM).

Most applications of VDMs to date have been implemented at the site scale. These efforts demonstrate that plant diversity affects ecosystem resilience in response to environmental change (Sakschewski et al. 2016; Powell et al. 2018). Regional-scale simulations show less threshold-driven response to global change than has been seen in early-generation DGVMs, with compensation among tree sizes and types (Levine et al. 2016; Sakschewski et al. 2016). While VDMs are a promising advance, a great deal of work is needed for these models to capture what is already known about vegetation dynamics and disturbance and also to synthesize and collect data critical for model parameterization and testing.

3.3 Vegetation Demography in Models

Workshop discussions considered how ESMs might be improved through better representation of climate-disturbance-vegetation interactions,

particularly through advanced VDMs. Summarized herein are the elements of plant demography (i.e., growth, regeneration, and mortality) expected to be important for vegetation responses to climate and environmental change, as well as disturbance responses, and how models can better capture these elements.

3.3.1 Plant growth

Plant growth responds to environmental change, and the differences among individuals, species, and functional groups determine the size structure and composition of communities. Both site-to-site differences and interannual variation in growth rates show strong effects of temperature and moisture variability, but with substantial differences among species and size classes (Clark et al. 2010, 2014). Strong interacting effects exist between climate variables and light availability; for example, plant response to soil water availability in the forest understory differs from that in canopy gaps (Clark et al. 2014). Nutrient availability also can be a strong constraint on growth, but carbon allocation to fine roots, mycorrhizae, or nitrogen-fixing symbionts that help plants acquire nutrients is not well understood, even though it can influence ecosystem carbon dynamics and competitive interactions.

The steady rise in atmospheric CO₂ since the preindustrial era also may be affecting plant growth, but understanding has been limited by the small number of stand-level experiments. Free-air CO₂ enrichment (FACE) experiments show increases in net productivity (Ainsworth and Long 2004; Norby et al. 2005) that can be constrained by nitrogen and/or phosphorus limitation (Norby et al. 2010; Ellsworth et al. 2017) and low light in the forest understory (Mohan et al. 2007), but these constraints have yet to be understood in complete mechanistic detail (Norby et al. 2016; Duursma et al. 2016; Hasegawa et al. 2015). The experimental evidence from mature forests suggests little CO₂ effect on production in older trees, but limited understanding of the restricted factors in these experiments contributes to large uncertainty in CO₂ effects on growth.

Because plant growth responses occur at the scale of individuals, ESMs have struggled to address these dynamics at larger scales. For example, because growth is typically assumed to be a priority for allocation, models tend to predict a stimulation of net biomass accumulation in response to increased atmospheric CO₂ (Zhang et al. 2015; Holm et al. in review). Errors in the prediction of growth can propagate to other processes in VDMs, as individual- or cohort-level processes are aggregated to landscape-level predictions. For example, rapid growth accelerates competitive dynamics, thereby increasing mortality (Zhu et al. 2015). Not all VDMs represent nutrient constraints on growth or on growth response to CO₂. *While VDMs already simulate plant growth and many factors that influence it, VDM growth responses across size classes and canopy positions to light, temperature, water balance, CO₂, and nutrients need to be evaluated against experimental data.*

3.3.2 Reproduction, recruitment, and dispersal

Reproduction and recruitment are responsible for plant persistence within current ecosystems, even with changing conditions, including disturbance regimes. **Reproductive output** varies among individuals, among species, and biogeographically (Leibhold et al. 2004; Clark et al. 2004; Minor and Kobe 2018). Some of this variation is explained by resource availability, including light (Clark et al. 2014; Wright and Calderón 2005), CO₂ (LaDeau and Clark 2001), and moisture (Clark et al. 2013, 2014; Lasky et al. 2016; Detto et al. 2018). For some taxa, especially species with canopy seedbanks, variation in reproductive potential also reflects historical disturbance regimes and age structure (e.g., Buma et al. 2013). **Plant establishment** is also environmentally sensitive. For example, water and temperature limitations interact at high elevations (Kueppers et al. 2017; Conlisk et al. 2018). The environmental sensitivity of establishment can vary by species and functional group (e.g., Engelbrecht et al. 2007; Uriarte et al. 2018), but inter-annual variability in resources may not explain much of the total variation (Ibáñez et al. 2009; Beckage and

Clark 2005; Hille-Ris Lambers et al. 2005). Establishment of seedlings further depends on seed predators (e.g., Bogdziewicz et al. 2016) and damping-off pathogens (Hersh et al. 2012; Kolb et al. 2016). Most VDMs simplify reproduction and recruitment, with limited or no environmental constraint on seedling emergence, establishment, or mortality (Trugman et al. 2016; Fisher et al. 2018). Recruitment biases in models affect small tree mortality through altered competition (Powell et al. 2018). *Improving the representation of these processes in models requires synthesis of existing data on seed production, germination, and establishment to help constrain model algorithms, as well as filling gaps in available data for key ecosystems and with respect to environmental factors.*

Dispersal is required for populations to repopulate large patches of high-severity disturbance where biotic legacies are scarce (Turner et al. 1998) and to occupy new habitats as the climate changes; thus, dispersal controls shifts in biome boundaries. Migration depends on factors controlling long-distance dispersal and reproductive output, which both must be understood for prediction (Clark et al. 2003). Observational (Clark et al. 2004, 2014; Jones and Mueller-Landau 2008; Uriarte et al. 2012) and experimental (Katul et al. 2005) approaches yield valuable dispersal data but provide incomplete information, making this aspect of vegetation dynamics inherently uncertain. Source-dependent dispersal across grid cells is not commonly enabled in vegetation models, limiting prediction of dispersal-induced lags in migration. The greatest lags are expected to come between climate change and vegetation change in regions with low topographic relief undergoing rapid environmental change, where climate shifts are expected to outrun the capacity of populations to migrate (Loarie et al. 2009). While difficult, addressing the challenge of modeling dispersal is important, because historical observations and future projections suggest complex responses of plant geographic distributions and biome boundaries to climate and environmental change (e.g., Kelly and Goulden 2008; Harsch et al. 2009; Zhu et al. 2012; Conlisk et al. 2017, 2018; Svenning and

Sandel 2013). *New approaches to modeling dispersal are likely required. Data synthesis and new observations and experiments also are needed to support model parameterization and testing.*

