

# Modeling the Terrestrial Biosphere

Joshua B. Fisher,<sup>1</sup> Deborah N. Huntzinger,<sup>2,3</sup>  
Christopher R. Schwalm,<sup>2</sup> and Stephen Sitch<sup>4</sup>

<sup>1</sup>Jet Propulsion Laboratory, California Institute of Technology, Pasadena, California 91109;  
email: jbfisher@jpl.nasa.gov

<sup>2</sup>School of Earth Sciences and Environmental Sustainability; <sup>3</sup>Department of Civil Engineering,  
Construction Management, and Environmental Engineering, Northern Arizona University,  
Flagstaff, Arizona 86011

<sup>4</sup>College of Life and Environmental Sciences, University of Exeter, Exeter EX4 4RJ,  
United Kingdom

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## Abstract

The land surface comprises the smallest areal fraction of the Earth system's major components (e.g., versus atmosphere or ocean with cryosphere). As such, how is it that some of the largest sources of uncertainty in future climate projections are found in the terrestrial biosphere? This uncertainty stems from how the terrestrial biosphere is modeled with respect to the myriad of biogeochemical, physical, and dynamic processes represented (or not) in numerous models that contribute to projections of Earth's future. Here, we provide an overview of the processes included in terrestrial biosphere models (TBMs), including various approaches to representing any one given process, as well as the processes that are missing and/or uncertain. We complement this with a comprehensive review of individual TBMs, marking the differences, uniqueness, and recent and planned developments. To conclude, we summarize the latest results in benchmarking activities, particularly as linked to recent model intercomparison projects, and outline a path forward to reducing uncertainty in the contribution of the terrestrial biosphere to global atmospheric change.

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## 1. THE TERRESTRIAL BIOSPHERE IN EARTH'S CLIMATE, OR "THE PRINCESS AND THE PEA"

In 1835, Hans Christian Andersen wrote a children's story about a young woman whose royal identity is established by a test of her physical sensitivity. The test, unbeknownst to her, was that a pea was placed in her bed, covered by 20 mattresses and 20 featherbeds. In the morning she lamented about the discomfort from the pea; only a real princess would have such sensitivity, thus verifying her claims to royalty.

Earth's land surface comprises less than a third of the total surface area, and the volume interacting with exchanges of heat, energy, and moisture dictating our planet's climate is far less relative to that of the ocean and atmosphere; the land surface is a figurative pea in the bed of Earth's climate. However, like the princess, Earth's future climate is particularly sensitive to uncertainties in changes on land (1, 2), especially with respect to the carbon cycle, which may contribute half of total uncertainty of physical climate properties (3). The breathing of the terrestrial biosphere dominates variability in global atmospheric CO<sub>2</sub> concentrations (4, 5).

The disproportionate influence of terrestrial biogeochemical uncertainty on Earth's climate uncertainty is something of a puzzle. Not only is the land surface disproportionately small, but the wealth of measurements, experiments, and overall information with respect to land surface properties is disproportionately large. How is it that terrestrial uncertainties exert such a powerful influence on climate uncertainty? The answer is hidden within how the terrestrial biosphere is modeled from the myriad of highly heterogeneous biogeochemical, physical, and dynamic processes represented (or not) in numerous models that contribute to projections of Earth's future.

## 2. A BRIEF HISTORY OF TERRESTRIAL BIOSPHERE MODELS

In 1849, Alexander von Humboldt published the first observational link between climate and plant geography (6). August Grisebach followed in 1872 with more detail in "Vegetation of the Earth: According to Climatic Arrangement. An Outline of Comparative Geography of Plants" (7). This inspired Wladimir Köppen, who in 1884, produced a vegetation-centric world temperature and precipitation climate classification system, commonly known as the Köppen–Geiger climate

classification system (8), thus spawning the beginning of predictive modeling in plant geography, including Leslie Holdridge's life zones system (9).

Such plant geography or biogeography models predict the spatial distribution of biomes (10). However, they do not explicitly account for the biogeochemical cycling of carbon, water, and nutrients nor for the biophysical interactions with heat, energy, and momentum. Moreover, plant biogeography models are assumed to be static and in equilibrium with climate, thereby missing dynamic changes in plant distribution with climate and between biomes (11–14).

The opposite of broad-scope, global-scale biogeography models have been gap models, or vegetation dynamics models, which have focused on individual plant behavior and response from interactions between other individuals within a community, typically a forest (15). These models have targeted such processes as establishment, succession, mortality, and competition for space, light, water, and nutrients. The individual-based models are computationally intensive, having been constructed from detailed observations, allometric relationships, and growth traits at the species level, and are therefore typically applied only in small regions. Such vegetation dynamics models have included, for example JABOWA, FORET, LINKAGES, FORSKA, ZELIG, SORTIE, HYBRID, and ED.

Vegetation dynamics models do not always preserve mass or energy balance (16), unlike terrestrial biogeochemistry models, which have been developed to describe the biogeochemical cycling of carbon, water, and nutrients through ecosystems. Early biogeochemistry models, including Miami, FOREST-BGC, TEM, CENTURY, BIOME-BGC, and DAYCENT, focused especially on carbon uptake on multiannual timescales. Biogeochemistry models have traditionally been stand-alone, offline, or uncoupled from the atmosphere. They provide fluxes to the atmosphere but have no check or constraint from the atmosphere on these fluxes, nor do changes in the uncoupled biogeochemistry models in any given time step have any impact on the atmospheric forcing in the subsequent time steps (17).

Biophysics models formed the foundation of soil-vegetation-atmosphere transfer (SVAT) mechanisms in land surface models (LSMs), or land surface schemes, coupled to climate and atmospheric general circulation models (GCMs) (18). Early biophysics models, including BATS and SiB, provided supporting-role atmospheric boundary conditions for the land-atmosphere exchange of energy, water vapor, and momentum. The structure of such models was focused on fast, subdaily time step processes interacting with equally fast atmospheric dynamics.

Until the late 1980s, all four groups of models—biogeography, vegetation dynamics, biogeochemistry, and biophysics—had largely been isolated from one another in development, but a series of meetings outside Vienna in 1988 and 1989 moved researchers toward integration (16). The amalgamation of these model groups formed a new class—dynamic global vegetation models (DGVMs) (19, 20)—or, more broadly, what are termed terrestrial biosphere models (TBMs), which include some or all from the class of DGVMs. Further integration with hydrological models and models of macrofauna continues to expand the TBMs, providing new tools and organizational structures for the emerging fields of macro- or global ecology.

More details on the developmental history of DGVMs and TBMs can be found elsewhere (16, 21–26). For model descriptions and terminology see the sidebar. A time series showing how the four types of models have trended in English books from Google Books Ngram Viewer can be seen in **Figure 1**.

### 3. PROCESSES OF TERRESTRIAL BIOSPHERE MODELS

We provide a (relatively) brief overview of 25 key processes generally included in many TBMs. These processes range from biophysical and biogeochemical cycling across carbon, water, and

## MODELS TERMINOLOGY RELATED TO THE TERRESTRIAL BIOSPHERE

**Biogeochemistry model:** cycling of carbon, water, and nutrients through ecosystems.

**Biogeography model:** spatial distribution of vegetation in equilibrium with climate.

**Biophysics model:** exchanges of energy, water vapor, and momentum across soil–vegetation–atmosphere continuum.

**Crop model:** yield of agricultural vegetation (crops) based on environmental and climatic drivers.

**Diagnostic model:** refers to the use of prescribed forcing data for a process that would otherwise be modeled (e.g., using remotely sensed greenness for phenology).

**Dynamic global vegetation model (DGVM):** explicitly couples biogeography, biogeochemistry, biophysics, and vegetation dynamics.

**Earth system model (ESM):** fully coupled and dynamic interactions between Earth's climate system of oceans, atmosphere, cryosphere (and lithosphere), and land surface (including vegetation).

**Ecological model:** evolution of ecosystem function and flora and/or fauna.

**Ecosystem demography model:** see vegetation dynamics model.

**Food-web model:** energy flow and biomass across trophic levels and positions.

**Forest model:** as in DGVM, though not necessarily with all components, applied to forests.

**Gap model:** see vegetation dynamics model.

**General circulation model (GCM):** changes in the atmosphere relative to ocean dynamics and, to a lesser degree, land surface properties; precursor to ESM.

**Global climate model:** same as the GCM, but with a focus on climate evolution.

**Hydrological model:** catchment-scale subsurface and surface transport processes of water, snow, and water quality.

**Land surface model (LSM):** can be part of ESM, evolved from biophysics to full DGVMs.

**Land surface scheme:** see LSM.

**Lotka-Volterra model:** changes in predator/prey abundance.

**Plant geography model:** same as biogeography model.

**Prognostic model:** refers to a type of model that simulates a relevant process internally (based on intermediate values in silico mechanistically, or process-based), as opposed to constraining the process via prescribed forcing data.

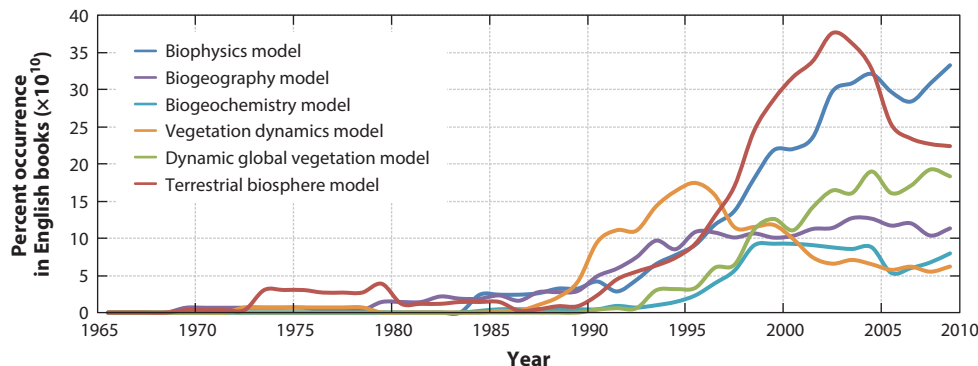
**Soil-vegetation-atmosphere transfer (SVAT) model:** same as biophysics model.

**Terrestrial biosphere model (TBM):** encompasses some or all DGVM submodels—biogeography, biogeochemistry, biophysics, and vegetation dynamics.

**Terrestrial ecosystem model:** see TBM.

**Vegetation dynamics model:** plant-to-community succession and resource competition.

nutrient stocks, fluxes, and transformations, as well as dynamic and ecological processes. The scales span from microscopic bacteria and pores on leaves to landscape dimensions. We focus on important and distinguishing features of each process, consider links and complications to TBM approaches for modeling each process, and provide references for more in-depth investigation (e.g., equations and parameterizations). We organize the processes into 4 categories: (a) leaf scale (3), (b) canopy scale (7), (c) plant scale (4), and (d) ecosystem scale (16). The TBM processes are shown in **Figure 2**.



**Figure 1**

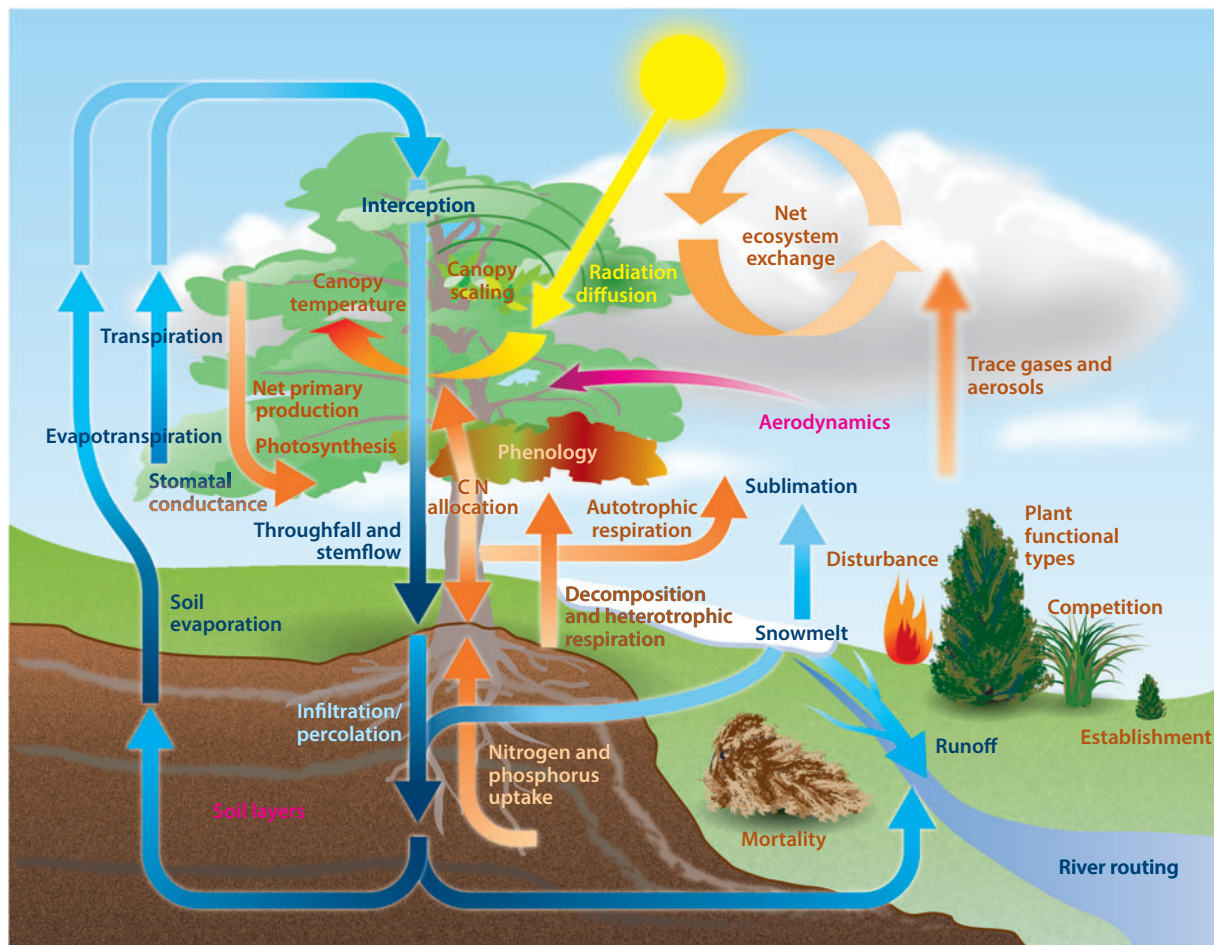
The history of how four classes of models—biophysics, biogeochemistry, biogeography, and vegetation dynamics—as well as the integrated dynamic global vegetation models and terrestrial biosphere models, have trended in terms of terminology/phrasing in English language books from 1965 to 2008 (from Google Books Ngram Viewer). Additional search terms include “land surface scheme” for biophysics models, “forest gap model” for vegetation dynamics models, and “terrestrial ecosystem model” for terrestrial biosphere models.

### 3.1. Leaf Scale

**3.1.1. Stomatal conductance.** Microns-large leaf pores called stomata exert an enormous influence on the entire planet. When stomata are open, plants take up  $\text{CO}_2$  from the atmosphere and release water to the atmosphere, providing water for precipitation. This is especially critical for biomes that rely entirely on this recycled water (27). However, stomata are not always open, and therein lies the modeling challenge: open too much and the modeled biosphere may take up too much  $\text{CO}_2$  and release too much water; open too little, and the opposite can occur (28).

Diurnally, stomata often close in the afternoon with root zone water depletion; alternatively, stomata may close because of large atmospheric water vapor deficits (dry air) in the afternoon (29). These controls on stomatal conductance extend seasonally through wet and dry periods and beyond (e.g., decadal) with changes in climate. Individual species may respond to the same controls in radically different ways—one species may keep stomata open under low moisture/dry air conditions, hedging that wet conditions will come soon, while continuing to gain carbon; another more conservative species may close stomata quickly, not wanting to risk cavitation (the formation of air bubbles in xylem that can expand and burst the vessels) (29). Species’ “choices,” or response thresholds, are generally evolutionarily and life-history based (29). Most TBMs do not model individual species (with notable exceptions), however, so encompassing these aspects into lumped plant functional types that TBMs use is a challenge. This biological control is a large source of uncertainty in TBMs; if the fluxes were purely environmentally or abiotically driven, the uncertainty would be much less.

Stomatal closure response is also a function of plant age and height; i.e., taller plants exert more capillary force on their xylem, so cavitation becomes a greater risk with height. Stomata can be damaged by ozone deposition, though this is rarely modeled (30, 31). The amount of individual stomata per individual leaf varies substantially from species to species, plant type to plant type, and with  $\text{CO}_2$  concentration. Finally, mesophyll conductance between stomata and chloroplasts is sometimes included with stomatal conductance or often ignored, yet it also provides a significant control on carbon and water exchange. All these aspects lend variability and uncertainty to modeling stomatal conductance.



**Figure 2**

The terrestrial biosphere as represented in terrestrial biosphere models.

**3.1.2. Photosynthesis and gross primary production.** The process of photosynthesis operates at the cellular and intercellular levels, replete with numerous enzymes, proteins, electrons, chemical transformations, and reactions. None of this is explicitly modeled in TBMs, and rightly so, as doing so for every photosynthesizing cell on the planet is computationally unwise, to say the least.

However, the primary photosynthate end-product of photosynthesis—usable carbon—is modeled as gross primary production (GPP), the rate of which is gross primary productivity. Necessarily, some assumptions, simplifications, and extrapolations of the more detailed photosynthetic process are required. TBM approaches to modeling photosynthesis divide into three camps (21): biochemical, light-use efficiency, and carbon assimilation.

The biochemical approach, also called enzyme kinetics, is most well-known as encapsulated by Farquhar et al. (32), with extensions and modifications to  $C_3$  and  $C_4$  plants (33, 34). This approach is the most commonly used by TBMs because it explicitly unifies carbon, water, and energy through stomatal conductance, bypassing molecular processes, and is relatively more robust in extrapolations over time (21, 35, 36). However, there are numerous tunable parameters that



lead to major differences among TBMs, and acclimation processes are not well represented in these approaches (16). Further variations with sunlit versus shaded leaves, temperature, and soil moisture constraints add to differences.

The light-use efficiency approach is powerful and well-constrained at large scales because the light used in photosynthesis, or the fraction of absorbed photosynthetically active radiation (fAPAR; 0.4–0.7  $\mu\text{m}$ ), can be measured globally, consistently, and reasonably accurately with satellite remote sensing instruments (37). Nonetheless, how much of that light gets converted to carbon is highly uncertain, with criticism raised over this approach for longer, climate-length timescales (21). Light-use efficiency approaches are particularly sensitive to light attenuation through the canopy and to differences in leaf properties, including nitrogen content.

Carbon assimilation approaches first calculate the maximum possible rate of GPP ( $V_{\text{cmax}}$ ), then downscale it with empirical multipliers based on environmental properties such as light, temperature,  $\text{CO}_2$ , nitrogen, and water, for example (38). Because of the critical dependency on empirical multipliers, and because those multipliers are not well characterized globally over space and time, TBMs that rely on carbon assimilation approaches may have large uncertainties from such domains (21).

An exciting new TBM approach to photosynthesis and GPP comes from fluorescence (i.e., solar-induced chlorophyll fluorescence, SIF) (39). Although the relationship between fluorescence and photosynthesis has been long established at the plant and field scales, recent global measurements of fluorescence from satellite remote sensing (e.g., GOSAT, GOME-2, OCO-2) now provide the same powerful constraint that fAPAR measurements have had on light-use efficiency approaches (40, 41). However, unlike the light conversion uncertainty in light-use efficiency approaches (e.g., light could be absorbed but not used in photosynthesis), fluorescence is a direct by-product of photosynthesis and has been shown to scale linearly with GPP at the global scale (40).

**3.1.3. Transpiration.** Like GPP, transpiration is governed by similar controls—stomatal conductance, radiation, dryness of the air, air temperature, leaf characteristics, soil moisture, and wind speed (including aerodynamic and boundary layer resistances) (42). Transpiration can even occur at night with a combination of imperfectly closed (leaky) stomata and dry air conditions (43). It is important for models neither to overestimate transpiration, potentially drying out the soil too much, nor to underestimate transpiration, potentially limiting the amount of water recycled back into precipitation.

Given the suite of controls, modeling transpiration has a large number of formulations, with different approaches weighting some controls over others (44). Typically, transpiration is unified into the Penman-Monteith (42) equation, though simplifications (45) and expansions (46) are also widely used. Sap flow measurements, eddy covariance, and remote sensing techniques can help constrain TBM estimates of transpiration.

## 3.2. Canopy Scale

**3.2.1. Canopy scaling.** Having described the processes that occur at the scale of individual leaves, how do we scale them up to all the leaves of an entire canopy? Leaf properties are not uniform throughout the canopy, varying in angle, size, thickness, age, nitrogen content, and light exposure (47, 48). One could ignore that variability and simply multiply an average leaf out to the total leaf area of the canopy; this is often done and is called the big leaf approach (49, 50). The strength of the big leaf approach is that it does not require knowledge of within-canopy variability for model parameterization and computation, and it can approximate canopy functioning relatively closely

(50, 51). Nonetheless, multilayered canopies that incorporate this variability with leaf area index (LAI; total leaf area per ground area) and account for stratified access to light have improved the performance of many TBMs (52). Schaefer et al. (36) reviewed 21 TBMs and found that about half (11) used a big leaf approach and half used a multilayer (two-leaf, shaded versus sunlit) approach.

Related to canopy scaling is radiation diffusion through the canopy, necessary to ensure that all vertically distributed processes requiring light/radiation are activated proportionally. Generally, Beer's law is invoked, whereby light decays exponentially from top to bottom depending on both what is in the way of the path (leaf area, thickness, angle, density) and where the light is coming from (solar zenith angle). The light stream may be partitioned into direct beam and diffuse components, and this partitioning impacts photosynthesis because these two types of light penetrate through canopies differently (52–55).

**3.2.2. Canopy temperature.** Canopy temperature indicates how much of the energy from radiation diffusion is converted to heat the physical structure of the canopy. Although important for energy balance and reporting of climate change, canopy temperature is highlighted here because well-established global remote sensing measurements of surface temperature can provide a strong constraint on the energy partitioning of TBMs (56).

**3.2.3. Interception.** Interception of precipitation (or sometimes fog) by the canopy is important because (a) wet leaves have minimal photosynthesis (reduced CO<sub>2</sub> transfer), (b) water returns to the atmosphere quickly because of high radiation exposure and few barriers (i.e., resistances), and (c) this is water that does not reach the ground for belowground processes requiring water. For some species, water can be incorporated directly into the leaves, though this is generally not modeled in TBMs. Most TBMs model interception as a straightforward function of precipitation and LAI (35, 57).

**3.2.4. Aerodynamics.** A key boundary condition that the land surface provides to atmospheric circulation is surface roughness, which is the physical vertical heterogeneity that reduces momentum and aerodynamic wind speed with friction (58). TBMs can specify how the roughness length varies between different plant types as well as heights. Aerodynamics alter leaf-to-air diffusion rates, affecting transpiration and CO<sub>2</sub> uptake.

**3.2.5. Phenology.** Phenology and leaf fall are critical processes in TBMs because these are gateway carbon transfer switches and pathways. Accurate phenology, which is particularly important in deciduous biomes, controls how much carbon is taken out of the atmosphere by the biosphere on seasonal and annual timescales. Too early budburst and/or too late senescence mean that TBMs will overestimate carbon uptake, and vice versa (59). Similarly, leaf fall, which is the primary carbon transfer to the soil, must be balanced delicately so as not to have too many or too few leaves on the canopy at any given time.

Typically, temperature is the largest determinant of temperate phenology in TBMs, with various temperature-based parameterizations, including thresholds, accumulations, and other combinations, though other approaches such as prescribed leaf onset/offset dates, day length/photoperiod, and carbon optimization strategies are also employed (21). Tropical phenology, i.e., raingreen phenology, has been driven primarily by moisture and radiation, given that temperature is relatively seasonally constant in the tropics (60). Because phenology and leaf fall are so important, many TBMs prescribe phenology from remotely sensed greenness indices and other derived products, moving these TBMs away from more prognostic and dynamic models



(37, 61). Recent TBM evaluations by Schwalm et al. (62), Schaefer et al. (36), and Huntzinger et al. (63) found that roughly one-third of TBMs used prescribed phenology.

**3.2.6. Plant functional types.** The last canopy-scale TBM component we include here, plant functional types (PFTs), is the most important of the canopy scale group (64–66). Every species, or individual for that matter, behaves and responds differently from others, but it is not possible to capture explicitly that diversity in TBMs. However, certain individuals behave more similarly to each other than to others, with distinct cutoffs noticeable along what might be considered a continuum of behavior (67–69). For instance, deciduous trees drop all their leaves every year, whereas other plants do not. TBMs must know when and where to turn on/off different processes (e.g., phenology), depending on whether or not a given plant or plant group abides by those processes. TBMs must balance the computational desire to have few plant groups versus the representative desire to model the world in comprehensive detail. PFTs are that compromise.

We include PFTs here in the canopy scale, as opposed to the plant scale (despite the word plant in the PFT term), because PFTs are generally organized based on canopy characteristics, though rooting depths are also included. These characteristics can include leaf size, leaf life span, radiation absorption, leaf area-to-mass ratio, leaf moisture retention, leaf nutrients, phenology, life form based on temperature survivorship, tree height, and successional stage. Distinctions and classes may be selected analytically using principal components analysis (70). Recently, there has been a move toward direct use of traits-based classification (71, 72).

Most TBMs have at least five PFTs—broadleaf evergreen tree, broadleaf deciduous tree, needleleaf deciduous tree, grass, and shrub—that can co-occur and compete for any given pixel (73). Further distinctions are sometimes made from those broad classes, including, for example,  $C_3$  versus  $C_4$  grasses, different crops, and climate-restricted plant types (74). This range of PFTs is acceptable both computationally and representatively, although it does not capture community functional diversity that may become important as diverse biomes respond to changing climate (16, 75). Of 50 TBMs recently reviewed (35, 62, 63), the number of PFTs ranged from 1 to 31.

### 3.3. Plant Scale

**3.3.1. Autotrophic respiration.** Not all the usable carbon from photosynthesis is assimilated into structural growth. Some of those sugars are consumed by plant cells for basic metabolism and repair, also known as maintenance respiration, thereby returning that carbon to the atmosphere. Some of those sugars are consumed in the process of building new tissue (in addition to the carbon assimilated directly into the tissue material), which is growth respiration. Together, maintenance and growth respiration constitute autotrophic respiration ( $R_a$ ) (76).

TBMs typically model  $R_a$ , and the components therein, with functions of temperature upon carbon stocks or the maximum potential of plants to take up carbon (33, 34). The temperature functions are often exponential, and their sensitivity to temperature is represented by the  $Q_{10}$  factor, which indicates the relative increase in the rate ( $Q_{10} = 1, 2, 3, \dots$ ) for each incremental  $10^\circ\text{C}$  increase in temperature (77). There may be subtle differences for leaves, stems, and roots, or some models may provide a lumped whole plant respiration (78). Schwalm et al. (62) catalogued 15 unique approaches to estimating  $R_a$  from 21 TBMs.