3.3.3 Mortality

Because the direct cause of individual tree mortality is rarely observed, predicting changes in stand-level mortality rates is a large, but feasible challenge when models properly capture mortality mechanisms (McDowell et al. 2013, 2016; Anderegg et al. 2015). Representation of tree mortality in VDMs fails to account for all major mechanisms of mortality (McDowell et al. 2018). Nearly all mortality of trees (except from fire and wind loss) is associated with low growth prior to death (Cailleret et al. 2017; Pederson 1998), and thus models that use the simplistic lower growth efficiency threshold to induce mortality still have promise to accurately simulate mortality (McDowell et al. 2011). The ED model assumes a constant tree density-independent background mortality rate determined by wood density (e.g., Kraft et al. 2010), carbon starvation due to shading or moisture stress (Moorcroft et al. 2001; Fisher et al. 2010), and frost damage (Albani et al. 2006). Drought directly affects mortality through interdependent processes of hydraulic failure and carbon starvation (McDowell et al. 2008; Adams et al. 2017). Representing these processes is now possible via development of hydraulic and carbon processes within some next-generation individual-based models (e.g., iLand) and VDMs (e.g., McDowell et al. 2013; Xu et al. 2016). Hydraulic failure has recently been added to two VDMs—ED2 and FATES (Christofferson et al. 2016; Xu et al. 2016)—but testing of the new processes is needed. Mortality from wind, insects and pathogens (Dietze and Matthes 2014), and herbivores (Pachzelt et al. 2015) are mostly absent from VDMs. Invasive species in the eastern United States continue to introduce new sources of mortality, often host-specific, due to the sometimes limited diet of alien insects and fungal pathogens (Eschtruth et al. 2006; Kolka et al. 2018), creating a challenge for vegetation models to address.

Sensitivity analyses and predictive tests are largely absent for mortality rates and the processes that can precipitate tree death, such as carbohydrate depletion and embolism (McDowell et al. 2011, 2018). As modelers add new mechanisms to better predict mortality, it is essential that experimental and observational data are available for testing the processes themselves and the emergent consequences at stand and landscape scales. *Model development and testing and mortality dataset development need to proceed simultaneously to understand and simulate the most important modes of mortality.*

3.4 Disturbance in Models

The workshop explicitly considered how ESMs might be improved through better understanding and representation of disturbance and its links to both environmental and vegetation changes. This section reports on important aspects of disturbance and how disturbance can be better represented in models, with emphasis on fire, insect outbreaks, and wind disturbance.

3.4.1 Fire

Current models often fail to reproduce interannual variability in fire metrics, and they do not capture the long-term reduction in burned area associated with management practices (Andela et al. 2017). Many fire models embedded within ESMs parameterize overall fire risk as a function of ignition, spread, and effects. Ignitions may be parameterized as a function of lightning strikes, human population density (Li et al. 2013), or a simple function of gross domestic product (GDP; Thonicke et al. 2010). Fire spread determines the area burned within a grid cell and depends on climate and weather variables that control the duration of the burn (e.g., humidity and temperature), wind speed, and fuel state (e.g., moisture, type, and amount). Fire effects are determined by the amount of aboveground biomass available to burn within a model grid cell and by combustion factors. However, the extreme conditions associated with large fire events and processes such as long-distance spotting are seldom included.

The climate-disturbance-vegetation interactions that control responses to climate change require a better

understanding of disturbance causes and feedbacks with vegetation. For example, tall trees with thick bark and lacking low branches can escape low-intensity fire damage. The interaction between climate and fuel requires tracking of multiple fuel classes (i.e., grasses, twigs, small and large branches, and trunks) and fuel states (e.g., moisture, bulk density, and surface area to volume). Fire modules such as SPITFIRE (adapted from Thonicke et al. 2010) track these details. When embedded within a demographic vegetation model like FATES, a fire model generates predictions of fire behavior, mortality that varies with cohort size and PFT traits, and subsequent regrowth and regeneration. Spatial patterns of trees, shrubs, and grasses that affect fire behavior are not represented in current VDMs. *The accuracy of predictions from current fire models remains unclear but would be enhanced by testing against experimental, remotely sensed, and ground observational data. Collaborations between modelers and field scientists are critical to achieving this goal.*

3.4.2 Insect outbreaks

Unlike fires, insect outbreaks arise from fluctuating population dynamics and can persist across multiple growing seasons, intensifying the stress experienced by host species (Seidl et al. 2017). Over the last three decades, bark beetles in the western United States have killed trees over twice the area impacted by fire (see Fig. 4, this page; Hicke et al. 2016). Rising temperatures have resulted in increased survival and relaxed range boundaries of mountain pine beetle, thus threatening eastern pine forests of North America (Rosenberger et al. 2018). Extreme events such as drought and heat waves can weaken trees, leading to increased insect outbreak frequency and intensity (Logan and Powell 2001; Bentz et al. 2010; Cudmore et al. 2010; Hicke et al. 2013). Invasive species can contribute to these impacts, through periodic defoliation or chronic mortality (e.g., gypsy moth; Davidson et al. 1999; Schäfer et al. 2014a) or more immediate impacts (e.g., potential extirpation of North American *Fraxinus* spp. by the emerald ash borer (Herms and McCullough 2014; Klooster et al. 2018) and *Tsuga*



Fig. 4. Lodgepole Pine Trees in Different Red and Gray Attack Phases During a Mountain Pine Beetle (*Dendroctonus ponderosae*) Outbreak on the Bridger-Teton National Forest, Wyoming. Bark beetles typically kill large-diameter trees, so outbreaks are often followed by rapid growth responses of understory vegetation and smaller trees. [Photo courtesy Monica Turner, University of Wisconsin–Madison.]

canadensis by the hemlock woolly adelgid (Eschtruth et al. 2006).