**3.3.2. Net primary production and allocation.** Net primary production (NPP) is the carbon taken up by GPP minus the amount consumed in  $R_a$ . NPP is a critical quantity because it reflects the amount of carbon removed from the atmosphere by plants integrated over time. Because NPP typically represents the difference between GPP and  $R_a$  in TBMs, the calculation of NPP

necessarily carries with it uncertainties and errors from inaccurate modeling of both GPP and  $R_a$ , making NPP potentially more uncertain, proportionally, than either GPP or  $R_a$  alone.

After using up some of the carbon gained from GPP for  $R_a$ , what does a plant (and TBM) do with the remaining carbon, or NPP? Options include new leaves, increased wood/stem height and girth, new fine and/or coarse roots, root exudates, transfer to symbiotic bacteria or mycorrhizae for nitrogen or phosphorus, plant defenses, stress-response emissions, reproduction (seeds, pollen, flowers, fruits), or storage as sugars or nonstructural carbohydrates (79–82).

TBMs typically optimize carbon allocation to maximize growth and carbon gain for survival and reproduction (83, 84). If they did not, then they would most likely be outcompeted. In a light-limited environment, this might mean allocating carbon with preference to leaves or height; in a moisture- or nutrient-limited environment, this might mean allocating carbon with preference to roots; in a disturbance-prone environment, the plants that survive may allocate more carbon to wood (83).

Most TBMs allocate carbon only to wood, roots, and leaves (the sum of which is the total biomass) (21), though new TBM developments are including more pathways (81, 85). Some models have fixed allocation amounts to the different plant storage pools (37, 86), others use proportional or allometric relationships so that allocations change nonlinearly with other storage pools (49, 87–89), and still others optimize allocation to maximize carbon gain typically for LAI (90).

Nitrogen (and other nutrient) allocation typically follows the carbon with fixed ratios for different carbon pools (85), though some models have dynamic nitrogen allocation (91). More development is needed to understand and model how carbon-to-nutrient ratios vary with space and time (92).

**3.3.3. Throughfall and stemflow.** The flow of canopy-intercepted precipitation down the stem (stemflow) or directly to the ground (throughfall) is rarely modeled in TBMs (35, 57); the impact on ecosystem functioning is minimal, with only very localized pockets of erosion and nutrient deposition prevalent. However, they are important with respect to spatial resolution and ecosystem functioning—precipitation that remains on the canopy instead of transferring to the ground leads to different rates of evaporation and carbon uptake.

## 3.4. Ecosystem Scale

**3.4.1. Soil layers/pools.** The number of soil layers and pools varies widely among TBMs yet can significantly affect the storage and cycling of carbon, water, and nutrients. In the Arctic, for example, a major current TBM focus is on centuries-old soil carbon stored in multiple layers beneath the rapidly thawing permafrost that, if and when exposed to the atmosphere, will add an enormous amount of  $\text{CO}_2$  and  $\text{CH}_4$  to the atmosphere (93, 94). The number of layers used in the soil thermal hydrological calculations has typically been different from the number of layers in the carbon calculations. Of the 50 total TBMs reviewed in other papers (35, 36, 62, 63), the number of soil layers ranged from 0 to 25, and the number of soil carbon pools varied from 0 to 9. Each soil layer needs new parameterization, so increasing the number of layers adds computational cost but potentially the gain of better representing turnover and storage rates of stored carbon and nutrients.

**3.4.2. Nitrogen and phosphorus uptake.** Most plants globally are limited in growth by the inability to access enough nitrogen or phosphorus (95, 96). However, most models providing climate projections to the Intergovernmental Panel on Climate Change (IPCC) do not include

nutrient cycles (97). This is not for lack of awareness—it is more a matter of the course of development, and many modeling groups are now actively working on nitrogen cycle development and implementation (next on the queue is the phosphorus cycle). Without the nitrogen cycle, the ability of the terrestrial biosphere to take up  $\text{CO}_2$  is overestimated (97). Among the first TBMs to implement a nitrogen cycle, CLM-CN showed “fundamentally altered behavior” with a reduction of terrestrial carbon uptake by 74% (98, p. 1), though other models have had a less drastic impact (99, 100).

Nitrogen must be made available to plants through soil decomposition and transformation pathways (85), then through any of a set of uptake mechanisms via (81) (*a*) the transpiration stream, (*b*) active root uptake, (*c*) symbiotic mycorrhizae, and (*d*) symbiotic nitrogen-fixing bacteria (available to only some plants). Nitrogen can also be resorbed or retranslocated from senescing leaves. All pathways except the transpiration stream require plants to expend a significant amount of carbon in return for nitrogen, usually more carbon than is available to expend, which results in growth limitation (81). Phosphorus is sourced primarily from mineral rock and is particularly limiting in older, more weathered tropical soils (96).

**3.4.3. Decomposition and heterotrophic respiration.** TBMs must delicately balance the rates of litter decomposition and subsequent  $\text{CO}_2$  release back to the atmosphere from heterotrophic respiration ( $R_h$ ) so that litter neither builds up too much in the models nor breaks down too quickly. This is a process that is executed by soil fauna—worms, termites, and other insects and beetles as well as, predominantly, bacteria and fungi—that eat dead plant material and in so doing respire  $\text{CO}_2$ . TBMs cannot model all of these biotic processes and instead model the end-products— $\text{CO}_2$  and different carbon and nitrogen compounds—from abiotic functions that control the rates of production. These functions are primarily based on temperature (e.g., with  $Q_{10}$ ) and moisture, as well as on carbon content and form (e.g., quality), but can also be stimulated by root exudates (101–104). One confusion often apparent when comparing TBMs is whether to specify root respiration as part of the soil ( $R_h$ ) or as part of the plant ( $R_a$ ), as this varies from model to model. Modeling  $R_h$  accurately is critical for understanding whether the terrestrial biosphere is, was, or will be a net carbon sink or source, especially as  $R_h$  responds differently from how GPP and NPP respond to changes in climate (19, 104).

**3.4.4. Net ecosystem exchange.** Net ecosystem exchange (NEE) is probably the most important output of all that is modeled by TBMs in the context of global change. Although not really a process, but more the outcome of a collection of processes, NEE represents how much carbon is stored or emitted from the land surface over time. If the terrestrial biosphere is a net carbon sink, then this helps to mitigate rising atmospheric  $\text{CO}_2$ ; if the terrestrial biosphere is a net carbon source, then this exacerbates atmospheric  $\text{CO}_2$  impacts.

The concept and definition of NEE have recently been clarified (105, 106). NEE, which is total ecosystem respiration ( $R_e$ , or  $R_a + R_h$ ) minus GPP, is in a sign convention “as seen” by the atmosphere: A positive value means that the land emits carbon, and a negative value means that the land takes up carbon. Oppositely, net ecosystem production (NEP), which is GPP minus  $R_e$ , switches the sign convention.

When including processes for carbon emissions other than  $R_a$  or  $R_h$ , such as fire, harvest, aquatic fluxes, fossil-fuel burning, cement production, lateral transfers, and other carbon gases such as  $\text{CH}_4$ , new terms are introduced. Net biome production (NBP) is NEP with fire. Some TBMs implicitly include disturbance fluxes with  $R_h$ . Net ecosystem carbon balance (NECB) is all the processes except fossil fuels and cement. Both NBP and NECB are often referred to as land uptake (105, 106).

Given both the importance of the carbon balance terms and the nuanced but potentially significant differences, it is critical that modelers and analysts be very clear on terminology among NEE, NEP, NBP, and NECB. These terms tend to vary around 0 plus or minus very small numbers, so small uncertainties can easily switch sink/source direction, and errors in sign reporting can be difficult to diagnose.

**3.4.5. Snowmelt and permafrost thaw.** Snowmelt and related frost and permafrost thaw are among the most difficult processes to model accurately, involving energy transfer through multiple layers of unevenly packed, colored, and exposed frozen water (107). Snowmelt is very easy to validate against observations because the comparisons are nearly binary between yes and no snow. But correct modeling of snowmelt and permafrost thaw is critical for turning processes on and off in TBMs, as well for hydrology from the melted water. There is very little congruence among TBMs for melt and thaw approaches, with temperature being the strongest driver, and not all TBMs model melt or thaw (35).

**3.4.6. Infiltration/percolation.** The rate that water moves vertically from the ground surface through the soil is infiltration (also called percolation). For TBMs, infiltration is important for the balance of how much water is available to plants in the root zone, how much water runs off to open water bodies, and how much water recharges aquifers and contributes to base flow of rivers. Infiltration is a function of how much water is at the starting point (surface); how much water is already in the soil; and soil characteristics such as texture, depth, and porosity (often influenced by roots). These controls are formulated to varying degrees in historic equations such as Darcy's Law, Horton's equation, Kostiaikov's equation, and the Green-Ampt method. Not all TBMs simulate infiltration, and those that do use a range of approaches extending from those equations, with some more complex and cover dependent, and others with simpler and sometimes uniform infiltration rates (35).

**3.4.7. Evapotranspiration.** Evapotranspiration (ET) is the sum of canopy transpiration, soil evaporation, and interception evaporation. Soil and interception evaporation are governed by the same controls on leaf/canopy transpiration, except without stomatal conductance, and with the addition of soil resistance for soil evaporation (46). ET can be expressed both in units of water (length per time, e.g., mm per day; consistent with volume per area per time; or, mass—1 kg of water is equal to 1 mm of water spread over 1 m<sup>2</sup>) or energy (latent heat flux, LE or  $\lambda E$ ; 2.45 MJ of energy is required to vaporize 1 kg of water at 20°C, so 1 kg of water is therefore equivalent to 2.45 MJ, and 1 mm of water is thus equal to 2.45 MJ per m<sup>2</sup>). ET is one of the most important integrating terms from TBMs, as ET uniquely links the water cycle, the energy cycle, and the carbon cycle (108). ET regulates the balance of net radiation into sensible versus latent heat, the former of which leads directly to a warming surface (42). Global remote sensing-based ET products can constrain ET from TBMs (109).

**3.4.8. Runoff, routing, and water balance.** After ET and infiltration, additional precipitation (or snowmelt) flows downhill as runoff carrying carbon and nutrients. Most TBMs model runoff simply as excess water above field capacity, with variants, though they do not always include the carbon and nutrients transport (35, 110).

Where does the runoff go? Rivers have variable widths, depths, and sinuous shapes affecting how much sediment (e.g., carbon, nutrients) is deposited and where, as well as how fast and how far water continues to run off against the pull of evaporation. However, most (but not all) TBMs

do not model river routing (35). They are typically coupled to separate river routing schemes, often including human abstraction of water.

It is essential that TBMs conserve mass, which includes ensuring that water inputs and outputs are balanced exactly. Most TBMs follow a bucket-based approach (including tipping bucket, leaky bucket) (35), which tends to be simpler than hydrological models that use much more advanced schemes such as probabilistic moisture distribution. The relative merits of these approaches remain unresolved (35); global remotely sensed terrestrial water storage from GRACE may help with assessment (111).

**3.4.9. Competition.** Competition among PFTs or within PFTs (e.g., age, size classes) for space, light, water, and nutrients is a key, defining feature that makes a TBM dynamic with respect to distribution of composition (112). This aspect becomes increasingly important over climate timescales when plant distributions shift with changing climate (113). The few DGVMs that simulate inter-PFT competition tend to use versions of Lotka–Volterra predator/prey equations (114). Dynamic TBMs are very sensitive to competition parameterization, potentially shifting from one biome into the next too early or too late. Applications to paleoclimate records help test this sensitivity and precision (16, 115).

**3.4.10. Establishment.** Another key dynamic feature is establishment, or how plants occupy new space. This can be regrowth from disturbance or natural mortality within a biome, or extension into new biome space with changing climatic conditions. Although the within-biome application formed the basis of the gap models that were foundational for modern dynamic TBMs (116), the biome-extension application is of considerable interest now within the context of climate change, such as the greening of the high northern latitudes (117). There is still much interest in within-biome establishment, as scientists try to distinguish between regrowth from disturbance versus other new growth to what would otherwise be considered old growth forests at equilibrium from factors such as CO<sub>2</sub> fertilization, nitrogen deposition, and changes to growing seasons (118, 119).

**3.4.11. Mortality.** If a tree falls in a forest. . . how did it die? Although a seemingly simple question, the answer is far from straightforward or resolved, yet it is profoundly important for maintaining TBM carbon balance and turnover (120, 121). Plants can die from hydraulic failure, carbon starvation, temperature extremes, and old age (preprogrammed lifetime). Hydraulic failure (cavitation, overheating, lack of water for photosynthesis) and carbon starvation (carbon demand for metabolism outweighs carbon uptake from GPP) are the leading hypotheses, they are not necessarily mutually exclusive, and disturbances exacerbate both of them (122). For biomes such as savannas, for example, which exist as a balance between trees and grass, modeled mortality must be balanced delicately between them so as not to switch the biome into a forest or grassland. Mortality algorithms range considerably across TBMs: productivity dependence, constant background rate, climate tolerances, size threshold, age, heat stress, negative carbon balance, shading, growth efficiency threshold, and carbon starvation (123).

**3.4.12. Disturbance.** Disturbances such as fires, wind, floods, landslides, and volcanic eruptions kill or reduce the functioning of vegetation in relatively punctuated and stochastic manners. Droughts and pests (insects/beetles, fungi, bacteria, viruses) do the same, but relatively less punctuated, and are sometimes considered disturbances and sometimes not. Erosion, grazing, invasive species, and sea level rise continue further out on the disturbance spectrum; tides and diurnal and seasonal cycling, while altering vegetation functioning, are not disturbances. All are natural parts of the terrestrial biosphere, though an anthropogenic influence is intimately tied to many of them

to varying degrees especially through land use (e.g., agricultural establishment and abandonment, pastoralism, logging). These disturbances are critical in reducing the modeled potential vegetation to a more realistic estimate of actual vegetation. Disturbances are very difficult to model at fine spatiotemporal scales; often, TBMs incorporate stochastic disturbance effects implicitly in turnover constants for vegetation carbon (22, 49, 86).

Of all the disturbances, fire removes the most biomass worldwide and is the top disturbance priority for development in TBMs. Fire models are often based on the operational yet complex framework of Rothelmer (124–126), though more simplistic formulations are also used (127).

**3.4.13. Trace gases and aerosols.** The terrestrial biosphere emits and absorbs more gases than just CO<sub>2</sub>, O<sub>2</sub>, and H<sub>2</sub>O, some of them very important for weather and climate (128). These include CH<sub>4</sub>, CO, H<sub>2</sub>, N<sub>2</sub>O, NH<sub>3</sub>, NO<sub>x</sub> (NO, NO<sub>2</sub>), and phytogetic/biogenic volatile organic compounds (VOCs; C<sub>5</sub>H<sub>8</sub>, C<sub>10</sub>H<sub>16</sub>, CH<sub>3</sub>OH).

Fire is a major source of many of these gases from the biosphere to the atmosphere, though plant and soil processes contribute significantly as well. VOCs are directly emitted from plants as defenses, attractors, and stress responses and can consume on average 1–2% and up to 10% of annual GPP (129). VOCs and NO<sub>x</sub> lead to secondary organic aerosols and tropospheric O<sub>3</sub>; these aerosols scatter and absorb radiation and influence cloud formation. Aerosols can also be sourced from dust.

N<sub>2</sub>O and CH<sub>4</sub> are potent greenhouse gases, with 298× and 25× the 100-year warming potential of CO<sub>2</sub>, respectively. Soil nitrification/denitrification controls the rate of N<sub>2</sub>O (and NO<sub>x</sub>) production. Natural CH<sub>4</sub> emissions come primarily from wetlands, but most CH<sub>4</sub> emissions come from anthropogenic rice agriculture. Although tropical wetlands represent a significant fraction of natural CH<sub>4</sub> emissions, much recent interest, especially from the TBM community, is in CH<sub>4</sub> emissions from the high degree of warming in Arctic wetlands (130).

## 4. THE MODELS

### 4.1. Parallel Earths, or “The Blind Men and the Elephant”

Around 500 BCE in the Indian subcontinent, Buddhist monks told the story of six blind men and an elephant. The six men gathered around the unknown object (the elephant), and each gave a different perspective of “truth” based on what each felt (tusk, tail, trunk, etc.). They were all in disagreement, all partially right, and all partially wrong.

In many respects, terrestrial biosphere modelers are like the blind men of the ancient parable. The models are often in partial or complete disagreement, yet each modeler seeks the truth, in this case the state and functioning of the terrestrial biosphere. All are partially right, and all are partially wrong; by working and communicating collaboratively, we may be able to see the elephant more clearly.

How many TBMs are currently in use and development? We compiled a nonexhaustive list of 75 TBMs (see **Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>). We attempted to include TBMs that were at least some combination of the four types of models (biogeography, biogeochemistry, biophysics, vegetation dynamics) that encompass DGVMs, and exclude models that were only one of those types, though this may not be perfect. Many of the models are replicates with slight modifications and development by independent teams.

We surveyed the modelers and asked, “What makes your model different from other models?” With a surprisingly high response rate of over 85%, responses ranged from models having (*a*) the first of a given process, (*b*) a unique approach to a process, (*c*) strengths of code organization, and



(*d*) strengths in application and validation. MC1, for example, was one of the first TBMs to have a detailed dynamic fire module. SiB3 has had one of the oldest and strongest performing photosynthesis modules. CENTURY had one of the first complete coupled nitrogen and phosphorus cycles. CABLE included one of the first phosphorus cycling coupled to an ESM. ED, HYBRID, aDGVM, ZELIG, and SEIB-DGVM model individual plants, and Ent is one of the first TBMs with vegetation demography to be coupled to a GCM.

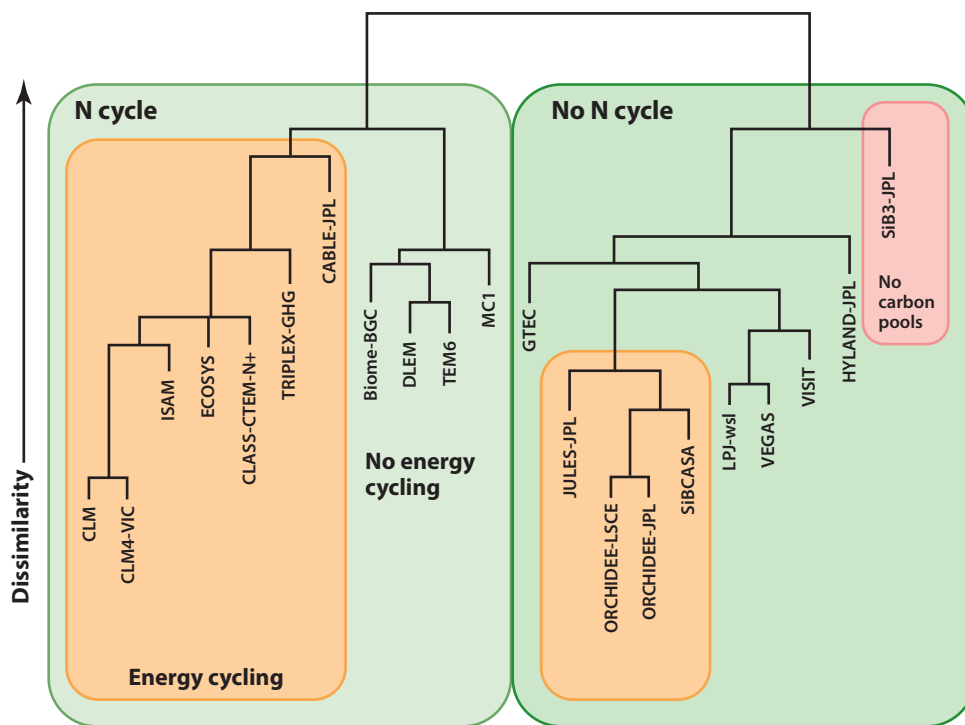
In terms of unique strengths, ORCHIDEE, CLM, TEM, and SiBCASA have among the most advanced permafrost models; SiBCASA also includes wind compaction and depth hoar on snow. TRIPLEX-GHG specializes in wetland dynamics. CENTURY includes complex agricultural practices and parameterizations for more than 40 different crop species. JeDi samples trait space across 15 parameters, allowing representation of plant diversity. aDGVM models the mutation, crossover, and trait inheritance of seeds. Catchment, CLM-VIC, and MATSIRO have explicit treatment of subgrid soil moisture variability and advanced hydrology. DLEM represents disturbance from insects and hurricanes. CARAIB can work with both PFTs and bioclimatic affinity groups; aDGVM also does not require PFTs. CABLE represents canopy turbulence. SiB3 utilizes a prognostic canopy air space. SiB3 and VISIT both model trace gases. SiBCASA prognostically couples  $^{13}\text{C}$  to photosynthesis; LPX-Bern and CLM both model  $^{13}\text{C}$  as well as  $^{14}\text{C}$ . Ent models foliage clumping impacts on canopy radiative transfer. BCC-AVIM determines carbon allocation based on LAI. The LPJ family optimizes  $V_{\text{max}}$  to environmental conditions for photosynthetic carbon gain. ISBA/SURFEX includes photosynthesis parameterization that captures a wide range of drought dynamics. HYBRID has advanced physiological parameterizations that handle acclimatization processes. SSiB is tightly constrained by the land-atmosphere interface.

JSBACH, Biome-BGC, HAL, HYBRID, LPJ, and GTEC modelers all expressed strengths in code structure, particularly with respect to clarity, modularity, and submodel evaluation. JULES is consistent both offline and coupled to an ESM and is consistent within weather and climate modeling applications. Noah-MP can run with multiple parameterization options to facilitate ensemble predictions; JSBACH can as well but to a lesser degree. CABLE has two alternative schemes for soil and snow. CLM is simply the largest TBM, with the most community input and largest number of processes.

CARAIB and LPX-Bern have demonstrated extensive testing against measurements, both with current climate and paleoclimate. H-TESEL is implemented into a weather forecasting system, which necessitates frequent review of the physics and parameterizations. TECO emphasizes data assimilation. CASA-GFED is tightly constrained by satellite data and has a long history of use and evaluation by the atmospheric carbon community. VEGAS and LPJ-GUESS have been applied and validated at multiple scales—paleoclimate, current climate, and future climate and on interannual and seasonal timescales of analysis.

All these models contribute to our understanding of the terrestrial biosphere and to projections of change. They encompass different combinations of the processes described in Section 3. Their differences define uncertainty, or at least a type of uncertainty (e.g., structural). Implicitly or explicitly, the ultimate aim is for model congruence (i.e., toward “truth”), or reducing the model spread—defined uncertainty.

One problem with this approach to uncertainty is that each model, in essence, gets one vote, regardless of skill or model independence. This in part leads to a bias of many similar models skewing the vote. Should similar models be grouped together or do more similar models indicate that there is some converged-upon truth that should influence the consensus? Not unsurprisingly, models have been developed primarily out of Europe and North America (**Supplemental Figure 1**). Our collective view of how the world functions could therefore be considered primarily how Europeans or North Americans view the world. Many of the formulations and parameterizations



**Figure 3**

Dendrogram showing overall model structural differences, as determined by Hamming distance, for 21 terrestrial biosphere models. Models in the same “tree” share similar structural characteristics. Models to the left include an explicit nitrogen (N) cycle, whereas those to the right do not. Further separation or clustering is by treatment of soil carbon pools and radiation/heat storage. (Adapted with permission from Reference 132.)

in our global models have been constructed based on measurements from ecosystems in these regions.

A more objectively rigorous approach to understanding TBM uniqueness or independence is through dendrograms, which are hierarchical cluster diagrams that can be used to visualize similarities and differences among models. Dendrograms can be constructed by sorting through binary responses in whether or not the models include a given process or attribute, then organizing the models in the diagram based on Hamming distance, with models grouped into branches by clusters of similar attributes (131). For example, Huntzinger et al. (132) constructed multiple dendrograms on 21 TBMs (**Figure 3**). Dendrograms can be used as hypotheses to explain patterns of TBM outputs.

## 4.2. The Global Picture(s)

For illustration, we briefly show some recent global estimates of 10 characteristic variables from 10 TBMs (**Figure 4**). Model outputs are for annual means from 1901 to 2010 from the TRENDY model intercomparison project (MIP) (133). We show output from the TRENDY S2 run—varying CO<sub>2</sub> and climate but keeping land use constant. To show model agreement/disagreement, we overlay the multimodel standard deviation on top of the multimodel means, coloring the model

disagreement red when the standard deviation is greater than the mean (inversely analogous to the stippling in the IPCC reports). We also plot the multimodel mean and standard deviation 110-year time series directly on top of the maps. Note the relative scales, in that NPP,  $R_a$ , and  $R_h$  are each approximately half of GPP globally. Similarly, vegetation carbon is half of soil carbon globally. Uncertainty typically swamps interannual variability for all variables except for NBP, which underlies the most regions of uncertainty.

One of the capabilities of TBMs is not only in simulating reality (or attempting to) but also in simulating multiple realities. These realities can manifest as differences in forcings to TBMs and are of particular interest for future projections, mainly because it is plausible that society can actually alter those forcings at will. Forcings include  $\text{CO}_2$  concentrations, nitrogen deposition, and land use/land cover change (LULCC), as well as climate in general; these are the dominant drivers of TBM response. Moreover, sensitivity tests to those drivers help us understand the innate functioning of the terrestrial biosphere, especially with nonlinearities and tipping points or thresholds.