Insect outbreaks are not included in current VDMs because of at least three key challenges. First, big-leaf representation of vegetation lacks the size structure that determines tree vulnerability to insect attack and affects insect population dynamics (Hadley and Veblen 1993). Second, current insect-induced tree mortality models omit interactions between vegetation and insects, modeling primarily at landscape scales. They lack differences in tree defenses (Powell and Bentz 2014) and insect population dynamics (Sturtevant et al. 2004). Empirical environmental relationships do not account for scale-dependent dynamics (Aukema et al. 2008; Krist et al. 2006). Finally, current models are generally species-specific, without clear connection to the PFTs in VDMs, but there are pathways forward. The multicohort nature of VDMs plus their ability to simulate hydraulic failure and carbon starvation allow VDMs to represent the vulnerability of plants to insect attack. By integrating predictions of plant vulnerability into models of insect populations that account

for landscape heterogeneity, VDMs eventually may overcome these challenges (Goodsman et al. 2018). *In the case of insect outbreaks, further model development, dataset development, and model testing are all needed to make significant advances in the ability to predict these disturbances.*

3.4.3 Wind

Wind damage is only beginning to be represented in ESMs (Chen et al. 2018). Wind damage and mortality were prescribed in the ED model using an empirical model relating wind speed to stem mortality and damage based on field measurements, forest inventory data, and change in the nonphotosynthetic vegetation in remote-sensing images before and after hurricanes (Fisk et al. 2013). There are several limitations to this approach. First, wind damage depends on the interaction of meteorological, topographic, and stand factors. Generally, mortality rates are high on ridges, in water-logged valleys, and in older stands (Tanner et al. 1991, 2014; Ostertag et al. 2005; Xi 2015). Second, the majority of wind-induced mortality is often delayed, resulting from branch and canopy damage during storms (Walker 1995; Uriarte et al. 2004), and remains poorly understood (Zimmerman et al. 1994). Third, species variation in wind-induced damage and mortality do not always align with successional life history classifications commonly used in PFT representations in VDMs. Instead, they depend on biomechanical characteristics of species, traits which are not part of current models. *To better capture the effects on forests of large-scale, damaging wind storms, including hurricanes, models require new schemes that represent size- and PFT-dependent damage and mortality. Parameterization and testing of these schemes need to opportunistically leverage major wind disturbances, such as the recent hurricanes Irma and Maria.*

3.4.4 Land cover change and management

Direct anthropogenic disturbance of the landscape alters ecosystem structure and function, influencing trajectories of vegetation dynamics. In different parts

of the globe, activities can include shifting cultivation, deforestation, urbanization, and abandonment. Few VDMs directly use emerging land-use datasets, including HYDE3.2 (Goldewijk et al. 2017) and LUH2 (Hurtt et al. 2011). Forest age-distribution datasets that are potentially useful include those documented in Poulter et al. (2018), Chazdon et al. (2016), Pan et al. (2011), and Bellasen et al. (2011). Land cover and natural disturbances that can be detected in inventory-derived and hybrids of inventory and remote-sensing products can be used to initialize models and evaluate historical trajectories of land cover. *To account for land use in simulations of past, present, and future vegetation dynamics, VDMs need to assimilate time series of land use and properly account for effects, both direct (e.g., tree harvest) and indirect (e.g., soil compaction). Emerging networks of research sites in secondary forests may provide useful test cases for the models.*

3.4.5 Disturbance recovery

Post-disturbance recovery encompasses many of the important feedbacks that impact ecosystem properties. Disturbances may accelerate ecosystem change, such as fire in tundra and boreal forest that promotes fire-dependent tree establishment (Lloyd et al. 2007; Johnstone et al. 2010b) and extreme droughts that caused a 90% die-off of piñon pines across the southwestern United States (Breshears et al. 2005). Variation among VDMs in their assumptions about reproduction and recruitment affects predictions of ecosystem trajectories following disturbance. Although differences in size thresholds for reproductive maturity and other reproductive traits can influence the structure of forests during succession, especially for conifer forests (Chapin et al. 1994; Turner et al. 2003), reproductive output is often only weakly influenced by plant size or age (Clark et al. 2014). It is, however, strongly influenced by tree damage (Uriarte et al. 2012). Current models generally neglect the varied reproductive strategies that determine responses to disturbance. Post-disturbance sprouting, which can be an important regeneration strategy following wind or fire, is rarely implemented in cohort-based models, IBMs (Mladenoff 2004; Holm et al. 2012), or VDMs.

Plant growth responses to the altered light and nutrient conditions after disturbance also are generally not included in current models [but see Uriarte et al. (2009) and Holm et al. (2017) for IBM examples]. *In addition to improving and evaluating the basic representation of reproductive output, recruitment, and dispersal, both experimental and observational datasets are required or need analysis to quantify the post-disturbance recovery process across varied ecosystems.*

3.5 Unique Challenges of Scale

The broad range of spatial scales at which disturbances affect ecosystem function poses major challenges for modeling efforts. Disturbances create spatial patterns that influence post-disturbance recovery through effects on seed and insect dispersal, air turbulence, leaf temperature, and light penetration (Peters et al. 2011). Succession and recruitment can be slow after large, severe, or compound disturbances (e.g., beetle, fire, and drought) due to limited seed supply or sprouting capacity, distance to reproductive trees, or repeated disturbance before recruitment reaches resistant life stages (Chambers et al. 2016; Carlson et al. 2017; Owen et al. 2017). VDMs capture limited spatial heterogeneity at the subgrid scale because topography and soil properties are shared across subgrid patches. Although

disturbance and recovery processes can influence ecosystem processes in adjacent patches on the landscape, patches within a VDM grid cell are not spatially explicit, thus missing the spatial contagion in disturbance (e.g., fire spread) and recovery (e.g., distance to seed sources). As ESMs operate at finer spatial scales, accurately representing connectivity within grid-cell patches and across grid cells will become more critical. *Workshop participants discussed strategies for capturing some aspects of spatially explicit processes in large-scale models; more effort is needed to fully scope the suite of related problems and develop solutions that remain computationally tractable but capture known emergent effects.*

In summary, recent advances in vegetation modeling at scales suitable for coupling with ESMs provide a potential foundation for capturing important ecosystem properties critical to Earth system simulation—particularly plant demography and its sensitivity to environmental variation. However, these new VDMs largely do not adequately represent important disturbances or their interactions with vegetation structure and dynamics. Further, resolving uncertainty in model algorithms and parameterization requires sustained effort and rigorous use of observations and experimental data to make progress.

4. New and Existing Data

Many of the foregoing modeling challenges are directly linked to data availability at relevant scales. Thanks to decades of demographic and other observations by the forestry and ecological research communities, there are a number of datasets available for advancing vegetation dynamics knowledge and vegetation demographic models. In addition, new approaches to observation and experimental manipulation are allowing greater insight into the critical processes underlying vegetation dynamics in response to chronic and abrupt environmental disturbances. The workshop considered virtues and limitations of current and emerging datasets and important gaps, which are summarized in this section.