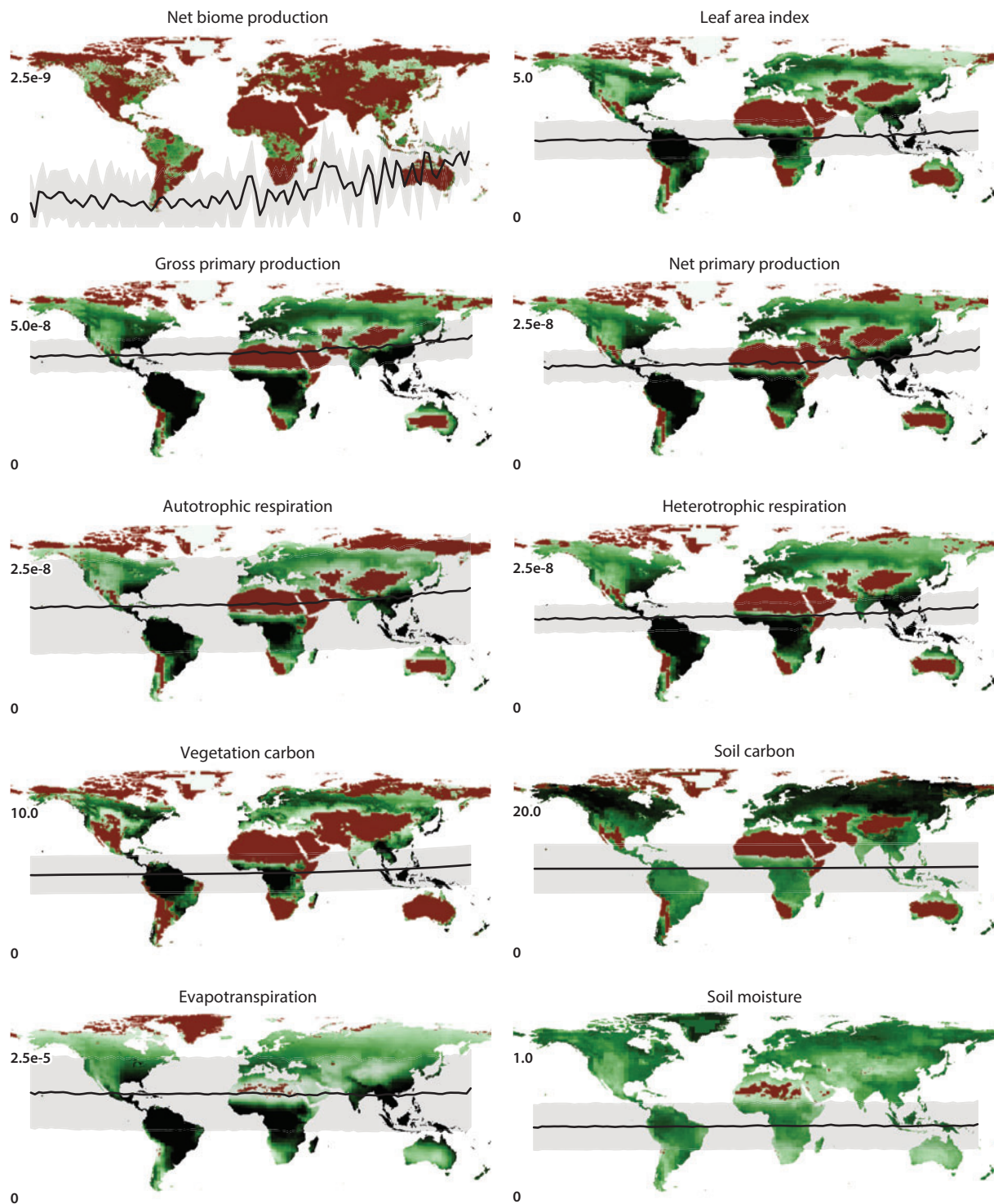
Warming an ecosystem may increase productivity up to a point, especially a cold ecosystem where rates of photosynthesis are slowed by temperature-dependent reaction rates; after such point, however, it may be too hot for vegetation, and soil respiration processes begin to dominate the net  $\text{CO}_2$  flux from the ecosystem (134, 135). But what is that point or threshold? Laboratory and some controlled field experiments may help, but the global terrestrial biosphere is more dynamic and diverse than these studies can sample, so TBMs allow for the testing of such sensitivities.

Similarly, increasing  $\text{CO}_2$  concentrations may stimulate a boost in productivity, at least initially, but nutrient availability rates may not keep pace with  $\text{CO}_2$  availability, and ecosystems may become progressively nutrient limited (136), at least until nutrient availability catches up. At what point does  $\text{CO}_2$  fertilization slow due to nutrient limitations? TBMs can help identify sensitivities.

Nitrogen deposition, like  $\text{CO}_2$ , acts as a fertilizer, thereby boosting productivity, at least initially. However, excessive nitrogen acidifies soils, which reduces productivity. Moreover, if an ecosystem is limited by other resources (e.g., phosphorus, light, temperature, moisture), then excessive nitrogen will do little to increase productivity (137, 138). Furthermore, a change to the nutrient regime could reduce biodiversity, e.g., supporting the dominance of plants or plant types that thrive on fertile grounds (139). A reduction in biodiversity could mean a loss in the ability of different plant types to capture different light and moisture environments, thereby reducing overall ecosystem productivity (140). TBMs can detect these changes quickly by integrating multiple aspects of ecosystem dynamics that may be difficult to capture in laboratory and field experiments.

Conversely, TBM sensitivity experiments are difficult to validate with measurements. Warming, nutrient fertilization, rainfall exclusion, watering, free air  $\text{CO}_2$  enrichment (FACE), and other manipulation experiments are essential to testing TBM sensitivities (141–144). But these experiments are insufficient to constrain global sensitivities (91, 119). Recently, Schimel et al. (118) used global atmospheric measurements and atmospheric flux inversion models in conjunction with TBM sensitivity experiments and in situ vegetation measurements to test the question of whether or not recent increases in land carbon uptake are due more to  $\text{CO}_2$  fertilization or to recovery from early deforestation. They found that TBMs that did not include  $\text{CO}_2$  fertilization (but did include climate and LULCC) were outside the bounds of atmospheric constraints;  $\text{CO}_2$  fertilization (with LULCC) positioned the TBMs directly within atmospheric constraints, supporting the hypothesis that recent land carbon uptake is due primarily to  $\text{CO}_2$  fertilization.

As an example, in the CLM4.5 TBM, over the last three decades the land surface takes up the most carbon when varying  $\text{CO}_2$  (i.e., increasing), especially in the tropics, which is consistent with the  $\text{CO}_2$  fertilization effect (**Supplemental Figure 2**). Nitrogen deposition also serves to increase carbon uptake, especially in the mid-northern latitudes, where much of the deposition



## Figure 4

Twentieth century (1901–2010) multimodel annual means with standard deviations overlaid for 10 variables for 10 terrestrial biosphere models from the TRENDY model intercomparison project (MIP) (varying CO<sub>2</sub> and climate; land use constant). Color scale goes from light to dark green (low to high). Red is where the standard deviation is larger than the mean. Scales on the left are for both the maps and the time series plots, the latter of which cover 1901–2010 laterally across each plot. Units are in kg m<sup>-2</sup> s<sup>-1</sup> for fluxes and kg m<sup>-2</sup> for stocks; soil moisture is in %/100.

has occurred. Climate change has helped carbon uptake in CLM4.5 in the high latitudes (e.g., longer growing seasons) but has hurt carbon uptake in the tropics (e.g., drought). CLM4.5 is particularly sensitive to LULCC, which has driven the model to produce very large emissions. Nonetheless, overall when all drivers are integrated, the large emissions from LULCC are offset by the cumulative gains from CO<sub>2</sub> fertilization, nitrogen deposition, and climate changes in the high latitudes; the total global carbon uptake over the last few decades for CLM4.5 is 0.01 PgC (petagrams of carbon) per year. Sensitivity analyses help us understand the impact of different drivers, and allow modelers to deduce the realism and patterns in sensitivity to those drivers with respect to their individual TBMs.

### 4.3. Model Intercomparison Projects and Benchmarking

Why do different models give different results for the same quantity? Different combinations of processes (Section 3) may be included between models (process inclusion). Moreover, for the same process, there may be different formulations, e.g., different parameterization approaches to photosynthesis/GPP discussed in Section 3.1.2 (process formulation). Or, for the same process and the same formulation, there may be differences in parameter specification, such as multiplier constants. For the same process, same formulation, and same parameterization, there may be differences whereby the process stops, starts, or switches (thresholds) (145). A given process might be completely identical in every respect between models, but the sensitivity or feedbacks between that process and other processes within the models may be different (internal feedbacks). Models may be perfect copies yet yield different results due to differences in driving or forcing data and spin-up/initialization (146).

Modelers may think they are constructing exact replicates of every possible point of difference but may in fact have differences of interpretation of any of those points, e.g., differences in net CO<sub>2</sub> flux definitions. Or modelers may simply overlook coding errors, including typos, for any step. Model versioning is also an important point of difference. The download/upload or storage of forcing data or model output may be unknowingly corrupted (data transfer). Finally, the final model output analysis may be in error by the analyst (or even the publisher).

Thus, uncertainties in, or variations across, TBMs are driven by a complex combination of factors. MIPs, which compare models to models, have been used as a starting point for understanding uncertainty or confidence in the model estimates. The spread of model results is an indicator of structural uncertainty. MIPs can also be used to better inform comparisons across models by eliminating as many of the controllable differences across models as feasible (e.g., choice of driver data, process inclusions, flux definition). Numerous MIPs have focused on TBMs, beginning even before the first TBMs were constructed (16)! MIPs have highlighted the role of the terrestrial biosphere in coupled models (e.g., PILPS, C4MIP; 1, 147). We briefly review some of the TBM-focused MIPs as they pertain to shaping the development and advancement of TBMs over the past 20 to 30 years.



One of the first organized TBM MIPs that focused on biogeochemistry models and DGVMs was the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) (12). VEMAP used common forcing data for seven models (Biome-BGC, CENTURY, GTEC, TEM, LPJ, DOLY, MC1). The results from the VEMAP Phase 1 activity clearly indicated the need for improved land use and disturbance information in models (148) and highlighted the importance of land use change, climate, and atmospheric CO<sub>2</sub> concentrations on land carbon sinks in the United States (149).

Around the same time as VEMAP, several parallel TBM MIPs were under way, including the Carbon-Cycle Model Linkage Project (CCMLP) (150) and the IGBP-sponsored Potsdam NPP MIP (151). During later stages of CCMLP, a series of experiments were conducted to evaluate the response of four TBMs (Bern, FBM, HRBM, and TEM) to changes in atmospheric CO<sub>2</sub>, time-varying temperature and precipitation, and historical land use changes (152). This semifactorial design (testing the influence of one driver at a time) showed that the large and opposing influences of historical land use (land carbon source) and CO<sub>2</sub> fertilization (land carbon sink) were the dominant influences on the terrestrial carbon cycle, with climatic changes (temperature and precipitation) having a much smaller and less consistent impact (152).

The Potsdam NPP MIP brought together 17 TBMs (CASA, GLO-PEM, SDBM, SiB2, TURC, Biome-BGC, CARAIB2.1, CENTURY4.0, FBM2.2, HRBM3.0, KGBM, PLAIO.2, SILVAN2.2, TEM4.0, BIOM3, DOLY, and HYBRID3.0) across three general classes—satellite-based models (5), models that simulated carbon fluxes using prescribed vegetation (9), and models that simulated both carbon fluxes and vegetation structure (3, 151). Interestingly, differences among simulated estimates of NPP could not be directly attributed to differences in model/process formulation and/or the different classes of models. The role of nutrients, however, did point to a differentiation in patterns of NPP simulation. Moreover, the Potsdam NPP MIP results suggested that most TBMs may be calibrated to an assumed total global NPP (153). A follow-on Potsdam DGVM MIP led to the creation of six new DGVMs (19).

These and other past MIPs informed model development and provided the foundation for more recent intercomparison efforts, such as the African Monsoon Multidisciplinary Analysis (AMMA) (154), the Wetland and Wetland CH<sub>4</sub> Intercomparison of Models Project (WETCHIMP) (130), the Large-Scale Biosphere–Atmosphere Experiment in Amazonia Data Model Intercomparison Project (LBA-DMIP) (155), the North American Carbon Program (NACP) Interim Site (62) and Regional Syntheses (63), the Trends in Net Land–Atmosphere Carbon Exchange (TRENDY) (156), and the Multi-scale Synthesis and Terrestrial Model Intercomparison Project (MsTMIP) (132).

Even though significant progress has been made in TBM development over the past 20 to 30 years, in many ways models have not progressed enough. We now have land use and land cover change data products (157), but we still lack robust historic disturbance data sets. Owing in part to the lack of sufficient disturbance-related drivers, disturbance events and impacts are still poorly described in many models. Similarly, many models still lack adequate representation of cropland and land management activities. As a result, we still see a large spread in TBM estimates of land fluxes and carbon stocks (132).

The many different TBMs provide many different answers, but which one is best? Is that even the right question to ask? If one model does better at carbon cycling, and another model does better at water cycling, are the two models equivalently good? What about a model that does better at diurnal cycling, another at seasonal cycling, and yet another at interannual variability? Is a model that does reasonably well across all dimensions better than a model that does exceptionally well across a few dimensions but poorly across others? What about a model that gets the right answer for the wrong reasons (equifinality)? Finally, how do we define best/better/good/well/poor/bad/skill/etc.?



Ultimately the answer depends on the purpose and the question. Much like cars, the fastest one is not always best—sometimes the user prefers the largest one, the smallest one, the cheapest one, the most durable, the one with the most amenities, or some sort of compromise. Thus, the “best” model is likely to change from question to question, and, ultimately, it is unlikely that there will be a universal best model (**Supplemental Figure 3**). Rather, different TBMs are suited to the purposes of the various users.

Nonetheless, TBMs must be evaluated objectively against a measure of “truth” to determine the expected accuracy for a given purpose. Although perturbed physics ensembles or variable initial conditions may be considered analytically from TBM simulation, benchmarking is a standardized evaluation of TBM consistency against a set of defined reference data sets (158). Benchmarking, also known as model–data intercomparison, model evaluation, or model validation, is a routine component of TBM development. Luo et al. (158) detailed the best practices in benchmarking studies, encapsulated into a four-step iterative workflow that focuses on the model aspects to be evaluated, reference data sets, and skill metrics that feed back to model improvement.

Skill metrics cover three types: (a) distance-based (e.g., RMSE,  $\chi^2$ ; how far apart are simulation and reference), (b) correlation (e.g.,  $r^2$ ; to what extent are simulation and reference in phase), and (c) distributional (e.g.,  $S_{\text{score}}$ ; how much do simulation and reference distribution overlap). As each type evaluates a different aspect of mismatch, they may yield dichotomous results (159, 160). Some evaluators combine metrics, but the inherent problem is how to weight each metric (161).

Benchmarking studies have not articulated or found consensus on a general framework or standard for benchmarking. A common simulation protocol is necessary but lacking (different model outputs due to different protocols change apparent skills), as are standardized reference data sets and skill metrics. Randerson et al. (161) made an early attempt at a TBM benchmarking system, applying it to two TBMs. Their benchmarking framework encompasses five metrics, each with multiple subcomponents, generating a total of eighteen skill metrics for each model. In contrast, Blyth et al. (162) emphasized the use of a single skill metric (RMSE) in their benchmarking system for JULES. In the NACP Interim Site Synthesis, Schwalm et al. (62) developed a three-dimensional skill surface emphasizing the  $\chi^2$  metric, which explicitly incorporates reference uncertainty. Kelley et al. (163) developed a benchmarking system that uses nine reference data sets (four gridded, five point-based), and five different score metrics that address interannual variability, seasonality, and long-term mean values; these include the normalized mean error, the normalized mean squared error, the mean phase difference, the Manhattan metric, and the squared chord distance.