4.1 Monitoring and Observational Plot Networks

Long-term datasets of vegetation structure and dynamics are critical for understanding how environmental variability affects growth, mortality, and regeneration and also for evaluating VDM predictions over multidecadal timescales. Some of the longest observational time-series data of vegetation dynamics (e.g., growth, mortality, and recruitment) in the Americas exceed four decades (McDowell et al. 2018). Many sites share methods and data through the global ForestGEO network (Anderson-Teixeira et al. 2015). The U.S. Department of Agriculture (USDA) Forest Inventory and Analysis (FIA) program comprises thousands of small plots, sampled at irregular intervals. While too small to represent stand structure, new approaches to estimate stand-level demography include the full size–species structure (Schliep et al. 2017; Clark et al. 2017), thus capturing indirect relationships between growth, survival, and fecundity. The uncertainty contributed by small plot area in inventory data depends on species diversity, so high-diversity tropical forests are especially challenging. Small FIA plots and the newly implemented vegetation structure plots in the U.S. National Ecological Observatory Network

(NEON; neonscience.org) have only sporadic representation of most species at most sites. However, the stratified random design and the deployment along important gradients with high temporal replication in NEON are valuable. The multiyear census interval available for most inventory networks poses the challenge of growth and mortality estimates spanning years of variable conditions, so sensitivity to weather and climate variability is necessarily damped, although diameter measurements at multiyear intervals are less subject to noise in the measurement. Where subsets of plots can be sampled each year, year effects and random effects allow for imputing missing years (Clark et al. 2014).

AmeriFlux, Long-Term Ecological Research (LTER), NEON, and Critical Zone Observatory (CZO) sites provide standardized data on vegetation and physical factors, including water, carbon, and energy balance, in the United States. Some sites were designed to address the consequences of disturbance or have proven useful in documenting the effects of disturbance on vegetation. The Sevilleta LTER (New Mexico) focuses on the ecotone (i.e., boundary) between grass- and shrub-dominated communities. Its multidecadal record of monitoring and experimental manipulations has documented widespread tree mortality in response to chronic drought, large fires, and insect outbreaks. These sudden and dramatic changes have altered biodiversity as well as evapotranspiration and net primary production. Other monitoring sites opportunistically capture disturbance and ecosystem recovery. For example, inventory plots and eddy covariance sites have been subjected to hurricanes at Luquillo Experimental Forest (Puerto Rico), strong and moderate El Niño droughts at Barro Colorado Island (Panama), fire in Yellowstone National Park (Wyoming; see Fig. 5, p. 17), and insect outbreaks (Wisconsin, New Jersey, and throughout the West) (Cook et al. 2008; Schäfer et al. 2014b). Flux data document the return of ecosystem processes to predisturbance levels,



Fig. 5. Dense Natural Regeneration of Lodgepole Pine Trees 15 Years After 1988 Yellowstone National Park Fires. Regeneration was common throughout the burned landscape, but whether or not this level of resilience will continue into the future as climate warms and disturbance regimes change is a key question. [Photo courtesy Monica Turner, University of Wisconsin–Madison.]

while inventory or LIDAR data capture structural recovery. Plot networks have allowed assessment of compound disturbances and linked disturbances.

The increasing number of monitoring data networks are providing valuable new insights that are critical to evaluating and informing developments in vegetation demographic models. While existing sites and networks provide opportunities for VDM model benchmarks, they largely do not track spatially extensive biome transitions or disturbance regimes. Studies that do capture disturbance and recovery data are diverse and often held by individual principal investigators, so there is a need to identify existing data sources and make them accessible for testing and parameterizing models. Existing networks might be augmented with measurements in high-priority ecosystems, across environmental gradients, or in landscapes subject to disturbance and recovery dynamics important to VDM predictions. Additional measurements of vegetation

structure and dynamics at eddy covariance sites would extend the value of past efforts.

4.2 Paleoecological Records

Evaluating VDMs is difficult due to the extended timescales over which vegetation dynamics play out. Historical data (e.g., public land surveys) and paleo proxies, including tree-ring, pollen, charcoal, and isotopic analyses, have the potential to inform longer-term processes related to landscape composition, structure, and function (Rollinson 2017; Marlon et al. 2008). One of the primary challenges in using paleo data with models is that most paleo proxies (e.g., pollen counts) do not match model outputs (e.g., PFT composition) and have considerable uncertainties. Paleo proxies also have uneven spatial and temporal distribution. For example, the pollen record is poor except in regions with high densities of lakes (e.g., glaciated North America and Eurasia), and packrat middens are rare outside arid regions.

Tree rings can allow direct comparisons between models and data. Analyses of dying and surviving trees consistently reveal that trees that have died had a multiyear, sometimes even multidecade, trend of decreasing growth and shifts in water stress (indexed via carbon isotopes) prior to mortality (McDowell et al. 2010; Wyckoff and Clark 2002; Berdanier and Clark 2016; Cailleret et al. 2017). This pattern exists for drought, temperature, and insect-induced mortality, although the mechanisms underlying growth declines are poorly understood. Depending on design, tree-ring datasets collected for ecological studies may be used to reconstruct historical stand-level biomass and productivity (Berner et al. 2017; Dye et al. 2016; Foster et al. 2014). Tree rings have sufficient temporal extent spanning large changes in climate, CO₂, and air pollution (Thomas 2013). Because measurements are sequential and annual, they provide evidence of lagged effects (Richardson et al. 2013; Zhang 2018). Tree-ring data collected in combination with other observations are likely most useful for VDM testing, but they must be considered in context. For example, many sites in the International Tree-Ring

Database (ITRDB) were selected for reconstruction of paleoclimate and, therefore, are biased toward climate-sensitive topographic positions or species (Brienen et al. 2012; Babst et al. 2017). Tree populations are often dominated by the smallest size classes, which respond to climate differently than the large individuals selected for climate reconstruction due to the interaction effects of climate variables with understory light and moisture levels (Clark et al. 2014). *While imperfect, paleoecological data—particularly tree-ring data—may be helpful in revealing lagged relationships between climate and vegetation change or disturbance and vegetation recovery that are important for vegetation models to capture but are difficult to directly observe on the landscape or in experiments.*

4.3 Manipulative Experiments

Experimental manipulations are important for understanding the mechanics of plant and ecosystem responses to novel, “out-of-sample” environmental conditions. Data from experiments are also valuable for calibration and evaluation of models, including whether or not models arrive at right answers (e.g., mortality) for the right reasons (e.g., hydraulic failure; McDowell et al. 2013). When framed in terms of testing the hypotheses embedded within models, these model-data comparisons have provided a number of insights that can subsequently impact model development to improve model accuracy (e.g., Medlyn et al. 2016; Powell et al. 2013; McDowell et al. 2013). VDM calibration requires demographic data across species and size classes, which are often missing from global change experiments focused on ecosystem processes or ecophysiology. The growing number of tree diversity experiments that manipulate density and plant functional types, while monitoring growth rate, canopy structure, and mortality, could be exploited for model calibration and evaluation. Drought, heating, and girdling experiments that affect tree mortality provide insight into the physiological basis of tree resistance and vulnerability to drought and elevated temperature (Gough et al. 2016; Kolka et al. 2018; Mau et al. 2018). Global change experiments that measure recruitment, growth, and/or mortality can help



Fig. 6. Piñon Pine Inside a Heated Open-Top Chamber Within the Rain-Out Shelter Plot at the Los Alamos Survival-Mortality Experiment (SUMO). Experimental tests of the individual and interactive effects of warming and drought on tree physiology and demography yield insights and tests needed for new vegetation models. [Photo courtesy Henry Adams, Oklahoma State University.]

address model predictions in response to chronic disturbances, such as elevated CO₂ or temperature (see Fig. 6, this page).

A suite of DOE-funded warming experiments [e.g., Alpine Treeline Warming Experiment (ATWE), Boreal Forest Warming at an Ecotone in Danger (B4WARMED), Harvard-Duke warming experiment, Spruce and Peatland Responses Under Changing Environments (SPRUCE), Survival-Mortality Experiment (SUMO), Tropical Responses to Altered Climate Experiment (TRACE), and Zero Power Warming] that focused on processes associated with multifactor drivers of vegetation dynamics is ripe for use in model-data comparison efforts. Despite past successes, discussions emphasized the need for experiments that manipulate disturbance regimes, plant diversity, or global change factors, particularly in factorial designs to allow testing for the independent and combined roles of different drivers. Building bridges between modelers and experimentalists early in experiment development can help ensure that new experiments generate the data products needed to address uncertainties in next-generation vegetation models.

4.4 Remote Sensing

Understanding how demographic rates within a site vary over time in response to environmental change must be paired with coarse-scale observation of spatial variation in climate, disturbances, soil, and vegetation. Remote sensing can be used to quantify vegetation properties along with disturbance and its impacts, and the technical capabilities and their value to modeling are growing rapidly (McDowell et al. 2015). Imaging spectroscopy (IS, also known as hyperspectral remote sensing) provides evidence of canopy functional traits and soil properties (e.g., Dahlin et al. 2013; Ollinger et al. 2002; Ustin et al. 2004; Serbin et al. 2015; Singh et al. 2015). These data are used to test model predictions involving carbon, water, and nutrient cycling (Rogers et al. 2017; Fisher et al. 2018). IS has the potential to scale up field measurements of foliar traits and to connect local-scale measurements to watershed scale and possibly larger (e.g., proposed National Aeronautics and Space Administration [NASA] Surface Biology and Geology satellite mission). Moderate-resolution (i.e., 100 m to 10 km) Earth-observing sensors can be used to detect stand-replacing disturbance, but they miss partial canopy disturbances. However, data fusion approaches can be used to decompose coarse-scale disturbance patterns to finer scales (e.g., Meng et al. 2018). High-resolution mapping of vegetation structure and function following disturbance is facilitated by NASA's many imaging systems, including the airborne G-LiHT and WorldView satellite constellation (e.g., Meng et al. 2017). *New data collection to add value to these missions could include targeted field surveys to attribute remotely detected disturbances to causes (e.g., insects, pathogens, and wind) for calibration and ground truthing. There are new opportunities to generate near-real time disturbance maps from remote-sensing datasets (e.g., Feng et al. 2018), which could be used to guide rapid-response field campaigns.*

Future satellite missions are expected to expand the set of physiological and structural measurements that can be captured remotely. Upcoming missions on the International Space Station, including Global Ecosystem Dynamics Investigation (GEDI; NASA

spaceborne LiDAR, launching November 2018), Ecosystem Spaceborne Thermal Radiometer Experiment on Space Station (EcoSTRESS; NASA thermal infrared, launched July 2018), and Japan's Hyperspectral Imager Suite (HISUI; JAXA hyperspectral imager, launch planned 2019), will provide expanded spatial coverage and over a wider range of the electromagnetic spectrum at finer spectral resolution (Stavros et al. 2017). Other systems include the NASA Surface Biology and Geology imaging spectrometer mission (NASEM 2018). Combined with existing and upcoming radar remote-sensing missions (i.e., Tandem-X, NISAR, BIOMASS, and ICESAT-2), data from these instruments are expected to provide global forest structure and dynamics information relevant for testing VDMs (Fisher et al. 2018). Raw data from valuable remote-sensing missions require considerable processing and interpretation to be used in concert with vegetation models. *Efforts to generate and distribute data products directly useful to VDM testing from these diverse new observations should be expanded.*

4.5 Bridging Scales in Observations

Observations of vegetation dynamics and disturbance, as well as the processes underlying them, range from subdaily, tissue-scale physiological stress responses to multidecadal, landscape-scale post-disturbance recovery. Vegetation models, including VDMs, that are coupled to ESMs represent processes across these scales, meaning that multiscale datasets collected at common sites over common time frames are particularly valuable. Pairing satellite and airborne remote sensing with ground-based observations, embedding new vegetation dynamic data collection efforts within sites that already have long-term monitoring of stand-scale carbon and water exchange, or collecting a suite of intensive measurements following episodic disturbance at a monitoring site can multiply the value of existing datasets. To be maximally valuable, data must be collected in ways that preserve observation error and the joint relationships between variables. *While such multiscale observational approaches have been identified previously, this workshop highlighted the need*

for multiscale observational efforts that explicitly address interactions between changing vegetation dynamics and disturbance regimes.

In summary, diverse observational and experimental data are critical components of advancing simulation of vegetation dynamics and disturbance in ESMs.

While existing datasets and monitoring networks are valuable, they also present challenges. Further, most global change experiments to date have not targeted

vegetation dynamics or disturbance processes. Therefore, there is a need for a new generation of publicly accessible datasets—ideally leveraging preexisting complementary observations and designed in coordination with modeling groups—that address uncertainty in vegetation responses. *Synthesis of existing observations, development of data products directly relevant to VDMs, and new observations and experiments targeting interactions among vegetation dynamics, climate, and disturbance are all priorities.*

5. Next Steps in Model-Data Fusion

As highlighted above, there are numerous opportunities for “model-data fusion” that leverage experimental and observational data as part of formal model calibration (assimilation) and evaluation (benchmarking). Taking full advantage of available information requires innovation in cyber-infrastructure, cloud computing, informatics, and statistical tools. In addition, model-data fusion could further benefit from model-data integration efforts pursued as a sustained, community-wide activity that is transparent, accessible, and interoperable across a range of models.