Abramowitz (164) attempted to standardize benchmarking experiments internationally. The Protocol for the Analysis of Land Surface models (PALS; <http://www.pals.unsw.edu.au/pals>) is an online benchmarking application that supports community-based standardized reference data sets, spatiotemporal resolutions, and skill metrics for model validation. PALS is aligned with the goals of the ongoing community benchmarking effort, the International Land Model Benchmarking project (ILaMB; <http://ilamb.org>).

Remotely sensed observations hold the most promise for reference data sets, as these observations are often global in scope and include relatively spatially consistent errors. These include measurements across hydrology—snow cover, soil moisture, freeze/thaw state, evapotranspiration/transpiration/evaporation, runoff, total water storage and groundwater; as well as carbon cycling—fluorescence and GPP, NPP, LAI and phenology, canopy height, biomass, PFTs, canopy nutrients, nutrient limitation, land surface temperature, and fire. Nonetheless, many of these remote sensing data sets have moved away from direct measurements through a model. For example, the MODIS NPP data set is not actually a direct measure of carbon flux; rather, NPP is modeled from measurements of vegetation greenness. There is a continuum of model influence embedded in

nearly every measurement, and this carries forward to ground-based measurements as well, which also carry with them scale mismatch problems to model grids. A key benchmarking decision is how much model contamination is allowable in a measurement to be used as a benchmark against TBMs. In theory, any data set can be used as a benchmark as long as it carries with it rigorously quantified uncertainty; a data set closer to a pure measurement would likely have less uncertainty, and subsequently more utility, than a data set with more uncertainty and that is probably more reliant on a model.

Although these frameworks promise great utility in quantifying model skill, understanding model output, and improving TBMs, the use of such frameworks across any representative sampling of TBMs being used in the community is as yet aspirational. These examples of benchmarking frameworks have been limited to a few models and are still being developed. This highlights the difficulty in agreeing on universal guidelines.

## 5. CONCLUSIONS AND FUTURE PROSPECTS

We opened this review with a puzzle—given the terrestrial biosphere’s small areal coverage and wealth of measurements, how is it that terrestrial uncertainties exert such a powerful force on the entire planet? We hope we have provided a glimpse into the context occupied by the terrestrial biosphere. Although relatively small in size, the terrestrial biosphere’s ability to take up or emit huge amounts of carbon, alter water cycling, and influence energy exchanges with the atmosphere is enormous. It is no wonder that Earth’s climate is sensitive to such a “pea.”

Moreover, although the wealth of terrestrial measurements is rich, it is not rich enough relative to the overwhelming complexity encompassed in the biogeography, biogeochemistry, biophysics, and vegetation dynamics of the terrestrial biosphere. We provided an overview of 25 processes included in TBMs and the difficulties and challenges with modeling each process. Fortunately (or unfortunately), there are hundreds of scientists developing and analyzing TBMs; ironically, this simultaneously advances understanding and promotes confusion. Paradoxically, analysts have found (but not explained why) the multimodel mean tends to show better skill against benchmarks than any one given model [62, 133; see also Cox et al. (119) and Knutti (165) for counterpoints]. Well-structured, well-executed, and well-participated MIPs are essential for clearing through the chaos and seeing the global terrestrial biosphere, and its sensitivities, thresholds, and tipping points, more clearly. Understanding how benchmark data sets can be used within these MIPs is a requirement.

The past five years have seen an explosion of activity in TBM development. Foci have been on basic parameterization of fundamental carbon and water processes, ensuring that photosynthesis and phenology are acceptable, strategizing on how to incorporate the complexity of soils, and staying on top of the latest in hot topics including nitrogen cycling, wetlands, and human dimensions of land management. In fact, these are the topics expressed by modelers in our survey responding to the question, “What parts/processes have you been developing in your model over the past 5 years?” We encapsulated these responses visually into a Wordle: a word cloud giving prominence to words that appeared more frequently in the survey responses (**Figure 5a**).

For comparison, we also asked, “What parts/processes do you expect to develop in your model over the next 5 years?” (**Figure 5b**). Many of the topics from the previous five years continue over the next five years, with a huge emphasis on nitrogen cycling, but with continuing developments in hydrology, disturbance, permafrost (and other Arctic processes), vegetation dynamics, and changes in land cover and land use. There is new interest in rethinking the definition of PFTs, with some modelers moving toward a species-level parameterization and continuous trait variation. Increasing complexity and computational costs come with interests in increasing the number of soil and canopy layers, increasing resolutions and assessing subgrid level signals. Disturbances other than



fire are garnering notice, as are new mechanisms related to photosynthesis such as fluorescence, carbonyl sulfide, and isotopes. Belowground processes such as exudates/priming, mycorrhizae, and phosphorus cycling are also on the horizon. There have been calls for including better (or any) representation of hydraulic redistribution, mechanistic mortality, community-level interactions, and photosynthetic and respiratory acclimation to changing temperature, water, and CO<sub>2</sub> (16, 123, 145). Finally, the elephant in the room is how to deal with human intervention, which can substantially alter what the natural terrestrial biosphere would otherwise do. Very few ecosystems have not been directly altered by humans; agriculture, forest, and rangeland management alter water, nutrients, and carbon cycling, as well as plant distribution.

Is there and should there be a ceiling to TBM complexity? Does adding more complexity improve TBM estimates? The trajectory of TBM development is marching toward increased realism and complexity. Computational demands aside, a very serious question is whether or not added realism outweighs error propagation from expanding unknown parameterizations. Increased complexity also adds to the risk of models being very much black boxes, where even the modelers lose track of how the models work. There is indeed a fine line at the center of this balance, with valid arguments on either side. For example, adding the nitrogen cycle to TBMs adds considerable complexity, and TBM responses to nitrogen cycle inclusions range from 7% to 74% reductions in carbon uptake (98–100). However, without the nitrogen cycle, TBMs may take up an impossibly unlimited-seeming amount of carbon, in addition to other impacts with nitrogen cycle fingerprints in space and time (97). We echo decades-old recommendations for emphasis on clarity, and even process modularity, as model developments march forward in time (12).

We also urge advancement in the maturity of benchmarking both at the global scale with remote sensing and at the ecosystem scale with intensive monitoring sites and experimental manipulations. It is essential that benchmarks have rigorous uncertainty quantification. Within a benchmarking framework, clear gaps must be identified so that TBMs are not advancing toward matching one aspect better at the expense of ignoring another aspect that has no benchmark. There should be a reward for TBMs that do well across all benchmarks, as opposed to being the best for any one benchmark. TBMs should excel well across benchmarks in space and time and demonstrate the correct sensitivities to changes in forcings, as shown in ecosystem experiments. TBMs should be tested against modern historical data and, if applicable, paleoclimatic data before being cleared for take-off into future projections.

Traditionally, measurements were often made without models in mind. Yet every process in TBMs was based on measurements, sometimes very sparse measurements, either explicitly or implicitly. When many TBMs were first being developed, there were fewer data, yet the early parameterizations still remain. Today, we live in a data revolution that allows modelers to reexamine the core assumptions, formulations, and parameterizations in their TBMs (4, 16, 67, 71, 166). Nevertheless, most data are collected at very high spatial and temporal resolutions, but with poor spatial coverage, or at coarse spatial and temporal resolutions, but with global coverage; intermediate scales are poorly data-constrained (167). Investigations should adhere to the “model-data handshake” paradigm whereby models directly inform measurements, and measurements feed back to enable model development—“model what you measure, measure what you model.” Modelers should develop radiative transfer processes to simulate more directly what satellites observe so that any modeling uncertainty on the part of the remote sensing data sets can be eliminated.

Like Andersen’s “Princess and the Pea,” TBMs have truly shown the disproportionately large impact of Earth’s terrestrial ecosystems on the Earth system as a whole. Although potentially giving some pain and discomfort, it is this impact that the pea had that was necessary for the princess to claim her royalty. TBMs will continue to make their mark on us into the future, and hopefully we too can live happily ever after.

## SUMMARY POINTS

1. Terrestrial biosphere models (TBMs) consist of any combination of four components: (a) biogeography (plant distribution), (b) biogeochemistry (carbon, water, and nutrients cycling), (c) biophysics (land-atmosphere exchange of energy, water vapor, and momentum), and (d) vegetation dynamics (establishment, succession, mortality, competition).
2. The number of processes included in a given TBM ranges from just a few to dozens, spanning leaf, canopy, plant, and ecosystem scales. As a result, there is a wide diversity of process inclusion, process formulation, and parameter specification across TBMs.
3. Differences in model output may be due to any combination of process inclusion, process formulation, parameter specification, thresholds, internal feedbacks, forcing data, spin-up, interpretation, coding errors, versioning, data transfer, or analysis.
4. Model intercomparison projects (MIPs) are critical for understanding and advancing TBM output and developments. Factorial sensitivity experiments help identify some of the dominant factors influencing model output.
5. Benchmarking is critical in terrestrial biosphere modeling efforts, and an agreed upon benchmarking framework is needed.

## FUTURE ISSUES

1. Terrestrial biosphere modelers are continuing to develop numerous processes in their models, including nitrogen cycling, hydrology, disturbance, permafrost, vegetation dynamics, and changes in land use and land cover.
2. TBMs continue to increase in complexity and discretization of soil and canopy layers.
3. A critical aspect of development is how to deal with human intervention.
4. New links to data sets on the ground as well as from remote sensing are guiding TBM development.
5. Buy-in to a benchmarking framework must garner consensus soon, and TBM development must be intimately tied to benchmarking model output.

## DISCLOSURE STATEMENT

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## LITERATURE CITED

1. Friedlingstein P, Cox P, Betts R, Bopp L, von Bloh W, et al. 2006. Climate-carbon cycle feedback analysis: Results from the C4MIP model intercomparison. *J. Clim.* 19:3337–53
2. Friedlingstein P, Meinshausen M, Arora VK, Jones CD, Anav A, et al. 2014. Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *J. Clim.* 27:511–26
3. Bodman RW, Rayner PJ, Karoly DJ. 2013. Uncertainty in temperature projections reduced using carbon cycle and climate observations. *Nat. Clim. Change* 3:725–29
4. Baldocchi D. 2008. ‘Breathing’ of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Aust. J. Bot.* 56:1–26
5. Keeling CD, Chin J, Whorf T. 1996. Increased activity of northern vegetation inferred from atmospheric CO<sub>2</sub> measurements. *Nature* 382:146–49
6. Von Humboldt A. 1849. *Aspects of Nature, in Different Lands and Different Climates; With Scientific Elucidations*. Transl. EJ Sabine. Philadelphia: Lea and Blanchard
7. Grisebach A. 1872. *Die Vegetation der Erde nach ihrer klimatischen Anordnung: Ein Abriss der vergleichenden Geographie der Pflanzen. Bd. I und II*. Leipzig: Verlag von Wilhelm Engelmann
8. Köppen W. 1884. Die Wärmezonen der Erde, nach der Dauer der heissen, gemässigten und kalten Zeit und nach der Wirkung der Wärme auf die organische Welt betrachtet. *Meteorol. Z.* 1:215–26
9. Holdridge LR. 1947. Determination of world plant formations from simple climatic data. *Science* 105:367–88
10. Emanuel WR, Shugart HH, Stevenson MP. 1985. Climatic change and the broad-scale distribution of terrestrial ecosystem complexes. *Clim. Change* 7:29–43
11. Prentice I, Solomon A. 1991. Vegetation models and global change. In *Global Changes of the Past*, ed. RS Bradley, pp. 365–83. Boulder, CO: UCAR/Off. Interdisc. Earth Stud.
12. VEMAP Memb. 1995. Vegetation/Ecosystem Modeling and Analysis Project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO<sub>2</sub> doubling. *Glob. Biogeochem. Cycles* 9:407–37
13. Neilson R, Running S. 1996. Global dynamic vegetation modelling: coupling biogeochemistry and biogeography models. *Glob. Change Terr. Ecosyst.* 2:451–65
14. Woodward FI, Lomas MR. 2004. Vegetation dynamics—simulating responses to climatic change. *Biol. Rev.* 79:643–70
15. Watt AS. 1947. Pattern and process in the plant community. *J. Ecol.* 35:1–22
16. Prentice I, Cowling S. 2013. Dynamic global vegetation models. *Encycl. Biodivers.* 2:607–89
17. Cox PM, Betts RA, Bunton CB, Essery RLH, Rowntree PR, Smith J. 1999. The impact of new land surface physics on the GCM simulation of climate and climate sensitivity. *Clim. Dyn.* 15:183–203
18. Sellers PJ, Dickenson RE, Randall DA, Betts AK, Hall FG, et al. 1997. Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science* 275:502–9
19. Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, et al. 2001. Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Glob. Change Biol.* 7:357–73
20. Sitch S, Huntingford C, Gedney N, Levy PE, Lomas M, et al. 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using 5 Dynamic Global Vegetation Models (DGVMs). *Glob. Change Biol.* 14:2015–39
21. Arora V. 2002. Modeling vegetation as a dynamic component in soil-vegetation-atmosphere transfer schemes and hydrological models. *Rev. Geophys.* 40:3-1–3-26