For complex VDMs that represent multiple interacting processes, calibration efforts will need to occur across data types, sites, and over time. VDMs can rely on a range of top-down and bottom-up observations (e.g., remote sensing, forest inventory, and eddy covariance), with each providing information about the processes of interest. Assimilating data types that inform processes operating on different spatial and temporal scales requires distribution theory that admits uncertainty at different levels. Absorbing uncertainty in data and process can be achieved via a hierarchical approach at the most basic level by including random effects. In- and out-of-sample prediction is one of the most effective ways to evaluate models. Although predictions of the future cannot be tested directly now, there can be many opportunities for out-of-sample prediction that provide the most basic tests of model performance. Model selection is available for evaluating different model structures. Variable selection can help determine which predictors to include in models (Cressie et al. 2009). Use of multiple, complementary datasets helps to isolate the roles of individual processes. Further, process simulators (e.g., Walker et al. 2018) can be used to evaluate individual process representations and assumptions before their incorporation into larger model frameworks, helping to reduce uncertainty and minimizing computational costs.

Model benchmarks are a suite of observations that can be used to evaluate models, enabling repeatable quantification of model successes and shortcomings. The most widely used set of benchmarks for global land surface models is the ILAMB test suite of gridded data products (Hoffman et al. 2017). No such analog yet exists for VDMs, although site-scale benchmarks of processes and subsequent vegetation dynamics have been developed for experimental drought settings (McDowell et al. 2013, 2016). Further, the Next-Generation Ecosystem Experiments (NGEE)–Tropics project has been developing site-scale benchmarks in Panama and Brazil. The Predictive Ecosystem Analyzer (PEcAn) project has established benchmarks from site-scale observations and experiments in a range of biomes. Ideally, benchmarks should be constructed to identify when models and their embedded hypotheses are capturing processes correctly (Medlyn et al. 2015). VDM benchmarking requires site (e.g., tree-size distributions, soil information, and topography) and meteorological data to specify initial and boundary conditions for the model(s) and plant trait information, which is used to parameterize models. For datasets that omit information on uncertainty, efforts might be needed to solicit additional information as part of benchmark development. More information on benchmarks and appropriate usage can be found in Hoffman et al. (2017). *Assembling model benchmarks, including uncertainty in observations, into standardized, community-accessible test suites or testbeds would increase the efficiency of model evaluation and avoid duplication of effort.*

Sensitivity analysis (SA) is used to quantify how variability in parameter estimates, as well as model process representation (Dai et al. 2017), affects variability in model predictions (Fieberg and Jenkins 2005). SA thus identifies the parameters and processes that most influence predictions (de Kroon et al. 2000) to determine (1) the input variables and feedbacks that have a large effect on response variables (Clark et al. 2013) or (2) the effect of prior knowledge on parameter

estimates (Gelman et al. 1995). Increasingly, the term uncertainty quantification (UQ) is used to describe methods that fully recognize and account for limited knowledge of a system, which can come from multiple sources (Beven 2016). SA and UQ help to prioritize processes that need to be better understood, sometimes addressable through the collection of new data or a synthesis of existing data. SA can suggest which additional measurements provide the largest reduction in model uncertainties (Dietze et al. 2014; LeBauer et al. 2013). *Wider application of SA and UQ could help prioritize measurements and guide model development.*

Workflows like PEcAn can also increase the efficiency of model evaluation (Hoffman et al. 2017). Dietze (2017) evaluates the contributions to predictions of five elements, including initial conditions, input uncertainty, parameter uncertainty, parameter variability, process heterogeneity (i.e., random effects), and process error (e.g., structural uncertainty, residual error, and inherent stochasticity). These sources of uncertainty are represented by probability

distributions. Distributions of inputs can be the basis for ensemble model predictions. For uncertain inputs, advances in remote sensing are enabling constraint of vegetation composition and structure at global scales. There is not yet an equivalent approach for belowground pools. State data assimilation approaches have been used in PEcAn and the National Center for Atmospheric Research (NCAR) Data Assimilation Research Testbed (DART). *More efficient workflows for model spin-up and initialization could advance the understanding of uncertainty and its effects on model predictions.*

Informal model evaluation and sensitivity testing are giving way to more formalized approaches that allow quantification of sources of uncertainty in models and that can identify priorities for model development and data collection. *Efforts to assemble data into formats and repositories where the information can be accessed and reused by the full community, as well as expanded use of SA/UQ approaches, will help accelerate model development and evaluation and should be encouraged.*

6. Priorities for Future Research

Interactions between vegetation, climate, and disturbance have consequential impacts on ecosystems that are poorly predicted by current ESMs. These interactions control biogeochemical cycles in ways that, in some cases, remain poorly understood, making them difficult to implement in models. While not an explicit focus of the workshop, the strong impacts of land use, past and present, are integral to these interactions and must be better understood.

Discussions highlighted several key areas that need progress in understanding and projecting vegetation dynamics and disturbances in the context of ESMs:

- **New Observations.** While there are considerable, if imperfect, sources of data on vegetation dynamics, the short- and long-term responses of vegetation dynamics to disturbance events and ways those responses vary across environmental gradients are inadequately documented by data (Section 4.1, 4.2). Strategically designed monitoring and observational studies in regions that will experience unplanned disturbance events need to be continued and expanded. Capacity to collect rapid-response observations at existing long-term study sites following important disturbance events (Lindenmayer et al. 2010) would also fill some important gaps. Observed variables need to incorporate stand structure and demographic rates (e.g., recruitment, growth, survival, and reproductive output), including spatial variation in these properties and environmental conditions. Also needed are more concentrated monitoring near boundaries between biomes, as well as more reliable capture of disturbance events, vegetation response, and feedback effects of vegetation on repeat disturbance. Monitoring along environmental gradients should be part of these design considerations.
- **New Experiments.** Experiments to partition the roles of different, but often correlated, environmental drivers of demographic change (e.g., chronic temperature rise versus abrupt drought events) are required to test the impacts of climate and environmental variation on vegetation demography (Section 4.3). Such new experiments should be developed in tandem with models to enable improved model design, process testing, and prediction.
- **Remote-Sensing Integration.** Integration of ground and remote-sensing data has already proven valuable and promises to improve, with new products being exploited by ESMs (Section 4.4).
- **Scaling Processes.** Process measurements, ranging from carbon starvation to seed dispersal and germination, in both experiments and observational networks, are required to ensure the connections between fast ecophysiological or phenological processes and slower demography, as well as between short- and long-term disturbance responses (Section 4.5). These connections require observations at fine and coarse scales and models that connect them (e.g., hierarchical frameworks). The connections from individual plants to landscapes may need to include size and spatial distributions of disturbance events because those spatial scales interact with processes like seed dispersal.
- **Sustained Model Development and Testing.** New modeling approaches that capture dominant modes of vegetation dynamics and disturbance are critical (Sections 3.2–3.4). Vegetation demographic models within ESMs were of particular interest to a number of participants in this workshop. These models show promise but require extensive evaluation, including sensitivity and uncertainty analysis. Model improvements are possible, but they require sustained effort to better simulate vegetation dynamics with and without disturbances. A critical test includes properly representing range shifts associated with seed dispersal and seedling survival

to reproductive ages. Simulation of processes driving mortality are still in their infancy but are critical to accurate simulations of vegetation demographics. Some disturbance processes are captured in existing models (e.g., fire and drought), but others require new development (e.g., insect outbreaks and wind), and all require evaluation against data.

- **Synthesis and Model-Data Fusion.** Synthesis and model-data fusion will accelerate with expanded availability of data and data products, from physiology and individual demography to stand-level aggregate variables (Section 5). Several discussants

are involved in development of testbeds that are currently limited by data availability. Discussions pointed out opportunities to leverage existing projects, sites, and experimental networks for new synthesis efforts.

Finally, discussions concluded that additional workshops and/or working groups that combine modelers with experimentalists are warranted. The combined disciplines represented at this workshop do not often meet together. While productive conversations identified key challenges, workshop participants have only begun to consider how collaborations might solve them.

7. Conclusions

The study of vegetation dynamics and disturbance has a rich history in ecology but has only recently been challenged to inform and predict ecosystem responses to environmental change at coarse scales of space and time. Advances in modeling approaches, as well as model evaluation, are critical to achieving robust predictions, particularly when coupled through water, energy, and biogeochemical cycles to other physical components of the Earth system. Synthesis of extensive existing data across diverse study systems and geographies is a near-term opportunity for generating insights; to be most effective, particularly for disturbance studies, such syntheses require participation by a broad cross section of scientists involved in field, modeling, and remote-sensing research. By and large, past global change experiments were not designed with vegetation dynamics or disturbance in mind; there are gaps in the availability of manipulative studies for confirming cause and effect inferred from observational

studies. A subset of experiments targeting these processes offers some initial opportunities for synthesis and scoping of required new experimental work. Ultimately, efforts to capture the many missing details that are involved in disturbance-vegetation-climate interactions may not improve predictions. Details that are well constrained by measurements at one scale do not necessarily improve models that predict at another scale. At the same time, the lack of adequate representation of vegetation dynamics and disturbance in ESMs has led to large uncertainties and biases in Earth system prediction, a consequence requiring developmental progress. A key challenge for the next decade is to identify which types of measurements can improve predictions of which variables. Overall, the community is eager to address these challenges with the goal of improving the ability to predict critically important vegetation dynamics and disturbances in the context of global change.

Appendix A. Workshop Agenda

U.S. Department of Energy Office of Science
Office of Biological and Environmental Research Workshop

Disturbance and Vegetation Dynamics in Earth System Models

March 15–16, 2018

Hilton Gaithersburg, 620 Perry Parkway, Gaithersburg, Maryland

Overarching workshop goal: The goals of this workshop are (a) to identify key uncertainties in current dynamic vegetation models that inhibit our ability to adequately represent vegetation in Earth System Models (ESMs) and (b) to identify and prioritize research directions that can improve models, including forest structural change and feedbacks and responses to disturbance. Failure to capture disturbance dynamics and feedbacks limits the utility of ESMs for predictive understanding. Large uncertainties discourage potential policy and decision-making applications. Focusing on the United States and its territories, this workshop will consider (a) dynamic processes that significantly affect terrestrial ecosystems and the coupled Earth system and (b) data constraints and modeling challenges important for future progress.

Day 1 – Thursday, March 15th (Darnestown/Gaithersburg Room)

8:00 a.m.	Continental breakfast (in the foyer to the meeting room)	
8:30 a.m.	Welcome, introductions, safety	Daniel Stover, Peter Wyckoff
8:45 a.m.	Welcome and the Climate and Environmental Sciences Division's (CESD) strategic investments in this workshop	Gary Geernaert
8:55 a.m.	Structure of workshop and report	James Clark and Lara Kueppers
9:10 a.m.	Session 1 – Representation of vegetation dynamics and disturbance in Earth system models and the uncertainties. Focus on prediction and novel approaches for the next-generation of models. Session description: Dynamic global vegetation models, developed to capture changes in the spatial distribution and local composition of plant functional types over time, have historically included some representation of vegetation dynamics and chronic and abrupt disturbances. However, these representations have been highly simplified in ways that cast doubt on model predictions. A variety of new approaches have been proposed that may better capture key vegetation response types, response times, and ecosystem vulnerabilities to extreme events. We will discuss the challenges of modeling vegetation dynamics and disturbance, current modeling strategies, and how they differ from each other and from classic dynamic vegetation models.	
9:10 a.m.	Plenary presentation 1.1: Observational priorities and Earth-system models	Robert Jackson, Stanford University
9:40 a.m.	Plenary presentation 1.2: Dynamic Vegetation Models: where next?	Rosie Fisher, National Center for Atmospheric Research
	10:10 a.m.	Break
10:30 a.m.	Breakout discussion session (two groups, each use the same Questions) Group 1 – Darnestown/Gaithersburg Room Breakout facilitator: Charlie Koven, Breakout rapporteur: Jackie Shuman	

Group 2 – Frederick Room**Breakout facilitator:** Anthony Walker, **Breakout rapporteur:** Ben Poulter**Questions for Session 1:****Q1.1:** Do current modeling approaches capture the important vegetation dynamics and their consequences for the Earth system? What are the gaps?**Q1.2:** Where do model predictions agree and disagree on vegetation responses to abrupt and chronic disturbances?**Q1.3:** What do we know about the different sources of uncertainty? Which ones pose the most critical problems for prediction?**Q1.4:** Where/when are current model predictions most unreliable? Consider estimates of mean states, responses, and their uncertainty.