22. Prentice CI, Bondeau A, Cramer W, Harrison SP, Hickler T, et al. 2007. Dynamic global vegetation modeling: quantifying terrestrial ecosystem responses to large-scale environmental change. In *Terrestrial Ecosystems in a Changing World*, ed. JG Canadell, pp. 175–92. Berlin: Springer
23. Moorcroft PR. 2006. How close are we to a predictive science of the biosphere? *Trends Ecol. Evol.* 21:400–7
24. Tang G, Bartlein PJ. 2008. Simulating the climatic effects on vegetation: approaches, issues and challenges. *Prog. Phys. Geogr.* 32:543–56
25. Fisher RA. 2013. Modelling plant ecology. In *Environmental Modelling: Finding Simplicity in Complexity*, ed. J Wainwright, M Mulligan, pp. 207–20. Hoboken, NJ: Wiley-Blackwell. 2nd ed.
26. Raupach M, Barrett D, Briggs P, Kirby J. 2005. Terrestrial biosphere models and forest-atmosphere interactions. In *Predictions in Ungauged Basins: International Perspectives on the State of the Art and Pathways Forward*, Vol. 301, ed. S Frank, M Sivapalan, K Takeuchi, Y Tachikawa, pp. 239–91. Oxfordshire, UK: IAHS Press
27. Eltahir EA, Bras RL. 1996. Precipitation recycling. *Rev. Geophys.* 34:367–78
28. Gedney N, Cox PM, Betts RA, Boucher O, Huntingford C, Stott PA. 2006. Detection of a direct carbon dioxide effect in continental river runoff records. *Nature* 439:835–38
29. Xu D-Q, Shen Y-K. 1997. Midday depression of photosynthesis. In *Handbook of Photosynthesis*, ed. M Pessarakli, pp. 451–59. New York: Marcel Dekker
30. Sitch S, Cox PM, Collins WJ, Huntingford C. 2007. Indirect radiative forcing of climate change through ozone effects on the land-carbon sink. *Nature* 448:791–94
31. Felzer B, Reilly J, Melillo J, Kicklighter D, Sarofim M, et al. 2005. Future effects of ozone on carbon sequestration and climate change policy using a global biogeochemical model. *Clim. Change* 73:345–73
32. Farquhar GD, Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* 149:78–90
33. Collatz GJ, Ball JT, Griwet C, Berry JA. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agric. Forest Meteorol.* 54:107–36
34. Collatz GJ, Ribas-Carbo M, Berry JA. 1992. Coupled photosynthesis-stomatal conductance model for leaves of C<sub>4</sub> plants. *Aust. J. Plant Physiol.* 19:519–38
35. Murray S, Watson I, Prentice I. 2013. The use of dynamic global vegetation models for simulating hydrology and the potential integration of satellite observations. *Prog. Phys. Geogr.* 37:63–97
36. Schaefer KM, Schwalm CR, Williams CA, Arain M, Barr AG, et al. 2012. A model-data comparison of gross primary productivity: results from the North American Carbon Program site synthesis. *J. Geophys. Res.* 117:G03010. doi: 10.1029/2012JG001960
37. Potter CS, Randerson JT, Field CB, Matson PA, Vitousek PM, et al. 1993. Terrestrial ecosystem production: a process based model based on global satellite and surface data. *Glob. Biogeochem. Cycles* 7:811–41
38. McGuire AD, Melillo JM, Joyce LA, Kicklighter DW, Grace AL, et al. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Glob. Biogeochem. Cycles* 6:101–24
39. van der Tol C, Verhoef W, Rosema A. 2009. A model for chlorophyll fluorescence and photo-synthesis at leaf scale. *Agric. Forest Meteorol.* 149:96–105
40. Frankenberg C, Fisher JB, Worden J, Badgley G, Saatchi SS, et al. 2011. New global observations of the terrestrial carbon cycle from GOSAT: patterns of plant fluorescence with gross primary productivity. *Geophys. Res. Lett.* 38:L17706. doi: 10.1029/2011GL048738
41. Joiner J, Guanter L, Lindstrom R, Voigt M, Vasilkov AP, et al. 2013. Global monitoring of terrestrial chlorophyll fluorescence from moderate spectral resolution near-infrared satellite measurements: methodology, simulations, and application to GOME-2. *Atmos. Meas. Tech. Discuss.* 6:3883–930
42. Monteith JL. 1965. Evaporation and the environment. *Symp. Soc. Explor. Biol.* 19:205–34
43. Fisher JB, Baldocchi DD, Misson L, Dawson TE, Goldstein AH. 2007. What the towers don't see at night: nocturnal sap flow in trees and shrubs at two AmeriFlux sites in California. *Tree Physiol.* 27:597–610
44. Fisher JB, Debiase TA, Qi Y, Xu M, Goldstein AH. 2005. Evapotranspiration models compared on a Sierra Nevada forest ecosystem. *Environ. Model. Software* 20:783–96

45. Priestley CHB, Taylor RJ. 1972. On the assessment of surface heat flux and evaporation using large scale parameters. *Mon. Weather Rev.* 100:81–92
46. Shuttleworth WJ, Wallace JS. 1985. Evaporation from sparse crops—an energy combination theory. *Q. J. R. Meteorol. Soc.* 111:839–55
47. Baldocchi D, Hutchison B, Matt D, McMillen R. 1985. Canopy radiative transfer models for spherical and known leaf inclination angle distributions: a test in an oak-hickory forest. *J. Appl. Ecol.* 22:539–55
48. Lloyd J, Patino S, Paiva R, Nardoto G, Quesada C, et al. 2010. Optimisation of photosynthetic carbon gain and within-canopy gradients of associated foliar traits for Amazon forest trees. *Biogeosciences* 7:1833–59
49. Friend AD, Stevens AK, Knox RG, Cannell MGR. 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecol. Model.* 77:233–55
50. Sellers P, Berry J, Collatz G, Field C, Hall F. 1992. Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sens. Environ.* 42:187–216
51. Friend A. 2001. Modelling canopy CO<sub>2</sub> fluxes: are ‘big-leaf’ simplifications justified? *Glob. Ecol. Biogeogr.* 10:603–19
52. Mercado LM, Huntingford C, Gash JH, Cox PM, Jogireddy V. 2007. Improving the representation of radiation interception and photosynthesis for climate model applications. *Tellus B* 59:553–65
53. Mercado LM, Bellouin N, Sitch S, Boucher O, Huntingford C, et al. 2009. Impact of changes in diffuse radiation on the global land carbon sink. *Nature* 458:1014–17
54. Spitters C, Toussaint H, Goudriaan J. 1986. Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. Part I. Components of incoming radiation. *Agric. Forest Meteorol.* 38:217–29
55. Brodersen CR, Vogelmann TC, Williams WE, Gorton HL. 2008. A new paradigm in leaf-level photosynthesis: Direct and diffuse lights are not equal. *Plant Cell Environ.* 31:159–64
56. Wan Z. 2008. New refinements and validation of the MODIS Land-Surface Temperature/Emissivity products. *Remote Sens. Environ.* 112:59–74
57. Murray SJ. 2014. Trends in 20th century global rainfall interception as simulated by a dynamic global vegetation model: implications for global water resources. *Ecohydrology* 7:102–14
58. Thom A. 1971. Momentum absorption by vegetation. *Q. J. R. Meteorol. Soc.* 97:414–28
59. Cadule P, Friedlingstein P, Bopp L, Sitch S, Jones CD, et al. 2010. Benchmarking coupled climate-carbon models against long-term atmospheric CO<sub>2</sub> measurements. *Glob. Biogeochem. Cycles* 24:GB2016. doi: 10.1029/2009GB003556
60. Poulter B, Heyder U, Cramer W. 2009. Modeling the sensitivity of the seasonal cycle of GPP to dynamic LAI and soil depths in tropical rainforests. *Ecosystems* 12:517–33
61. Sellers PJ, Meeson BW, Hall FG, Asrar G, Murphy RE, et al. 1995. Remote sensing of the land surface for studies of global change: models—algorithms—experiments. *Remote Sens. Environ.* 51:3–26
62. Schwalm CR, Williams CA, Schaefer K, Anderson R, Arain MA, et al. 2010. A model-data intercomparison of CO<sub>2</sub> exchange across North America: results from the North American Carbon Program site synthesis. *J. Geophys. Res.* 115:G00H5
63. Huntzinger DN, Post WM, Wei Y, Michalak AM, West TO, et al. 2012. North American Carbon Program (NACP) regional interim synthesis: terrestrial biospheric model intercomparison. *Ecol. Model.* 232:144–57
64. Woodward FI, Cramer W. 1996. Plant functional types and climatic change: introduction. *J. Veg. Sci.* 7:306–8
65. Harrison SP, Prentice IC, Barboni D, Kohfeld KE, Ni J, Sutra J-P. 2010. Ecophysiological and bioclimatic foundations for a global plant functional classification. *J. Veg. Sci.* 21:300–17
66. Díaz S, Cabido M. 1997. Plant functional types and ecosystem function in relation to global change. *J. Veg. Sci.* 8:463–74
67. Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, et al. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–27
68. Prentice IC, Meng T, Wang H, Harrison SP, Ni J, Wang G. 2011. Evidence of a universal scaling relationship for leaf CO<sub>2</sub> drawdown along an aridity gradient. *New Phytol.* 190:169–80

69. Wright IJ, Reich PB, Cornelissen JH, Falster DS, Garnier E, et al. 2005. Assessing the generality of global leaf trait relationships. *New Phytol.* 166:485–96
70. Fyllas NM, Quesada CA, Lloyd J. 2012. Deriving plant functional types for Amazonian forests for use in vegetation dynamics models. *Perspect. Plant Ecol. Evol. Syst.* 14:97–110
71. Kattge J, Diaz S, Lavorel S, Prentice I, Leadley P, et al. 2011. TRY—a global database of plant traits. *Glob. Change Biol.* 17:2905–35
72. Pavlick R, Drewry DT, Bohn K, Reu B, Kleidon A. 2013. The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. *Biogeosciences* 10:4137–77
73. Poulter B, Ciais P, Hodson E, Lischke H, Maignan F, et al. 2011. Plant functional type mapping for earth system models. *Geosci. Model Dev.* 4:993–1010
74. Bonan GB, Levis S, Kergoat L, Oleson KW. 2002. Landscapes as patches of plant functional types: an integrating concept for climate and ecosystem models. *Glob. Biogeochem. Cycles* 16(5):5–1–5–23. doi: 10.1029/2000GB001360
75. Fisher JB, Sikka M, Sitch S, Ciais P, Poulter B, et al. 2013. African tropical rainforest net carbon dioxide fluxes in the twentieth century. *Philos. Trans. R. Soc. B* 368:20120376
76. Thornley JHM, Cannell MGR. 2000. Modelling the components of plant respiration: representation and realism. *Ann. Bot.* 85:55–67
77. Lloyd J, Taylor JA. 1994. On the temperature dependence of soil respiration. *Funct. Ecol.* 8:315–23
78. Cannell MGR, Thornley JHM. 2000. Modelling plant respiration: some guiding principles. *Ann. Bot.* 85:45–54
79. Phillips RP, Brzostek E, Midgley MG. 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon–nutrient couplings in temperate forests. *New Phytol.* 199:41–51
80. Phillips RP, Erlitz Y, Bier R, Bernhardt ES. 2008. New approach for capturing soluble root exudates in forest soils. *Funct. Ecol.* 22:990–99
81. Fisher JB, Sitch S, Malhi Y, Fisher RA, Huntingford C, Tan S-Y. 2010. Carbon cost of plant nitrogen acquisition: a mechanistic, globally-applicable model of plant nitrogen uptake and fixation. *Glob. Biogeochem. Cycles* 24:GB1054. doi: 10.1029/2009GB003621
82. Malhi Y, Doughty C, Galbraith D. 2011. The allocation of ecosystem net primary productivity in tropical forests. *Philos. Trans. R. Soc. B* 366:3225–45
83. Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193:30–50
84. Iwasa Y, Roughgarden J. 1984. Shoot/root balance of plants: optimal growth of a system with many vegetative organs. *Theor. Popul. Biol.* 25:78–105
85. Ostle NJ, Smith P, Fisher RA, Woodward FI, Fisher JB, et al. 2009. Integrating plant-soil interactions into global carbon cycle models. *J. Ecol.* 97:851–63
86. Foley JA, Prentice IC, Ramankutty N, Levis S, Pollard D, et al. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Glob. Biogeochem. Cycles* 10:603–28
87. Cox PM. 2001. *Description of the TRIFFID dynamic global vegetation model*. Hadley Cent. Tech. Note 24, Met Office, London. [http://www.metoffice.gov.uk/media/pdf/9/h/HCTN\\_24.pdf](http://www.metoffice.gov.uk/media/pdf/9/h/HCTN_24.pdf)
88. Running SW, Hunt ER Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. In *Scaling Processes Between Leaf and Landscape Levels*, ed. JR Ehrlinger, C Field, pp. 141–58. San Diego, CA: Academic
89. Sitch S, Smith B, Prentice CI, Arneth A, Bondeau A, et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Glob. Change Biol.* 9:161–85
90. Haxeltine A, Prentice IC. 1996. A general model for the light-use efficiency of primary production. *Funct. Ecol.* 10:551–61
91. Zaehle S, Medlyn BE, De Kauwe MG, Walker AP, Dietze MC, et al. 2014. Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate Free-Air CO<sub>2</sub> Enrichment Studies. *New Phytol.* 202(3):803–22

92. Ghimire B, Riley WJ, Koven CD. 2013. *Improving representation of nitrogen uptake, allocation, and carbon assimilation in the Community Land Model*. Presented at Am. Geophys. Union Fall Meet., Dec. 9–13, San Francisco
93. Tarnocai C. 2006. The effect of climate change on carbon in Canadian peatlands. *Glob. Planet. Change* 53:222–32
94. Koven CD, Ringeval B, Friedlingstein P, Ciais P, Cadule P, et al. 2011. Permafrost carbon-climate feedbacks accelerate global warming. *Proc. Natl. Acad. Sci. USA* 108:14769–74
95. Fisher JB, Badgley G, Blyth E. 2012. Global nutrient limitation in terrestrial vegetation from remote sensing. *Glob. Biogeochem. Cycles* 26:GB3007. doi: 10.1029/2011GB004252
96. Davidson EA, Howarth RW. 2007. Nutrients in synergy. *Nature* 449:1000–1
97. Hungate BA, Dukes JS, Shaw MR, Luo Y, Field CB. 2003. Nitrogen and climate change. *Science* 302:1512–13
98. Thornton PE, Lamarque J-F, Rosenbloom NA, Mahowald NM. 2007. Influence of carbon-nitrogen cycle coupling on land model response to CO<sub>2</sub> fertilization and climate variability. *Glob. Biogeochem. Cycles* 21:1–15
99. Zaehle S, Friend AD, Friedlingstein P, Dentener F, Peylin P, Schulz M. 2010. Carbon and nitrogen cycle dynamics in the O-CN land surface model. II: The role of the nitrogen cycle in the historical terrestrial C balance. *Glob. Biogeochem. Cycles* 24:1–14
100. Thomas RQ, Zaehle S, Templer PH, Goodale CL. 2013. Global patterns of nitrogen limitation: confronting two global biogeochemical models with observations. *Glob. Change Biol.* 19(10):2986–98
101. Ryan MG, Law BE. 2005. Interpreting, measuring, and modeling soil respiration. *Biogeochemistry* 73:3–27
102. Thompson MV, Randerson JT, Malmström CM, Field CB. 1996. Change in net primary production and heterotrophic respiration: How much is necessary to sustain the terrestrial carbon sink? *Glob. Biogeochem. Cycles* 10:711–26
103. Tuomi M, Vanhala P, Karhu K, Fritze H, Liski J. 2008. Heterotrophic soil respiration—comparison of different models describing its temperature dependence. *Ecol. Model.* 211:182–90
104. Rustad LE, Huntington TG, Boone RD. 2000. Controls on soil respiration: implications for climate change. *Biogeochemistry* 48:1–6
105. Hayes D, Turner D. 2012. The need for “apples-to-apples” comparisons of carbon dioxide source and sink estimates. *Eos Trans. Am. Geophys. Union* 93:404–5
106. Chapin FS III, Woodwell G, Randerson JT, Rastetter EB, Lovett G, et al. 2006. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9:1041–50
107. Essery R, Morin S, Lejeune Y, Menard C. 2013. A comparison of 1701 snow models using observations from an alpine site. *Adv. Water Resour.* 55:131–48
108. Fisher JB, Whittaker RH, Malhi Y. 2011. ET come home: a critical evaluation of the use of evapotranspiration in geographical ecology. *Glob. Ecol. Biogeogr.* 20:1–18
109. Fisher JB, Tu K, Baldocchi DD. 2008. Global estimates of the land-atmosphere water flux based on monthly AVHRR and ISLSCP-II data, validated at 16 FLUXNET sites. *Remote Sens. Environ.* 112:901–19
110. Murray SJ, Foster PN, Prentice IC. 2011. Evaluation of global continental hydrology as simulated by the Land-surface Processes and eXchanges Dynamic Global Vegetation Model. *Hydrol. Earth Syst. Sci.* 15:91–105
111. Murray SJ. 2013. Present and future water resources in India: insights from satellite remote sensing and a dynamic global vegetation model. *J. Earth Syst. Sci.* 122:1–13
112. Moorcroft PR, Hurtt GC, Pacala SW. 2001. A method for scaling vegetation dynamics: the Ecosystem Demography model (ED). *Ecol. Monogr.* 71:557–86
113. Haxeltine A, Prentice IC. 1996. BIOME3: an equilibrium terrestrial biosphere model based on eco-physiological constraints, resource availability, and competition among plant functional types. *Glob. Biogeochem. Cycles* 10:693–709
114. Arora VK, Boer GJ. 2006. Simulating competition and coexistence between plant functional types in a dynamic vegetation model. *Earth Interact.* 10:1–30
115. Cowling SA. 1999. Simulated effects of low atmospheric CO<sub>2</sub> on structure and composition of North American vegetation at the Last Glacial Maximum. *Glob. Ecol. Biogeogr.* 8:81–93

116. Bugmann H. 2001. A review of forest gap models. *Clim. Change* 51:259–305
117. Piao S, Friedlingstein P, Ciais P, Zhou L, Chen A. 2006. Effect of climate and CO<sub>2</sub> changes on the greening of the Northern Hemisphere over the past two decades. *Geophys. Res. Lett.* 33:L23402
118. Schimel D, Stephens BB, Fisher JB. 2014. The effect of increasing CO<sub>2</sub> on the terrestrial carbon cycle. *Proc. Natl. Acad. Sci. USA*. In press
119. Cox PM, Pearson D, Booth BB, Friedlingstein P, Huntingford C, et al. 2013. Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. *Nature* 494:341–44
120. Sala A, Piper F, Hoch G. 2010. Physiological mechanisms of drought-induced tree mortality are far from being resolved. *New Phytol.* 186:274–81
121. Keane RE, Austin M, Field C, Huth A, Lexer MJ, et al. 2001. Tree mortality in gap models: application to climate change. *Clim. Change* 51:509–40
122. McDowell N, Pockman WT, Allen CD, Breshears DD, Cobb N, et al. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol.* 178:719–39
123. McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends Ecol. Evol.* 26:523–32
124. Rothermel RC. 1972. *A mathematical model for predicting fire spread in wildland fuels*. Res. Pap. INT-115, US Dep. Agric., US Forest Serv., Ogden, UT
125. Prentice I, Kelley D, Foster P, Friedlingstein P, Harrison S, Bartlein P. 2011. Modeling fire and the terrestrial carbon balance. *Glob. Biogeochem. Cycles* 25:GB3005
126. Thonicke K, Spessa A, Prentice I, Harrison S, Dong L, Carmona-Moreno C. 2010. The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: results from a process-based model. *Biogeosciences* 7:1991–2011
127. Arora VK, Boer GJ. 2005. Fire as an interactive component of dynamic vegetation models. *J. Geophys. Res.* 110:G02008. doi: 10.1029/2005JG000042
128. Arneth A, Sitch S, Bondeau A, Butterbach-Bahl K, Foster P, et al. 2010. From biota to chemistry and climate: towards a comprehensive description of trace gas exchange between the biosphere and atmosphere. *Biogeosciences* 7:121–49
129. Peñuelas J, Llusà J. 2004. Plant VOC emissions: making use of the unavoidable. *Trends Ecol. Evol.* 19:402–4
130. Melton JR, Wania R, Hodson EL, Poulter B, Ringeval B, et al. 2013. Present state of global wetland extent and wetland methane modelling: conclusions from a model inter-comparison project (WETCHIMP). *Biogeosciences* 10:753–88
131. Hamming RW. 1950. Error detecting and error correcting codes. *Bell Syst. Tech. J.* 29:147–60
132. Huntzinger D, Schwalm C, Michalak A, Schaefer K, King A, et al. 2013. The North American Carbon Program Multi-scale synthesis and Terrestrial Model Intercomparison Project—Part 1: Overview and experimental design. *Geosci. Model Dev.* 6:2121–33
133. Piao S, Sitch S, Ciais P, Friedlingstein P, Peylin P, et al. 2013. Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO<sub>2</sub> trends. *Glob. Change Biol.* 19:2117–32
134. Melillo JM, Borchers J, Chaney J, Fisher H, Fox S, et al. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO<sub>2</sub> doubling. *Glob. Biogeochem. Cycles* 9:407–38
135. Natali SM, Schuur EAG, Rubin RL. 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *J. Ecol.* 100:488–98
136. Luo Y, Su BO, Currie WS, Dukes JS, Finzi A, et al. 2004. Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *BioScience* 54:731–39
137. Fisher JB, Malhi Y, Torres IC, Metcalfe DB, Weg MJ, et al. 2013. Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes. *Oecologia* 172:889–902
138. Chapin FS III, Bloom AJ, Field CB, Waring RH. 1987. Plant responses to multiple environmental factors. *Bioscience* 37:49–57
139. Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, et al. 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70:153–226



140. Baldocchi DD. 2005. The role of biodiversity on the evaporation of forests. In *Forest Diversity and Function: Temperate and Boreal Systems*, Vol. 176, ed. M Scherer-Lorenzen, C Körner, E-D Schulze, pp. 131–48. Berlin: Springer
141. Harte J, Shaw R. 1995. Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science* 267:876–80
142. Shaver GR, Chapin FSI. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. *Ecology* 61:662–75
143. Fisher RA, Williams M, Da Costa AL, Malhi Y, Da Costa RF, et al. 2007. The response of an Eastern Amazonian rain forest to drought stress: results and modelling analyses from a throughfall exclusion experiment. *Glob. Change Biol.* 13:2361–78
144. Norby RJ, DeLucia EH, Gielen B, Calfapietra C, Giardina CP, et al. 2005. Forest response to elevated CO<sub>2</sub> is conserved across a broad range of productivity. *Proc. Natl. Acad. Sci. USA* 102:18052–56
145. Galbraith D, Levy PE, Sitch S, Huntingford C, Cox P, et al. 2010. Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. *New Phytol.* 187:647–65
146. Shi M, Yang Z-L, Lawrence DM, Dickinson RE, Subin ZM. 2013. Spin-up processes in the Community Land Model version 4 with explicit carbon and nitrogen components. *Ecol. Model.* 263:308–25
147. Henderson-Sellers A, Yang Z, Dickinson R. 1993. The project for intercomparison of land-surface parameterization schemes. *Bull. Am. Meteorol. Soc.* 74:1335–49
148. Schimel DS, Braswell BH, Parton WJ. 1997. Equilibration of the terrestrial water, nitrogen, and carbon cycles. *Proc. Natl. Acad. Sci. USA* 94:8280–83
149. Schimel D, Melillo J, Tian H, McGuire AD, Kicklighter D, et al. 2000. Contribution of increasing CO<sub>2</sub> and climate to carbon storage by ecosystems in the United States. *Science* 287:2004–6
150. Kicklighter DW, Bruno M, Dönges S, Esser G, Heimann M, et al. 1999. A first-order analysis of the potential rôle of CO<sub>2</sub> fertilization to affect the global carbon budget: a comparison of four terrestrial biosphere models. *Tellus B* 51:343–66
151. Cramer W, Kicklighter D, Bondeau A, Moore B III, Churkina G, et al. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Glob. Change Biol.* 5:1–15
152. McGuire A, Sitch S, Clein J, Dargaville R, Esser G, et al. 2001. Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO<sub>2</sub>, climate and land use effects with four process-based ecosystem models. *Glob. Biogeochem. Cycles* 15:183–206
153. Nemry B, Francois L, Gérard JC, Bondeau A, Heimann M. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of the seasonal atmospheric CO<sub>2</sub> signal. *Glob. Change Biol.* 5:65–76
154. Redelsperger J-L, Thorncroft CD, Diedhiou A, Lebel T, Parker DJ, Polcher J. 2006. African Monsoon Multidisciplinary Analysis: an international research project and field campaign. *Bull. Am. Meteorol. Soc.* 87:1739–46
155. de Gonçalves LGG, Borak JS, Costa MH, Saleska SR, Baker I, et al. 2013. Overview of the Large-Scale Biosphere–Atmosphere Experiment in Amazonia Data Model Intercomparison Project (LBA-DMIP). *Agric. Forest Meteorol.* 182–183:111–27
156. Sitch S, Friedlingstein P, Gruber N, Jones SD, Murray-Tortarolo G, et al. 2013. Trends and drivers of regional sources and sinks of carbon dioxide over the past two decades. *Biogeosci. Discuss.* 10:20113–77
157. Hurtt G, Chini L, Frolking S, Betts R, Feddema J, et al. 2011. Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim. Change* 109:117–61
158. Luo YQ, Randerson JT, Abramowitz G, Bacour C, Blyth E, et al. 2012. A framework for benchmarking land models. *Biogeosciences* 9:3857–74
159. Schwalm CR, Huntzinger DN, Michalak AM, Fisher JB, Kimball JS, et al. 2013. Sensitivity of inferred climate model skill to choice of benchmarking datasets and evaluation decisions. *Environ. Res. Lett.* 8:024028
160. Kelley DI, Prentice IC, Harrison SP, Wang H, Simard M, et al. 2013. A comprehensive benchmarking system for evaluating global vegetation models. *Biogeosciences* 10:3313–40



161. Randerson JT, Hoffman FM, Thornton PE, Mahowald NM, Lindsay K, et al. 2009. Systematic assessment of terrestrial biogeochemistry in coupled climate-carbon models. *Glob. Change Biol.* 15:2462–84
162. Blyth E, Clark D, Ellis R, Huntingford C, Los S, et al. 2011. A comprehensive set of benchmark tests for a land surface model of simultaneous fluxes of water and carbon at both the global and seasonal scale. *Geosci. Model Dev.* 4:255–69
163. Kelley DI, Prentice IC, Harrison SP, Wang H, Simard M, et al. 2012. A comprehensive benchmarking system for evaluating global vegetation models. *Biogeosciences* 10:3313–40
164. Abramowitz G. 2012. Towards a public, standardized, diagnostic benchmarking system for land surface models. *Geosci. Model Dev.* 5:819–27
165. Knutti R. 2010. The end of model democracy? *Clim. Change* 102:395–404
166. Keller M, Schimel DS, Hargrove WW, Hoffman FM. 2008. A continental strategy for the National Ecological Observatory Network. *Front. Ecol. Environ.* 6:282–84
167. Schimel D, Fisher JB, Pavlick R, Asner GP, Saatchi S, et al. 2014. Observing terrestrial ecosystems and the carbon cycle. *Glob. Change Biol.* In press



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