11:30 a.m.

Working lunch and small discussion groups

12:30 p.m.

Session 2 – Vegetation dynamics critical to Earth system responses and opportunities for advancing prediction**Session description:**

Recent promising advances in dynamic vegetation modeling do not yet accommodate key dynamics within ecosystems and across the landscape that could importantly affect predictions. The missing processes are not equally important for predicting water, energy, and biogeochemical cycles at regional scales or their risks to natural resources or communities. We will discuss vegetation changes that could have large impacts on climate and natural resources but are either not adequately represented in models or are readily evaluated. We will also discuss opportunities for advancing predictive capabilities.

12:30 p.m.

Plenary presentation 2.1: Beyond light and nutrients:
Disturbance as a driver of forest structure and function

Maria Uriarte, Columbia University

1:00 p.m.

Plenary presentation 2.2: Disturbance-vegetation dynamics:
Key needs for getting them rightMonica Turner, University
of Wisconsin, Madison

1:30 p.m.

Break

1:45 p.m.

Breakout discussion session (Two groups, each use the same Questions)**Group 1 – Darnestown/Gaithersburg Room****Breakout facilitator:** Jeremy Lichstein, **Breakout rapporteur:** Shawn Serbin**Group 2 – Frederick Room****Breakout facilitator:** Ben Bond-Lamberty, **Breakout rapporteur:** Kyla Dahlin**Questions for Session 2:****Q2.1:** What processes are known to be important to climate and natural resources but are not adequately represented or tested in dynamic vegetation models?**Q2.2:** What strategies from landscape, gap dynamic, or other modeling frameworks could be leveraged by next-generation DGVMs?**Q2.3:** What are the major challenges to advancing predictive capabilities of DGVMs?**Q2.4:** Given sensitivity of existing models (or what we know!), what processes are highest priority?

2:45 p.m.

Session 3 – New methods and datasets needed to estimate and predict dynamics at regional to continental scales**Session description:**

Dynamic Global Vegetation Models (DGVMs) that project future ecosystem structure and function, including disturbance responses, make use of diverse observational and experimental data that are integrated in creative ways. DGVMs and ESMs engage in extrapolation that inevitably generates large

predictive uncertainty. This session will focus on the potential middle ground for modeling dynamic data at scales that can be more directly assimilated into ESMs. Objectives include the identification of data sets and modeling strategies that can improve the data-model connections that lead to more tractable predictions. We will also discuss priorities for new observations and experiments needed to inform predictions of disturbance and vegetation dynamics.

2:45 p.m.	Plenary presentation 3.1: Regional vegetation prediction on the data scales, with connections to ESMs	James Clark, Duke University
3:15 p.m.	Plenary presentation 3.2: Approaches to better understanding of vegetation dynamics	Nate McDowell, Pacific Northwest National Laboratory
3:45 p.m.	Break	
4:00 p.m.	Breakout discussion session (2 groups, each use the same Questions) Group 1 – Darnestown/Gaithersburg Room Breakout facilitator: Mike Dietze, Breakout rapporteur: Jane Foster Group 2 – Frederick Room Breakout facilitator: Kiona Ogle, Breakout rapporteur: Sean McMahon Questions for Session 3: Q3.1: What are the creative new approaches for directly fitting DGVMs to data? Q3.2: What is the availability of data for model benchmarking or validation (remote-sensing, eddy flux, demography plots, and experiments)? Q3.3: Where should new measurements focus to make the most significant and rapid advancements (e.g., particular biomes or ecosystems, measurement gaps identified by empiricists, and processes that models find are highly-sensitive)?	
5:00 p.m.	Wrap-up and plan for Day 2	
5:15 p.m.	Adjourn	

Day 2 – Friday, March 16th (Darnestown/Gaithersburg Room)

8:00 a.m.	Emerging topics from Day 1 and Introduction to Day 2	Lara Kueppers, James Clark
8:30 a.m.	Report outs from Day 1 discussions Session 1 (10 minutes per group) Session 2 (10 minutes per group) Session 3 (10 minutes per group)	
9:30 a.m.	Identify writing groups, leads, and assignments	
10:00 a.m.	Break	
10:20 a.m.	Writing groups	
12:00 p.m.	Lunch and progress report outs from writing groups	
1:00 p.m.	Continue writing groups	
2:45 p.m.	Wrap-up including next steps, report, and paper?	Peter Wyckoff, James Clark, Lara Kueppers
3:00 p.m.	Adjourn	

Appendix B. Participants and Affiliations

James Clark, Workshop Co-Leader

Duke University

Lara Kueppers, Workshop Co-Leader

University of California, Berkeley, and
Lawrence Berkeley National Laboratory

Brian Aukema

University of Minnesota

Ben Bond-Lamberty

University of Maryland and
Pacific Northwest National Laboratory

Kyla Dahlin

Michigan State University

Mike Dietze

Boston University

Andrew Eckert

Virginia Commonwealth University

Rosie Fisher

National Center for Atmospheric Research

Jane Foster

University of Vermont

Jennifer Holm

Lawrence Berkeley National Laboratory

Robert Jackson

Stanford University

Charlie Koven

Lawrence Berkeley National Laboratory

Beverly Law

Oregon State University

Jeremy Lichstein

University of Florida

Nate McDowell

Pacific Northwest National Laboratory

Sean McMahon

Smithsonian Institution

Rebecca Montgomery

University of Minnesota

Kiona Ogle

Northern Arizona University

Benjamin Poulter

National Atmospheric and Space Administration
and Montana State University

Karina Schäfer

Rutgers University

Erin Schliep

University of Missouri

Shawn Serbin

Brookhaven National Laboratory

Jacquelyn Shuman

National Center for Atmospheric Research

Monica Turner

University of Wisconsin

Maria Uriarte

Columbia University

Anthony Walker

Oak Ridge National Laboratory

Chonggang Xu

Los Alamos National Laboratory

Department of Energy

Andrew Flatness

Gary Geernaert

Justin Hnilo

Renu Joseph

Dorothy Koch

David Lesmes

Sally McFarlane

Shaima Nasiri

Rick Petty

Daniel Stover

Tristram West

Peter Wyckoff (AAAS Science and Technology Policy
Congressional Fellow; University of Minnesota)

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